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Article

The Conservation and Restoration of Riparian Forests along Caribbean Riverbanks Using Legume Trees

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Abstract: In the actual context of global change and biodiversity depletion, soil bioengineering represents an important tool for riparian ecosystem restoration and species conservation. Various techniques have already been implemented, but their adaptation still must be carried out in Caribbean Islands biodiversity hotspots, where suitable species remains unknown. Nitrogen-fixing legumes are particularly relevant for ecological restoration and the diversity of native Caribbean legume trees is promising in the search for suitable species for soil bioengineering. We hypothesized that Caribbean legume tree species present a growth performance and set of biotechnical traits compatible with their use in soil bioengineering. We selected five native legume trees, adapted to riparian environments, in different ecosystems (swamp forest, evergreen seasonal forest, rainforest) based on their ecology, resistance to disturbance and seed production characteristics. We measured root traits relevant for soil bioengineering on nursery grown 3-month-old seedlings. Despite their differences in sensitivity to herbivory and in growth strategies, the selected species have a high potential for use in soil bioengineering, with high seed production, high germination rates—from 88 to 100%—, and 100% survival rates, and are therefore compatible with large scale plant material production. We provided practical guidance tools for their integration into soil bioengineering techniques.

Keywords: nitrogen-fixing legumes; tropical riparian ecosystem; nature based solutions; soil bioengineering; *Inga ingoides* (Rich.) Willd.; *Inga laurina* (Sw.) Willd.; *Lonchocarpus heptaphyllus* (Poir.) DC.; *Lonchocarpus roseus* (Mill.) DC.; *Pterocarpus officinalis* (Jacq.)



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1. Introduction

In the context of global change and the erosion of biodiversity, ecosystem restoration and species conservation are priorities [1], particularly in places under high anthropogenic pressure such as riparian areas [2]. Riparian belts, at the interface between terrestrial and freshwater habitats, are of disproportionate importance relative to their spatial extent [3]. Although they only represent 1.4% of continental land surfaces, riparian zones and related floodplains contribute to more than 25% of all terrestrial ecosystem services [4]. Riparian areas worldwide are increasingly affected by urban development, industrial uses and agricultural expansion, which disrupt their structure and function [5,6]. In the “Caribbean Island hotspot”, i.e., one of the 35 world hotspots of biodiversity, wildlife is both rich and threatened, with a high level of endemism [7]; the Guadeloupe archipelago is remarkably biodiverse: native terrestrial vegetation comprises 1706 native vascular species [8],

distributed over 34 ecosystem types [9,10]. The riparian ecosystems of Guadeloupe, particularly those close to human activities, are highly impacted by pollutions, deforestation, degradation and invasive alien species [11].

Soil bioengineering is a nature based solution that responds to societal challenges efficiently and adaptively and contributes to human wellbeing through its efficacy in controlling erosion and nurturing biodiversity [12]. It can be defined as the inclusion of vegetation into engineering designs to improve and protect slopes, embankments and structures from problems associated with erosion and other types of shallow slope failures [13]. Vegetation can positively impact soil degradation processes such as surface erosion and shallow landslides. Woody vegetation can exert a positive influence on the soil water regime and, thus, on slope stability [14]. Root systems of woody vegetation provides additional soil strength and cohesion, increasing the stability of shallow soils on steep slopes [15]. In shallow soils, tree roots may deeply penetrate the soil to anchor into a more stable substrate [16]. In the upper soil horizons, dense lateral root systems form a stabilizing membrane [17] and larger tree roots can provide reinforcement across planes of weakness along the flanks of potential slope failures [18]. Bioengineering techniques, such as brush layers, fascines, vegetated crib walls or brush mattresses, immediately protect stream banks and provide a combination of the benefits of immediate hazard control and long term stabilization due to plant reinforcement effects [19–21].

In soil bioengineering, the main construction materials are living plants or plant parts. The selection of adequate plant species with the biotechnical characteristics required by the projects conditions the success of works' implementation [22–24]. Native and site specific plants well adapted to the local ecological conditions are recommended for the successful development of the works and for avoiding the introduction and development of invasive alien species, as well as biogenetical contamination [25]. Soil bioengineering is an important tool for the restoration of riparian ecosystems, as it promotes the recruitment and growth of native plant species along riverbanks [26]. The active introduction of early successional species can trigger successional trajectories of riparian communities [27–30]. It improves riparian habitat quality and allows the development of native plant communities during secondary succession [31,32]. Soil bioengineering facilitates the partial recovery of some of the main ecological functions previously provided by riverbanks and now degraded, e.g., ecological corridor, biodiversity support or depollution [28,33,34], and contributes to climate change mitigation through carbon sequestration [35]. Beyond its ability to restore ecosystems, soil bioengineering can also be used as a conservation tool for endangered plant populations [36].

