

The Effect of Restoration Treatment Soils and Parent Tree on Tropical Forest Tree Seedling Growth

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Abstract

Restoration treatments can impact the growth and development of tree seedlings; however, it is often difficult to discern whether responses are driven by changes in microclimate, biotic interactions, or soil properties. To isolate for the latter, we quantified the growth response of four species [*Ocotea puberula* (Lauraceae); *Otoba novogranatensis* (Myristicaceae); *Pseudolmedia mollis* (Moraceae); *Senna papillosa* (Fabaceae)] grown under similar shade-house conditions in soils collected from 6 - 7 year old active (four species plantation) and passive restoration plots (natural recovery), and nearby reference forest sites in Costa Rica. We also evaluated the role of parent tree by collecting individuals from five mother trees. We measured height, above- and below-ground biomass, and determined root: shoot ratios (RSR). Species differed markedly in their responses. *Ocotea*, and to a lesser extent *Pseudolmedia*, were largely driven by parent tree. In contrast, *Senna* showed a strong soil response for all variables with more growth in active than passive restoration soils; reference forest seedlings were typically intermediate. An interaction suggested that some genotypes are more responsive to different soil properties than others. *Otoba* had higher soil-driven RSR in both restoration treatments. Surprisingly most soil nutrients, including %N, were similar or significantly lower in active restoration soils, suggesting that seedlings are responding to differences in soil microbial communities or more labile nutrients (e.g., NH₄⁺ and NO₃⁻). Active restoration appears to facilitate the growth of other species by improving certain soil properties. Additionally, genotypes are an important driver of seedling vigor and some species may be more responsive to subtle differences in soil properties than others.

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Keywords

Active Restoration, Costa Rica, Forest Recovery, Passive Restoration, Tropical Forest

1. Introduction

Forest restoration efforts typically include the practice of planting tree seedlings to increase canopy cover and accelerate the pace of forest recovery (Chazdon, 2008; Lamb, Erskine, & Parrotta, 2005). The restoration strategy selected, as well as the density of planting and species selection, can have strong effects on the growth of planted seedlings, subsequent naturally establishing seedlings, or individuals introduced as part of later enrichment planting efforts (Cole, Holl, Keene, & Zahawi, 2011; Paquette, Bouchard, & Cogliastro, 2006; Schweizer, Gilbert, & Holl, 2013). Seedling growth can be affected by a number of factors among them site-specific biotic and abiotic soil variables (Aldrich-Wolfe, 2007; Butterfield, 1996; Lawrence, 2003; Paul, Catterall, Pollard, & Kanowski, 2010), herbivory (Gerhardt, 1993; Holl & Quiros-Nietzen, 1999), provenance or genotype (Iakovoglou, Misra, Hall, & Knapp, 2007), and competition with or facilitation by existing vegetation (Gomez-Aparicio, 2009; I. C. G. Vieira, Uhl, & Nepstad, 1994).

Survival and growth of tree seedlings are strongly affected by the type of habitat in which they are planted (e.g., Benitez-Malvido, Martinez-Ramos, Camargo, & Ferraz, 2005; Cole et al., 2011; Raman, Mudappa, & Kapoor, 2009; D. L. M. Vieira, Scariot, & Holl, 2007). For example, Camargo, Ferraz, and Imakawa (2002) found considerable variation in seedling survival and growth after direct-seeding species in pasture, secondary and mature forest in the Brazilian Amazon, and responses were largely species specific. In turn, past research at our study site found that seedling allocation to above- and below-ground biomass was strongly influenced by the restoration treatment (Cole et al., 2011). It was unclear, however, whether differences in allocation and/or growth rates were driven by in situ microclimatic conditions (e.g., light or water availability), biotic interactions, or by differences in nutrient availability. Numerous tropical fertilization studies have shown a seedling response effect to enhanced nutrient availability in both greenhouse and field experiments (e.g., Davidson et al., 2004; Gehring, Denich, Kanashiro, & Vlek, 1999; Lawrence, 2003; Singh, Jha, & Singh, 2000) but these studies do not consider the effect of restoration treatments on soil properties. Paul et al. (2010) controlled for this by growing seedlings under greenhouse conditions using soils harvested from several tropical forest restoration and reference sites in Australia. Although they found differences, they were largely attributed to potential allelopathic properties in soils at one habitat and to within habitat type differences in pH and nitrate rather than a result of restoration treatments *per se*.

