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Forest Restoration at Berenty Reserve, Southern Madagascar: A Pilot Study of Tree Growth Following the Framework Species Method

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Abstract: Forest conservation and restoration are urgently needed to preserve key resources for the endemic fauna of dry southern Madagascar. This is a priority in the shrinking, seasonally dry forest of Berenty, a private reserve in Southern Madagascar. However, to provide a basis for forest restoration, a study of tree growth and regeneration in this unique biome is essential. A three-year planting program of native and endemic species was initiated in 2016. Three trial plots were established in forest gaps, with varying microclimates and soil conditions: one on the riverside, one in the mid-forest and the third in a degraded dryland area. We planted 1297 seedlings of 24 native tree species with plantings spaced at 1 m and 1.5 m and measured their height and stem diameters and recorded seedling mortality. We also recorded plant recruitment on the plots from the nearby forest. The main findings were that growth was best on the mid-forest plot planted at 1 m. Seedling mortality was highest on the riverside plot for the 1 m seedlings and least in the mid-forest at both planting distances. Recruitment was highest in the mid-forest at both planting distances and high also at 1.5 m by the river. These results are intended to aid future forest restoration on the Reserve and may serve as a reference for restoration of other dry forests in Madagascar. Finally, since species identification is central to the project, we collected, prepared and catalogued tree specimens to form a reference collection in an herbarium under construction in a new Research Centre at the reserve.

Keywords: conservation; planting program; dryland; growth; mortality; recruitment; reference collection

1. Introduction

Madagascar has one of the highest concentrations of endemic species anywhere on Earth [1], but these species are now severely threatened by deforestation. The threat is nowhere greater than in the dry south, due to a fast-rising human population and their need for building materials, fuel and grazing for the zebu cattle that form the basis of their society [2–4]. Conservation is urgently needed, but although in Madagascar there are many conservation areas [5], there is little government money to support local conservation and few of the forests are fully protected [6].

In Madagascar, primary forest has been reduced to coastal fragments including humid evergreen tropical forests, clinging to steep mountains on the eastern seaboard and, to the south and southwest, seasonally dry deciduous forests [7]. Much has been written about dry deciduous forests in Central and South America and Africa concerning their general characteristics, structure and floristic composition [8,9], but in dry southern Madagascar, such studies are scant. These include a species list compiled by the Groupe des Spécialistes des Plantes de Madagascar [10]; Crowley [11] described the location, distinctive biodiversity features and threats to this semi-arid biome and Aronson et al. [12] produced a comprehensive inventory of overall tree diversity and endemism.

A detailed analysis was published for the Beza Mahafaly Reserve by Sussman and Rakotozafy [13], with this covering the density, diversity, floristic composition, structure and regeneration patterns of the forest vegetation, but it lacks insights into tree growth or planting practices that could be used to guide restoration of the forest ecosystems at the Private Reserve of Berenty our study site 230 km southeast of Beza Mahafaly.

Berenty is a prime example of environmental conservation in a region that is otherwise suffering deforestation at an unprecedented rate [14]. The Reserve has been owned and protected by the de Heaulme family since 1936, but as early as 1973 primatologists noticed that the forest was shrinking and degrading [15,16]. It was clear that reasons for increasing degradation needed investigation [17].

Tree ring analysis showed that the dominant species in the gallery forest, *Tamarindus indica* (tamarind), has a median age of nearly 200 years and wherever a tree dies and falls direct sunlight reaches the forest floor allowing the invasion of an African vine (*Cissus quadrangularis*), prickly shrubs and tall grasses (notably *Panicum maximum*), which suffocate emerging seedlings and saplings. Around the remaining forest areas, edge effects including the invasion of vines and shrubs, the mortality of large trees and growth of secondary species, threaten the existing canopy forest [18]. Thus, although anthropogenic reasons for deforestation, common elsewhere in Madagascar are not a problem, the gallery forest at Berenty is threatened by age decline and *C. quadrangularis* invasion. In the Reserve, a vine clearance program is ongoing and forest restoration is in prospect.

For restoration to succeed, knowledge of tree species biology and ecology is essential [19]. Without it, any forest restoration attempt could fail or, even worse, damage an already fragile ecosystem. In 2016, we initiated a 3-year forest restoration trial following the general principles of the framework species method advocated by Elliott et al. [20], with further rules for its application set out by Di Sacco et al. [21].

Following the method, our work included a comparison of growth rates and mortality of species planted 1 m and 1.5 m apart, in three different forest locations, near the river, mid-forest and in the dryland area, with the objective of determining where species best thrive with respect to their location, planting distance and species performance. The project's long-term goal is to arrest forest decline and restore biodiversity levels to those typical of the remaining forest fragments, thus conserving key resources for the lemurs and other endemic fauna. It is intended that the knowledge gained could also provide a basis for forest restoration in other seasonally dry forests in southern Madagascar.

2. Study Area

Berenty Reserve, (25°00′20″S 46°18′05″E) lies on the banks of the Mandrare River, 18 km from the south coast at an altitude of around 30 m a.s.l (Figure 1). Mean annual precipitation is 500 mm, with a dry season from April to September, but rainfall is extremely variable (Figure 2). The floodplain is laced by ancient river channels (paleochannels), with the oldest of these underlying a steep 10-m high bank on the perimeter of the Reserve formed during a period of river downcutting [22]. Tree regeneration is fostered in the shallow paleochannels where leaf litter retains moisture particularly during the rainy season (October to April). The striking red soils above the flood plain are iron-rich unconsolidated sands overlying Archaean basement rock. In contrast, the alluvial sediments on the floodplain are derived largely from rhyolite a quartz-rich, mildly alkalic feldspar from the Androy lava flow, which covers a large part of the upstream river catchment [23].