Nitrogen-fixing species, such as legume species (family: Fabaceae) or *Alnus incana* (L.) Moench, are highly valuable in soil bioengineering contexts where disturbed soils tend to be poor. These species are capable of fixing N_2 by bacterial symbiosis, increasing soil C and N contents as well as rates of N mineralization and other N transformations [14,37,38]. Thus, N-fixing species improve the local nutritional status of the soil and can increase the production of neighboring species [39–41]. Some legume species have been widely used as pioneer plants in the recovery and restoration of degraded areas in the tropics [42–45]. They also display a series of biotechnical traits that make them particularly useful for soil bioengineering, e.g., a fast growth rate and quick regeneration after disturbance. For soil bioengineering, species must also be easy to propagate, either by a sufficiently large number of seeds, or by cuttings [13,19,46].

Soil bioengineering is currently developing in the Neotropics [47–49], but there are remaining gaps in the necessary knowledge. Botanical knowledge strongly influences the development and transferability of soil bioengineering techniques and is one of the key aspects of successful project implementation [49]. Some Neotropical legume tree species have already been used in soil bioengineering, e.g., *Gliricidia sepium* (Jacq.) Walp. [13,50], or *Erythrina* sp. [19,49]. Others, such as *Haematoxylon campechianum* L., *Leucaena leucocephala* (L.) de Wit, *Inga* species or *Albizia lebeck* (L.) Benth., have also been recommended [13,19]. However, in some areas, such as the Caribbean islands, recourse to

native species is limited by the lack of knowledge available regarding their characteristics and their compatibility with soil bioengineering methods. The native flora of Guadeloupe includes 19 N-fixing legume tree species, which is promising in terms of suitable species for soil bioengineering. Recent experiments have shown the difficulty of propagating native Caribbean legume tree species by cuttings in conditions compatible with soil bioengineering [51], and further investigations on germination and seedling establishment are needed to provide adequate guidance for both researchers and practitioners.

Focusing on the seedling establishment phase, we hypothesized that the selected Caribbean legume tree species showed growth performance and biotechnical traits that make them suitable for use in soil bioengineering. Since available information is scarce, the objective of this study was to improve the scant knowledge of Caribbean legume trees in order to define the best way to use them, according to their ecosystem type and operational constraints. Germination, growth, survival, susceptibility to herbivory were assessed and biotechnical traits of interest for soil bioengineering were quantified.

2. Materials and Methods

2.1. Species Selection and Description

Species selection was based on a review of published and grey literature (technical reports, thesis, notes) [9,11,52,53] and expert evaluation of native nitrogen-fixing legume trees found in Caribbean riparian formations. Specific traits conducive to soil bioengineering, such as ecological status, strong response to disturbance, abundant seed production, and ease of seed harvest, were considered as selection criteria. The five species selected for their potential compatibility with soil bioengineering were *Inga ingoides* (Rich.) Willd., *Inga laurina* (Sw.) Willd., *Lonchocarpus heptaphyllus* (Poir.) DC., *Lonchocarpus roseus* (Mill.) DC., and *Pterocarpus officinalis* Jacq. All are widespread in the Neotropics, except *L. roseus*, whose range is limited to the Caribbean. They differ in ecology and ecological amplitude [53,54]. In Guadeloupe, *Inga ingoides* and *Inga laurina* are the species with the widest geographical and altitudinal range, between 0 and 700 m above sea level (asl), in seasonal evergreen forests and rainforests. *L. heptaphyllus* reaches 500 m asl. *L. roseus*, a strictly riparian species, and *P. officinalis*, the dominant species structuring swamp forests, have more restricted suitable environments and are only met at low elevations (0–150 m and 0–15 m asl, respectively). According to the literature, fruit production varies in season and duration from one species to the next (Table 1). *I. ingoides* can produce fruits all year long, whereas the other species produce seeds over shorter periods.

2.2. Seed Collection

Seed collection was carried out from July to December 2020 in Guadeloupe between 0 and 300 m asl. Phenological data for these tree species were extracted from the literature to plan the harvest [9,53]. Fruits were collected from five or more healthy individuals from 3 to 6 distant populations, except for *L. roseus*, a critically endangered species, of which only two populations remain in Guadeloupe [8]. Mature fruits from *I. ingoides* and *I. laurina* were collected directly from the tree using a telescopic pole. Nondecayed fruits from *L. heptaphyllus*, *L. roseus* and *P. officinalis* were collected from the ground. Fruits were stocked in sealed plastic bags at ambient temperature, in the shade, and seeds were sown within the next 24 h. Seeds were separated from the fruit wall and, for *I. ingoides* and *I. laurina*, the sweet pulp was also removed. For *L. roseus*, it was empirically observed that removing a portion of the seed coat away from the root axis triggers germination. We therefore carried out this mechanical scarification of the seed integument for this species.

