Forest Ecology and Management 404 (2017) 289–293

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Seed desiccation tolerance and dispersal in tropical dry forests in Colombia: Implications for ecological restoration

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ARTICLE INFO

Keywords:
Late successional forest
Late successional species
Orthodox seeds
Seed bank

ABSTRACT

The widely documented loss of tropical dry forests (TDFs) is a consequence of multiple and complex causes. The conservation status of Colombian TDFs is critical; currently, these forests only occupy eight percent of their original cover. Evidence shows that TDFs have a low probability of natural regeneration and may require ecological restoration. Seeds are central to the existence, permanence, and dynamics of plant communities in forests. Seeds exhibit a varied set of traits that exerts control on plant communities by limiting or facilitating plant establishment. According to previous research, in TDFs, most seeds are small, dry, and wind-dispersed, with a high drought tolerance (orthodox storage behavior).

In this study, available information on the fruits and seeds of tree species distributed in Colombian TDFs was synthesized. Twelve Colombia TDFs datasets were selected, which included species' individual occurrences and diameters at breast height. For each TDF, the most important species were selected, and the literature was searched for their seed storage behaviors, dispersal syndromes, and general fruit and seed attributes. In contrast to initial expectations, the search results suggested that the most common dispersal syndrome of the most important species was animal dispersal, followed by wind dispersal. Thirty-nine species were found that were not currently naturally established and should be introduced by active restoration. Most of these species had capsule and drupe fruits. The most common dispersal syndrome was animal dispersal, and the most common seed storage behavior was orthodox. Dominance of animal-dispersed species exacerbates fragmentation and habitat loss in TDFs, making available niches difficult to colonize and reducing the ability of seeds to reach degraded sites. Orthodox germination of seeds can facilitate seed storage in *ex situ* germoplasm banks to overcome low seed availability and/or forest soil seed bank.

1. Introduction

The loss of tropical dry forests (TDFs) has been widely documented as due to multiple and complex causes (Janzen, 1988). The most documented causes are land use changes for agricultural production and cattle pastures (Pennington et al., 2009) and in some regions, for illegal logging and increased tourism (Quesada and Stoner, 2004). In Colombia, the conservation status of TDFs is critical; most mature forests have disappeared and currently only 8% of their original cover remains (Pizano and Garcia, 2014).

Evidence shows that TDFs have a low probability of natural regeneration (Rico-Gray and García, 1992). The establishment of later successional tree species is severely limited by the absence of viable soil seed banks and poor seed dispersal (Ashton et al., 2001; Cabin et al., 2002; Janzen, 2002). As a result, TDF conservation requires ecological restoration (*i.e.,* actions to assist the recovery of degraded, damaged, or destroyed ecosystems) (SER 2004).

The first mechanism of natural regeneration includes seed rain and soil seed banks, which both relate to seed attributes. Seeds show a variety of morphological and physiological traits that exert control on the plant community and play an important role in limiting or facilitating the establishment of soil seed banks, which can remain viable in the soil for several years or are ephemeral (Walck et al., 2005). Available information suggests that seeds attributes of most TDF trees differ from those in tropical wet forests (Baskin and Baskin, 1998; Morellato et al., 2000), such as smaller sizes, higher desiccation-tolerance levels (*i.e.,* orthodox), wind-dispersal, and seed dormancy (Baskin and Baskin, 1998; Figueiredo, 2002; Gentry, 1995; Khurana and Singh, 2001; Vieira and Scariot, 2006). These TDF seed attributes appear to have a strong influence on plant community composition, because they are involved in natural regeneration, and in this way can be used to aid the recovery of the TDFs. In this study, available information about seed dispersion syndromes and seed storage, the two key attributes to support natural TDF regeneration, were synthesized and assessed for potential

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http://dx.doi.org/10.1016/j.foreco.2017.08.042
Received 17 March 2017; Received in revised form 23 August 2017; Accepted 25 August 2017
Available online 09 September 2017
0378-1127/