It is well known that the genetic stock or seedling provenance of a particular species can determine its degree of adaptability to a particular set of conditions (e.g., Iakovoglou et al., 2007; Khurana & Singh, 2001; Raddad, 2007; Ruiz et al., 2013). As such, genotype is considered important in restoration practice and it has been factored into some tropical reforestation studies (Butterfield, 1996; Nichols, Rosemeyer, Carpenter, & Kettler, 2001). Nonetheless it is rarely tested directly in restoration (e.g., Bischoff, Steinger, & Muller-Scharer, 2010), and the potential response of genotype to different restoration treatments has not been evaluated.

The goal of this study was to determine whether restoration treatment, through the alteration of soil properties, could impact the growth response of native tree seedlings. We also evaluated the role of parent tree. We used the framework from a large-scale and long-term restoration project in southern Costa Rica (Cole, Holl, & Zahawi, 2010; Holl, Zahawi, Cole, Ostertag, & Cordell, 2011; Zahawi, Holl, Cole, & Reid, 2013), where 13 - 1-ha sites were established between 2004 and 2006 in a mixed-agricultural landscape. The restoration treatments include a passive strategy (no seedlings planted) and an active strategy (mixed-species tree plantation of four species, of which two are N-fixers). Aside from the potential impact of leguminous trees on soil N through fixation, past research in these sites and nearby younger secondary forests (Celentano et al., 2010) showed that: 1) litter fall biomass was lower in passive plots than active restoration or secondary forest; 2) leaf fall N concentration was highest in active restoration plots; and 3) leaf fall Ca, Mg, and K were highest in secondary forest. In the current study, we compared the growth of four native tree species in soils collected from passive restoration, active restoration, and reference forest sites. To control for environmental factors we ran the study in a controlled greenhouse setting.

2. Methodology

This study was carried out between November 2012 and May 2013 in the greenhouse facilities of the Las Cruces Biological Station (LCBS; 8°47'7"N; 82°57'32"W) in Coto Brus county, southern Costa Rica. The field station is located at 1200 m ASL and receives a mean annual rainfall of ~4000 mm, with a distinct dry season between January and March. Diurnal temperatures typically range between 13°C - 26°C.

Soils were collected from five active and passive restoration plots, as well as from five nearby reference forest plots within a few days of planting. Restoration sites were 6.5 - 7.5 yr old at the time of soil collection. Passive restoration sites were dominated by a mix of pasture grasses with scattered shrubs and small trees. Active restoration sites had a sparse understory and a dense canopy of the four planted tree species: *Terminalia amazonia* (J.F. Gmel.) Exell [Combretaceae], *Vochysia guatemalensis* Donn. Sm. [Vochysiaceae], *Erythrina poeppigiana* (Walp.) Skeels, and *Inga edulis* Mart. [Fabaceae]. Reference forests are fragments of the original premontane forest that was present prior to the broad expansion of agriculture in the area starting in the early 1960s. For more details on restoration design and initial plot management see [K. D. Holl et al. \(2011\)](#) and [Zahawi et al. \(2013\)](#).

Soils between 0 - 15 cm depth were collected from at least five locations within five 50 × 50 m plots of each of the three habitat types. Soils were transported to the LCBS greenhouse and mixed with rice straw hulls to enhance drainage. We used 15 × 20 cm plastic bags for the study, which were placed on benches to insure proper drainage and prevent predation by rodents.