2.3. Experimental Conditions of Cultivation

Twenty to forty seeds, depending on the species, were planted 2 cm deep in 2 l containers filled with a mixture of pozzolana and top layer of agricultural ferralsols (*v:v* 3/4:1/4). Irrigation to field capacity maintained a favorable water balance throughout the

experiment. After germination, the established seedlings were left in the containers for three months, protected from light stress under a shadehouse (60% light reduction).

Table 1. Fruiting phenology, ecology and geographical distribution of five legume tree species of the study area. Shaded areas indicate the fruiting period. Data extracted from [9,53,55].

Species	Months												Ecosystem	Description Biogéography	
	J	F	M	A	M	J	J	A	S	O	N	D			
<i>Inga ingoides</i> (Rich.) Willd.														Seasonal evergreen forest/rainforest	Native to the Lesser Antilles (Dominica, Guadeloupe, Marie Galante, Martinique, St. Lucia, St. Vincent), Margarita, Trinidad, and South America (Bolivia, Brazil, Colombia, French Guiana, Guyana, Peru, Suriname, Venezuela).
<i>Inga laurina</i> (Sw.) Willd.														Seasonal evergreen forest/rainforest	Native to Cuba, Hispaniola, Puerto Rico, Virgin Islands (St. Croix, St. John, St. Thomas, Tortola, Virgin Gorda), the Lesser Antilles (Antigua, Barbados, Dominica, Grenada, Guadeloupe, Marie Galante, Martinique, Montserrat, Saba, St. Kitts, St. Lucia, St. Vincent), Trinidad, Mexico, Central America and South America (Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, French Guiana, Guatemala, Honduras, Mexico, Nicaragua, Panama, Paraguay, Peru, Suriname, Venezuela).
<i>Lonchocarpus heptaphyllus</i> (Poir.) DC.														Seasonal evergreen forest	Native to Cuba, Hispaniola, Jamaica, Puerto Rico, the Lesser Antilles (Guadeloupe, Martinique, St. Kitts, St. Lucia), Margarita, Trinidad (cultivated), Central America and South America (Costa Rica, Ecuador, Guyana, French Guiana, Mexico, Panama, Suriname, Venezuela).
<i>Lonchocarpus roseus</i> (Mill.) DC.														Riparian seasonal evergreen forest	Native to the Lesser Antilles (Guadeloupe, Martinique), Hispaniola and Puerto Rico.
<i>Pterocarpus officinalis</i> (Jacq.)														Swamp forest	Native to Cuba, Hispaniola, Jamaica, Puerto Rico, the Lesser Antilles (Dominica, Grenada, Guadeloupe, Marie Galante, Martinique, St. Lucia, St. Vincent), Trinidad, Mexico, Central America and South America (Belize, Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Guatemala, Guyana, Honduras, Mexico, Nicaragua, Panama, Peru, Suriname, Venezuela).

2.4. Seed Mass, Germination, Herbivory and Survival

Prior to sowing, each fresh seed was weighed, and its dry mass was estimated from the following equation:

$$\text{Estimated seed dry mass (g)} = \text{Fresh Seed mass (g)} \times \frac{\text{Mean dry mass (g)}}{\text{Mean fresh mass (g)}}$$

Mean fresh and dry mass were calculated on ten seeds, and dry mass was obtained after oven drying at 80 °C for 72 h.

Germination was recorded at cotyledon emission. At the end of the three-month period, survival and herbivory were recorded.

2.5. Biotechnical Traits of Seedlings

After three months, 15–24 healthy seedlings per species were uprooted. Roots were cleaned. Stem length and taproot length and diameter were measured. Aerial and root parts were oven dried at 80 °C for 72 h and then weighed (shoot and root biomass). The root to shoot ratio was calculated. These biotechnical traits were chosen for their importance for soil bioengineering purposes.

2.6. Statistical Analysis

Statistical analyses were performed with the Xlstat (Addinsoft) software. Nonparametric Kruskal Wallis tests, in combination with a posthoc Conover–Iman’s test, was used to reveal significant differences in traits between the five species. A principal component analysis (PCA) was conducted to position the species in relation to one another according to their traits.

