

Black Soldier Fly Frass Fertilizer Outperforms Traditional Fertilizers in Terms of Plant Growth in Restoration in Madagascar

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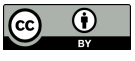
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Black Soldier Fly Frass Fertilizer Outperforms Traditional Fertilizers in Terms of Plant Growth in Restoration in Madagascar

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Abstract

Black soldier fly frass (BSFF) is a nutrient-rich organic byproduct with growing potential as a sustainable fertilizer. While its effects on crops have been studied, its impact on tree seedling development for reforestation remains poorly understood. This study evaluated the effect of BSFF on the growth and survival of two native Malagasy tree species: the fast-growing *Dodonaea madagascariensis* and the slow-growing *Verpis macrophylla*. A six-month nursery experiment tested three BSFF application rates (half-, one-, and two-fold nitrogen equivalence), along with cattle manure, synthetic NPK, and a no-fertilizer control. The survival was highest in the half-fold BSFF (95% for *D. madagascariensis*, 87.5% for *V. macrophylla*) and lowest in BSFF two-fold (0% and 22.5%, respectively) treatments. NPK also significantly reduced the survival (5% for *D. madagascariensis*, 17.5% for *V. macrophylla*). The growth responses were most pronounced in *D. madagascariensis*, where the BSFF half- and one-fold treatments led to height growth rates that were 2.0–2.7 times higher than that of the control, cattle manure, and NPK treatments, and diameter growth that was 1.8–2.3 times higher. The biomass accumulation was also significantly higher under the BSFF half- and one-fold treatments for *D. madagascariensis*. In contrast, *V. macrophylla* showed limited response to the treatments. These findings indicate that calibrated BSFF application can enhance seedling performance in reforestation efforts, particularly for fast-growing species. Notably, the growth rate of *D. madagascariensis* doubled (in terms of cm/month) under optimal BSFF treatment—a critical advantage, as time is a key constraint in reforestation and faster growth directly supports more efficient forest restoration. This highlights BSFF's potential as a sustainable and locally available input for forest restoration in Madagascar.

Keywords: black soldier fly frass; *Dodonaea madagascariensis*; *Verpis macrophylla*; forest restoration; fertilizer application; Madagascar

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1. Introduction

Madagascar is renowned for its exceptional biodiversity. Approximately 80% of its flora and fauna is endemic, and 90% of these are forest-dependent [1–3]. This biodiversity is under increasing threat due to deforestation, agricultural expansion, and other anthropogenic activities that lead to significant habitat loss and ecosystem degradation [4,5]. Native forests now cover just 10% of Madagascar's land area, and deforestation continues to be a persistent problem [6]. If current deforestation trends continue, only 0.7% of Madagascar's forest cover will be left by 2070, with climate change worsening the situation [7–9].

There is an urgent need for ecological restoration to expand habitat cover and reconnect degraded forest fragments to prevent biodiversity extinctions [10,11]. Madagascar has committed to the African Forest Landscape Restoration Initiative (AFR100), aiming to restore 4 million ha of its degraded land by 2030 [12]. Sustainable approaches to restoration practices that integrate scientific and local knowledge are important to ensure the success of this initiative [13]. Effective restoration depends on the reestablishment of native plant communities to promote long-term ecosystem resilience and functionality [14,15]. Many factors make forest restoration in Madagascar particularly challenging, one of which is nutrient-poor soils [13]. In the highland forest of central Madagascar, which is one of the island's most endangered ecosystems [1], soils are already highly weathered and low in fertility [16]. Deforestation can exacerbate these problems by reducing organic matter, leaching nutrients, and potentially stifling regeneration [16]. Studies in the central highlands show that seedlings have lower survival rates when planted further from the forest edge, likely due to dense, nutrient-poor soils with little to no topsoil [17,18]. Planting seedlings in these degraded soils limits their chance of survival, hence the importance of producing seedlings with vegetative vigor and a good nutritional condition.

One of the critical constraints in forest restoration is time, particularly in regions facing urgent biodiversity loss and climate change impacts. The speed at which planted seedlings establish and grow influences both ecological recovery and socio-economic viability [19,20]. Slow seedling development can delay canopy closure, prolonging their vulnerability to weeds, fire, and herbivory, while increasing mortality rates and maintenance costs [21]. This, in turn, delays the return of key ecosystem services such as carbon sequestration, erosion control, and habitat provision [19,20]. Accelerating early growth is therefore a critical goal in restoration planning, helping to reduce intervention needs and improve project outcomes [21]. Strategies to enhance seedling performance—including improved nursery practices, nutrient supplementation, and adaptive species selection—are essential, particularly in highly degraded or fragmented landscapes where natural regeneration is limited [22]. As such, accelerating early growth stages is essential to improve restoration success and reduce maintenance costs [22]. The use of fertilizers in forest management, particularly during the nursery phase, is a common practice aimed at enhancing early seedling growth and improving their overall performance after being transplanted to forest restoration sites [23]. Rotowa et al. [24,25] showed that the substrate and fertilization used in the nursery influence seedlings' growth and nutrient allocation one year after outplanting.

Insect frass, a byproduct of insect farming, is increasingly being investigated as a potential alternative fertilizer for enhancing plant nutrition and soil fertility [26,27]. Applying insect frass to soils has been shown to increase soil fertility, improve plant resistance to biotic and abiotic stress, and increase plant nutrient uptake [26,28,29]. In Madagascar, recent studies have shown that cricket frass can improve vegetable growth in local agricultural settings [30]. The black soldier fly (BSF) (*Hermetia illucens*, L (Diptera: Stratiomyidae)) is an effective recycler of organic waste, converting it into nutrient-rich organic fertilizer that can support crop production and soil health management [31,32], and contributing to circular bioeconomy as a result [27]. Black soldier fly frass (BSFF) is among the best studied types of insect frass fertilizers [27]. Many studies have demonstrated that BSFF has a positive impact on plant growth and yields [29,33,34], but negative effects of frass application such as stunted growth have also been reported due to its phytotoxic properties [35,36]. However, most studies have focused on assessing the response of herbaceous crops [29,37–40], while none has investigated the effects of BSFF on trees to the best of our knowledge.