We tested four native tree species: *Ocotea puberula* (Rich.) Nees [Lauraceae], *Otoba novogranatensis* Moldenke [Myristicaceae], *Pseudolmedia mollis* Standl. [Moraceae], and *Senna papillosa* (Britton & Rose) H. S. Irwin & Barneby [Fabaceae]. Species were chosen that are well represented in forest fragments in the area, and were producing seeds at the time of initiation of the study. Seeds were harvested from at least five mother trees for all species and germinated in trays prior to planting, with the exception of *Ocotea* and *Senna* where seedlings were harvested directly beneath mother trees (bare-rooted) and planted immediately into planter bags (*Ocotea* $\mu = 12.4 \pm 3.4$ cm and *Senna* $\mu = 6.1 \pm 1.4$ cm at time of transplant). For *Senna*, only three mother trees were located.

Five seedlings (one from each mother tree)/treatment/site were transplanted into bags ($n = 75$ seedlings/species) and grown under uniform shade cloth conditions. At the end of the study (4 - 6 mo after planting), final height measurements were taken (to the nearest mm) and seedlings were harvested and dried at 65°C for a minimum of 24 hr to determine above-ground (AGB) and below-ground (BGB) biomass. Root: shoot ratios (RSR) were calculated for all species.

2.1. Soil Analyses

In July 2012 we collected 25, 2.5-cm diameter × 15-cm deep soil cores across each plot. Cores were mixed, air dried, passed through a 2-mm sieve, and analyzed for pH, Bray II P, and major cations using Mehlich III extractions following standard procedures at Brookside Laboratories, Knoxville, OH (see www.blinc.com/worksheet_pdf/SoilMethodologies.pdf and [Gavlak, Horneck, Miller, & Kotuby-Amarcher, 2003](#) for details on protocols). Percent C and N were quantified at Brookside Laboratories using an Elementar Vario EL Cube elemental analyzer.

2.2. Data Analysis

All species were analysed separately. A two-way ANOVA was used to determine the effects of soil type and parent tree, on height, AGB and BGB, and RSR for each species. A two-way interaction of soil type × parent tree was included in models when possible; for two species (*Otoba*, *Pseudolmedia*) interactions with parent tree were not possible due to some seedling mortality. A one-way ANOVA was used to compare soil properties among the three habitats. For all analyses soil collection site was included in the model as a random factor. A post-hoc Tukey HSD LSMeans test was used to determine differences among statistically significant dependent variables when necessary ($p < 0.05$). All statistical analyses were conducted with JMP 10.0 (2012) and standard error is reported throughout.

3. Results

Survival of seedlings was high for all species (>95%), with the exception of *Otoba* (~70%). The latter was

largely due to a predation event at the onset of the study, which resulted in damage to a number of seedlings, most of which subsequently died and were removed from all further analyses. Mean height and range (95% quantiles) at the conclusion of the study varied by species *Ocotea* ($\mu = 15.0$ cm; 9.5 - 22.6); *Otoba* ($\mu = 15.5$ cm; 6.0 - 24.9); *Pseudolmedia* ($\mu = 7.1$ cm; 2.0 - 13.6); and *Senna* ($\mu = 10.2$ cm; 4.4 - 17.0), and final above- and below-ground biomass varied considerably by species (Figure 1).

3.1. Soil Type & Parent Tree Effects on Growth

The four species showed markedly different responses to soil type and parent tree (Table 1). Three species showed a response to parent tree. Parent tree affected height primarily and to a lesser extent AGB of *Ocotea*; height, AGB, and BGB of *Pseudolmedia*; and only BGB of *Senna*. In contrast, *Senna* had a strong response to soil type for all growth measures and *Pseudolmedia* a significant but weaker response. *Senna* was the only species to show an interactive effect of soil and parent tree on growth, suggesting that certain parental genotypes are more responsive to treatment differences than others. *Senna* height was significantly greater inactive restoration and reference forest soils, whereas AGB and BGB were only greater inactive vs. passive restoration soils; biomass values for reference forest soils were intermediate (Table 1, Figure 1). In turn, *Pseudolmedia* had greater AGB in active vs. passive restoration soils, with reference forest individuals intermediate. *Otoba* was the only species to show a difference in RSR; interestingly, passive (0.82 \pm 0.04) and active (0.82 \pm 0.04) restoration soils resulted in higher mean *Otoba* RSR as compared to seedlings grown in reference forest soils (0.60 \pm 0.04).