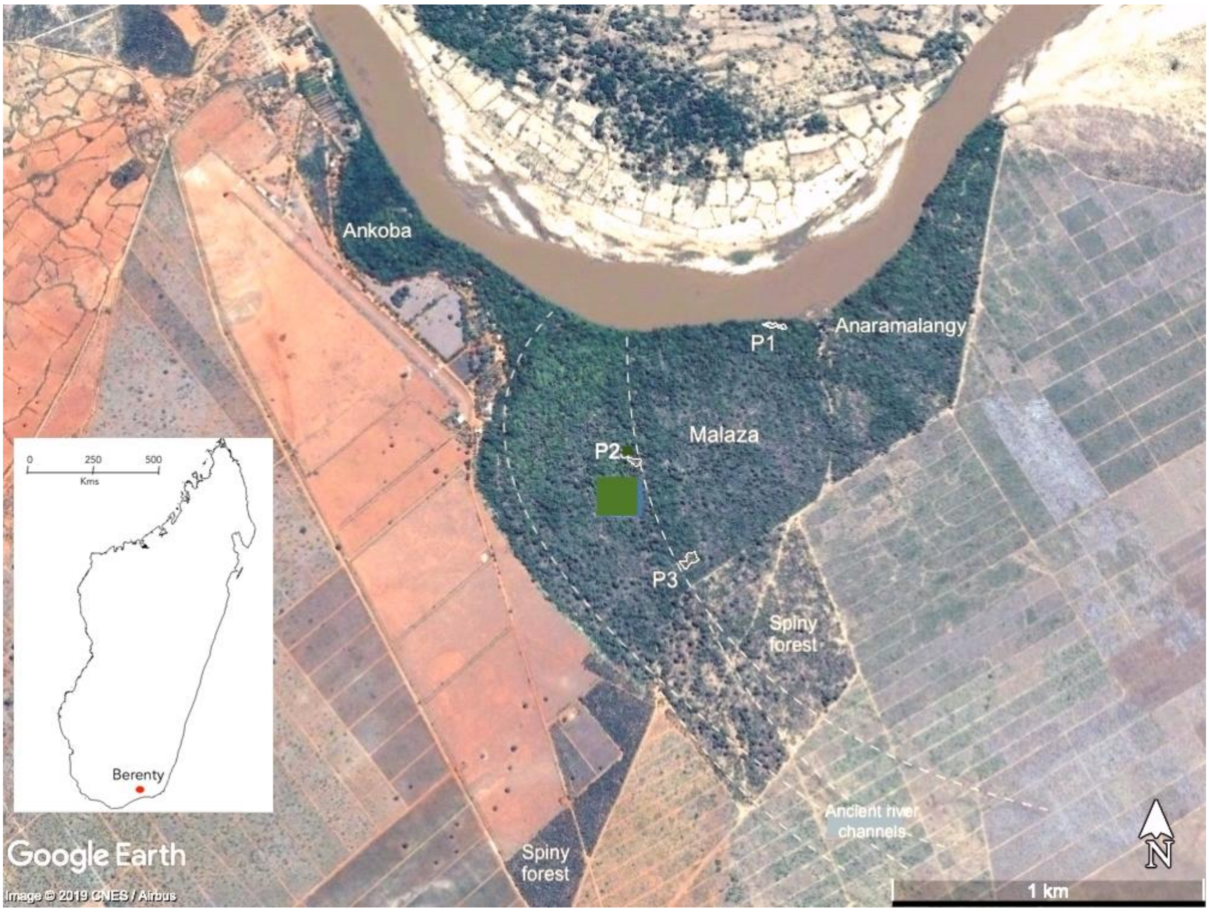

Figure 1. Berenty Reserve showing main forest areas, plot positions and ancient river channels.

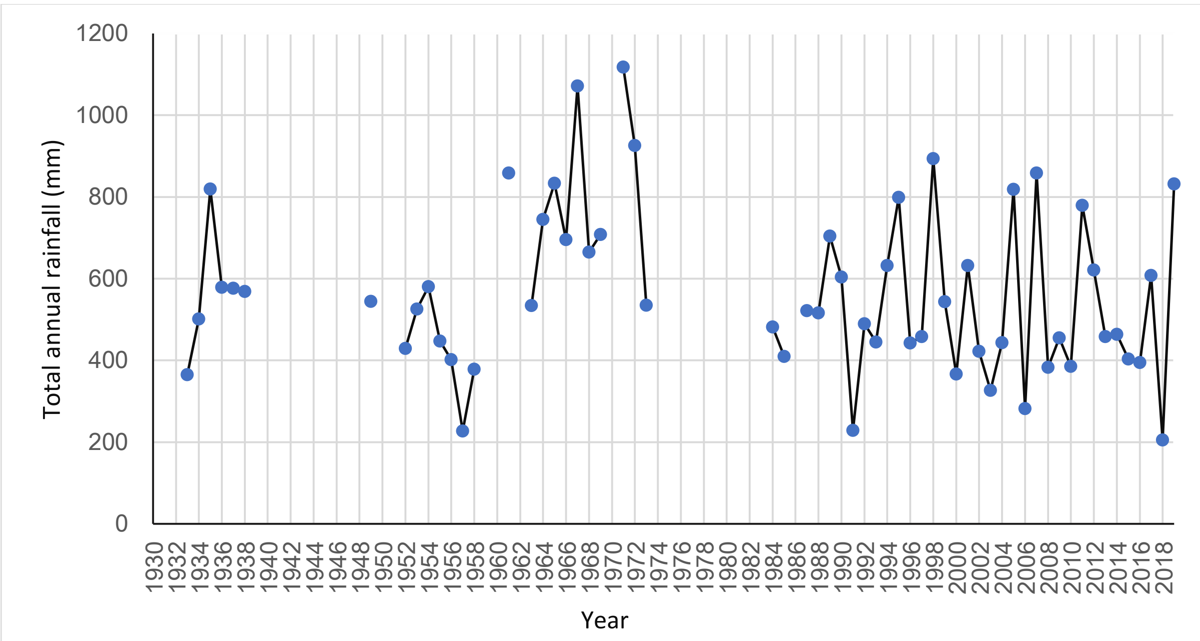

Figure 2. Annual rainfall totals at Berenty Reserve from 1933 to 2019. With data collected at Berenty Sud by Mr Rakotomalala and Henry de Heaulme. The gaps denote missing records.

The forest in Malaza, the main part of the Reserve where we carried out our work, may once have covered the whole floodplain, but today it is divided into closed canopy gallery forest, limited to a 100–150 m-wide band of tamarind trees up to 30 m tall and lower canopy species by the riverside. Transitional forest with large trees (15–30 meters tall) and lower canopy species (under 15 m) generally decline in abundance with increasing distance from the river. The eastern half of the former forest where large trees are rare has become degraded with patchy cover of dryland trees (mostly under 15 m) together with the *C. quadrangularis* vine and prickly shrubs.

Malaza, covering around 100 ha, has been protected since 1936. Ankoba, joined by a corridor to the northwest corner of Malaza, is a 15-ha patch of secondary forest that has been protected since the 1950s, while Bealoka, a gallery forest with an area of 110 ha that lies up-river 6.5 km to the northwest, has been protected since 1985. Anaramalangy, on the east side of Malaza, and divided from it by a cattle trail leading to the river, is a patch of 36 ha where protection has been less effective due to ingress of cattle and invasion of *C. quadrangularis*. Remnants of unique spiny forest vegetation, well adapted to the arid conditions, cover the gentle valley slopes south of Malaza [24,25].

3. Materials and Methods

3.1. Restoration Trial Plots

In Malaza three experimental plots, P1, P2 and P3, were established in 2016 in degraded openings. P1 on the riverbank had become invaded by vines following the death of a tamarind tree. P2 in the mid-forest covered an area burnt in 2006 and P3 was a degraded dryland area where almost all the large canopy species had died, identified as stage 2 degradation by Elliott et al. [26] (p. 68). P1 and P2 covered approximately 600 m^2 each, while P3 covered 900 m^2. All three plots were flat, but that on the riverbank had tall trees only on its forest edge to the south. P2 in the mid-forest had tall trees on three sides and a track flanked by an ancient dry river channel to the east and P3 was open with only two tall trees. Detailed maps were made of all the plantings, mortality and existing trees on every plot (Figure S1a–c).