3. Results

3.1. Germination, Herbivory and Survival

As indicated by their seed mass, the species studied had different seed resources, *P. officinalis* showing the highest value and *L. heptaphyllus* the lowest (Figure 1). The germination rate was high (>88%) in all species, and all the seedlings exhibited a remarkably high survival rate at 3 months, with 100% for all species. Germination was fairly synchronous within each species, the stem appearing within 4–5 days after sowing in all individuals. *L. heptaphyllus* showed a high rate of herbivory, as 75% of the seedlings displayed some trace of leaf-cutting ant or snail attacks; the other species appeared to sustain less damage (Figure 1).

3.2. Biotechnical Traits of Seedlings

The first two axes produced by the PCA captured 79% of the total variance, i.e., 57% for the first axis and 22% for the second (Figure 2, Table 2). The main variables contributing to the first axis were shoot and root biomass, stem length and root diameter on the positive side. The main variables contributing to the second axis were root to shoot ratio and root length on the positive side. *P. officinalis* displayed the highest aboveground and belowground biomass, with the greatest mean stem length (reaching 37 cm at three months). Its root system was the most developed, with the highest values in both mean length (21 cm) and mean diameter (0.5 cm). At the other end of the range, *L. heptaphyllus* exhibited the lowest mean root diameter and mean biomass values. The other species had a mean stem height ranging between 14 and 18 cm and a mean root length ranging between 16 and 19 cm. *I. laurina* and *L. roseus* seedlings reached a significantly greater root diameter than *I. ingoides*. Interspecies differences in biomass allocation patterns were also noted. *I. ingoides*, *I. laurina* and *L. heptaphyllus* had the highest mean root to shoot ratio, ranging between 0.49 and 0.55, while, at the other end of the scale, *L. roseus* had the lowest (0.36). *P. officinalis* exhibited an intermediate mean value (0.45) (Figure 3). Seed mass was positively linked to aboveground ($R^2 = 0.65$, $p < 0.001$) and belowground ($R^2 = 0.68$, $p < 0.001$) biomass. The data presented in this study are available in Table S1 (supplementary material).

	<i>I. ingoides</i>	<i>I. laurina</i>	<i>L. heptaphyllus</i>	<i>L. roseus</i>	<i>P. officinalis</i>
Dry seed mass (g)	0.338	0.531	0.122	0.234	1.198
N	33	32	41	19	27
Fresh seed mass	0.55 ± 0.04 bc	0.92 ± 0.02 cd	0.18 ± 0.01 a	0.3 ± 0.01 ab	2.40 ± 0.1 d
Germination rate	97%	97%	88%	95%	92%
Herbivory rate	12.50%	3%	75%	0%	12%



Figure 1. Mean dry seed mass calculated from 10 oven dried seeds, fresh seed mass (± standard error, different alphabetic designations indicate significant differences between species according to Kruskal-Wallis’ test ($p < 0.05$) and Conover-Iman peer-to-peer comparison procedure), and germination and herbivory rates, reported for N individuals of the five species studied. Pictures represent typical 3-month-old seedlings, and seeds.