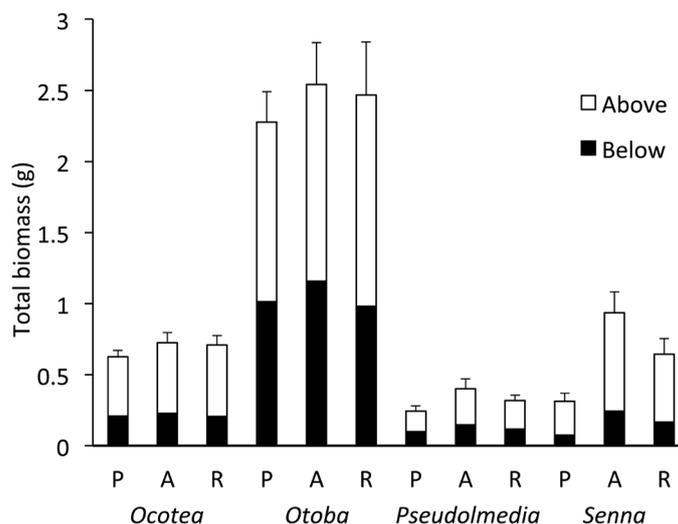


Figure 1. Final above- and below-ground seedling biomass grouped by habitat type (p = Passive restoration, A = Active restoration, R = Reference forest) and species. Standard error bars for both biomass values combined are shown.

Table 1. Two-way ANOVA comparing height (Ht), above-(AGB) and below-(BGB) ground biomass, and root/shoot ratio (RSR) responses of four tree seedling species to soil type and parent tree. Statistically significant differences ($p < 0.05$) are highlighted in bold; a (-) indicates the interaction was not assessed due to missing parent tree replicates.

Species	Soil Type				Parent Tree				Soil Type \times Parent Tree			
	Ht	AGB	BGB	RSR	Ht	AGB	BGB	RSR	Ht	AGB	BGB	RSR
<i>Ocotea puberula</i>	0.4126	0.2531	0.6743	0.5171	<0.0001	0.0284	0.1293	0.0558	0.6423	0.2457	0.2170	0.9117
<i>Otoba novogranatensis</i>	0.4917	0.6453	0.7673	0.0006	0.0716	0.1039	0.0493	0.7684	-	-	-	-
<i>Pseudolmedia mollis</i>	0.1696	0.0329	0.1378	0.1121	0.0155	0.0151	0.0024	0.5977	-	-	-	-
<i>Senna papillosa</i>	0.0001	0.0002	0.0008	0.3569	0.2434	0.2041	0.3837	0.3101	0.0318	0.0225	0.0592	0.5983

3.2. Soil Nutrients

Half of the measured soil properties (e.g., %N, %OM, P, and most micronutrients) were similar across the three habitats (**Table 2**). CEC, Ca, and Mg were higher in reference forests than both restoration treatment soils, whereas pH, K, base saturation, and Fe were lowest in active restoration, with passive restoration soils typically intermediate. Cu showed the reverse pattern.

4. Discussion

Our results show that active restoration improves soil properties, which can enhance seedling growth of some species. Three of four species showed a direct growth or allocation response to soils from different habitats; in general species grown in active restoration soils had the highest growth and passive restoration the lowest with intermediate values in reference forests. This is an interesting outcome as the seedling development stage in ontogeny typically results in high mortality (e.g., [Augsburger & Kitajima, 1992](#)) and restoration strategies that help seedlings reach the sapling stage more rapidly may be important for the long-term recruitment and survival of tree individuals. The only other greenhouse study to directly evaluate the effect of soil properties collected inactive pasture, restoration and reference forest soils on seedling growth found that species responded more to within treatment than among treatment differences in nutrient availability ([Paul et al., 2010](#)).