Unlike wetter tropical climates where 1.8 m is an optimum distance for forest restoration [26] (pp. 76, 127, 130), at Berenty rainfall is highly variable (Figure 2) and canopy closure is likely to take longer. Hence, closer planting distances were trialed, with the choice of 1 m and 1.5 m distances suggested by the naturally close spacing of understory trees in the gallery forest.

To test the effects on growth of different planting distances, each plot was divided into two sections, with seedlings in one section planted at 1 m and in the other at 1.5 m apart (Table 1; Figure 3).

Table 1. Planting distances plot areas and seedling numbers.

Plot	P1	P1	P2	P2	P3	P3
Planting distance	1 m	1.5 m	1 m	1.5 m	1 m	1.5 m
Area (m^2)	305	309	278	354	346	556
Seedling numbers	251	142	257	166	268	213

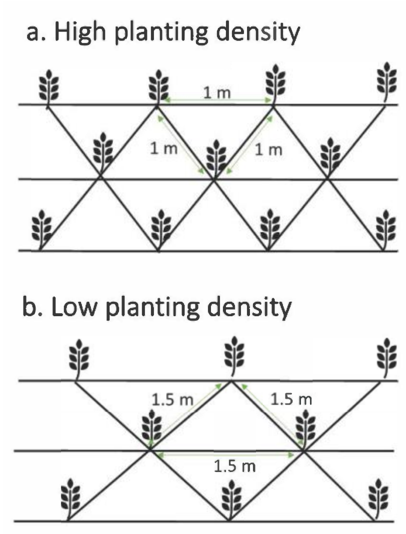

Figure 3. Planting design for the (**a**) high density (1.0 m) and (**b**) low density (1.5 m) planting treatments.

3.2. Species Selection, Planting and Measurement

A total of 1297 seedlings of 24 species belonging to 15 families of common native or endemic trees were planted in 2016, with the species chosen based on surveys in 2011–2014 (Table 2). The seedling species were classified as upper canopy, lower canopy and dryland species according to their growth characteristics in the forest.

Table 2. Planted species with the family, botanical and local names.

	Family	Species	Local Name
1.	Fabaceae	*Acacia rovumae* *	Rovontsy
2.	Fabaceae	*Albizia polyphylla* *	Halomboro
3.	Salvadoraceae	*Azima tetracantha* *	Filofilo
4.	Fabaceae	*Bauhinia decandra*	Tangatanganala
5.	Cannabaceae	*Celtis bifida*	Bemavo
6.	Cannabaceae	*Celtis gomphophylla*	Hazompotsy
7.	Cannabaceae	*Celtis madagascariensis*	Tsilikantsifaka
8.	Burseraceae	*Commiphora aprevalii* *	Daro
9.	Rubiaceae	*Coptosperma nigrescens* *	Mantsake
10.	Boraginaceae	*Cordia caffra*	Varogasy
11.	Capparaceae	*Crateva excelsa*	Keleogny
12.	Euphorbiacae	*Euphorbia tirucalii*	Famata
13.	Malvaceae	*Grewia androyensis*	Tabarike
14.	Malvaceae	*Grewia calvata var. arbuscula*	Andapary
15.	Sapindaceae	*Neotina isoneura*	Volely
16.	Anacardiaceae	*Poupartia* sp.	Magoe
17.	Violaceae	*Rinorea greveana*	Tsatsaky
18.	Salvadoraceae	*Salvadora angustifolia*	Sasavy
19.	Apocynaceae	*Strophanthus boivinii*	Kapoke
20.	Loganiaceae	*Strychnos madagascariensis*	Dagoa
21.	Apocynaceae	*Tabernaemontana coffeoides*	Feka
22.	Fabaceae	*Tamarindus indica* *	Kily
23.	Rubiaceae	*Tricalysia dauphinensis* *	Hazombalala
24.	Ximeniaceae	*Ximenia perrieri*	Kotro

* Species that are native but not endemic, as defined by Phillipson et al. [25].

The seedlings were planted in compost and forest soil 50:50, with wood chippings placed as a mulch around the base of each seedling to conserve moisture and prevent weed growth. Holes for seedlings were dug 40 × 40 × 40 cm; each hole was numbered, and the species were labelled with their vernacular names.

To assess the growth of the planted seedlings 2016–2018, we chose four key variables: height and root collar diameter growth rates; the mortality of the seedlings and recruitment from the forest.

Seedlings were measured after planting in July 2016 and between July and August in 2017 and in 2018. The measurements were height to terminal bud and root collar diameter taken using a meter tape and a Vernier caliper, respectively. Dead individuals were recorded every year and qualitative data on seedling health from visual cues, such as wilting or leaf-loss, were recorded together with the presence or absence of competing weeds (mostly grasses). In 2017 and 2018, the positions and the identity of species recruited from the surrounding forest were also recorded. The forest owner established daily watering, with this carried out all year round. To provide shelter from the sun, the owner also had small roofs constructed over the seedlings on P2 and P3, where most existing trees were under 15 m tall and only provided light shade. The long narrow plot P1 on the riverbank had a tall *Celtis bifida* growing in the middle and lower canopy shade trees at either end (Figure S1a).

3.3. Soil Sampling and Plant Identification

Soil samples were collected from the plots and across the forest at a depth of 5 and 25 cm [27] and analyzed at the School of Geography and the Environment, University of Oxford. Soil grain size distribution was analyzed using a Malvern 2000 Mastersizer with a gradistat program used for soil interpretation. Soil pH was measured using a Hanna pH meter. Organic content percentage was based on loss from Ignition and moisture was calculated as a percentage of the dry weight after drying the soil at 60 °C for 3–4 days until a constant weight was reached.

Additionally, to gain a better understanding of the plant diversity in Malaza, voucher specimens from 76 mature tree species (16 of these are awaiting botanical determination) were collected starting with the species used in the trials, together with their flowers, fruit and seeds where available. Other species occurring less frequently were also collected for the benefit of future researchers and to form part of the record. Curation involved identifying the species and linking their botanical names to the local vernacular names, drying, pressing, photography and descriptions, with each specimen laid out on a card for eventual inclusion in a prospective herbarium.

3.4. Data Analysis

The only methods available for analysis of the effects on seedling growth due to the inevitable plot differences: location in the forest, soil, moisture and shade from existing trees, were application of significance tests.

Relative growth rates (RGR) were calculated using the equation:

$$\mathrm{RGR} = \frac{\ln(\mathrm{M}_2) - \ln(\mathrm{M}_1)}{\mathrm{T}_2 - \mathrm{T}_1} \quad (1)$$

where M_1 and M_2 are the height or root collar diameter at time 1 (T_1 = 2016) and time 2 (T_2 = 2018). The increase in the natural log of the height and root collar diameter was divided by the time interval in which measurements were taken (365 days). Mortality rates (in percentages) were calculated as the number of dead individuals of a species divided by the total individuals planted in 2016 for each plot and for each planting distance.