With the growing practice of farming insects for food and feed in Madagascar, BSFF is now a locally available and increasingly accessible byproduct. The reported positive impact of BSFF on crop production suggests that this byproduct could play an important

role in supporting ecosystem restoration in the region. One key element for the success of reforestation projects is the production of large quantities of healthy native plant seedlings with robust growth [41]. Seedling production in the nursery is crucial for forest restoration efforts, with fertilization being one of the important factors to consider in producing high-quality seedlings [23,42]. This study aims to experimentally assess the effect of BSFF as a novel, organic fertilizer for native seedling production in Madagascar. Specifically, we measured the survivorship, growth, and biomass accumulation of two of Madagascar's endemic and contrasting successional forest species seedlings: *Dodonaea madagascariensis* Radlk. (Sapindaceae), a fast-growing pioneer species, and *Verpis macrophylla* (Baker) I. Verd. (Rutaceae), a later-successional species. The seedlings were grown in a nursery experiment under six different treatments (three doses of BSFF, cattle manure, NPK, and no fertilizer) for a period of six months.

2. Materials and Methods

2.1. Study Site

The experiment was carried out in a nursery at the Madagascar Biodiversity Center in Antananarivo—Madagascar (18.932° S, 47.525° E) from August 2024 to February 2025. Total average annual rainfall was 1100 mm, and temperatures ranged from 14 °C to 28 °C, similar to where the studied species naturally occur [43].

2.2. Species

The two species used in this study are endemic and common in humid forests of central Madagascar. *Dodonaea madagascariensis*, a fast-growing tree, was selected as the early-successional species and *Verpis macrophylla*, a slow-growing tree, was selected as the late-successional species [44]. Seeds from Ambohitantely Special Reserve (central highlands) were germinated in a substrate composed of 50% soil and 50% sand. Each species was planted at a similar developmental stage (maximum height between ca. 5 and 10 cm) in a 1 L pot filled with substrate at 80% of its volume and placed under 40% shade cloth for protection from direct sunlight. The seedlings were watered daily.

2.3. Substrate and Fertilizer

The substrate used was a mix of soil and sand, to which the appropriate dose of fertilizer was added, following the practices of nursery growers in the region. The standard substrate ratio is 1:1:1 (v/v) of soil, sand, and cattle manure. The soil is ferralitic, characteristic of central Madagascar [45], and originated from a former pine woodland area in Ankatso University, <10 km away from the nursery. The sand was river sand bought in local stores.

We compared BSFF with cattle manure (CM), NPK 11-22-16, and no fertilizer. The BSFF was from Valala Farm Research Lab at MBC—Antananarivo, where BSFs are farmed with conventional chicken feed during the first seven days, and with spent grain from the eighth day to harvest. Although different treatments of frass such as composting [27] and recirculation [46] are suggested, the BSFF that we used was fresh frass without any post-treatment. It was sun-dried for four days, not sifted, and stored for three weeks before application. We sent the BSFF sample to the FOFIFA/CENRADERU ("Centre National de Recherche Appliquée au Développement Rural") laboratory to determine its macro- and micronutrient content (Table 1).

Table 1. BSFF nutrient content.

C (%)	N Total (%)	C/N Ratio	P Total (%)	K (%)	Ca (%)	Na (%)	Mg (%)	Mn (mg/kg)	Cu (mg/kg)	Fe (mg/kg)	pH
39.7	3	13.2	3.09	0.36	0.063	0.02	5.04	180.8	48.6	2563.8	7.88

Fertilizer doses were calculated by nitrogen input, using the standard dose of locally utilized cattle manure as baseline (65 g/1 L pot, supplying 0.65 g of N). In total, six treatments were applied: one control (no fertilizer), one dose of cattle manure (CM: baseline), three doses of BSFF (half-fold BSFF, one-fold BSFF, and BSFF two-fold, supplying, respectively, half, 100%, and twice the nitrogen of the baseline), and one dose of NPK (equivalent to the baseline). Details on substrate composition and nitrogen input per treatment are presented in Table 2.

Table 2. Nitrogen input and substrate composition per 1 L pot, for each treatment.

Treatment	BSFF Half-Fold	One-Fold BSFF	BSFF Two-Fold	Cattle Manure	NPK	Control
N input (g)	0.325	0.65	1.3	0.65	0.65	0
Volume of fertilizer (l)	0.03	0.06	0.12	0.27	0.01	0
Volume of sand (l)	0.38	0.37	0.34	0.27	0.40	0.4
Volume of soil (l)	0.38	0.37	0.34	0.27	0.40	0.4

2.4. Experimental Design

The experiment followed a completely randomized design (CRD) with the response to six treatments of two species being studied. Each treatment was represented by 40 individuals, for a total of 240 individuals per species and 480 individuals for the entire experiment. Treatment locations were fully randomized to account for any unobserved spatial variation within the shade house.

2.5. Data Collection

The seedlings were planted on 1 August 2024, and the first measurements were taken on 7 August 2024. The stem basal diameter (mm) of seedlings was measured with a Vernier caliper (Finder, Almese, Italy), and height (cm) from the substrate surface to the tip of the topmost leaf was measured with a ruler. Additionally, the number of leaves was counted.

End measurements were taken on 4 February 2025 (182 days after first measurements). Roots were gently washed to minimize loss of fine root biomass. Each seedling was divided into belowground biomass (cut at the root collar) and aboveground biomass (all aboveground material). Plant material was stored in paper bags and oven-dried at 70 °C for 72 h, then weighed to determine dry mass with a three-decimal-place accuracy (Canglan Technology, Guizhou, China).

2.6. Statistical Analysis

All statistical analyses and figures were produced in the R version 4.4.1 [47]. Seedlings' survival proportion was calculated by dividing the number of surviving plants by the total number of plants initially planted, and the standard error was calculated using Greenwood's formula [48]. Seedlings' stem diameter, height, and leaf number were calculated as the difference between final and initial measurements, and expressed as monthly growth by dividing the total growth by the six-month duration. The effect of treatments on seedlings' survival and growth was calculated through the generalized linear models ("glm") function

from the "stats" R package [47], using the Binomial, Gaussian, and Poisson families for the analysis of survival, height and diameter, and leaf number, respectively. Post hoc analyses were carried out using Tukey's honestly significant difference (HSD).

3. Results

3.1. Seedlings Survival

For both species, the different types of fertilizer resulted in significant differences in seedling survival ($p < 0.001$) (Figure 1). The survival was the highest in the half-fold BSFF treatment for *V. macrophylla* (87.5%), while the two-fold BSFF significantly lowered the species' survival (22.5%, $p < 0.001$) compared to the control (77.5%). None of the *D. madagascariensis* seedlings treated with two-fold BSFF survived to the end of the experiment. The NPK treatment also significantly lowered the seedling survival for both species (5% for *D. madagascariensis*, and 17.5% for *V. macrophylla*) compared to all other treatments except the two-fold BSFF treatment ($p < 0.001$ for all). The plants treated with cattle manure had similar survival proportions (95% for *D. madagascariensis* and 85.7% for *V. macrophylla*) compared to the half-fold BSFF (95% for *D. madagascariensis* and 87.5% for *V. macrophylla*) and one-fold BSFF (77.5% for *D. madagascariensis*, and 62.5% for *V. macrophylla*) treatments for both species.

