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► **To cite this version:**

Octavie Toublanc-Lambault, Robin Pouteau, Marion Davezies, Manon Marron, Anthony Pain, et al..
Environmental Correlates for Seed Desiccation Sensitivity of New Caledonian Plant Species. Pacific
Science, 2019, 73 (2), pp.231-248. 10.2984/73.2.5 . hal-03377263

HAL Id: hal-03377263

<https://hal.umontpellier.fr/hal-03377263>

Submitted on 14 Oct 2021

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Article in *Pacific Science* · April 2019

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Source: Pacific Science, 73(2) : 231-248

Published By: University of Hawai'i Press

URL: <https://doi.org/10.2984/73.2.5>

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Environmental Correlates for Seed Desiccation Sensitivity of New Caledonian Plant Species¹

Octavie Toublanc-Lambault,² Robin Pouteau,³ Marion Davezies,² Manon Marron,² Anthony Pain,⁴ Bruno Fogliani,⁴ and Philippe Marmey^{2,5,6}

Abstract: Efficient *in situ* and *ex situ* conservation strategies are urgently needed in biodiversity hotspots, where high concentrations of endemic plant species are undergoing exceptional loss of habitat. In particular, determining seed desiccation sensitivity is a key prerequisite to design storage methods useful for *ex situ* programs. In this study, we explored seed desiccation sensitivity and its link with phenological and morphological traits as well as with the environmental variables for 45 New Caledonian plant species. Desiccation sensitivity was quantified through RH50, that is, the relative humidity at which 50% of initial viable seeds died. RH50 was found to be positively associated with the initial seed water content, seed mass, precipitation seasonality, precipitation of the warmest quarter, and presence in rainforest habitats. In contrast, the ability of species to endure desiccation increased in drier habitats such as dry forest. We also found that desiccation sensitivity was consistent at the genus level. These new data provide the basis to establish conservation plans for a large array of plant species in New Caledonia. Moreover, this study may help us to better understand the underlying mechanisms of desiccation sensitivity and to predict desiccation sensitivity of other taxa within the New Caledonian flora on the basis of taxonomy, functional traits and environmental features.

Keywords: South Pacific, tropical biodiversity, conservation, hotspot, storage

NEW CALEDONIA IS AN ARCHIPELAGO in the South Pacific Ocean recognized as one of the global biodiversity hotspots (Myers et al. 2000, Roberts et al. 2002). This ca. 18,000 km² archipelago hosts 3371 native plant species, 73% of which are endemic (Jaffre et al. 2001, Morat et al. 2012). The flora of New Caledonia also stands out among other floras for its very distinctive nature: the presence of several primitive groups including the emblematic *Amborella trichopoda* which is sister to all

other extant angiosperms (Soltis et al. 2008), the importance of families belonging to the core Eocene flora, and the presence of intense speciation (Morat et al. 2012). This exceptional biological richness results from a complex biogeographical history and a wide variety of environments including an extreme diversity and specificity of edaphic conditions (Jaffre 1993, Morat 1993, Pillon et al. 2010). The geological history of New Caledonia, with its phase of total submersion at the end of

¹This program was partly funded by the South Pacific Integrated Observatory for Environment and Terrestrial

Pacific Science (2019), vol. 73, no. 2:231–248 doi:10.2984/73.2.5 (Supplemental materials for this article are available on BioOne (<https://bioone.org/journals/pacific-science/current>) and Project MUSE (<https://muse.jhu.edu/journal/166>))

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and Marine Biodiversity (GOPS). Manuscript accepted 29 August 2018.

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the Eocene, its covering by a slice of oceanic lithospheric mantle during emersion and its sudden re-emersion 37 million years ago, led to the presence of ultramafic substrates now covering more than one third of the main island (Paris 1981, Pelletier 2006), with a flora that has adapted to these edaphic conditions (Jaffre 1996, Pillon et al. 2010, Morat et al. 2012, Isnard et al. 2016).

The climate of New Caledonia is affected by tropical and temperate influences. The latter are however reduced by the maritime environment and the quasi-permanent presence of the trade wind (Maitrepierre 2012). There are two main seasons in New Caledonia: a hot or cyclonic season, from January to March, and a cool season, from June to September. Transitions between these two seasons are also distinguished, in particular by the presence of a dry season from August to November, which is characterized by low rainfall and low temperature at night but high temperature during the day.

The nature and distribution of actual contrasting habitats observed in New Caledonia are thought to be linked to climatic conditions, topography, substrates, and the effects of human activity. Main vegetation units include a dense evergreen rainforest (called rainforest hereafter), a sclerophyllous forest (dry forest), the maquis, savannas, halophytic vegetation, wetland vegetation, and dense secondary shrublands (Morat et al. 1981). New Caledonian species and their association with these vegetation units have been specified (Jaffre et al. 2001, Morat et al. 2012, Munzinger et al. 2016). Natural habitats have experienced profound shrinkage over the last centuries (Jaffre et al. 1998) and remain highly threatened by urban and economic development, such as mining activities (Pascal et al. 2008, L'Huillier et al. 2010), fire (McCoy et al. 1999), invasive species (Pascal et al. 2006), and climate change (Bellard et al. 2014).

Desiccation tolerance is the ability of a seed to survive cellular water withdrawal without irreversible damage and to resume its metabolic activities after rehydration (Leprince and Buitink 2010). Historically, seeds were first classified into two categories, orthodox or recalcitrant, for their response to *ex situ*

storage according to their level of tolerance to desiccation (Roberts 1973). Orthodox seeds can tolerate dehydration without damage, while recalcitrant seeds do not survive dehydration. A third seed class was identified as intermediate, and these seeds tolerate a certain level of dehydration (compared to recalcitrant seeds) but lose viability more rapidly at low temperature than orthodox seeds (Ellis et al. 1990). The observed variability in the level of desiccation tolerated by species favored the hypothesis of a continuum of desiccation tolerance among species (Berjak and Pammenter 1994, Dussert et al. 1999, Sun 1999).

Multiple abiotic constraints may have influenced seed ecology and, therefore, biodiversity dynamics (Walck et al. 2011, Long et al. 2015). The ability of a seed to survive desiccation plays a major role in species regeneration (Tweddle et al. 2003). Unlike desiccation tolerant (orthodox) seeds that can survive with a very low moisture content, desiccation sensitive seeds need a high moisture content to remain viable (Berjak and Pammenter 2008). Desiccation sensitive seed plants are most commonly found in humid tropical or subtropical forests, which provide a favorable environment for germination and establishment of young seedlings (Dickie and Pritchard 2002, Tweddle et al. 2003), even though long distance dispersal may select for seed desiccation tolerance, even in tropical and subtropical islands (Carlquist 1974). In contrast, desiccation tolerant seed plants are widely represented in drier environments (Hong and Ellis 1998, Delgado and Barbedo 2012). Approximately 92% of the known species of flowering plants bear desiccation tolerant seeds (Long et al. 2015). Of the 8% of known species with desiccation sensitive seeds, some species may however belong to areas with temperate climates (Finch-Savage 1992, Leon-Lobos and Ellis 2002). Desiccation sensitivity was shown to possibly be related to phenology (Hong and Ellis 1997, Hong and Ellis 1998, Daws et al. 2005, Daws et al. 2006) and season specificities (Dussert et al. 2000, Tweddle et al. 2003) and appeared to occur in all the major seed-plant taxonomic groups (Dickie and Pritchard 2002, Wyse and Dickie 2017).