The statistical package R was employed for data analyses [28] (R Core Team, v3.6.2, 2019), with the packages' ggplot2' [29] and 'forcats' [30]) used to create the plots and the package 'dplyr' [31] to manage and arrange the data. The differences in the means of height and root collar diameter relative growth rates were tested using the Mann–Whitney U-test, after testing for normal distribution using the Shapiro–Wilk test. Mean rates of relative growth rates and mortality for years 2016–2018 (2016–2018 here onwards) were used throughout the analysis.

4. Results

4.1. Relative Growth Rates

Relative growth rates were consistently higher at the 1 m planting distance (Figure 4). Both height (RGR-H) and root-collar diameter (RGR-RCD) relative growth rates were significantly higher on P1 and P2 but lacked significance on P3 (Table 3).

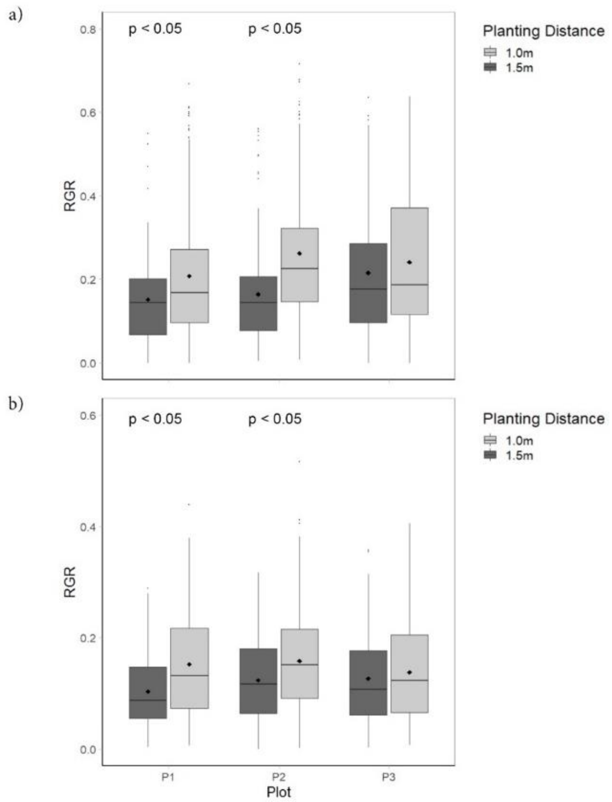

Figure 4. Seedling relative growth rates, 2016–18, per planting distance measured as: (**a**) height and (**b**) root collar diameter. The results are shown for all the plots (P1, P2 and P3).

Table 3. Mann–Whitney U-Test results comparing significance of differences in the relative growth rates by planting distance (1 m vs. 1.5 m) of all species within the plots.

RGR-H			RGR-RCD		
Plot	**W Statistic**	***p*-Value**	**Plot**	**W Statistic**	***p*-Value**
P1	7324.5	0.00048 *	P1	7416.5	0.00078 *
P2	23,808	<0.00001 *	P2	19,517	0.02212 *
P3	14,854	0.2296	P3	14,486	0.4331

* = significant at the 0.05 level.

Overall, the relative mean height-growth rate was higher at the 1 m planting distance for 19 out of 24 of the planted species (79%) (Figure 5a), and for 16 out of the 24 planted species (66.6%) when measured as root collar diameter growth rates (Figure 5b).

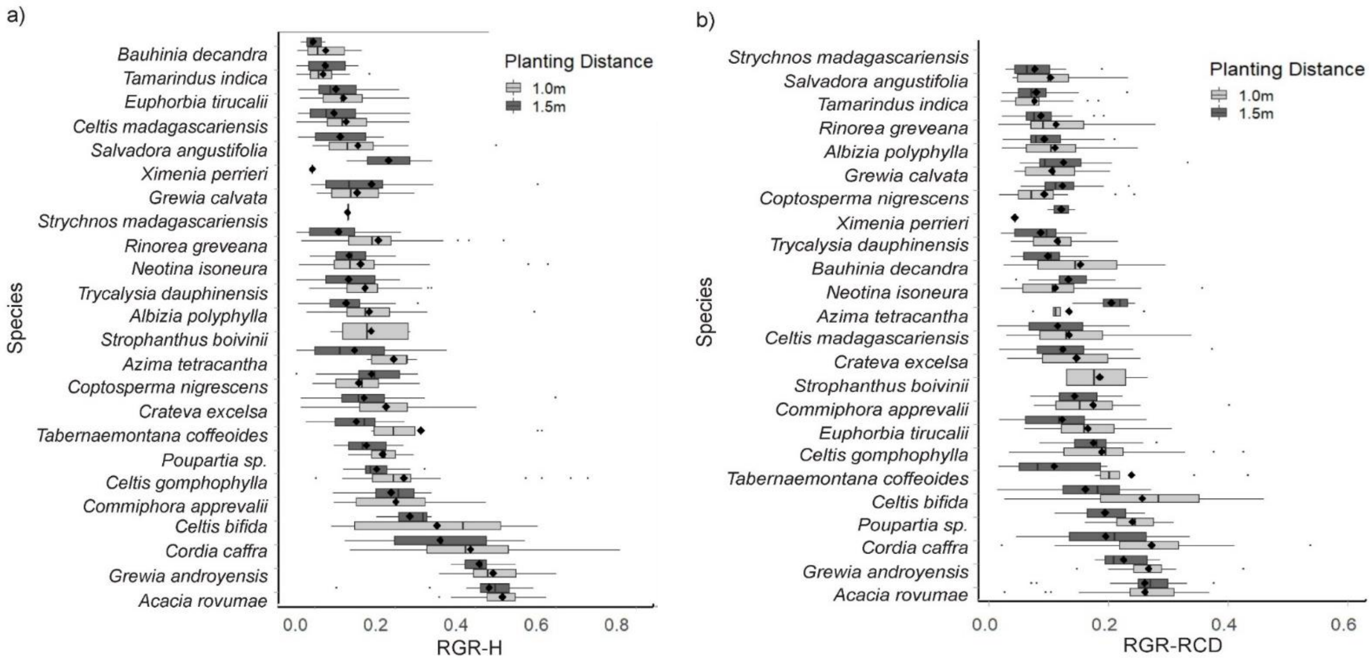

Figure 5. Comparison of planting distance and species mean relative growth rates on the three plots combined: (**a**) height, (**b**) root collar diameter. *Strychnos madagascariensis* lacks a boxplot since only one seedling survived.

Our RGR results (Figure 6a) show that the growth of the three canopy types, upper canopy, lower canopy and dryland species, is poorly related to their type or their growth rates for height. Upper canopy species and dryland species span the range. By contrast, lower canopy species mostly span the middle of the range with only one, *Bauhinia decandra*, at the lower end of the range. Some species, e.g., *Coptosperma nigrescens* and *Strophanthus boivinii*, are shown as dryland species but may also grow in lower canopy positions in the forest, although they may initially need light [18]. *Crateva excelsa*, an upper canopy species, also has recruits on P1 and P2 in both shaded and dryland areas.