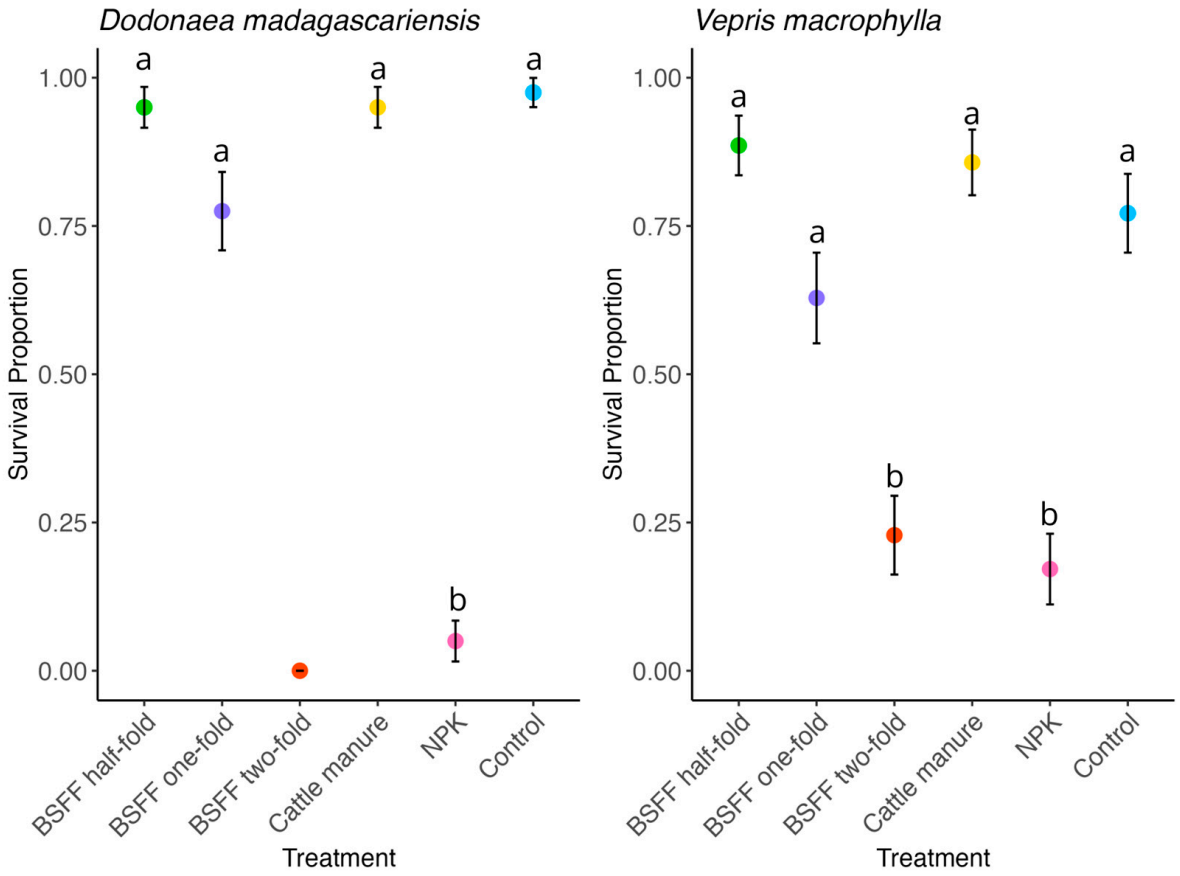


Figure 1. Survival proportion across six different fertilizer treatments (half-fold BSFF = 0.325 g of N/plant; one-fold BSFF = 0.65 g of N/plant; two-fold BSFF = 1.3 g of N/plant; cattle manure = 0.65 g of N/plant; control = 0 g of N/plant; NPK = 0.65 g of N/plant). Final number of plants alive is reported in Figure 2 for each treatment and species. Different letters above each treatment level represent statistically significant differences (Tukey post hoc, $p < 0.05$). Error bars indicate the standard error of survival proportions.