There is an urgent need to improve our knowledge of seed ecology in hotspots in order to conserve their outstanding biodiversity. To determine whether seed desiccation sensitivity is correlated with environmental factors, a study was conducted on seeds of species collected in different locations in New Caledonia. Morphological data and physiological results combined with data of bioclimatic variables were analyzed. Such an analysis may be useful in predicting possible adaptation of the species to disturbed environments and in determining suitable strategies for *ex situ* conservation.

MATERIALS AND METHODS

Seed Collection and Measurements

The Noumea (NOU) herbarium database (<http://herbier-noumea.plantnet-project.org>) was used to extract information on species occurrences, habitat distribution, fruiting season, and accessibility. Field missions were conducted to collect seeds or label plants likely to produce fruits in the near future. Harvested seeds were temporarily placed in plastic bags in the field then stored at room temperature (average temperature of 25 °C) in darkness up to two days until analysis in the laboratory. For each collected species, we recorded the following information: the type of vegetation in which the species was found, GPS coordinates, the type of fruit and its color at maturity, the number of seeds per fruit, seed length, and the mass of seeds. Length measurements were made on 10 seeds per species then averaged. Mass measurements were made several times per species (with a variable number of seeds depending on the species, ranging from 1 to 100) then averaged to 10 seeds. Scarification or treatment according to local and common usage was applied to some species (i.e. scarification for *Alphitonia neocaledonica*, rinsing with soap liquid for *Pittosporum* species) when necessary.

Seed Desiccation Sensitivity Assays

Water content (WC) was expressed in percentage of fresh weight basis ($\% = \text{gH}_2\text{O} \times \text{gFW}^{-1} \times 100$). Initial water content (iWC)

was WC of seed within 2 days of collection. Seeds were desiccated by equilibration using a range of atmospheres whose relative humidity varied between 9 and 92% at 25 °C (Dussert et al. 1999). Nine relative humidity (RH) levels were obtained using saturated salt solutions of KOH, $\text{C}_2\text{H}_3\text{KO}_2$, MgCl_2 , K_2CO_3 , NH_4NO_3 , NaCl, $(\text{NH}_4)_2\text{SO}_4$, KCl and KNO_3 for a RH of 9%, 23%, 34%, 45%, 62%, 75%, 81%, 85%, and 92%, respectively. Each saline solution was placed in a separate closed container. Seeds were placed in nets in closed containers without touching the saline solution, and in up to 4 closed containers per RH. When equilibrium moisture content was reached (no more mass variation), seed batches of a closed container (corresponding to one RH) were split into two parts, one part (from 2 to 100 seeds) to establish the sorption isotherm and the other part (from 30 to 100 seeds) for the germination tests. For germination assays, seeds were sown in a mixture of potting soil and perlite (50/50) and placed in a greenhouse with controlled humidity. Temperature and light were not controlled, allowing a natural temperature differential and day/night cycle. For some species, germination was also tested on vermiculite and/or hydrophilic cotton moistened with water in a greenhouse or incubator at 25 °C. The germination was monitored and recorded weekly by counting numbers of germinated seeds until one month after no new seeds germinated. The emergence of the radicle was used as a criterion of germination. Seed desiccation sensitivity was quantified by the RH50 value, which is the relative humidity at which 50% of the initial seed viability (control germination) was lost (measured at final stage of germination monitoring).

Species Distribution

Species occurrences were compiled from the NOU herbarium database. For each occurrence, the following information was extracted: elevation, bioclimatic variables (BIO1 for annual mean temperature, BIO3 for isothermality, BIO4 for temperature seasonality, BIO7 for annual temperature range, BIO12 for annual precipitation, BIO13 for precipitation

of wettest month, BIO14 for precipitation of driest month, BIO15 for precipitation seasonality, BIO17 for precipitation of driest quarter of the year, BIO18 for precipitation of warmest quarter of the year) from the WorldClim global climate database (www.worldclim.org), and frequency on ultramafic soil was determined from the database of geographical information of New Caledonia (www.georep.nc). The mean, amplitude and standard deviation of each environmental variable were then computed at the species level.

Statistical Analysis

Statistical analyses including linear regressions and principal component analyses (PCA) were carried out using Xlstat software (Addinsoft, USA). The RH50 value was estimated by non-linear regressions (least squares, quasi-Newton method) using Solver software (Frontline Systems Inc, USA) according to the following function: G (Germination observed for a given RH) = $(GMAX)/(1 + \exp((RH - RH50)^a))$ (Dussert et al. 1999).

RESULTS

Targeted Species and Habitat Associations

Fruits and/or seeds were collected from on 100 plants belonging to 68 species in 33 families 49 genera, of which 52 (76%) were endemic, 15 (22%) indigenous and one (1%) exotic (Table 1). Fruit and/or seed collections were done when fruits were mature (change of color) and at the estimated time of natural dispersal (opening of the fruit to release seeds for some species). The Myrtaceae was the most represented family with eight genera and 13 species, including species with five in the genus *Syzygium*, one of which was the exotic species *Syzygium cumini*. The second most frequent family was the Pittosporaceae represented by a single genus (*Pittosporum*) and six species.

The 68 species occur in the seven vegetation units according to Florical (Munzinger et al. 2016), and some species were found in several units (Table 1 and Figure 1). Rainforest was the most represented habitat with 39 species (57%), followed by maquis

(34 species, 50%), dry forest (15 species, 22%), halophytic vegetation (six species, 9%), secondary shrubland (six species, 9%), wetland vegetation (three species, 4%), and savannas (one species, 1%). Among the 32 species (47%) specific to a single vegetation unit, 14, 11, 3 and 4 species were specific to rainforest, maquis, dry forest and halophytic vegetation respectively, with 13, 11, 2 and 0 species being endemic, respectively within each vegetation unit.

Fruit and Seed Features

Six types of fruits were identified as berries, capsules, drupes, achene, follicle and pods, the first three being the most frequent with a cumulative proportion of 91% of species (Figure 2A). Fruits were predominantly brown (26 species, 38%), red (12 species, 18%) or black (11 species, 16%) (Figure 2B). Zoochory was by far the most common dispersal mode with 47 species (69%) (Figure 2C). A total of 20 species (29%) had a single seed per fruit while 24 species (35%) had more than five seeds per fruit (Figure 2D). The mass of 10 seeds was below or equal to 0.5 g for two thirds of species, and to 0.1 g for 20 species (29%) (Figure 2E). Seven species (10%) had a 10 seed mass above 10 g. A total of 55 species (81%) had a seed length of less than 10 mm including 30 species (44%) with a seed length of less than 5 mm (Figure 2F). Five species (7%) had seeds longer than 20 mm including by ascending order: *Syzygium cumini*, *Pleiolima longipetiolata*, *Calophyllum inophyllum*, *Diospyros macrocarpa* and *Diospyros brassica* (Supplemental Table S1).