4.2. Mortality Rates

Mortality rates of the species are shown in Table 4 and Figure 7a,b. Seedling mortality was highest on P3 (27.03% or, excluding *Ximenia Perrieri*, 17.84%), followed by P1, with a mortality rate of 23.4%. The lowest mortality (10.4%) occurred on P2. Mortality was consistently higher on the plots at a planting distance of 1.5 m, although a Welch two-sample *t*-test showed no significant difference (at the 0.05 level) between mortality rates for the planting distances on any of the plots (P1: p-value = 0.2828, df = 29.066; P2: p-value = 0.4351, df = 28.388; P3: p-value = 0.2938, df = 29.862) for all the plots combined (Figure 7a). Plant mortality on the 1.5 m plots was higher (74.44%) than on the 1 m plots (51.9%). Nevertheless, this difference was not statistically significant (p-value = 0.0936, df = 100).

Figure 7b shows that the species with the maximum overall mortality was *Celtis bifida* (an upper canopy species) with a mortality of 62% on the 1 m plots and 89% on the 1.5 m plots. Further, almost none of the *X. perrieri* species, which were only planted on P3, survived (a mortality of 95% on the 1 m planted plots and 91% on the 1.5 m plots). The other species showing the highest mortality rates were *Coptosperma nigrescens*, with 82% mortality planted at 1 m and 60% planted at 1.5 m, and *Tabernaemontana coffeoides*, with 89% mortality at 1 m and 100% mortality at 1.5 m.

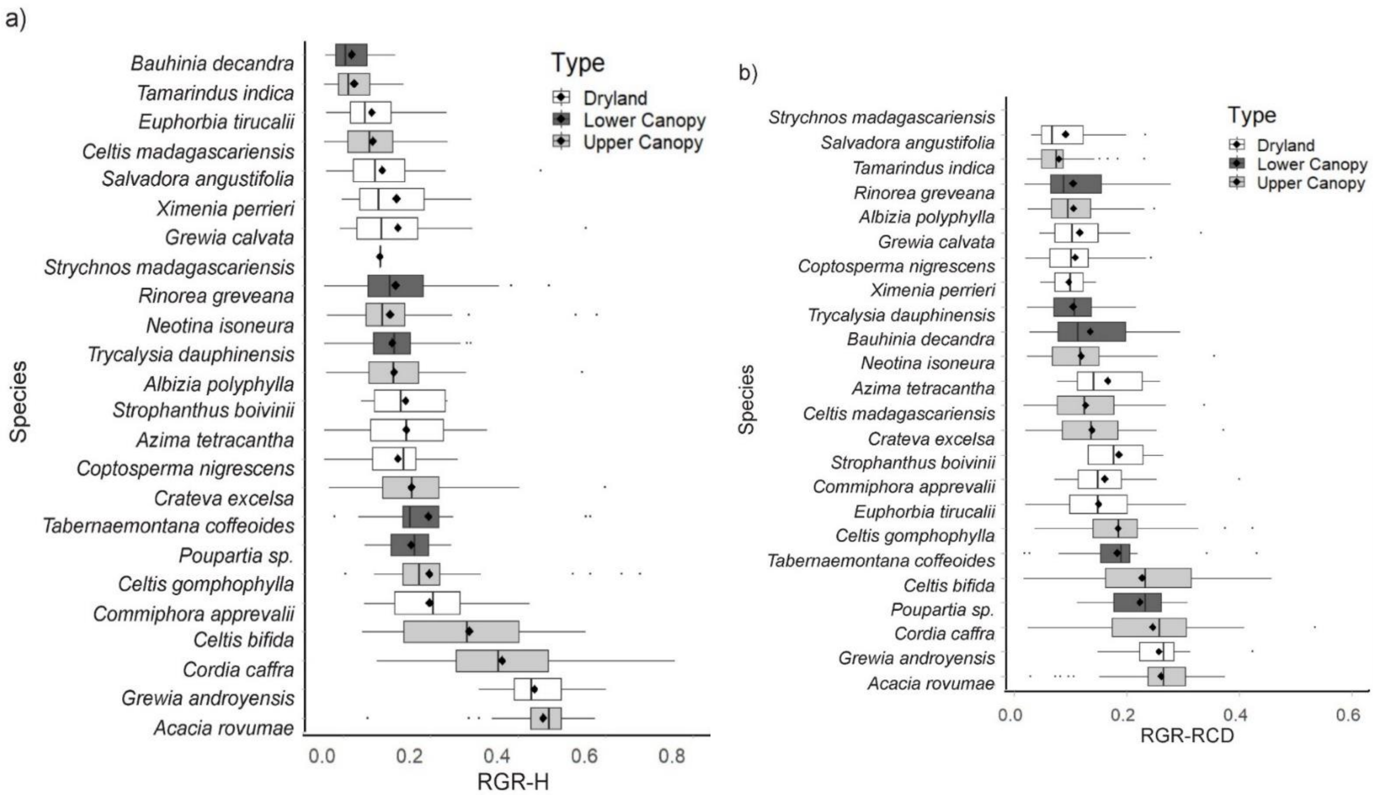

Figure 6. Species relative growth rates according to canopy type: (**a**) height, (**b**) root collar diameter.

Table 4. Dead seedlings and percent mortality per plot and planting distance. n/p = not planted. 0 = all seedlings survived.

	Mortality 2017–2018					
Plot	P1 1 m	P1 1.5 m	P2 1 m	P2 1.5 m	P3 1 m	P3 1.5 m
Total seedlings planted	251	142	257	166	268	213
Species						
Acacia rovumae	2	4	4	7	0	0
Albizia polyphylla	2	1	0	0	0	1
Azima tetracantha	n/p	n/p	0	0	n/p	1
Bauhinia decandra	5	2	n/p	n/p	n/p	n/p
Celtis bifida	10	7	7	9	n/p	n/p
Celtis gomphophylla	1	0	0	0	1	0
Celtis madagscariensis	4	4	1	1	n/p	n/p
Commiphora aprevalii	n/p	n/p	0	0	4	2
Coptosperma nigrescens	10	2	1	2	0	3
Cordia caffra	0	1	0	0	0	0
Crateva excelsa	0	0	0	1	1	2
Euphorbia tirucalii	0	0	n/p	n/p	0	0
Grewia androyensis	0	0	n/p	n/p	6	13
Grewia calvata	n/p	n/p	2	4	7	6
Neotina isoneura	8	4	0	3	0	1
Poupartia sp.	0	1	0	0	n/p	n/p
Rinorea greveana	4	3	0	0	3	5
Strophantus boivinii	0	n/p	n/p	n/p	n/p	n/p
Salvadora angustifolia	n/p	n/p	0	0	0	1

Table 4. *Cont.*

	Mortality 2017–2018					
Strychnos madagascariensis	n/p	n/p	n/p	n/p	n/p	2
Tabernaemontana coffeoides	0	4	0	0	n/p	n/p
Tamarindus indica	2	1	1	1	0	1
Tricalysia dauphinensis	5	5	0	0	3	0
Ximenia perrieri	n/p	n/p	n/p	n/p	41	26
Dead plants	53	39	16	28	66 (25 *)	64 (38 *)
Total plot mortality	92		44		130 (63 *)	
Mortality/planting distance/plot	21.1%	27.5%	6.2%	16.9%	24.6% (9.32% *)	30.04% (17.84% *)
Mortality/plot	23.4%		10.4%		27.03% (13.09%*)	
Total planted = 1297 (1226 *) Total Dead = 266 (199 *) Mortality for all plots = 20.5% (16.23% *)						

* Mortality percentages with *X. perrieri* seedlings discounted.