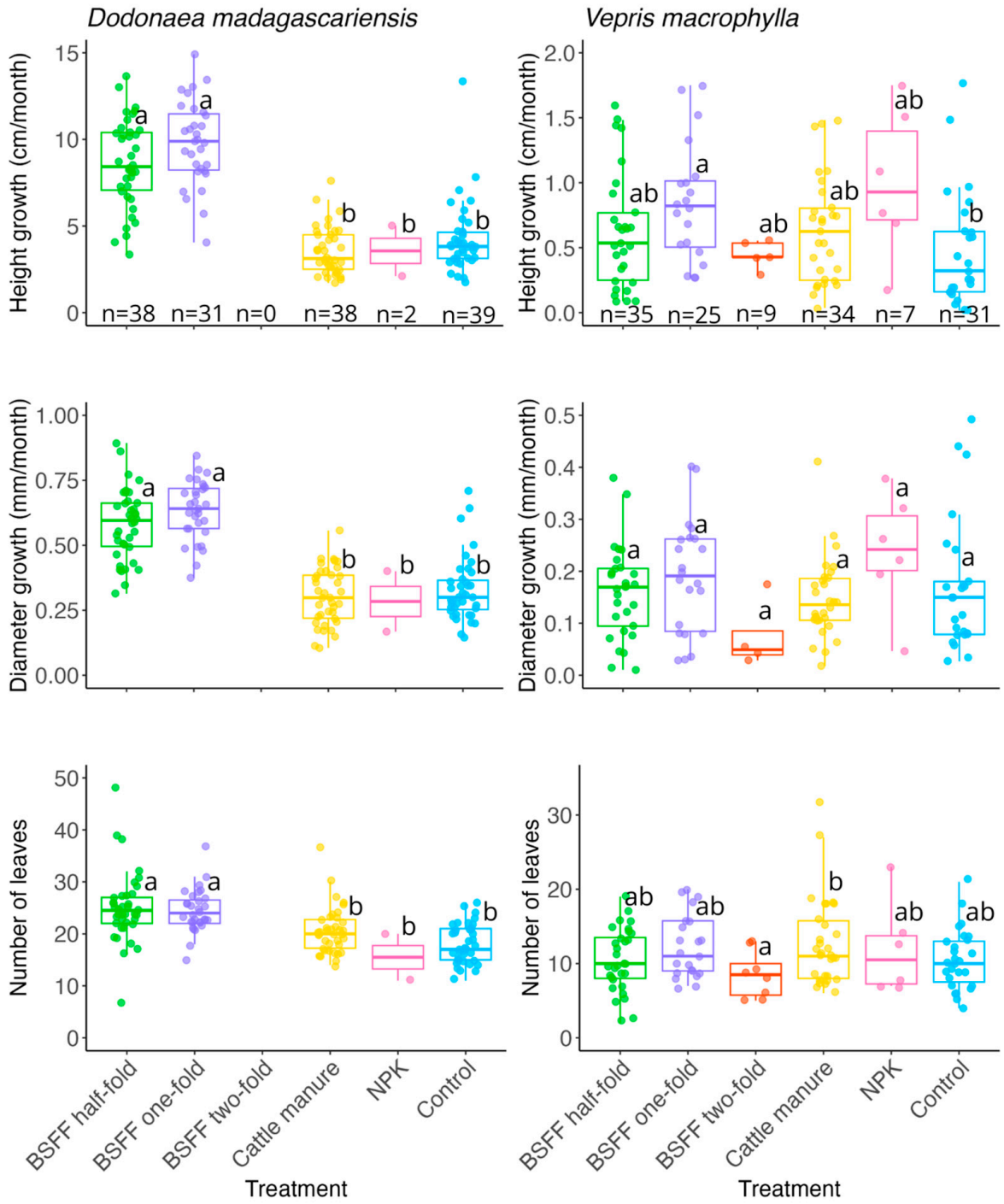


Figure 2. Species' height and diameter growth and final number of leaves across six different fertilizer treatments (half-fold BSFF = 0.325 g of N/plant; one-fold BSFF = 0.65 g of N/plant; two-fold BSFF = 1.3 g of N/plant; cattle manure = 0.65 g of N/plant; control = 0 g of N/plant; NPK = 0.65 g of N/plant). For *D. madagascariensis*, all plants treated with two-fold BSFF died by the end of the experiment. Different letters above each plot represent significant statistical differences (Tukey post hoc, $p < 0.05$).

3.2. Seedlings Growth and Biomass

The half-fold and one-fold BSFF treatments significantly improved the monthly height and diameter growth and increased the final number of leaves for *D. madagascariensis* compared to all other treatments (all $p < 0.05$) (Figure 2). The seedlings treated with half-fold BSFF grew in height on average 2.4, 2.0, and 2.4 times faster than those treated with

cattle manure, control, and NPK, respectively. The one-fold BSFF treatment increased the monthly height growth by 2.7, 2.3, and 2.7 compared to the cattle manure, control, and NPK treatments, respectively. The *D. madagascariensis* treated with half-fold BSFF and one-fold increased in diameter 1.9 and 2.1 times faster than the plants treated with cattle manure; 1.8 and 2 times faster than control treatment plants; and 2 and 2.3 times faster than the plants treated with NPK, respectively.

For *V. macrophylla*, a height growth difference was only found between plants in the one-fold BSFF and control groups, where the former grew on average 2.3 times faster than the latter. The treatments did not have any significant effect on the diameter growth for *V. macrophylla*. The leaf number was lowest with the two-fold BSFF treatment, which had a similar value to all other treatments except cattle manure ($p < 0.05$).

For both species, the different treatments showed significant differences in seedling biomass, with stronger responses being observed for *D. madagascariensis* compared to *V. macrophylla* (Figure 3). The half-fold and one-fold BSFF treatments showed significantly higher aboveground and belowground biomass compared to the other treatments for *D. madagascariensis* (all $p < 0.001$), except for the aboveground biomass of the plants treated with NPK. For *V. macrophylla*, the two-fold BSFF treatment significantly lowered the aboveground and belowground biomass compared to the two other BSFF treatments.

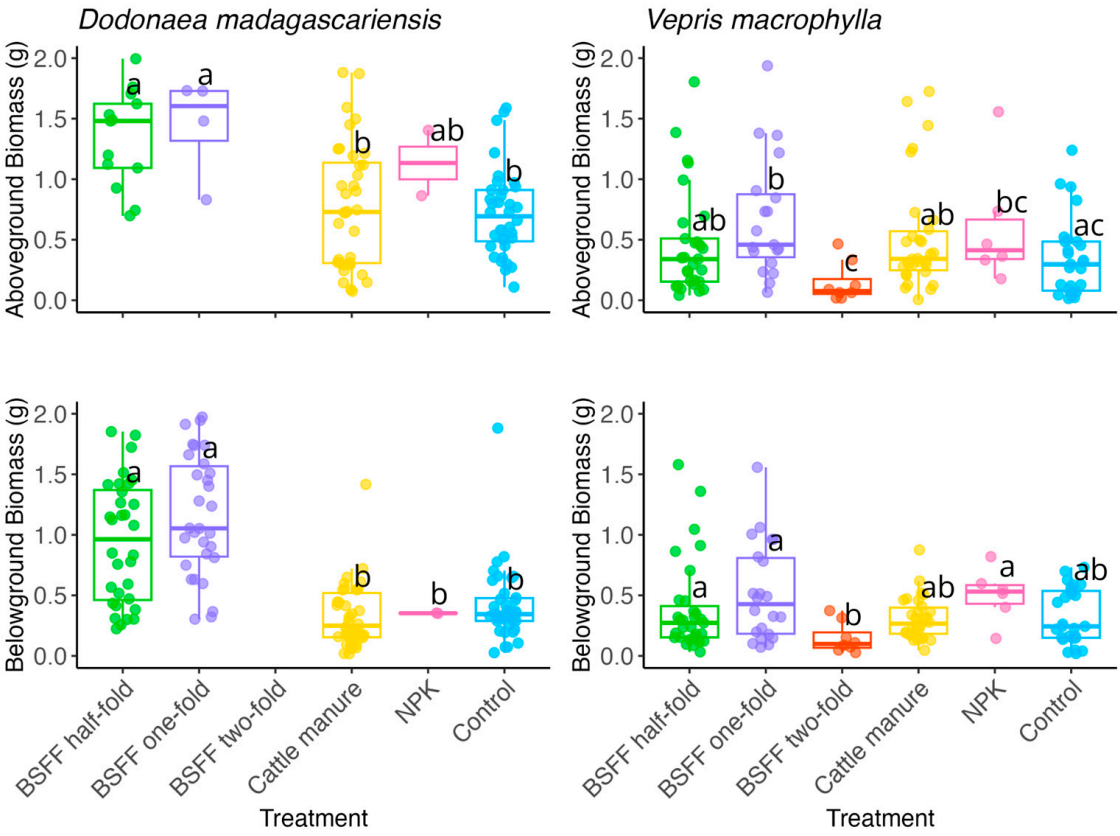


Figure 3. Species dry aboveground and belowground biomass across six different fertilizer treatments (half-fold BSFF = 0.325 g of N/plant; one-fold BSFF = 0.65 g of N/plant; two-fold BSFF = 1.3 g of N/plant; cattle manure = 0.65 g of N/plant; control = 0 g of N/plant; NPK = 0.65 g of N/plant). For *D. madagascariensis*, all plants treated with two-fold BSFF died by the end of the experiment. Different letters above each plot represent significant statistical differences (Tukey post hoc, $p < 0.05$).