Water Content and Isotherms

Nine species (13%) had an initial water content (iWC) below 10% (*Atractocarpus rotundifolius*, *Geniostoma densiflorum*, *Joinvillea plicata* ssp. *plicata*, *Oxera brevicalyx*, *Oxera pulchella* spp. *grandiflora*, *Santalum austrocaledonicum* var. *austrocaledonicum*, *Scaevola balansae*, *Schefflera candelabrum*, *Tristaniopsis glauca*). A total of 27 species (40%) had an iWC between 10 and 20%, and another 27 species (40%) between 20 and 50%. Only five species

TABLE 1

List of Species whose Fruits and Seeds were Collected for Analysis, with Details According to the Angiosperm Phylogeny Working Group and to the Florical Database (Munzinger et al. 2016) of the Family they Belong to, in Parentheses Vegetative Units in Which they can be Found, and in Brackets the Status with regard to Their Origin

Amborellaceae: <i>Amborella trichopoda</i> (F)[E]
Araliaceae: <i>Meryta denhamii</i> (FL)[E], <i>Polyscias pancheri</i> (M)[E], <i>Schefflera candelabrum</i> (F)[E]
Asphodelaceae: <i>Dianella adenanthera</i> (FL)[I]
Atherospermataceae: <i>Nemuaron vieillardii</i> (F)[E]
Calophyllaceae: <i>Calophyllum caledonicum</i> (F)[E], <i>Calophyllum inophyllum</i> (G)[I]
Casuarinaceae: <i>Gymnostoma deplancheanum</i> (FM)[E]
Celastraceae: <i>Peripterygia marginata</i> (M)[E]
Chloranthaceae: <i>Ascarina rubricaulis</i> (FN)[E]
Cunoniaceae: <i>Geissois racemosa</i> (FS)[E], <i>Pancheria alaternoides</i> (MR)[E]
Cyperaceae: <i>Gabnia aspera</i> (LM)[I]
Dilleniaceae: <i>Hibbertia pancheri</i> (FM)[E]
Ebenaceae: <i>Diospyros brassica</i> (F)[E], <i>Diospyros fasciculosa</i> (FL)[I], <i>Diospyros macrocarpa</i> (F)[E], <i>Diospyros vieillardii</i> (FM)[E]
Ericaceae: <i>Styphelia pancheri</i> (FM)[E]
Escalloniaceae: <i>Polyosma leratii</i> (F)[E]
Fabaceae: <i>Dendrolobium umbellatum</i> (G)[I], <i>Sophora tomentosa</i> (G)[I]
Goodeniaceae: <i>Scaevola balansae</i> (FM)[I], <i>Scaevola cylindrica</i> (MN)[I]
Joinvilleaceae: <i>Joinvillea plicata</i> ssp. <i>plicata</i> (MN)[I]
Lamiaceae: <i>Oxera brevicalyx</i> (LM)[E], <i>Oxera nerifolia</i> (FM)[E], <i>Oxera pulchella</i> spp. <i>grandiflora</i> (L)[E], <i>Oxera sulfurea</i> (LM)[E]
Loganiaceae: <i>Geniostoma densiflorum</i> (FN)[E], <i>Neuburgia novocaledonica</i> (F)[I]
Malphighiaceae: <i>Acridocarpus austrocaledonica</i> (M)[E]
Malvaceae: <i>Hibiscus tiliaceus</i> (GN)[I], <i>Thespesia populnea</i> (G)[I]
Meliaceae: <i>Dysoxylum canalense</i> (FM)[E]
Monimiaceae: <i>Hedyocarya cupulata</i> (F)[E], <i>Kibarpopsis caledonica</i> (F)[E]
Myrtaceae: <i>Arillastrum gummiferum</i> (FM)[E], <i>Eugenia gacognei</i> (LM)[E], <i>Myrtastrum rufopunctatum</i> (M)[E], <i>Pleurocalyptus pancheri</i> (FM)[E], <i>Syzygium auriculatum</i> (F)[E], <i>Syzygium cumini</i> (GN)[X], <i>Syzygium longifolium</i> (FR)[E], <i>Syzygium multipetalum</i> (FM)[E], <i>Syzygium pancherii</i> (FM)[E], <i>Tristaniopsis glauca</i> (M)[E], <i>Uromyrtus emarginata</i> (M)[E], <i>Xanthostemon aurantiacus</i> (MR)[E], <i>Xanthostemon macrophyllus</i> (M)[E]
Picrodendraceae: <i>Austrobuxus buerlimannii</i> (F)[E]
Pittosporaceae: <i>Pittosporum cberrieri</i> (L)[E], <i>Pittosporum coccineum</i> (FL)[E], <i>Pittosporum gracile</i> (FM)[E], <i>Pittosporum poumense</i> (M)[E], <i>Pittosporum scytobophyllum</i> (M)[E], <i>Pittosporum simsonii</i> (F)[E]
Rhamnaceae: <i>Alphitonia neocaledonica</i> (FL)[E], <i>Emmenosperma pancherianum</i> (L)[I]
Rubiaceae: <i>Atractocarpus rotundifolius</i> (M)[E], <i>Atractocarpus vaginatus</i> (M)[E], <i>Psychotria baillonii</i> (F)[E]
Rutaceae: <i>Sarcomelicope argyrophylla</i> (FM)[E]
Santalaceae: <i>Santalum austrocaledonicum</i> var. <i>austrocaledonicum</i> (FL)[E]
Sapindaceae: <i>Dodonaea viscosa</i> ssp. <i>viscosa</i> (LM)[I]
Sapotaceae: <i>Pleioluma longipetiolata</i> (FM)[E]
Thymelaeaceae: <i>Wikstroemia indica</i> (FL)[I]

G: halophytic vegetation; F: rainforest; L: dry forest; M: maquis; N: dense secondary shrublands; R: wetland vegetation; S: savannas. E: endemic, I: indigen, X: exotic.

had an iWC above 50%: *Ascarina rubricaulis*, *Pleioluma longipetiolata*, *Dysoxylum canalense*, *Nemuaron vieillardii* and *Polyosma leratii*.

Regarding the establishment of sorption isotherms (Figure 3), *Acridocarpus austrocale-*

donicus and *Nemuaron vieillardii* were not tested because of an insufficient number seeds. Another three species whose seeds were too light to establish correct sorption isotherms were not retained for analysis (i.e.

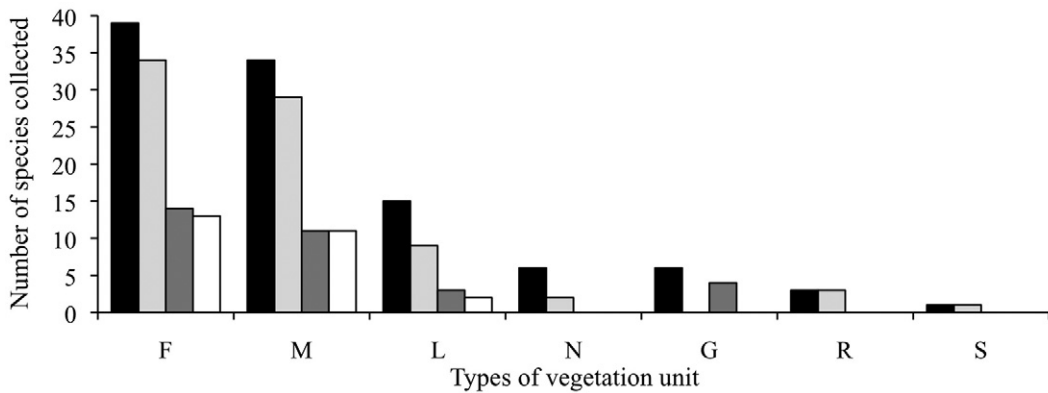


FIGURE 1. Frequencies of the 68 targeted species in the main vegetation units (corresponding codes are given below): black bars refer to species of any origin non-exclusively found in a vegetation unit, light grey bars refer to endemic species non-exclusively found in a vegetation unit, dark grey bars refer to species of any origin specific to a vegetation unit, and white bars refer to endemic species specific to a vegetation unit. F: rainforest; M: maquis; L: dry forest; N: dense secondary shrublands; G: halophytic vegetation; R: wetland vegetation; S: savannas.