Directly measured soil variables showed a markedly different pattern to that found for growth. Most variables that differed (e.g., pH, CEC, cations, base saturation), were highest in reference forest and lowest in active restoration soils with values in passive restoration soils either intermediate or similar to active restoration, indicating that restoration treatments retained poorer soil conditions overall as compared to reference forest. The only variable with greater values in active restoration as compared to reference forest was Cu; Cu can be important for lignin formation ([Goransson, 1998](#)), but is not typically a primary limiting nutrient.

Surprisingly, percent soil N did not vary among habitats, despite notable differences in leaf fall N concentration in active restoration plots, and higher leaf litter in active restoration and young secondary forest plots in our

Table 2. Mean \pm SE for soil properties and micronutrients compared across two restoration treatments and reference forest. Differences among treatments indicated by letter ($p < 0.05$) and are highlighted in bold.

	Soil Type			F (<i>p</i>)
	Passive Restoration	Active Restoration	Reference Forest	
C (%)	7.29 \pm 1.15	7.84 \pm 1.10	7.85 \pm 1.97	1.13 (0.3752)
N (%)	0.58 \pm 0.08	0.66 \pm 0.08	0.62 \pm 0.15	1.23 (0.3476)
OM (%)	17.59 \pm 2.57	19.26 \pm 2.65	19.15 \pm 4.87	0.87 (0.4595)
pH	5.42 \pm 0.07 ab	5.24 \pm 0.10 b	5.53 \pm 0.22 a	8.22 (0.0140)
CEC (meq/100 g)	13.05 \pm 2.54 b	14.16 \pm 3.04 b	22.78 \pm 3.06 a	8.47 (0.0133)
Bray II P (mg/kg)	10.20 \pm 1.98	8.40 \pm 0.51	11.00 \pm 1.29	1.43 (0.3020)
Ca (mg/kg)	1124 \pm 215 b	1180 \pm 223 b	2112 \pm 88 a	7.61 (0.0176)
Mg (mg/kg)	196.8 \pm 25.2 b	171.4 \pm 30.8 b	398.3 \pm 24.3 a	19.89 (0.0010)
K (mg/kg)	177.8 \pm 34.6 a	84.2 \pm 15.0 b	213.0 \pm 27.4 a	5.36 (0.0475)
Na (mg/kg)	26.80 \pm 0.66	29.80 \pm 1.24	28.00 \pm 2.48	1.80 (0.2307)
Base saturation (%)	61.05 \pm 2.12 ab	55.28 \pm 3.14 b	64.41 \pm 3.55 a	8.24 (0.0140)
Fe (mg/kg)	68.6 \pm 15.8 ab	53 \pm 13.74 b	88.75 \pm 25.47 a	4.77 (0.0490)
Mn (mg/kg)	22.60 \pm 7.97	23.80 \pm 11.66	25.50 \pm 3.71	0.02 (0.9834)
Cu (mg/kg)	7.42 \pm 0.7 a	7.51 \pm 0.72 a	5.48 \pm 0.51 b	7.00 (0.0232)
Zn (mg/kg)	2.46 \pm 0.80	1.87 \pm 0.37	3.24 \pm 0.62	1.10 (0.3795)
Al (mg/kg)	1912 \pm 113	2035 \pm 96	1716 \pm 74	3.29 (0.1000)