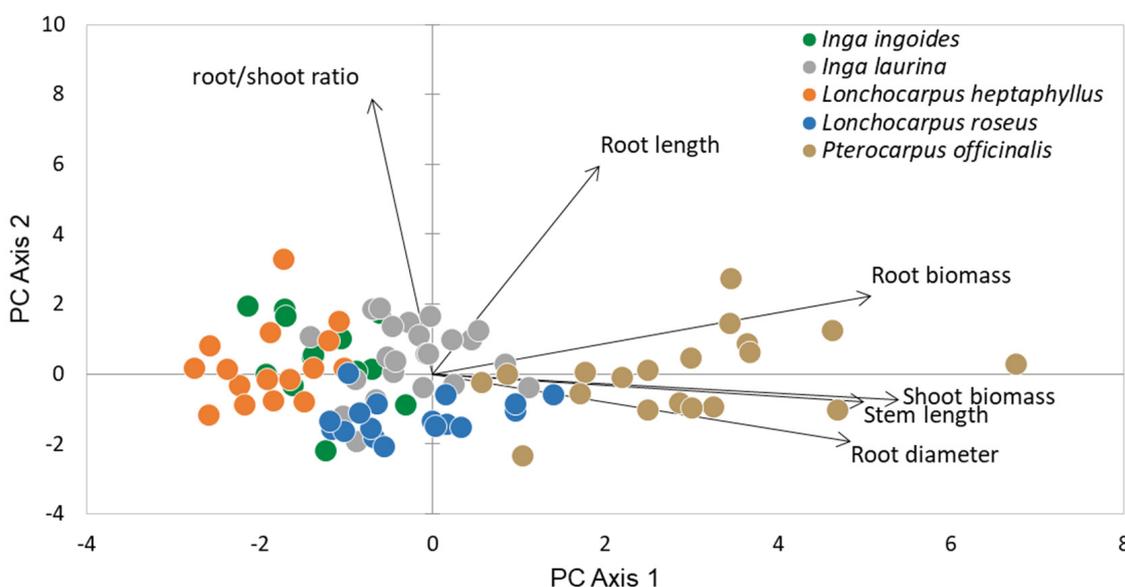


Figure 2. Principal components analysis (PCA) on six traits of soil bioengineering interest, for 93 seedlings from five riparian legume tree species.

Table 2. Eigenvector scores of plant traits on the three main PCA axes, obtained from a matrix of 6 traits \times 90 individuals from 5 species. Values are ranked in order of absolute magnitude along PCA 1. The inertia accounted for by each axis is indicated between brackets.

	PCA1 (57%)	PCA2 (22%)	PCA3 (12%)
Shoot biomass	0.521	−0.071	−0.085
Root biomass	0.490	0.214	−0.312
Stem length	0.482	−0.076	0.197
Root diameter	0.466	−0.186	−0.159
Root length	0.187	0.574	0.756
Root/Shoot	−0.068	0.761	−0.509