Ascarina rubricaulis, *Pancheria alaternoides*, *Tristaniopsis glauca*). Among the 68 species, a total of 42 species (62%) were desiccated over the range of RHs, and a total of 48 species (71%) desiccated at the two extreme RH (9 and 92%). Seeds of some species reached equilibrium after only 3 days, and seeds of a few species were removed after 3 weeks. Seeds equilibrated in controlled atmospheres of 9% RH had a final WC ranging from 0.69% (*Gymnostoma deplancheanum*) to 18.48% (*Dianella adenanthera*). For seeds equilibrated at 92% RH, this range was between 10.83% (*Gymnostoma deplancheanum*) and 68.20% (*Dysoxylum canalense*).

Germination Tests

Germination significantly differed among species. Three species showed no germination (*Acridocarpus austrocaledonicus*, *Polyscias pancheri*, *Xanthostemon macrophyllus*) and one species (*Pancheria alaternoides*) had a very low germination of 0.1%. A total of 23 species (34%) had germination below 50%, 13 species (19%) below 10%, 45 species (66%) above 50% among which 11 species (16%) had a germination of 100%: *Atractocarpus vaginatus*, *Calophyllum caledonicum*, *Dendrolobium umbellatum*, *Diospyros brassica*, *Oxera sulfurea*, *Pittosporum cherrieri*, *Pittosporum scythophyllum*,

Syzygium cumini, *Syzygium longifolium*, *Syzygium multipetalum* and *Uromyrtus emarginata*.

Habitat Correlates for Fruit and Seed Features

Relationships between iWC and seed features (size, mass (log transformed), and germination) were analyzed using linear regressions (Table 2). iWC was positively correlated with seed size and seed mass; however, no correlation was found with germination rates. A similar linear regression analysis was performed between iWC and ecological categories (vegetation units), dispersal syndrome and type of fruits (Table 2). Among significant correlations, iWC was positively associated with rainforest and one type of fruit (berry); it was negatively associated with dry forest, anemochory and fruits with above 5 seeds.

Desiccation Sensitivity

A pool of 23 species (34%) was not used in this analysis due to an insufficient number of seeds that germinated. Species displayed different germination rates according to the level of seed desiccation (Supplemental Figure S1). Desiccation sensitivity of 45 species (66%) was quantified through the RH50 value (Figure 4 and Table 3). 29 species (64%)

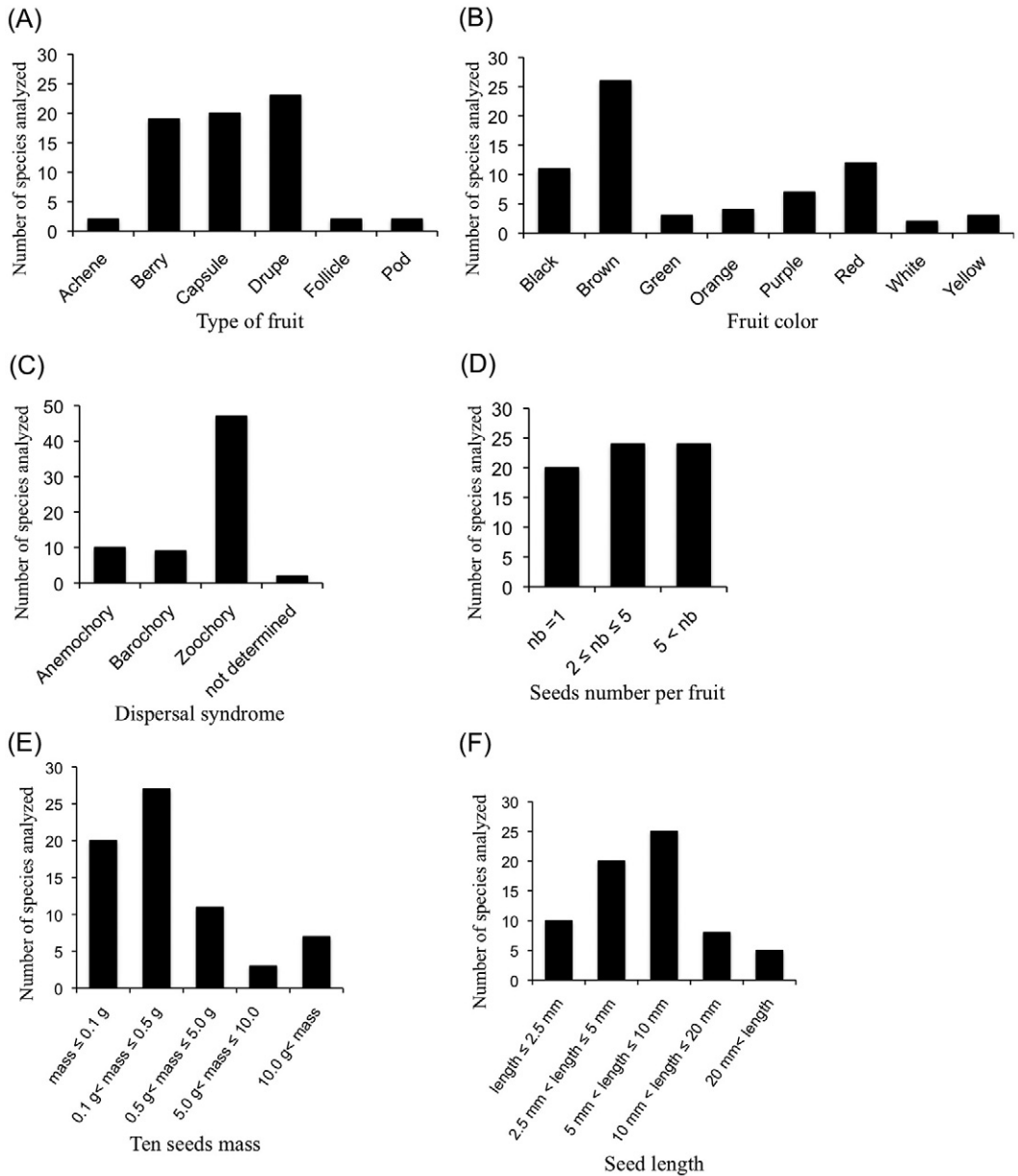


FIGURE 2. Frequencies of species with respect to fruit type (A), mature fruit color (B), dispersal syndrome (C), number of seeds per fruit (D), mass of 10 seeds (g) (E), and seed length (mm) (F).

had a germination of 50% or more for seeds that were equilibrated in RH below 20% (e.g. *Pittosporum cherrieri*; Figure 4A), suggesting a substantial tolerance to desiccation of seeds. Four species (9%) had an RH50 between 20

and 60% (e.g. *Diospyros fasciculosa*; Figure 4B), and 12 species (26%) an RH50 above 60% (e.g. *Syzygium multipetalum*; Figure 4C), suggesting a moderate and high sensitivity to desiccation, respectively.

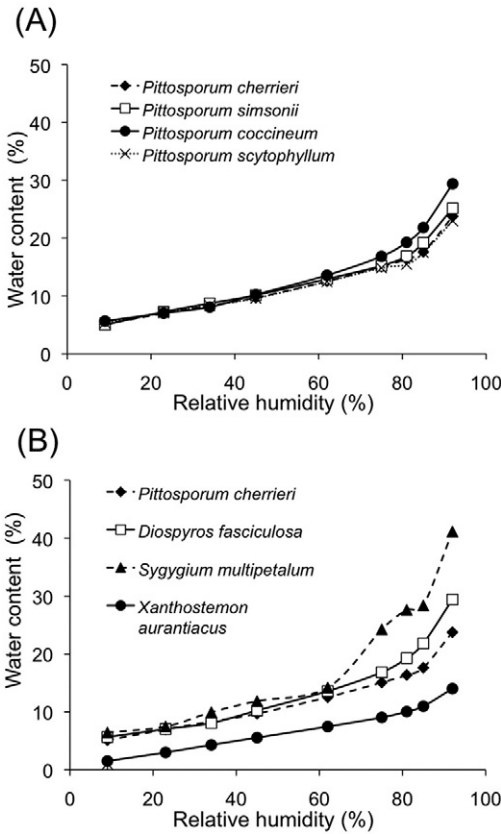


FIGURE 3. Water sorption isotherm curves at 25 °C for (A) four species of *Pittosporum* genus and (B) four species of four different genera. The water content percentage at different relative humidity is expressed on a fresh weight basis. Species were chosen to display (A) the similarity of isotherms observed for species of the same genus and (B) the variability of isotherms observed between species of different genera.