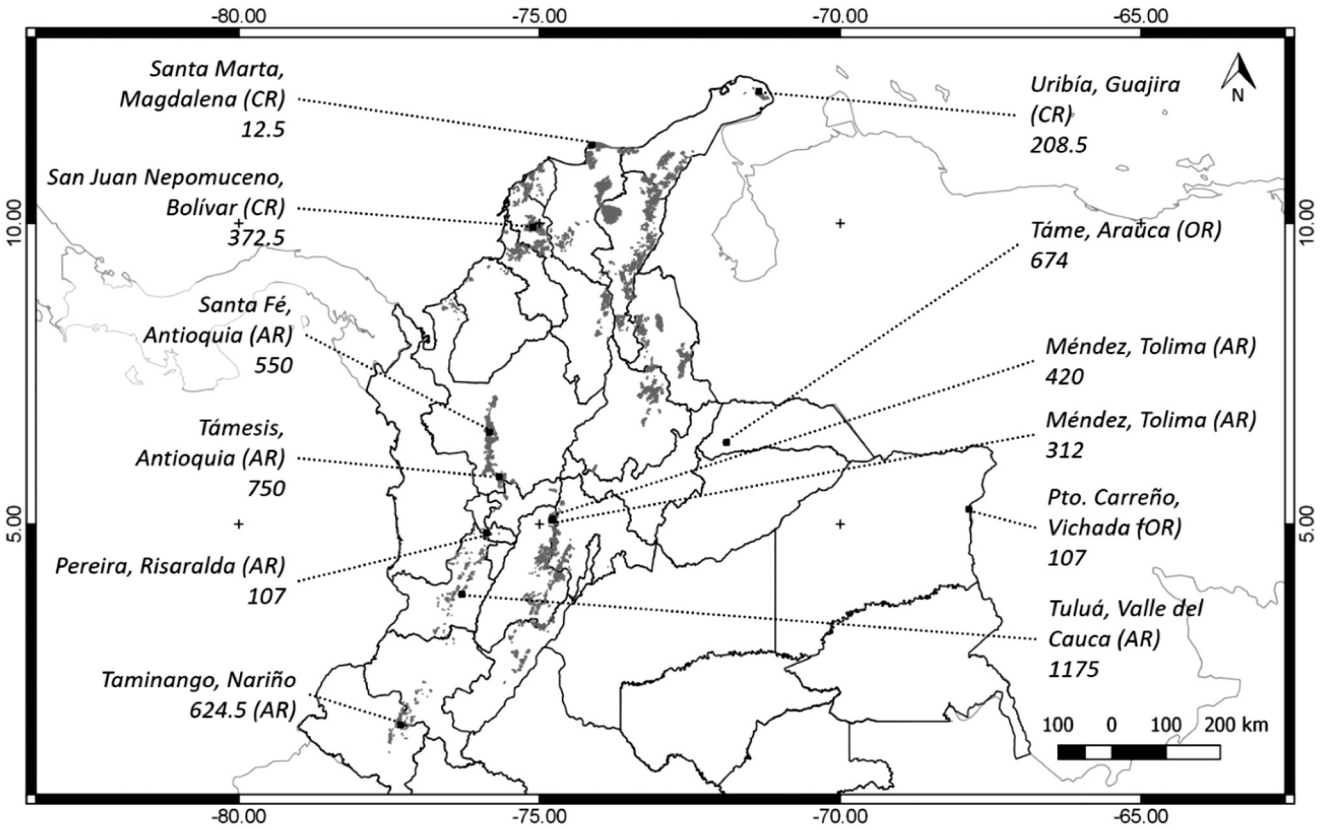

Fig. 1. Locations of tropical dry forest in Colombia included in the project "Bosques Secos de Colombia" leaded by the Alexander von Humboldt Institute. Data are available at Global Biodiversity Information Facility (GBIF; http://www.gbif.org/dataset). Information included municipality and department. Parenthetic information indicates the natural regions (AR, Andina Region; OR, Orinoquia Region; CR, Caribe Region), and number indicates altitude over sea level.

ecological restoration planning.

2. Seeds and restoration ecology

Managing tree species for direct seeding or plant propagation requires comprehensive knowledge of the physiology, morphology, and ecology of seed species (Martinez-Ramos, 1985). For example, plant dispersal syndromes, which include morphological, physiological and phenological characteristics associated with types of dispersal agents are influential in regenerative and successional processes in tropical ecosystems (Quesada et al., 2009). Seed dispersal exerts control over the locations of where seeds successfully germinate (Wenny, 2001).

Seed dispersal should ensure that seeds and/or fruits find a desirable place with appropriate light, water, temperature, and nutrients to promote germination and plant establishment (Norden, 2014). Seed dispersal deficits, due to a limited or absent dispersal agent (*i.e.,* animals) or low seed quantity and/or quality in terms of viability (Aide and Cavelier, 1994; Alvarez-Buylla and Martínez-Ramos, 1990; Holl, 1999; Zimmerman et al., 2000), limit natural regeneration and constrain ecological restoration efforts. Seidler and Plotkin (2006) recognized six dispersal syndromes based on fruit anatomy and morphology: ballistic (explosive capsule); gravity (nut, absent wings); gyrations (winged nut); and wind (capsule, pod, winged nut); animal medium fruit, (berry, drupe, capsule) and animal large fruit. In TDFs, most tree species have small wind-dispersed seeds (Justiniano and Fredericksen, 2000; Vieira and Scariot, 2006) that can be dispersed over long distances to colonize remote sites (Khurana and Singh, 2001).

In addition, in TDFs dispersion occurs in the dry season so seeds must undergo desiccation before germinating when the first rains arrive; a seed's storage behavior is a key attribute (Ceccon and Hernandez, 2009). Seed storage behavior is based on the seed's response to dehydration which exerts control on community structure and forest regeneration. Seed storage behavior is related to its persistence in the soil: dehydration-sensitive seeds that have short lives represent a high-risk regeneration strategy (Tweddle et al., 2003). Knowledge of a seed storage behavior is necessary to determine the most suitable way to handle seeds during collection (Hong, 1996). To understand seed storage behavior, terms defined by Roberts (1973) were used. *Orthodox* refers to seeds that can be dried to low moisture contents (2–5%) without damage, and in contrast, *recalcitrant* refers to seeds that cannot survive desiccation below a comparatively high (12–31%) moisture content. These traits are useful as a starting point for further investigations into plant attributes related to species arrival and establishment in order to promote natural regeneration and ecological restoration.

The main purpose of the current study was to synthesize research related to seed dispersal syndromes and seed storage behaviors in Colombian TDFs, and to discuss their implications on TDFs ecological restoration. Most species in TDFs were expected to have wind-dispersed seeds (Vieira and Scariot, 2006) with high desiccation tolerance (orthodox) (Hong et al., 1998). The implications of these plant attributes on restoration ecology using target species as the most important species is also discussed. Finally, species conservation status in the International Union for Cosnervation of Natura (IUCN) Red List of Threatened Species database and the Colombian Red list were reviewed to prioritize species for ecological restoration.

3. Materials and methods

3.1. Data collection

Species-occurrence data in Colombian TDFs are accessible via the