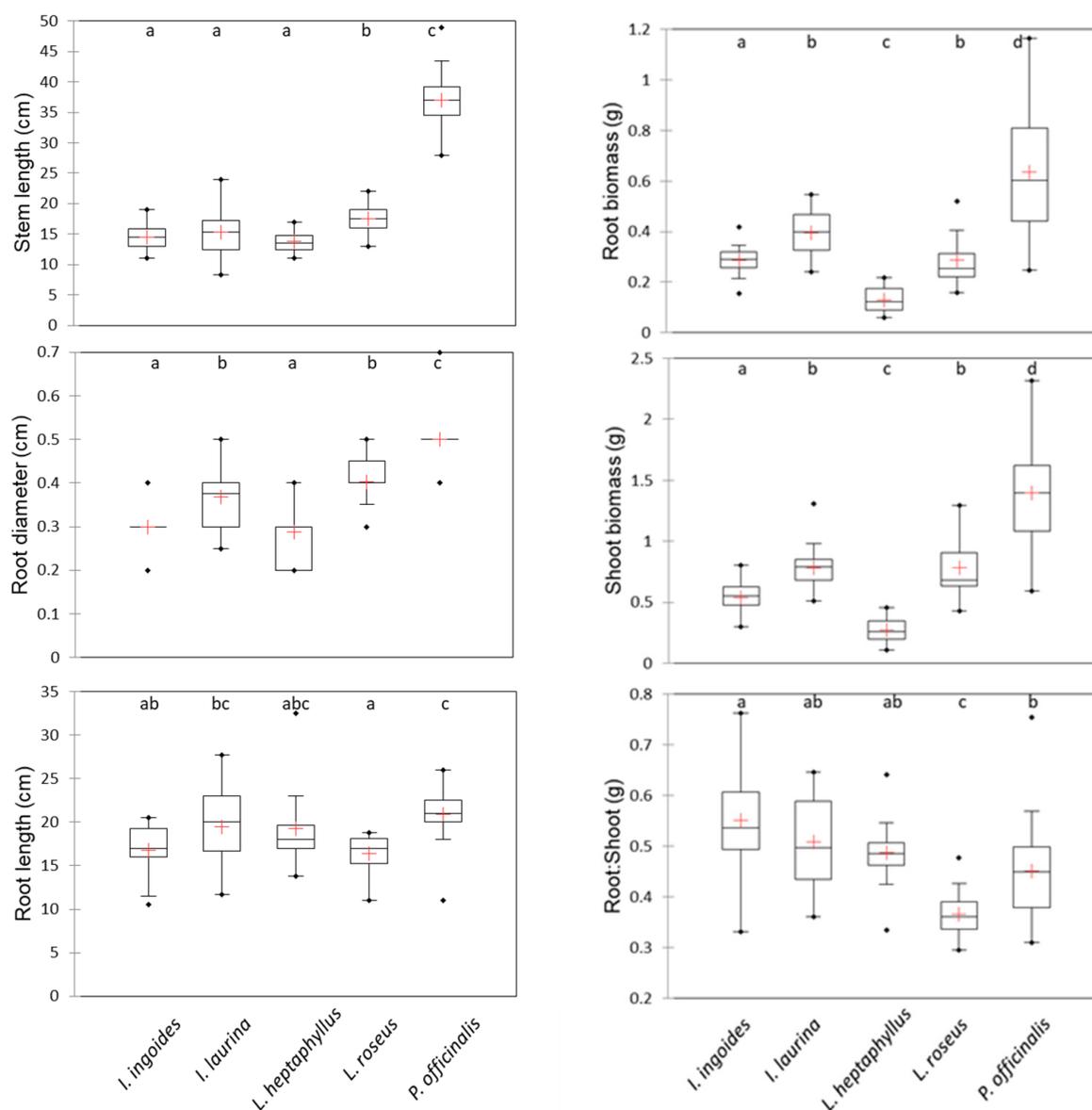


Figure 3. Boxplot per trait for the five legume tree species studied (*I. ingoides* $n = 15$; *I. laurina* $n = 24$; *L. heptaphyllus* $n = 16$; *L. roseus* $n = 17$; *P. officinalis* $n = 20$). Boxplot mid lines represent medians, red crosses represent means, boxes represent the 25th and 75th quartile values, whiskers represent 1.5x the interquartile range, and points represent outliers. For each trait, different alphabetic designations indicate significant differences between types according to Kruskal–Wallis test ($p < 0.05$) and Conover–Iman peer to peer comparison procedure.

4. Discussion

The Caribbean riparian legume species studied exhibited high germination and survival rates in our experimental conditions. However, we identified differences in sensitivity to herbivory, growth and a set of morphological traits, reflecting differences in performance and allocation strategies between species during the establishment phase.

4.1. Species Traits and Strategies

The germination rates of the species studied were higher than 88% and are among the highest reported for neotropical tree species. In a previous large scale study, conducted in comparable experimental conditions, a large variability in the germination of tropical tree was reported. Of over 100 species from the seasonal evergreen forest, only 11% presented germination rates higher than 80%. Lower germination rates were recorded for congeneric *Inga* species (between 83 and 91%), *Lonchocarpus* species (54%) and *Pterocarpus* species (77%) [56]. However, our results are consistent with another study on tropical pioneer or early successional trees, in which 75% of the species (without dormancy) showed a germination rate higher than 70% [57]. The high germination rate of Caribbean riparian legume tree species can be linked to their early successional ecological status. Pioneer species are known to exhibit the frequent production of abundant small seeds that usually germinate after dispersal, a fast establishment strategy that can be useful in frequently disturbed ecosystems [57,58]. In addition, our results provide evidence that the high germination rates recorded in continental neotropics for *I. ingoides* (80–90%) [59,60] and *I. laurina* (90–100%) [61,62] are also a characteristic of Caribbean populations and reveals the high germination potential of these two *Lonchocarpus* species.

After three months of growth, all studied species presented a survival of 100%. In literature, seedling survival in tropical species is mostly addressed on in situ experiments, regarding plant response to environmental drivers such as resources availability [63–65] or community effects [66]. This high survival is consistent with previous results on neotropical species conducted in natural conditions with comparable climatic conditions [67]. Germination potential and seedling survival do not seem to be a constraint for natural regeneration or for large scale nursery production.

Our results highlight interspecific differences in sensitivity to herbivory, with *L. heptaphyllus* particularly sensitive (75% of seedlings damaged) compared with all the other species (less than 13% of seedlings damaged). These differences could be explained by the existence of defense mechanisms. It has been hypothesized that species interactions, including between plants and herbivores, are stronger in the tropics. This would promote the intensification and diversification of plant defenses [68,69] as well as plant plasticity in N-acquisition strategy [70,71], particularly in legume species, which are more attractive because of their higher N content [72]. *I. laurina* is known to produce chemical compounds involved in pest defense [45,73] and the seeds of *P. officinalis* contain hypaphorine, which is disliked by a wide range of seed-eating rodents [74]. Given their low herbivory rate, *L. roseus* seedlings can also be suspected to have developed defense mechanisms.

The selected species showed root to shoot ratios ranging from 0.3 to 0.75 g·g⁻¹, this range is consistent with values reported in a greenhouse experiment for 44–60 days studying neotropical legume species from a lowland forest [75]. The root to shoot ratio of the selected seedlings appears also comparable with those reported in an in situ study on the growth and root traits of one year seedlings, encompassing 37 species of Bolivian moist forest [76]. However, the three month seedlings of the present study presented a much lower total dry biomass, between 0.8 to 2 g, than the 1 to 35 g recorded on the one-year seedlings of the Bolivian study. The average root length reported for the Bolivian seedling species where 7 ± 3 cm, a value two fold lower than those of the Caribbean seedlings species of the present study [76]. This difference could be explained by the competition occurring in natural conditions or by the differences in substrates characteristics. Indeed, the root length of the species from the present study displayed comparable values than those recorded

in a greenhouse experiment on 6 month old African seedlings, ranking between 15 and 30 cm [77].