study sites (Celentano et al., 2011). Increased N availability may have also occurred through potential fixation by planted legumes (Nichols & Carpenter, 2006); interestingly, the latter study reported a similar lack of difference in soil N despite higher growth rates of planted seedlings. Wood, Lawrence, Clark, and Chazdon (2009) found a strong response to leaf litter addition in a lowland wet forest with enhanced N and P reported in the subsequent litter as well as increased litter production, but no difference in incremental growth of trees over 2 yr. The apparently contrasting trends in seedling growth rates and soil nutrients in these and our study can be explained two ways. First, a meta-analysis of greenhouse fertilization studies showed that seedlings often respond to nutrient additions in high light conditions by accumulating higher nutrient concentrations in their leaves, rather than responding with increased growth (Lawrence, 2003). Second, there may have been differences in more labile forms of N (e.g., nitrate, ammonia), microbial community activity or composition (Araujo et al., 2013), allelopathic chemicals (Paul et al., 2010), or mycorrhizal inoculum potential (Allen, Allen, Egerton-Warburton, Corkidi, & Gomez-Pompa, 2003) that could have affected growth responses none of which we measured.

Similar growth responses were reported in a direct-seeding experiment by Cole et al. (2011) who planted directly into our restoration plots. Seedlings had greater final biomass in active restoration sites as compared to young secondary forest or passive plots after 2-yr, but the study also reported higher RSR in passive restoration sites suggesting that nutrient limitation maybe impeding the development of seedlings in these habitats. Surprisingly, only *Otoba* showed a difference in RSR in our study, and the pattern was slightly different with higher RSR in both restoration soil types as compared to reference forest. This disparity, and the lack of differences in RSR in our study in general, could be due to a number of reasons. First, the study by Cole et al. (2011) was done in situ and site-specific factors (such as light availability or herbivory) may have influenced RSR more strongly than nutrient limitation. Second, the current study lasted only six months in order to avoid seedlings from becoming root bound in their containers, which may have not been enough time to develop strong differences in RSR. Finally, although three of four species had exhausted their seed reserves, a number of *Pseudolmedia* seedlings still retained seeds with visible endosperm reserves present which may have masked potential effects of RSR in this species.

Our results are consistent with many prior studies that have demonstrated the importance of using good genetic stock in restoration projects as some genotypes are more suitable for establishing under stressful conditions than others (Butterfield, 1996; Nichols et al., 2001). Furthermore, *Senna* showed an interactive effect of parent tree and soil type indicating that some genotypes may respond more positively to altered soil properties than others. *Senna* was also the only early successional species evaluated in the study and the species may have a greater range of adaptation to respond to subtle differences in nutrient availability than later successional species (Lawrence, 2003). In evaluating the establishment patterns of a common Amazonian tree, Barbosa, Misiewicz, Fine, and Costa (2013) found that genotypes were separated along soil nutrient gradients suggesting that adaptation to local site conditions is important. Certainly research in restoration ecology has demonstrated the importance of using local genotypes (e.g., Bischoff et al., 2010) and whereas using a diversity of genotypes is often suggested in the absence of local availability, adaptation to local conditions of a particular restoration site may be a more important consideration (Jones, 2013; Wilkinson, 2001) than the actual distance from a source population.

Future studies should examine further the role that seed and seedling genetic stock could play in restoration efforts. Although the value of acquiring varied genetic stock is mentioned in a number of forestry studies, few have examined the importance this may play in successful restoration efforts. Additional studies could also compare seedling growth rates under different soil attributes for longer time periods, as well as look at the effects of ongoing nutrient inputs through leaf litter. Whereas a clear signal was found in this 6-mo study, this pattern could shift over time where initial differences in growth at the seedling stage are lost or possibly become more pronounced.

5. Conclusion

Results show that actively planting trees as a restoration strategy, and particularly N-fixing species, can affect soil properties with beneficial species-specific responses for establishing tree seedlings. If taken alone, it could be argued that such results may affect the long-term successional trajectory of recovering forests. However, additional site-specific factors such as the degree of light availability in the understory and competition for other limiting resources can also impact the long-term survival and growth of establishing tree seedlings. In addition,

the genetic stock of seeds or seedlings is an important consideration in restoration work, as some genotypes appear to respond better to stressful conditions than others. Accordingly, active restoration strategies should seek balanced interventions that enhance resource availability and forest recovery without impeding it in other ways.

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