Species Distribution along Environmental Gradients

Linear regressions performed on the 45 species showed that RH50 was significantly correlated to iWC ($R = 0.825$), seed mass ($R = 0.819$), and rainforest ($R = 0.350$). Seed mass was significantly correlated to maquis ($R = -0.350$), and iWC was significantly correlated to rainforest ($R = 0.323$) and dry forest ($R = -0.334$) (Table 4). No significant correlation was found between these variables and germination. The distribution of occurrences

TABLE 2

Correlations of Seed Initial Water Content with Seed Features, Habitat Association, Dispersal Syndrome, the Type of Fruit, and Number of Seeds per Fruit for 68 New Caledonian Plant Species

	Water Content	
	<i>R</i>	<i>P</i>
Seed size	0.377	0.002
Seed mass	0.424	0.000
Germination	0.010	0.938
<i>Vegetation Unit</i>		
Dryforest	-0.286	0.018
Maquis	-0.095	0.443
Rainforest	0.353	0.003
Secondary shrub	0.041	0.738
Other VUs	-0.073	0.554
<i>Dispersal syndrome</i>		
Anemochory	-0.255	0.036
Barochory	-0.068	0.581
Zoochory	0.184	0.133
<i>Type of fruit</i>		
Berry	0.274	0.024
Capsule	-0.164	0.180
Drupe	-0.035	0.779
Other type	-0.111	0.368
1 seed per fruit	0.088	0.475
2 to 5 seeds per fruit	0.182	0.424
Above 5 seeds per fruit	-0.266	0.028

Significant correlations at a 5% threshold are in bold.

of the 45 studied species extracted from the herbarium represented the entirety of New Caledonia (Supplemental Figure S2). The analysis of RH50 values along environmental gradients revealed no significant correlation with elevation or prevalence on ultramafic substrates, nor with the standard deviation and amplitude of any bioclimatic variables. However, RH50 was correlated to the mean of three bioclimatic variables related to rainfall (BIO13, BIO15 and BIO18) with R equal to 0.405, 0.343, and 0.432, respectively (Table 4). The Pearson correlation coefficient of a similarity matrix between BIO13 and BIO18 was found to be close to 1 for the whole bioclimatic data set from New Caledonia and for all occurrences (data not shown). Only BIO15 and BIO18 were then retained for the

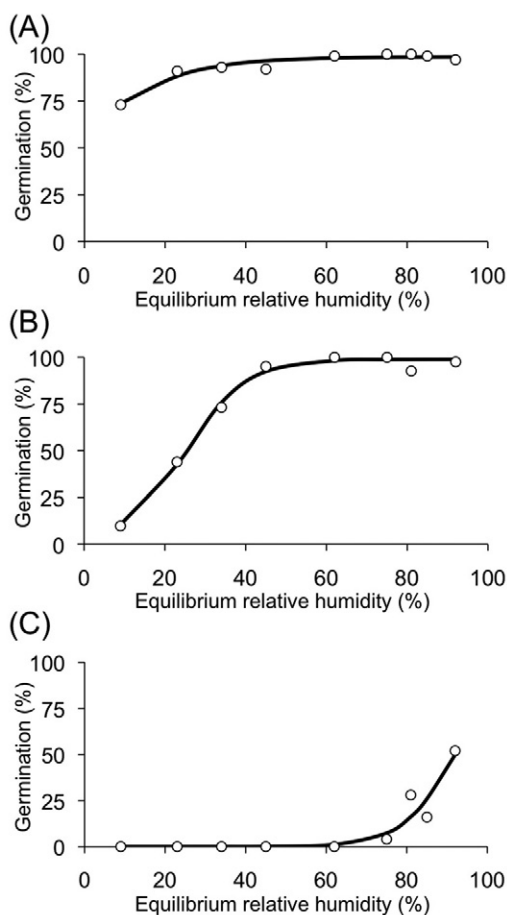


FIGURE 4. Relationship between seed germination and equilibrium relative humidities that modulated seed desiccation for *Pittosporum cherrieri* (A), *Diospyros fasciculosa* (B), *Syzygium multipetalum* (C). (°) is observed germination percentage of seeds; (—) is fitted pattern of the desiccation sensitivity model as computed by the Quasi-Newton method. The three species were chosen to display the three types of seed desiccation sensitivity observed (tolerant, sensitive, very sensitive).

analysis. The PCA performed on variables related to physiological seed data (RH50, iWC, germination, mass), seeds number per fruit, bioclimatic data (6 bioclimatic variables retained), environmental data (elevation mean, frequency on ultramafic soils), with vegetation units (VUs) to which the species could belong (rainforest, dry forest, maquis, other VUs) and the variable “fruit with more

than 5 seeds” used as supplementary variables, showed that more than 88% of the variance was explained by the four main principal components (PC1–PC4) (Table 5). No less than 11 out of the 12 active variables were significantly correlated to the first two components (PC1–PC2), which accounted for more than 68% of the variance (Figure 5). Variables associated with precipitation (BIO12, BIO17 and BIO18) contributed to PC1 whereas RH50, together with variables previously shown to be significantly correlated with RH50 (i.e. iWC, seed mass, rainforest), contributed to PC2. Interestingly, BIO15 (precipitation seasonality) also contributed to PC2. PC2 was significantly positively correlated with RH50 ($R = 0.838$), seed mass ($R = 0.836$), iWC ($R = 0.750$), BIO15 ($R = 0.721$), and rainforest ($R = 0.381$). In addition to being correlated with precipitation variables, PC1 was also significantly positively related to elevation ($R = 0.751$) and frequency on ultramafic soils ($R = 0.525$), and negatively to BIO1 (mean annual temperature) ($R = -0.827$) and dry forest ($R = -0.641$).

A PCA analysis was then performed on the same active variables but not the RH50 variable, and with the same supplementary variables. Species were divided into three classes according to their RH50 value. Thus, species whose values were equal to or less than 20, between 20 and 60, greater than 60, were then considered to have seeds tolerant, sensitive or very sensitive to desiccation, respectively. The distribution of the three desiccation sensitivity classes (tolerant, sensitive and very sensitive) in the PCA was distinctive (Figure 6). Species with very sensitive seeds were almost entirely associated to positive values of PC2 which was correlated to seed mass, iWC, precipitation seasonality and rainforest. Among the 12 species identified as having seeds highly sensitive to desiccation, five were specific to the rainforest, five were possibly found in rainforest and in maquis, and one was possibly found in rainforest and wetland vegetation. The four species classified as sensitive to desiccation were from various vegetation units (dry forest, halophytic vegetation, maquis, rainforest) and pooled in the same area of the PCA plot. Species with desiccation tolerant seeds were spread along PC1 and almost entirely in the lower part of PC2, with

TABLE 3
Seed Desiccation Sensitivity Quantified by the RH50 value for 45 New Caledonian Plant Species