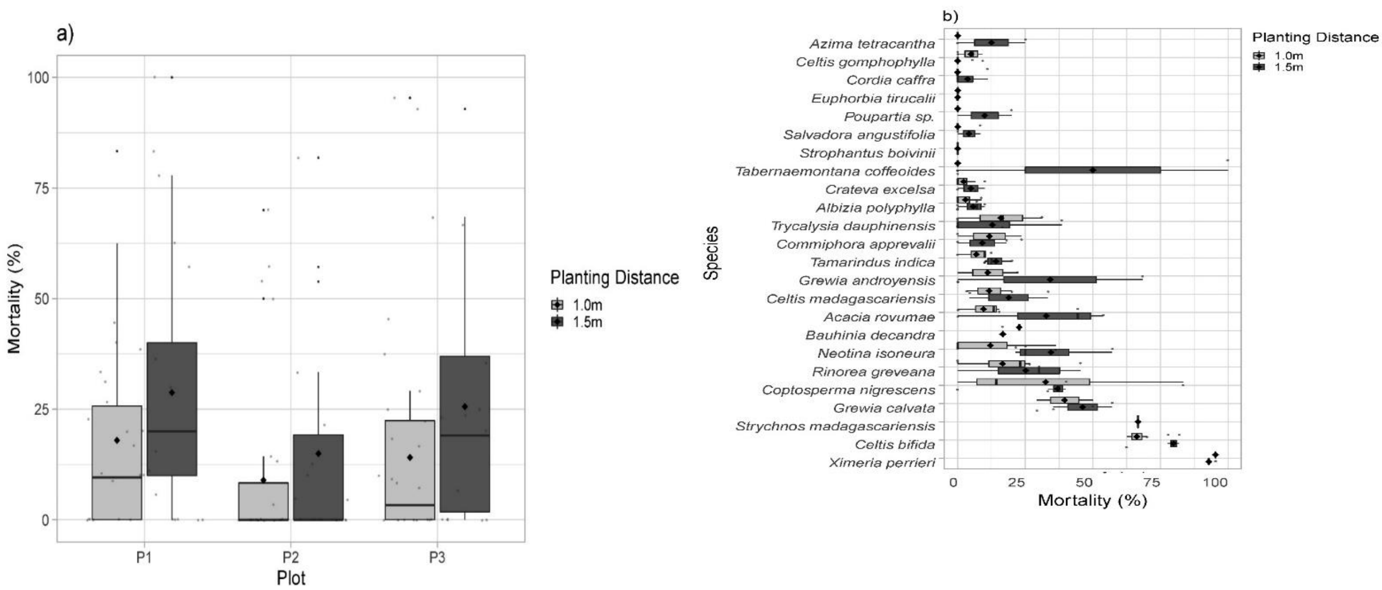

Figure 7. Species mortality on the 3 plots: (**a**) all species combined and (**b**) species in relation to planting distance. The lines drawn across the box plots indicate median mortality, with dots for the means.

4.3. Recruitment from the Forest

Self-planted wild recruits emerged on all the plots (Table 5). *Crateva excelsa* vigorously colonized both P1 and P2 in the mid-forest, while tamarind mostly colonized on the more open P1 by the riverside (it is notable that under the closed canopy very few tamarind seedlings survive more than two years). By August 2019, recruits supplied an average of 3.5% of the total of all species on P1 and P2, with the relatively larger percentage on P1 and P2 among the seedlings planted at 1.5 m intervals. On P3, not counting the shrub *Ximenia perrieri* and a plant locally named 'Miange', recruitment is 0.6% mainly made up from *Kosteletkya diplocrater.* This dryland species can grow as a shrub or small tree up to 5 m tall.

Table 5. Numbers of recruits and percentages of species colonizing the planted plots after 3 years.

Species	Number of Recruits						Total Recruits
	P1 (1 m)	P1 (1.5)	P2 (1 m)	P2 (1.5)	P3 (1 m)	P3 (1.5)	
Tamarindus indica	3	2	1				6
Crateva excelsa	2	4	3	6			15
Rinorea greveana		2			1		3
Tricalysia dauphinensis		1					1
Allophyllus decaryi		1		1			2
Neotina isoneura			1				1
Salvadora angustifolia			1	1			2
Tabernaemontana coff.				4			4
Kosteletzkya diplocr.					1	8	9
Miagne (shrub)					13		13
Ximenia perrieri (shrub)					8	4	12
Albizia polyphylla						1	1
Total recruits per sub-plot planting distance	5	10	6	12	23 (2)	13 (1)	
Total recruits per plot	15		18		36(3 *)		
Percentage of recruits per planting distance	1.9	6.5	2.2	7.1	3.4 (0.7 *)	6.1 (0.5 *)	
Percentage of recruits per plot	3.3		3.9		7.4(0.6 *)		

* If shrubs are removed, Plot 3 has only three recruits, with this affecting the percentages.

4.4. Soils

Generally, the soil samples can be classified as poorly sorted, very coarse silty, medium sand defined as belonging to the muddy sand textural group typical of river sediments from an igneous source, with this reflecting the basaltic–rhyolitic origin of the floodplain sediments [23].

Soil samples taken at 5 cm depth in the gallery forest along the riverbank are typified by sand percentages averaging 72% and silt averaging 28%, while in the transitional forest, percentages vary between 33% to 86% sand and 14% to 67% silt with higher percentages of silt on the western side of the forest contrasting with sand in the higher energy environment near the river [17]. The silt percentage in the paleochannels lies between 54% and 67% (except T9 at 46%). The highest variability was found in the eastern degraded area suggesting a complex history of changing channel regimes. Clay percentages average 2.7 with a range from 0.7% to 3.8%. Soil moisture levels were lowest near the river and highest in the mid-forest, while organics were also lowest near the river, but higher in the mid forest and in parts of P3.

The pH, at 25 cm depth on the plots, averaged 5.8, contrasting with an average pH of 8.5 in the dryland area with this possibly reflecting exposure to higher temperatures and aridity [32,33]. This pH was further supported by Hartley et al. [34] who maintain that dryland soils in low lying areas tended to be more alkaline compared to up-slope soils. A pH of 8.5% was also found in the oldest paleochannel defining the western margin of Malaza (Table 6).

Table 6. Soil Characteristics. For the locations of the transects (T) see Winchester et al. [17]. C = Sampling circle; (GF) = Gallery forest within 150 m of the riverbank; (P) Paleochannel; (D) Dryland.