4. Discussion

Restoration efforts in Madagascar are critical to restoring ecosystem functions and ensuring the survival of the country's unique biodiversity. For forest restoration projects to be effective, a sufficient quantity of native seedlings that enjoy robust vegetative growth and optimal health must be produced. Here, we show that, with a calibrated dose, BSFF can enhance seedling growth and survival and thus support the rapid recovery of forest landscapes in restoration projects.

Our results showed that, of the three doses of BSFF that were tested, the seedling survival was highest with the half-fold and one-fold BSFF treatments, although these results are not significantly different from the control and cattle manure treatments (Figure 1). At the highest dose (two-fold), the survival proportion significantly decreased, which was comparable to the effect of NPK. Other studies showed similar results, where high frass application rates were toxic to plants and led to growth inhibition and yield reduction [35,36,49,50]. Setti et al. [36] suggest that the phytotoxicity of BSFF results from a general lack of maturity and stability. This is a result of the rapid bioconversion of organic waste by BSF larvae, which can be remedied through post-treatment processes such as thermophilic composting [27]. Composting can contribute to the reduction of phytotoxic compounds [51] and improve the suitability of BSFF as a fertilizer for cultivation [27]. The use of untreated BSFF in this study aimed to assess its potential as a readily available input for reforestation, particularly in contexts where access to composting infrastructure is limited. While post-treatment may enhance the maturity and stability of BSFF, our findings suggest that, even in its untreated form, BSFF can improve seedling performance at appropriate application rates. Future research should directly compare treated and untreated BSFF to optimize its use and minimize potential phytotoxic effects.

Similar to our results for NPK application, a significant reduction in the number of transplanted tree seedlings that survived (including *D. madagascariensis*) was also found with an application of NPK at a rate of 4 g of N per plant [17]. Pareliussen [17] cautions that the use of chemical fertilizers on reforestation sites may impede the establishment of native forest species. The prolonged and excessive application of chemical fertilizers leads to soil degradation, including nutrient imbalance, reduced microbial diversity, and a decline in overall soil fertility [52]. Moreover, chemical fertilizers can contaminate groundwater and surface water through leaching and runoff, which can lead to significant ecological damage [52]. While our experiment was not designed to determine the specific level at which NPK becomes toxic, the reduced survival of seedlings might be due to the fertilization level being too high for these tree species and thus leading to toxicity.

In terms of seedling growth, our results showed that the application of the two lowest doses of BSFF resulted in a significantly more rapid gain in height, diameter, number of final leaves, aboveground biomass, and belowground biomass (Figures 2 and 3) for *D. madagascariensis*. These findings are in line with previous studies that demonstrate positive effects on growth and productivity among plants where BSFF was applied as an organic fertilizer [29,33,34,53]. BSFF is a nutrient-rich fertilizer due to its high organic matter content, essential macro and micronutrients, high mineralization rate, and rapid nutrient availability that can improve soil fertility and optimize plant nutrient uptake [54]. In addition to its nutrient content, insect frass has been shown to enhance plant growth through other biological mechanisms. Insect frass contains microbial biomass, chitin, and plant-growth-promoting compounds such as phytohormones, which play a role in stimulating root development, enhancing plant immune responses, and improving overall vigor [27,55,56]. Consistent with the nutrient quality analysis of BSFF by Beesigamukama et al. [57], our BSFF has a C/N ratio (13.2) and pH (7.8) (Table 1) that are adequate to support optimal plant nutrition. The pH of BSFF usually ranges between 7.0 and 8.0, which

is optimal for nutrient availability and thus supports plant growth [58]. Moreover, this pH range supports the proliferation of beneficial bacterial communities that contribute to plant health and soil quality [33].

The improved growth of seedlings treated with BSFF compared to cattle manure, the standard fertilizer used in nurseries for reforestation in Madagascar, supports growing evidence that insect frass is an effective and sustainable fertilizer. Previous studies have shown that BSFF and other insect frass types have nutrient compositions that are similar to those of traditional manures, such as poultry manure, particularly in its nitrogen, phosphorus, and carbon content [59,60]. However, frass may offer better nutrient availability, as insect digestion tends to reduce the total nitrogen while increasing the amount that is readily available to plants [60]. Beyond plant performance, insect frass production carries a lower environmental impact than that of traditional livestock, using fewer resources and emitting less greenhouse gases [61–63].

As seedling availability is one of the major constraints in forest restoration efforts [22], the accelerated growth that we observed during the early stages of development can support rapid seedling production to meet the growing demand for forest and landscape restoration initiatives [42]. Additionally, the improved growth parameters observed in our experiment—including increased height, diameter, and belowground biomass—suggest enhanced seedling quality and vigor, which might improve seedling survival and growth after transplantation into the field [23]. Specifically, seedlings with a larger size can more effectively capture sunlight and photosynthesize, which facilitates rapid establishment and growth in the field [64,65]. A larger stem diameter, which is associated with greater root mass [66], means more surface area for absorbing water and maintaining a proper water balance. This in turn will help seedlings survive better in dry conditions after planting [67,68]. Such morphological attributes are critical as they make seedlings better equipped to overcome transplanting stress and allow them to become effectively coupled to the restoration site [23].

The early-successional, fast-growing species (*D. madagascariensis*) studied in our experiment showed a stronger positive growth response to BSFF than the late-successional species *V. macrophylla*. *D. madagascariensis* has been suggested to be one of the most suitable candidates for initiating reforestation efforts in the central highlands of Madagascar due to its ability to quickly establish canopy cover and improve microclimatic and soil conditions, which facilitates the establishment of other, more sensitive late-successional species [44]. The application of BSFF might benefit early-successional species more than slower-growing late ones. Late-successional species may require longer-term support to achieve comparable growth performance. However, too few species were included in this study to strongly support this conclusion. The way that early and late-successional species respond to BSFF could have impacts on the resource management plans of restoration projects. More field tests and studies with other native species are needed to fully understand species-specific responses and interactions with BSFF and to confirm these results, and much remains to be learned about the application of BSFF for optimal plant nutrition.