Species	RH50	Species	RH50
<i>Amborella trichopoda</i>	9.0	<i>Oxera pulchella</i> spp. <i>grandiflora</i>	9.0
<i>Arillastrum gummiferum</i>	9.0	<i>Oxera sulfurea</i>	9.0
<i>Atractocarpus vaginatus</i>	44.3	<i>Pittosporum cherrieri</i>	9.0
<i>Austrobuxus buerlimannii</i>	9.0	<i>Pittosporum coccineum</i>	9.0
<i>Calophyllum caledonicum</i>	83.0	<i>Pittosporum gracile</i>	9.0
<i>Calophyllum inophyllum</i>	68.7	<i>Pittosporum poumense</i>	9.0
<i>Dendrolobium umbellatum</i>	9.0	<i>Pittosporum scytbophyllum</i>	9.0
<i>Diospyros brassica</i>	90.0	<i>Pittosporum simsonii</i>	10.7
<i>Diospyros fasciculosa</i>	25.1	<i>Pleioluma longipetiolata</i>	77.0
<i>Diospyros macrocarpa</i>	92.0	<i>Scaevola balansae</i>	9.0
<i>Diospyros vieillardii</i>	77.0	<i>Scaevola cylindrica</i>	9.0
<i>Dysoxylum canalense</i>	85.0	<i>Sophora tomentosa</i>	56.0
<i>Emmenosperma pancherianum</i>	9.0	<i>Styphelia pancheri</i>	9.0
<i>Gabnia aspera</i>	9.0	<i>Syzygium auriculatum</i>	70.2
<i>Geissois racemosa</i>	9.0	<i>Syzygium cumini</i>	42.2
<i>Geniostoma densiflorum</i>	9.0	<i>Syzygium longifolium</i>	66.3
<i>Gymnostoma deplancheanum</i>	9.0	<i>Syzygium multipetalum</i>	92.0
<i>Joinvillea plicata</i> ssp. <i>plicata</i>	9.0	<i>Syzygium pancherii</i>	75.2
<i>Kibaropsis caledonica</i>	82.5	<i>Tristaniopsis glauca</i>	9.0
<i>Meryta denhamii</i>	17.3	<i>Uromyrtus emarginata</i>	9.0
<i>Myrtastrum rufopunctatum</i>	9.0	<i>Wikstroemia indica</i>	9.0
<i>Oxera brevicalyx</i>	9.0	<i>Xanthostemon aurantiacus</i>	9.0
<i>Oxera nerifolia</i>	9.0		

RH50 value is the relative humidity at which 50% of the initial seed viability (control germination) is lost.

TABLE 4

Correlations of Seed Features (Desiccation Sensitivity Value [RH50], Seed Mass [Mass], Seed Initial Water Content [Water content]) with Habitat Association ([Rainforest], [Dry forest], [Maquis]) and Bioclimatic Variables [BIO13], [BIO15], [BIO18] for 45 New Caledonian Plant Species

	RH50		Mass		Water content	
	R	P	R	P	R	P
Mass	0.819	<0.0001				
Water content	0.825	<0.0001	0.698	<0.0001		
Rainforest	0.350	0.018	0.261	0.083	0.323	0.030
Maquis	-0.157	0.302	-0.350	0.018	0.026	0.864
Dry forest	-0.335	0.025	-0.108	0.480	-0.334	0.025
BIO13	0.405	0.006	0.156	0.305	0.364	0.014
BIO15	0.343	0.021	0.456	0.002	0.251	0.096
BIO18	0.432	0.003	0.196	0.198	0.380	0.010

Only vegetation units and bioclimatic variables that displayed significant correlations with these seed features are shown. Significant correlations at a 5% threshold are in bold.

TABLE 5

Correlations between Variables and the Four First Principal Components Resulting from Principal Component Analysis (PCA) Performed on 45 New Caledonian Plant Species

	PC1	PC2	PC3	PC4				
RH50	0.177	0.838	(0.702)	0.401	-0.179			
iWC	0.226	0.750	(0.562)	0.453	-0.161			
Germination	-0.175	0.204		0.283	0.906	(0.821)		
Seed mass	-0.141	0.836	(0.699)	0.394	0.001			
Freq on UM	0.525	(0.274)	-0.413	0.396	-0.206			
Elevation	0.751	(0.564)	0.390	-0.448	0.074			
BIO1	-0.827	(0.684)	-0.266	0.396	-0.085			
BIO4	0.684	(0.468)	-0.557	0.294	0.067			
BIO12	0.955	(0.912)	0.064	0.028	0.056			
BIO15	-0.458		0.721	(0.520)	-0.432	-0.056		
BIO17	0.948	(0.900)	-0.199	0.152	0.038			
BIO18	0.767	(0.589)	0.493	-0.236	0.062			
Seeds + 5	0.013		-0.419	-0.155	-0.046			
Dry forest	-0.641	(0.672)	-0.216	-0.134	-0.046			
Maquis	0.276		-0.283	0.099	-0.153			
Rainforest	0.279		0.381	(0.482)	-0.099	-0.190		
Other VUs	0.035		-0.078	0.038	0.144			
Eigen value	4.733	(39.444)	3.514	(29.283)	1.467	(12.225)	0.950	(7.918)

Significant correlations of variables to the principal components are indicated in parentheses. Variables were seed traits (desiccation sensitivity value [RH50], initial water content [iWC], germination percentage [Germination], seed mass), frequency on ultramafic soils [Freq on UM] and elevation, bioclimatic variables ([BIO1], [BIO4], [BIO12], [BIO15], [BIO17], [BIO18]). Variables such as vegetation units ([dry forest], [maquis], [rainforest], [Other VUs]) and "fruit with more than 5 seeds" (seeds + 5) were qualitative variables. The last row displays the eigen value of each PC and the corresponding percentage of total variance explained.

23 species (out of 29) possibly found in dry forest and/or maquis. Out of the 10 species possibly found in dry forest, nine had desiccation tolerant seeds. Among species classified according to their RH50 values, *Amborella trichopoda* had a unique position in the PCA plot.

DISCUSSION

Our study describes for the first time an analysis of seed desiccation sensitivity for species of the New Caledonian flora. The tolerance or sensitivity of seeds to desiccation was determined for 45 species, and for the first time for 31 of them, along with a search for predictive criteria such as morphophysiological characters and environmental factors.

A total of 33 families, 49 genera and 68 species were covered by this study, with one family, eight genera and 52 species being endemic. Our analyses of fruit and seed traits performed on 68 species revealed that fruits were mainly berries and drupes, and that zoochory was the most widespread dispersal

mode. Frequencies of these traits within rainforest species (39 species) were similar to those found in a previous study on the reproductive traits of 123 New Caledonian rainforest tree species (Carpenter et al. 2003). Great attention was given to the stage of fruit maturity at the time of collection, and to the viability of the seeds prior experiments (e.g. elimination of empty seeds). Some species, however, showed low germination percentages, thus only 45 species were analyzed for seed desiccation sensitivity. Species with seeds sensitive to desiccation were shown to occur in all the major seed-plant taxonomic groups (Dickie and Pritchard 2002). Recent studies estimating the proportion of seed plants with desiccation sensitive seeds (Wyse and Dickie 2017), and based on taxonomic relatedness (FitzJohn et al. 2014), showed that more than 98% of the genera are monomorphic for the seed desiccation trait. Our study was an opportunity to determine the status of desiccation sensitivity of 45 species. Desiccation sensitivity or tolerance was determined