2018 at 25 cm	Sand %	Silt %	Clay %	pH	Organics %	Moisture %
1 Dryland	52.6	47.4	2.3	9.1	4.4	6.1
2 Dryland	31.2	68.8	3.3	9		10.8
3 Dryland	35.6	64.4	3.3	7.5		7.2
4 Dryland-regrown spiny	31.1	68.9	3.6	8.6		9.3
Riverside	45.5	54.5	3.5	7.1	2.5	11.9
Paleochannel by10 m bank	38.1	61.9	3.7	8.5		9.1
			2016 at 25 cm			
P1-1	68.6	31.4	2.3	5.8	2.5	1.85
P1-2	48.2	51.8	2.9	5.4	6	2.1
P1-3	44.5	55.5	2.9	5.4	8	4.5
P1-4 (GF)				5.8	7.4	5.8
P2-1	44.9	55.1	3.8	5.9	10.5	26.0
P2-2	48.9	51.1	3.7	6.0	8.5	16.4
P3-1	35.6	64.4	3.7	5.7	11.5	5.9
P3-2	39.0	61.0	3.3	5.8	14	6.5
P3-3	66.2	33.8	1.8	6	6.5	10.6
		2014 at 5 cm				
T1 C3	33.3	66.7	3.0	7.5	17	
T1 C4	37.0	63	3.6	7.5	16	
T2 C1 (GF)	74	26	1.3	7.1	6	
T3 C1 (GF)	62.6	37.4	1.9	7.4	16	
T3 C5 (GF)	63.2	36.8	2.0	7.0	6	
T3 C9 (GF)	75.4	24.6	1.3	7.3	7	
T5 C4 (P)	40.6	59.4	3.8	7.3	21	
T6 C3 (GF)	85.8	14.2	0.7	6.5	4	
T7 C8 (GF)	70.4	29.6	1.7	7.6	10	
T8 C2	47.4	52.6	2.7	7.3	14	
T9 C2 (P)	53.8	46.2	2.4	7.3	38	
T12 C6 (D)	61.3	38.7	2.2	6.6	8	
T13 C6 (D)	54.7	45.3	2.4	7.1	6	
T14 C9 (PD)	33.3	66.7	3.7	7.0	6	
T15 C7 (PD)	46.3	53.7	3.2	7.4	11	
T16 C1	72.3	27.7	1.4	4.4 *	13	

* The low pH of T16 suggests this sample was taken from a urine-soaked patch.

5. Discussion

Restoration efforts in Madagascar are crucial for recovery of ecosystem functions and survival of the country's unique biodiversity. Around Berenty, much of the landscape, once covered in closed-canopy gallery forest, has been given to large-scale sisal plantations. The Reserve is, therefore, of utmost importance as one of the few remaining patches of natural vegetation in the area. Since there is very little information about the biology of the local native and endemic plant species, our work is important in that it provides insights into the conditions under which these species may best thrive on restoration projects.

5.1. Berenty Compared with Beza Mahafaly

For the purpose of future restoration in southern Madagascar, it is instructive to compare the native and endemic species from Berenty with those found at Beza Mahafaly. Despite the distance separating the two forests, there are some interesting similarities and differences. Compared with Berenty, Beza Mahafaly on River Sakamena lies at a higher altitude (100–200 m) with a higher average rainfall (750 mm/year) [35,36].

The common features are *Tamarindus indica* the dominant canopy species in Malaza's gallery forest near the river, together with *Acacia rovumae*, *Quisivianthe papinae* and *Albizia polyphylla*, while lower canopy trees (<15 m tall) include *Euphorbia tirucalii*, *Salvadora angustifolia*, *Azima tetracantha*, *Crateva excelsa*, *Grewia* spp. and *Coptosperma nigrescens* (Syn. *Enterospermum pruinosum*).

Differences include five species at Beza Mahafaly not present at Berenty and two species at Berenty lacking at Beza Mahafaly: one an upper canopy tree, *Neotina isoneura* and the other a lower canopy species, *Rinorea greveana*. Sussman and Rakotozafy [13] (p. 247) comment that the forest on the soils further from the river is 50% more dense with more grass and herbs and with large trees more widely spaced and that the forest vegetation is distinctly patchy, due to subtle topographical features, shading, natural troughs in the land and a variable sand fraction, with these last two likely related to periodic flooding. Probably for the same reasons, Berenty also shows similar environmental variability. Species differences may be due to altitude and rainfall or possibly to a lack of protection prior to 1986 when Beza Mahafaly became fully protected—50 years after Berenty.

Similarities in terms of species composition suggest that the main findings from our study could be useful for restoration projects in other dry forests on the island, but given the local nature of restoration, such projects should initially also gather basic plant growth information.

5.2. Planting Density, Recruitment, and Mortality

The aim of close planting using the framework species method is that it promotes rapid canopy closure, conserves soil moisture and shades out weeds [26], with fast-growing species planted around slow growing ones to provide shade. Our findings were that the fastest growing species were *Celtis bifida*, *Cordia caffra*, *Grewia androyensis* and *Acacia rovumae* (Figures 5 and 6).

The finding that the 1 m planting distance favors early growth on all the plots as compared with that at 1.5 m is promising but should be investigated over a much longer period to find out if tree death will occur as a result of competitive thinning, as maintained by Elliott et al. [26] (p. 219). With this in mind, seedlings that died were not replaced. It is hoped that this will both help to randomize the regimented appearance of the plantings and provide space for self-planted recruits from the forest.

A comparison of mortality and recruitment (Tables 4 and 5) shows that although mortality was highest on P1 at both distances (discounting the dryland shrub *X. perrieri* on P3) recruitment from the forest was highest at 1.5 m on P1 and P2. On these two plots, recruits included 50% of the species from across the chosen range, while recruits on plot P3 were limited almost exclusively to *X. perrieri* and Miange and to *Kosteletzkya diplocrater*, another dryland species not present under the closed canopy and thus not included in the planting program.

There are several factors that could account for the different levels of species recruitment on the plots. Seed, deposited either by wind or fauna, is available from the dense forest flanking P1 and P2, while P3 is surrounded only by degraded shrubs with few seed trees offering feeding for the fauna.

Daily watering may be another factor: the experience of the Reserve's management has shown that watering is essential for the first three years. However, *X. perrieri* whose planted seedlings almost all perished may be sensitive to the amount of water, with this suggested by the high numbers of un-watered recruits, self-seeded from the surroundings, growing between the 1 m plantings, with half the number growing in the dryer soil between the 1.5 m plantings (Table 5).

Grewia androyensis is another dryland species with high seedling mortality on P3 at 1.5 m, but unlike *X. perrieri* this species lacked recruitment. And although the quantity of watering may have been one problem [37], another could also be due to shading from the small roofs that the Reserve management believed necessary to protect seedlings from the sun on sites P2 and P3, or due to transplant shock or some other nursery-related treatment. In general, the low percentage of other recruits on degraded P3, highlights the problems for regeneration in this arid sunlit area.