The results of this study indicate that BSFF, when applied at calibrated doses, can significantly enhance seedling survival and growth in nursery settings. This positions BSFF as a valuable organic input for producing the robust, high-quality seedlings that are essential for large-scale forest restoration. Unlike conventional chemical fertilizers, BSFF not only supplies key nutrients but also contributes to improved soil structure and microbial health, which are critical for long-term soil fertility and resilience [56]. As such, BSFF represents a sustainable, locally available, and resource-efficient solution for supporting restoration efforts in Madagascar and similar contexts.

5. Conclusions

This study highlights the potential of black soldier fly frass (BSFF) as a practical and sustainable organic fertilizer for native tree seedling production in forest restoration initiatives. As a nutrient-rich byproduct of insect-based waste processing, BSFF offers an innovative way to support reforestation while promoting circular economy practices. The findings show that applying BSFF at low rates can provide measurable benefits for seedling development, particularly in fast-growing species. In contrast, excessive application led to negative outcomes, which underlines the need for dose calibration tailored to individual species' requirements. By demonstrating both the benefits and limitations of BSFF use, this study supports its role as a safe and environmentally responsible input that can complement and strengthen broader restoration strategies. While this study focused on assessing the direct effects of BSFF on seedling survival and morphological growth parameters, we acknowledge that BSFF likely influences a broader range of soil and plant physiological processes. Future research should incorporate measurements of soil properties, nutrient dynamics, microbial community composition, and plant physiological traits (e.g., chlorophyll content, root development, and water use efficiency) to better understand the mechanisms underpinning BSFF's effects and to optimize its application for ecological restoration.

Although this study focuses mainly on the six-month nursery growth phase, the positive effects of BSFF on seedling survival, growth, and biomass accumulation suggest important implications for their future performance after planting. These early gains in development may help seedlings establish themselves more quickly and compete more effectively in challenging field conditions, which can increase the chances of long-term restoration success. Early-stage growth plays a critical role in determining how well seedlings adapt to their environment, resist stress, and survive over time. Therefore, the strong nursery performance observed in this study provides useful insight into the seedlings' potential for continued growth and establishment once transplanted. Understanding this connection between early growth and field success is essential for improving restoration outcomes, especially in degraded or resource-limited sites. To build on these findings, a follow-up field experiment is currently underway to monitor the survival and growth of these seedlings after outplanting, which will help evaluate the long-term effectiveness and ecological relevance of BSFF application in real restoration settings.

More broadly, the findings of this study contribute valuable insights into how resource-efficient reforestation practices can be designed to align not only with biodiversity conservation objectives but also with global restoration commitments. To fully realize the potential of BSFF as a restoration tool, it is crucial to conduct field trials across a broader spectrum of native species, habitat types, and climatic conditions. This will help determine the extent to which the observed nursery-stage benefits, such as improved seedling growth, can be sustained in real restoration conditions, where environmental stressors and biotic interactions play a significant role. Such trials would also provide a more robust understanding of species-specific responses to BSFF and inform adaptive management strategies.

Furthermore, assessing the long-term ecological outcomes of BSFF-treated seedlings, including their survival rates, contribution to canopy closure, and role in facilitating natural regeneration, is vital for evaluating the practical viability of BSFF. As Madagascar continues to face pressures from deforestation and land degradation, developing science-based, scalable methods for native forest recovery is more important than ever. Ongoing interdisciplinary research and collaboration with local practitioners will be important in refining BSFF applications, ensuring that they are ecologically sound, culturally appropriate, and economically feasible. Ultimately, advancing the use of BSFF in reforestation efforts holds promise not only for enhancing ecosystem resilience and biodiversity in

Madagascar but also for informing restoration practices in other tropical regions facing similar environmental challenges.

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References

1. Ganzhorn, J.U.; Lowry, P.P., II; Schatz, G.E.; Sommer, S. The biodiversity of Madagascar: One of the world's hottest hotspots on its way out. *Oryx* **2001**, *35*, 346–348. [CrossRef]
2. Goodman, S.M.; Benstead, J.P. Updated estimates of biotic diversity and endemism for Madagascar. *Oryx* **2005**, *39*, 73–77. [CrossRef]
3. Allnutt, T.F.; Ferrier, S.; Manion, G.; Powell, G.V.N.; Ricketts, T.H.; Fisher, B.L.; Harper, G.J.; Irwin, M.E.; Kremen, C.; Labat, J.-N.; et al. A method for quantifying biodiversity loss and its application to a 50-year record of deforestation across Madagascar. *Conserv. Lett.* **2008**, *1*, 173–181. [CrossRef]
4. Myers, N.; Mittermeier, R.A.; Mittermeier, C.G.; da Fonseca, G.A.B.; Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **2000**, *403*, 853–858. [CrossRef]
5. Harper, G.J.; Steininger, M.K.; Tucker, C.J.; Juhn, D.; Hawkins, F. Fifty years of deforestation and forest fragmentation in Madagascar. *Environ. Conserv.* **2007**, *34*, 325–333. [CrossRef]
6. Vieilledent, G.; Grinand, C.; Rakotomalala, F.A.; Ranaivosoa, R.; Rakotoarijaona, J.R.; Allnutt, T.F.; Achard, F. Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biol. Conserv.* **2018**, *222*, 189–197. [CrossRef]
7. Opdam, P.; Wascher, D. Climate change meets habitat fragmentation: Linking landscape and biogeographical scale levels in research and conservation. *Biol. Conserv.* **2004**, *117*, 285–297. [CrossRef]
8. Ramiadantsoa, T.; Ovaskainen, O.; Rybicki, J.; Hanski, I. Large-scale habitat corridors for biodiversity conservation: A forest corridor in Madagascar. *PLoS ONE* **2015**, *10*, e0132126. [CrossRef]
9. Morelli, T.L.; Smith, A.B.; Mancini, A.N.; Balko, E.A.; Borgerson, C.; Dolch, R.; Farris, Z.; Federman, S.; Golden, C.D.; Holmes, S.M.; et al. The fate of Madagascar's rainforest habitat. *Nat. Clim. Change* **2020**, *10*, 89–96. [CrossRef]
10. Brancalion, P.; Niamir, A.; Broadbent, E.; Crouzeilles, R.; Barros, F.; Almeyda, A.M.; Baccini, A.; Aronson, J.; Goetz, S.; Reid, J.L.; et al. Global restoration opportunities in tropical rainforest landscapes. *Sci. Adv.* **2019**, *5*, eaav3223. [CrossRef]
11. Strassburg, B.B.N.; Iribarrem, A.; Beyer, H.L.; Cordeiro, C.L.; Crouzeilles, R.; Jakovac, C.C.; Junqueira, A.B.; Lacerda, E.; Latawiec, E.; Balmford, A.; et al. Global priority areas for ecosystem restoration. *Nature* **2020**, *586*, 724–729. [CrossRef]
12. African Forest Landscape Restoration Initiative (AFR100). Available online: www.wri.org/our-work/project/african-restoration-100 (accessed on 3 June 2025).