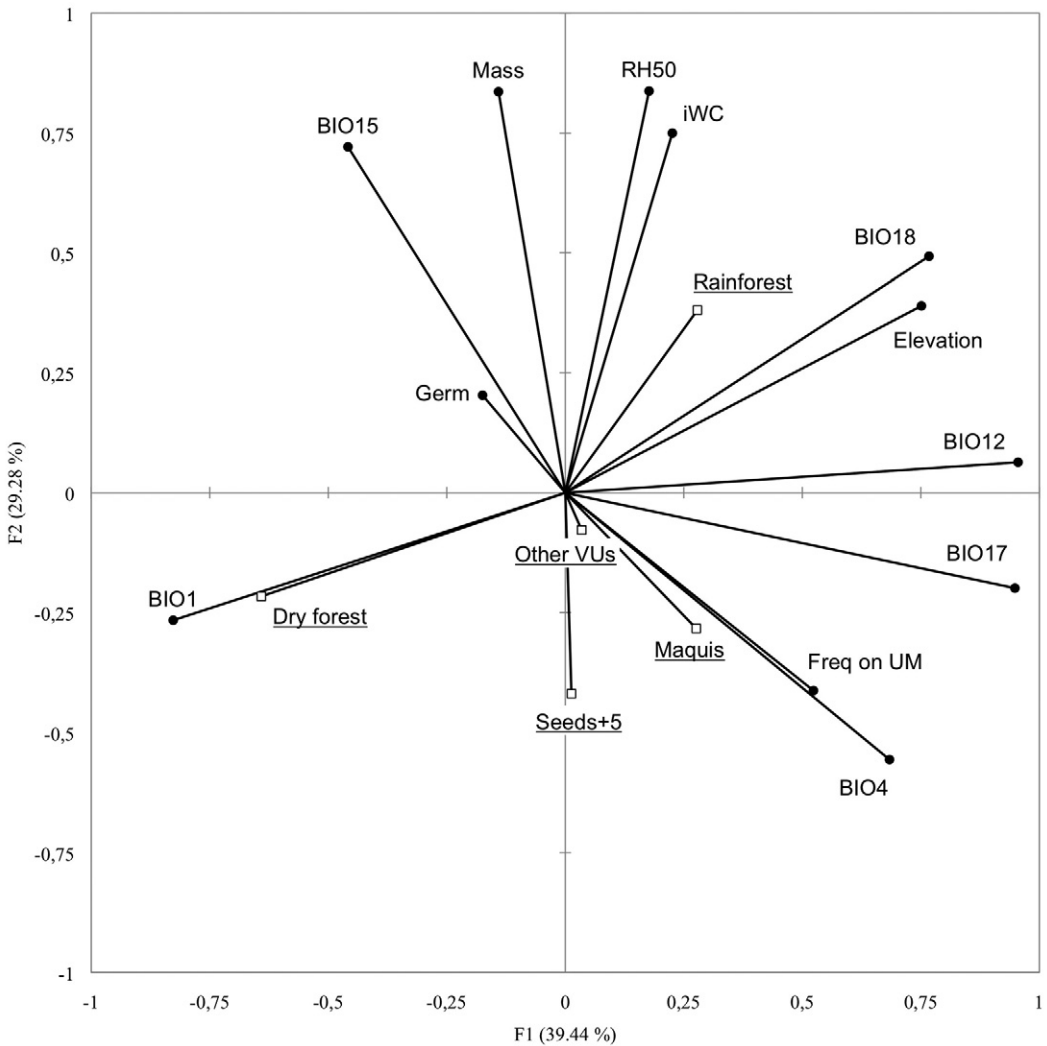


FIGURE 5. Principal Component Analysis (PCA) plot showing the multivariate variation among 45 New Caledonian plant species in terms of seeds traits (seed mass [MASS], initial water content [iWC], germination percentage [Germ], seed desiccation sensitivity value [RH50]), environmental data (elevation [elevation], frequency on ultramafic soils [Freq on UMI]), bioclimatic variables ([BIO1], [BIO4], [BIO12], [BIO15], [BIO17], [BIO18]), vegetation units ([rainforest], [dry forest], [maquis], [Other VUs]) and fruit with more than 5 seeds [Seeds + 5]. All variables were active, with the exception of vegetation unit qualitative variables (rainforest, dry forest, maquis, other VUs) and variable “fruit with more than 5 seeds” which were supplementary variables and are indicated by an underline. Axes F1 and F2 explain 68.72% of variance. Vectors indicate the direction and strength of each variable to the overall distribution.

for the first time for 31 species. Some genera had species characterized for desiccation sensitivity for the first time, especially these genera: *Atractocarpus*, *Austrobuxus*, *Emmenosperma*, *Kibaropsis*, *Styphelia*. Our results confirmed a status characterized, or determined

as probable, by previous studies for another 13 species (Bailly et al. 1986, L’Huillier et al. 2010, Royal Botanic Gardens Kew 2016, Zongo et al. 2016, Villegente et al. 2017). The exception was for *Sophora tomentosa*, a species specific to halophytic vegetation in New Caledonia (with

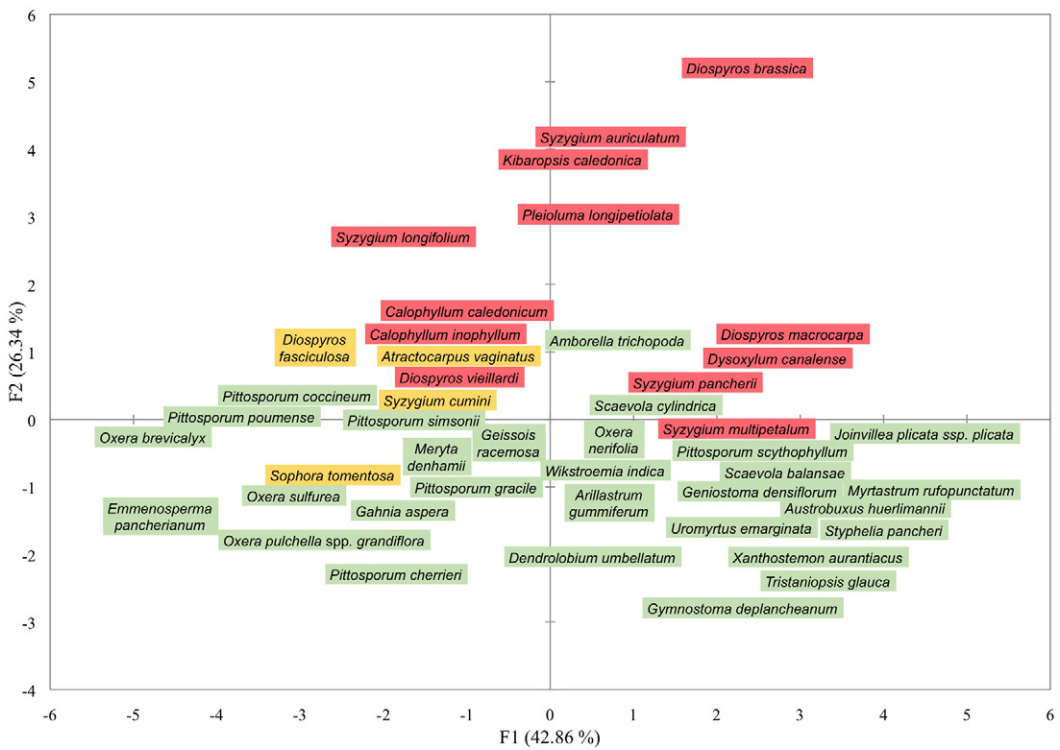


FIGURE 6. Distribution of the 45 New Caledonian plant species in the Principal Component Analysis (PCA) plot using variables such as seeds traits (seed mass [Mass], initial water content [iWC], germination percentage [Germ]), environmental data (elevation [elevation], frequency on ultramafic soils [Freq on UM]), bioclimatic variables ([BIO1], [BIO4], [BIO12], [BIO15], [BIO17], [BIO18]), vegetation units ([rainforest], [dry forest], [maquis], [Other VUs]) and fruit with more than 5 seeds [Seeds + 5]. All variables were active, with the exception of vegetation unit qualitative variables (rainforest, dry forest, maquis, other VUs) and variable “fruit with more than 5 seeds” which were supplementary variables. Axes F1 and F2 indicate 69.20% of variance. Species background colors depend on their RH50 value: green for species whose values were equal to or less than 20, yellow for species whose values were between 20 and 60, red for species whose values were greater than 60.