Concerning the 2006 fire on P2, the advantaged growth rate suggests that the past fire event has not limited growth here. Although the long-term effects of fire on the physical properties of soil can range from a single season to many decades, with fire killing mycorrhizal fungi and beneficial microorganisms and reducing organic matter [36]. Research has shown that low intensity fires may increase nutrient availability and soil fertility leading to an increase in mineralization and available nutrients [38].

5.3. Climate Change

A record of rainfall at Berenty, 1983 to 2019, shows high variability with very little trend (Figure 2). Silva et al. [39] point out that where gallery forests have access to ample water, they may be buffered against the effects of climate change. However, at Berenty there are years when the river can flood the forest floor and years when it dries completely; this is likely to occur more frequently with increased warming [40] and this could negatively affect the nutrient balance: specifically, the carbon, nitrogen and phosphorus content of the soil [32]. Although the spiny forest species at Berenty have evolved to withstand aridity, the species in the closed canopy and transitional forest may be challenged, especially where old trees are dying on the margins of the canopy area allowing sunlight to reach the forest floor and the ingress of *C. quadrangularis*.

5.4. Study challenges

There is a lack of published studies on natural regeneration, seedling growth and forest restoration in Madagascar. Thus, comparisons between our study and others was not possible. It has been proposed that dry forests in Madagascar have a low regeneration capacity due to slow plant growth rates because of the arid environment. However, few studies have been empirically tested [41].

Plant species identification was also a challenge from the start. Apart from this, a major problem for the analysis was the variable quality of the data. Taking precise measurements of stems and root collar diameters can be challenging when large numbers of measurements are involved, assistants are comparatively untrained and site visits by the authors are limited to short periods once a year so that control of the plots is intermittent. There was also variability in seedling quality, with the roots of many plants in the nursery growing through their containers into the ground so that roots were ruptured on transplanting.

A further problem was that the plots varied in terms of shade, soil conditions and moisture availability, with this illustrated by the lack of significance for the relative growth rates on Plot 3.

5.5. Ongoing Work

Our 3-year study provided a starting point for future work and a basis for a long-term study of tree growth in this unique environment. In the immediate future further plots should be established where advancing degradation is threatening the margins of the closed canopy. A planting distance of 1.3 m should be trialed for comparison with growth at the 1 m and 1.5 m planting distances. At the same time, non-planted control plots should be set up in similar areas to provide essential baseline data against which subsequent changes in biodiversity and tree growth rates can be compared [26] (pp. 242–252).

There were three species, *Strychnos madagascariensis*, *Bauhinia decandra*, and *Strophantus boivinii* that could merit further planting trials. Either too few individuals were planted and/or their plantings were limited to too few plots (Table 4). To assist future planting designs, Figures 5 and 6 reveal the fastest growing species; these are *Celtis bifida*, *Poupartia* sp., *Cordia caffra*, *Grewia androyensis* and *Acacia rovumae.*

Further research is needed to quantify varying degrees of shade by existing trees. Apart from planting distances and soil characteristics, shade variations could be a factor contributing to differences in growth rates. For example, shade is particularly dense on P1 for the 1.5 m plantings and P2 has low numbers of existing trees but is surrounded by tall canopy species reducing the amount of direct sunlight in the early mornings and, more importantly, in the hot evenings. High numbers of existing trees were present on parts of P3, although these were all dryland species with small light-colored leaves that did little to shade the ground.

Watering treatments should also be evaluated to determine how watering could affect below-ground biomass and root structure and long-term performance of the plants under water stress. A final topic could be research into the reasons for tamarind seedlings failing to thrive under the canopy: potential reasons include the degree of shade or an allelopathic reaction to leaf and bark toxins or mycorrhizal negative plant-soil feedback under mature tamarinds [42,43].

6. Conclusions

6.1. Location, Planting Density and Species Performance

The main conclusions from the study were that for the combined species relative mean height growth rates for seedlings on P2 grew faster planted at 1 m than on the other two plots, on P2 at 1.5 m growth was slower than elsewhere. However, root seedling mortality (discounting *Ximenia perrieri*) was highest on P1 at 1 m and least on P2 at both planning distances (Table 4 and Figure 7). Recruitment (also discounting *X. perrieri*) was highest on P2 at 1.5 m closely followed by P1 at 1.5 m; it was extremely low on P3 (Table 5).

Although most of the species grow fastest at the 1 m planting distance, there are a few that do better at 1.5 m, notably: *Tamarindus indica* and *Neotina isoneura*, with these being giants of the upper closed-canopy forest.

The data on individual relative growth rates, mortality and recruitment of the 24 species planted at Berenty will be useful for the planning and management of future plantings (Figure 5a,b).

The three canopy types showed no clear relationship between relative growth rates and type (Figure 6). Both upper canopy and dryland rates were distributed across the range, while lower canopy rates were restricted to low to medium growth with respect to height, but with the rate expanding into the upper register as regards root collar diameter increase.

Although there are many environmental factors that we did not quantify (in particular shade differences, which need further investigation), the advantaged growth in the mid-forest may also be due to differences in soil composition and moisture levels. At Berenty, soil organics and moisture levels were lowest near the river and highest in the mid-forest, with silt predominating in the western sector of the forest and sand in the higher energy environment near the river. Percentages of sand and silt elsewhere in the forest were variable consequent upon the changing course of river channels over time (Figure 1).

6.2. Future Prospects

Future growth rates will undoubtedly change as the planted seedlings age and competition becomes a limiting factor. To better establish planting patterns, density and growth rates of the various species, measurements should be repeated over several years, to track the performances of the species, including their survival, mortality and recruitment from the forest.

Throughout the planting trials, we have been collecting, pressing and cataloguing tree specimens (including both their common and scientific names) to form a reference collection in an herbarium in a new Research Centre that will include a veterinary clinic and a meeting hall, with visual displays and educational material for school children. The center's aim is to demonstrate the very special nature of this environment, both for the local people and visitors, while also potentially providing a locus for reference material from the forest and potentially for the flora of the whole southern biome.

The wider significance of this study is that it focuses on which common native trees thrive best, where and under what conditions. It provides initial data on tree growth characteristics for forest restoration that could contribute to the preservation of endangered ecosystems across Madagascar's southern region. This study was only a beginning: it is intended to provide a platform for further studies. It is hoped that the details on growth rates, survival and recruitment of species in this unique biome will be generally of interests for applied research on biodiversity restoration and conservation elsewhere [44].

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/land10101041/s1, Figure S1 (a–c): maps of the three plots showing seedling numbering, existing trees and mortality 2016–2018.

Author Contributions: R.S. and A.M.-B. carried out the statistical analysis with description of methods and also helped with editing. J.M. collected, named, prepared and catalogued the tree species as a basis for the future herbarium. V.W. was mainly responsible for the text. B.M. and T.P.V. carried out the establishment of a further stage of reforestation and all of the above carried out the field work. F.D. generously supported us all and was instrumental in getting the whole team together. All authors have read and agreed to the published version of the manuscript.

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