Data on seedling performance, biomass allocation and root traits are scarce for tropical forest species. The few studies available have used different, hardly comparable plant material and experimental designs, explaining the wide disparities reported in performance and traits [75,78,79]. As biomass allocation patterns and root traits are known to be influenced by environmental conditions and plant ontogeny [80,81], our results contribute to fill a gap in the knowledge of tropical legume tree seedlings establishment.

Species were distributed along the two main axes of the PCA, which reflected their variation in the studied traits. The first axis could be interpreted as the establishment strategy axis, along which species are ranked from slow to fast establishers. The second axis reflects resource allocation into the root system. *P. officinalis* was the best performing species, exhibiting the fastest seedling establishment (highest biomass) and rapid development of the root system (greatest root length), permitting quick anchorage that is well adapted to swamp forest conditions, where the water level can vary throughout the year [82]. This species, capable of withstanding brackish water and frequent floods [82], has promising potential for riverbank stabilization purposes. *I. ingoides* and *L. heptaphyllus* displayed opposite trait values to *P. officinalis* and seem less likely to achieve deep soil stabilization early on. However, both remain of interest for enriching species diversity on work sites and diversifying root system architectures, which would probably contribute to improve soil cohesion [15]. *I. laurina* and *L. roseus* exhibited intermediate growth characteristics. *L. roseus* invests in the development of its aerial system, whereas *I. laurina* gives precedence to the development of its root system.

Interspecies differences in performance can be linked to seed characteristics. The seedlings of larger seeded species, *Pterocarpus officinalis* and *Inga laurina*, tend to perform better than those of smaller seeded species, such as *I. ingoides* and *L. heptaphyllus*. They benefit from greater initial seed resources and are, therefore, better provisioned for their establishment [83]. The metabolism of *L. roseus* performed particularly well, since this small seeded species, by investing more in its shoots, acquired a comparatively large biomass.

4.2. Which Species, When and Where?

On Caribbean islands, highly diverse pedoclimatic conditions on small areas support complex floristic assemblages [9,10,84]. The species selected and studied here cover a broad ecological spectrum (Table 1), providing practitioners with a range of options adapted to different ecological conditions, from brackish estuarine to rainforest. In addition, most of these species have a geographical distribution that extends beyond the Caribbean territory [53,54] and are still relevant in a wider Neotropical context (Table 1).

In tropical regions, the time available for implementing soil bioengineering projects is mostly limited to the beginning of the rainy season. Seedling availability and seed stock management are therefore key aspects to consider when planning projects [19]. Whereas *I. ingoides* produces seeds all year round, for *I. laurina* and *L. heptaphyllus*, seed collection for seedling production is highly dependent on the phenology of in situ populations because both species have a short seed production period and, moreover, their recalcitrant seeds cannot endure the loss of only a small proportion of water and it is not possible to store them, for practical purposes [85,86]. Seed physiology in *L. roseus* is unknown but for the fact that germination is triggered by the scarification of its hard seed coat. This kind of dormancy has been reported in other legumes [87,88] and unpublished assays revealed that its germinative capacity can be retained for 6 months after seed collection, supporting the hypothesis that seeds of this species could be stored at least for a few months. As regards *Pterocarpus officinalis* seed conservation appears possible in certain conditions since seeds inside floating fruits have been found to retain their germinative capacity for more than 2 months in fresh water—but only for 2 weeks in sea water [82,89]. Further investigations on the longevity and storage conditions of *L. roseus* and *P. officinalis* seeds would help to design appropriate seed conservation protocols and guide seed storage management.

4.3. Using Legume Species in Soil Bioengineering

The active reintroduction of plants in degraded areas can be achieved by planting cuttings or seedlings, or by sowing seeds. The propagation of riparian Caribbean legume tree species by cuttings in soil bioengineering field conditions has been found to be very difficult [51], excluding this option for these N₂-fixing species. However, since the five selected species produce sufficient quantities of seeds that are easy to collect, they can still be used in soil bioengineering and introduced as seedlings or saplings, with older established plantation sites usable as living stocks, providing donor trees for subsequent projects. Their synchronous cohort establishment, with seedling emergence within the first 3 months, is a bonus for nursery production and work site maintenance. In the field, rooted seedlings can be directly planted through a geotextile or incorporated into a range of soil bioengineering techniques, such as vegetated cribwalls, live gratings, brush layers, retaining walls, benches, hedge layerings or live spurs [13,19,90–92]. Even though a cultivated nursery stock is preferable, direct seeding is also possible in soil bioengineering [93] and we can imagine developing innovative methods such as the integration of legume tree seeds into dead fascines.