13. Culbertson, K.A.; Treuer, T.L.; Mondragon-Botero, A.; Ramiadantsoa, T.; Reid, J.L. The eco-evolutionary history of Madagascar presents unique challenges to tropical forest restoration. *Biotropica* **2022**, *54*, 1081–1102. [CrossRef]
14. Broadhurst, L.M.; Lowe, A.; Coates, D.J.; Cunningham, S.A.; McDonald, M.; Vesk, P.A.; Yates, C. Seed supply for broadscale restoration: Maximizing evolutionary potential. *Evol. Appl.* **2008**, *1*, 587–597. [CrossRef]
15. Society for Ecological Restoration International Science & Policy Working Group. *The SER International Primer on Ecological Restoration*; SER: Boston, MA, USA, 2004.
16. Vågen, T.G.; Shepherd, K.D.; Walsh, M.G. Sensing landscape level change in soil fertility following deforestation and conversion in the highlands of Madagascar using Vis-NIR spectroscopy. *Geoderma* **2006**, *133*, 281–294. [CrossRef]
17. Pareliussen, I.; Olsson, E.G.A.; Armbruster, W.S. Factors limiting the survival of native tree seedlings used in conservation efforts at the edges of forest fragments in upland Madagascar. *Restor. Ecol.* **2006**, *14*, 196–203. [CrossRef]
18. Miandrimanana, C.; Reid, J.L.; Rivoharison, T.; Birkinshaw, C. Planting position and shade enhance native seedling performance in forest restoration for an endangered Malagasy plant. *Plant Divers.* **2019**, *41*, 118–123. [CrossRef]
19. Chazdon, R.L. Beyond deforestation: Restoring forests and ecosystem services on degraded lands. *Science* **2008**, *320*, 1458–1460. [CrossRef] [PubMed]
20. Brancalion, P.H.S.; Viani, R.A.G.; Strassburg, B.B.N.; Rodrigues, R.R. Finding the money for tropical forest restoration. *Unasylva* **2015**, *245*, 41–50.
21. Rodrigues, R.R.; Lima, R.A.F.; Gandolfi, S.; Nave, A.G. On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. *Biol. Conserv.* **2009**, *142*, 1242–1251. [CrossRef]
22. Palma, A.C.; Laurance, S.G.W. A review of the use of direct seeding and seedling plantings in restoration: What do we know and where should we go? *Appl. Veg. Sci.* **2015**, *18*, 561–568. [CrossRef]
23. Grossnickle, S.C. Why seedlings survive: Influence of plant attributes. *New For.* **2012**, *43*, 711–738. [CrossRef]
24. Rotowa, O.J.; Małek, S.; Jasik, M.; Staszel-Szlachta, K. Substrate and fertilization used in the nursery influence biomass and nutrient allocation in *Fagus sylvatica* and *Quercus robur* seedlings after the first year of growth in a newly established forest. *Forests* **2025**, *16*, 511. [CrossRef]
25. Rotowa, O.J.; Małek, S.; Kupka, D.; Pach, M.; Banach, J. Innovative peat-free organic substrates and fertilizers influence growth dynamics and root morphology of *Fagus sylvatica* L. and *Quercus robur* L. seedlings one year after planting. *Forests* **2025**, *16*, 800. [CrossRef]
26. Poveda, J. Insect frass in the development of sustainable agriculture. A review. *Agron. Sustain. Dev.* **2021**, *41*, 5. [CrossRef]
27. Lopes, I.G.; Yong, J.W.; Lalander, C. Frass derived from black soldier fly larvae treatment of biodegradable wastes: A critical review and future perspectives. *Waste Manag.* **2022**, *142*, 65–76. [CrossRef]
28. Poveda, J.; Jiménez-Gómez, A.; Saati-Santamaría, Z.; Usategui-Martín, R.; Rivas, R.; García-Fraile, P. Mealworm frass as a potential biofertilizer and abiotic stress tolerance-inductor in plants. *Appl. Soil Ecol.* **2019**, *142*, 110–122. [CrossRef]
29. Menino, R.; Felizes, F.; Castelo-Branco, M.A.; Fareleira, P.; Moreira, O.; Nunes, R.; Murta, D. Agricultural value of black soldier fly larvae frass as organic fertilizer on ryegrass. *Heliyon* **2021**, *7*, e05855. [CrossRef] [PubMed]
30. Andrianorosoa Ony, C.; Solofondranohatra, C.L.; Ramiadantsoa, T.; Ravelomanana, A.; Ramanampamonjy, R.N.; Hugel, S.; Fisher, B.L. Effect of cricket frass fertilizer on growth and pod production of green beans (*Phaseolus vulgaris* L.). *PLoS ONE* **2024**, *19*, e0303080. [CrossRef]
31. Lalander, C.H.; Fidjeland, J.; Diener, S.; Eriksson, S.; Vinnerås, B. High waste-to-biomass conversion and efficient *Salmonella* spp. reduction using black soldier fly for waste recycling. *Agron. Sustain. Dev.* **2015**, *35*, 261–271. [CrossRef]
32. Beesigamukama, D.; Mochoge, B.; Korir, N.K.; Fiaboe, K.K.; Nakimbugwe, D.; Khamis, F.M.; Subramanian, S.; Wangu, M.M.; Dubois, T.; Ekesi, S.; et al. Low-cost technology for recycling agro-industrial waste into nutrient-rich organic fertilizer using black soldier fly. *Waste Manag.* **2021**, *119*, 183–194. [CrossRef] [PubMed]
33. Choi, S.; Hassanzadeh, N. BSFL frass: A novel biofertilizer for improving plant health while minimizing environmental impact. *Can. Sci. Fair J.* **2019**, *2*, 41–46.
34. Coudron, C.; Spranghers, T.; Elliot, D.; Halstead, J. *Insect Breeding: Lab Scale and Pilot Scale Experiments with Mealworm and Black Soldier Fly*; BioBoost: Roeselare, Belgium, 2019.
35. Temple, W.D.; Radley, R.; Baker-French, J.; Richardson, F. *Use of Enterra Natural Fertilizer (Black Soldier Fly Larvae Digestate) as a Soil Amendment*; Enterra Feed Corporation: Langley City, BC, Canada, 2013.
36. Setti, L.; Francia, E.; Pulvirenti, A.; Gigliano, S.; Zaccardelli, M.; Pane, C.; Caradonia, F.; Maistrello, B.S.L.; Ronga, D. Use of black soldier fly (*Hermetia illucens* (L.), Diptera: Stratiomyidae) larvae processing residue in peat-based growing media. *Waste Manag.* **2019**, *95*, 278–288. [CrossRef]
37. Kawasaki, K.; Kawasaki, T.; Hirayasu, H.; Matsumoto, Y.; Fujitani, Y. Evaluation of fertilizer value of residues obtained after processing household organic waste with black soldier fly larvae (*Hermetia illucens*). *Sustainability* **2020**, *12*, 4920. [CrossRef]