seeds collected on a small island), and found to be seed desiccation sensitive in our study. Seed-plant species issued from halophytic vegetation such as mangroves, may produce desiccation sensitive seeds (Wyse and Dickie 2017), but the contradictory status observed with regard to seed desiccation requires further studies on this species. For genera in which other species have previously been studied, our results showed an identical status regarding sensitivity to desiccation. The genus *Diospyros* displays a contradictory status with 21 orthodox-probable or orthodox species and 11 desiccation sensitive or sensitive-probable species (Royal Botanic Gardens Kew 2016); the four *Diospyros* species analyzed in our study revealed sensitivity to

desiccation. Our study included four genera with several species: *Diospyros*, *Oxera*, *Pittosporum* and *Syzygium*, with four, four, six and five species, respectively. Desiccation sensitivity was shown to be conserved for species within the same genus, with species *Oxera* and *Pittosporum* being tolerant and those of *Diospyros* and *Syzygium* being sensitive. Thus, our results could help to define the trait of seed desiccation sensitivity for other New Caledonian species belonging to the genera we evaluated.

Our analysis covered species that could be found in various types of vegetation, including rainforest, dry forest or maquis. We showed a positive association between seed desiccation sensitivity and seed water content, seed size,

seed mass, and the presence in rainforest. Seed size, together with the latitudinal gradient, have been shown to be closely linked to vegetation types, and positively with rainforest (Moles et al. 2007). Seed mass has been found to be greater for desiccation-sensitive species (Dickie and Pritchard 2002, Daws et al. 2006), and desiccation-sensitive species occur most commonly in wet tropical forests (Dickie and Pritchard 2002, Tweddle et al. 2003). Other studies on tropical forest taxa showed similar correlations with species' sensitivity to desiccation and seed mass (Daws et al. 2005, Daws et al. 2006, Hamilton et al. 2013). Ecological conditions that favor desiccation sensitivity were also suggested to select for large seed size (Tweddle et al. 2003). Large seeds were shown to enhance seedling survivorship under a low light canopy (Foster 1986, Leishman and Westoby 1994). In our study, presence of the species in rainforest was significantly correlated to seed desiccation sensitivity and seed water content; however the correlation was not significant with seed mass. Species found in dry forest were likely to produce seeds tolerant to desiccation, supporting the assumption that the proportion of species with desiccation sensitive seeds is lower in drier than wetter habitats (Hong and Ellis 1998, Tweddle et al. 2003, Delgado and Barbedo 2012).

The New Caledonian flora originates from relatively recent long-distance dispersal events (after a re-emersion 37 Mya ago) followed by *in situ* speciation (Grandcolas et al. 2008, Espeland and Murienne 2011, Pillon 2012). Diversification of the flora occurred (Pintaud et al. 2001, Pillon et al. 2009) in a high diversity of habitats due to great variation in climate, topography and geology recognized to constrain species distributions (Jaffre 1993, Morat 1993). Our study showed that seed desiccation sensitivity is positively correlated to precipitation of the warmest quarter of the year and precipitation seasonality. These climate correlates together with rainforest habitat may favor the probability that a species will produce desiccation sensitive seeds. Our findings suggested correlations between vegetation units and desiccation sensitivity. Species from drier habitats are likely to have seeds non-sensitive to

desiccation, and species from rainforest have seeds more likely to be sensitive to desiccation. These results are consistent with the extant literature (Tweddle et al. 2003, Pritchard et al. 2004). Species from the understory of tropical rainforest are more likely to have large seeds and therefore to be sensitive to desiccation (Foster 1986, Tweddle et al. 2003, Daws et al. 2006). The singular species *Amborella trichopoda* is only found in the rainforest understory and produces small seeds. The desiccation tolerance observed for this species may be the result of the conservation of ancestral morphological or ecophysiological traits (Fourcade et al. 2015, Villegente et al. 2017).

The biodiversity of New Caledonia is threatened by habitat loss associated with mining activities, agriculture, fire and urban planning (Bouchet et al. 1995, Gillespie and Jaffre 2003, Pascal et al. 2008). Global climate change may represent a major additional threat to island biodiversity, with a high number of insular endemic plants species already considered as endangered or critically endangered (Caujape-Castells et al. 2010, Harter et al. 2015).

Established in accordance with criteria from the International Union for Conservation of Nature (IUCN), a list of the threatened flora of New Caledonia is updated periodically by a local red list authority (RLA) committee (<http://endemia.nc/en/page/laliste-rouge>). So far, more than 1000 species have been evaluated; 40% of them were identified as endangered, with 95 species being classified as critically endangered (CR), 175 as endangered (EN), 149 as vulnerable (VU) and more than 30% were classified as least concern (LC). But these numbers might increase in the course of climate change. Indeed, a modeling analysis of the potential impact of climate change on the whole New Caledonian tree flora predicted a general decrease of species area of occupancy and major losses in local species richness (Pouteau and Birnbaum 2016). Among the 68 species targeted in our study, 19 have been evaluated according to IUCN criteria (vulnerable, near threatened, least concern) and 10 are protected by local policies. In our study we determined the sensitivity to desiccation of 13

of 19 and 9 of 10 species, respectively. Among species tested for sensitivity to desiccation and mentioned by the RLA committee, nine have desiccation tolerant seeds (*Amborella trichopoda*, *Emmenosperma pancherianum*, *Geissois racemosa* and all *Pittosporums species*), one has desiccation sensitive seeds (*Diospyros fasciculosa*), and three have desiccation very sensitive seeds (*Diospyros brassica*, *Diospyros macrocarpa*, *Diospyros vieillardii*) with *Emmenosperma pancherianum*, *Pittosporum cherrieri* and *Pittosporum scythophyllum* having the status of vulnerable (VU) and *Diospyros vieillardii* of near threatened (NT).

Seed desiccation tolerance or sensitivity has a direct impact on techniques that can be used for conservation. Desiccation tolerant seeds can be stored successfully using conventional techniques (drying and storage at low temperatures) (Roberts 1973, Roberts and Ellis 1989). However, desiccation sensitive (intermediate or recalcitrant) seeds must be stored using biotechnology methods, preferably by cryopreservation (Walters et al. 2013). The present study identified morphophysiological seed characteristics and environmental factors that can be used to predict seed desiccation sensitivity. Such analysis will be prominent in determining seed behavior for storage and methods to use for long-term storage and other conservation plans. Our study will contribute to decision-making to be put in place for *ex situ* biodiversity conservation strategies for threatened species in New Caledonia. In addition, our analysis of predictors for seed sensitivity or tolerance desiccation will inform land managers to define species suitable for integration into revegetation strategies of disturbed environments to maintain or restore biodiversity.

ACKNOWLEDGMENTS

Authors are grateful to the Province Sud de Nouvelle-Calédonie and Province Nord de Nouvelle-Calédonie for permission for seed collection. The authors thank Dr J. Read (Monash University, Australia) for providing some data regarding fruits and seeds traits, and C. Chambrey for her assistance in field missions.

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