4.4. Caribbean Legume Tree Species for Restoring and Conserving Riparian Forests

In Guadeloupe, despite their globally recognized diversity and patrimonial value, natural ecosystems are being degraded at a critical rate and 150 ha of forest are lost every year [94]. Beyond the emergency need to conserve the remaining natural ecosystems and threatened species, the restoration of degraded forests is an important issue. Nitrogen-fixing legume tree species are recognized as pivotal in tropical forest restoration, in that they facilitate the establishment of more complex and resilient communities [45,95,96]. They are, consequently, of particular interest for riparian forest restoration using soil bioengineering techniques. All the species selected and studied here are highly compatible with soil bioengineering in low cost conditions, due to high seed availability, fast germination and seedling development, high seedling survival rates and effective N₂-fixing root nodulation [52]. *I. laurina* and *P. officinalis* have already been used successfully in forest restoration programs in Brazil and the Caribbean [82,96,97]. Our results confirm the good performances of these species during their establishment phase. Beyond its ability to restore ecosystems, soil bioengineering can also be used as a conservation tool for endangered plant populations [36]. In Guadeloupe, the conservation of *L. roseus* is a major issue: endemic to the Caribbean, it is classified as critically endangered in the regional IUCN red list. This strictly riparian species is greatly threatened by the destruction of its natural habitat [8]. The few known stations concern limited areas, at low elevation and under strong anthropic pressure, persisting amid densely urbanized zones. Field observations in the remaining natural populations in Guadeloupe indicate a rapid spontaneous regeneration. This species is very common in riparian areas in Martinique [53]. Integrating *L. roseus* into soil bioengineering projects should, therefore, be encouraged for the additional purpose of its conservation.

In addition to being a biodiversity hot spot [7], the Caribbean is also a climate hot spot [98], i.e., a region for which potential climate change impacts on the environment or different activity sectors can be particularly pronounced. The species studied belong to different ecosystems along an altitudinal gradient from dry to moist forest. In the lesser Antilles, climate change scenarios predict an increase in temperature and a decrease in precipitation [99]. This will probably lead to the modification of plant community structure and composition, through the induced drought mortality of sensitive species [100,101] and the upward migration of species currently located at lower altitudes [102,103]. It then would be relevant to conduct further investigation on the drought response of selected species for soil bioengineering, in order to better identify the species adapted to the future drier conditions. Some riparian species of the present study (*I. ingoides* and *I. laurina*) display a wide ecological amplitude, a high dispersal ability, and can be distributed in different ecosystems, whereas others have a narrower distribution (*P. officinalis* and *L. heptaphyllus*)

or are located in a few numbers of stations (*L. roseus*). Soil bioengineering, by creating the opportunity to plant whatever desired and adapted species, represents a promising tool to assist species migration, by expanding the range of species that are at risk of extinction by climate change to new locations [104,105]. That is the case of *P. officinalis* and *L. roseus*, which are threatened by the decrease and fragmentation in their habitats. Their current narrow habitats, located close from the coastline, are constrained by urbanization on one side, and by the rising ocean level at the other side [94]. Soil bioengineering and other planting opportunities are relevant, to contribute to the conservation of those species. Soil bioengineering may also have positive benefits for climate mitigation by the sequestration of carbon [35]. Vegetated land surfaces hold more carbon in their soil and biomass than do surfaces with civil engineering works that are sparsely vegetated or where vegetation is absent [106].

5. Conclusions

This study adds to the current knowledge on legume trees for riparian restoration including soil bioengineering techniques. All the species studied here display performances and traits that allow their inclusion in soil bioengineering techniques and the large scale plant material production necessary to implement soil bioengineering designs. Our experimental results open a new avenue for the use of native N-fixing species and are therefore innovative and important for soil bioengineering in the Caribbean, both for practitioners and researchers. Evidence from this study shows that using legume trees can conserve and restore Caribbean riparian forests. Their high seed availability, fast germination and seedling development, high seedling survival rates and effective N₂-fixing root nodulation demonstrate their potential to induce the fast installation of early succession stage of riparian forests. The inclusion of threatened and structuring species in restoration programs can contribute to the conservation of an entire type of threatened riparian ecosystem.

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