38. Beesigamukama, D.; Mochoge, B.; Korir, N.; Musyoka, M.; Fiaboa, K.K.M.; Nakimbugwe, D.; Khamis, F.M.; Subramanian, S.; Dubois, T.; Ekesi, S.; et al. Nitrogen fertilizer equivalence of black soldier fly frass fertilizer and synchrony of nitrogen mineralization for maize production. *Agronomy* **2020**, *10*, 1395. [CrossRef]
39. Anyega, A.O.; Korir, N.K.; Beesigamukama, D.; Changeh, G.J.; Nkoba, K.; Subramanian, S.; Van Loon, J.J.A.; Dicke, M.; Tanga, C.M. Black soldier fly-composted organic fertilizer enhances growth, yield, and nutrient quality of three key vegetable crops in Sub-Saharan Africa. *Front. Plant Sci.* **2021**, *12*, 680312. [CrossRef] [PubMed]
40. Rehan, I.; Lopes, I.G.; Murta, D.; Lidon, F.; Fareleira, P.; Esteves, C.; Moreira, O.; Menino, R. Agronomic potential of *Hermetia illucens* frass in the cultivation of ryegrass in distinct soils. *Insects Food Feed.* **2024**, *1*, 1–16. [CrossRef]
41. Nunes, S.; Gastauer, M.; Cavalcante, R.B.; Ramos, S.J.; Caldeira, C.F., Jr.; Silva, D.; Rodrigues, R.R.; Salomão, R.; Oliveira, M.; Souza-Filho, P.W.M.; et al. Challenges and opportunities for large-scale reforestation in the Eastern Amazon using native species. *For. Ecol. Manag.* **2020**, *466*, 118120. [CrossRef]
42. Haase, D.L.; Davis, A.S. Developing and supporting quality nursery facilities and staff are necessary to meet global forest and landscape restoration needs. *Reforesta* **2017**, *4*, 69–93. [CrossRef]
43. Centre de Recherches, D'études et D'appui à L'analyse Économique à Madagascar (CREAM). *Monographie Région Analamanga*; Centre de Recherches, D'études et D'appui à L'analyse Économique à Madagascar (CREAM): Antananarivo, Madagascar, 2013.
44. Pareliussen, I. Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar. Ph.D. Thesis, Norwegian University of Science and Technology, Trondheim, Norway, 2004.
45. Ramifehiarivo, N.; Brossard, M.; Grinand, C.; Andriamananjara, A.; Razafimbelo, T.; Rasolohery, A.; Razafimahatratra, H.; Seyler, F.; Ranaivoson, N.; Rabenarivo, M.; et al. Mapping soil organic carbon on a national scale: Towards an improved and updated map of Madagascar. *Geoderma Reg.* **2017**, *9*, 29–38. [CrossRef]
46. Lopes, I.G.; Wiklicky, V.; Vinnerås, B.; Yong, J.W.H.; Lalander, C. Recirculating frass from food waste bioconversion using black soldier fly larvae: Impacts on process efficiency and product quality. *J. Environ. Manag.* **2024**, *366*, 121869. [CrossRef] [PubMed]
47. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2020. Available online: https://www.r-project.org/ (accessed on 15 August 2024).
48. Greenwood, M. The natural duration of cancer. *Rep. Public Health Med. Subj.* **1926**, *33*, 1–26.
49. Newton, L.; Sheppard, C.; Watson, D.; Burtle, G.; Dove, R. *Using the Black Soldier Fly, Hermetia illucens, as a Value-Added Tool for the Management of Swine Manure*; Animal and Poultry Waste Management Center, North Carolina State University: Raleigh, NC, USA, 2005.
50. Alattar, M.; Alattar, F.; Popa, R. Effects of microaerobic fermentation and black soldier fly larvae food scrap processing residues on the growth of corn plants (*Zea mays*). *Plant Sci. Today* **2016**, *3*, 57–62. [CrossRef]
51. Song, S.; Ee, A.W.L.; Tan, J.K.N.; Cheong, J.C.; Chiam, Z.; Arora, S.; Lam, W.N.; Tan, H.T.W. Upcycling food waste using black soldier fly larvae: Effects of further composting on frass quality, fertilizing effect and its global warming potential. *J. Clean. Prod.* **2021**, *288*, 125664. [CrossRef]
52. Pahalvi, H.N.; Rafiya, L.; Rashid, S.; Nisar, B.; Kamili, A.N. Chemical Fertilizers and Their Impact on Soil Health. In *Microbiota and Biofertilizers*; Springer: Cham, Switzerland, 2021; pp. 1–20.
53. Yaacobi, G.; Shouster-Dagan, I.; Opatovsky, I.; Baron, Y.; Richter, H.; Bashan, I.; Steinberg, S. The Potential of the Black Soldier Fly Bioconverted Rearing Substrate as a Plant Growth Enhancer. In *Book of Abstracts Insecta Conference*; ATB: Potsdam, Germany, 2019.
54. Beesigamukama, D.; Mochoge, B.; Korir, N.; Ghemoh, C.J.; Subramanian, S.; Tanga, C.M. In situ nitrogen mineralization and nutrient release by soil amended with black soldier fly frass fertilizer. *Sci. Rep.* **2021**, *11*, 14799. [CrossRef]
55. Basri, N.E.A.; Azman, N.A.; Ahmad, I.K.; Suja, F.; Jalil, N.A.A.; Amrul, N.F. Potential applications of frass derived from black soldier fly larvae treatment of food waste: A review. *Foods* **2022**, *11*, 2664. [CrossRef]
56. Hénault-Ethier, L.; Quinche, M.; Reid, B.; Hotte, N.; Fortin, A.; Normandin, É.; de La Rochelle Renaud, G.; Zadeh, A.R.; Deschamps, M.-H.; Vandenberg, G. Opportunities and challenges in upcycling agri-food byproducts to generate insect manure (frass): A literature review. *Waste Manag.* **2024**, *176*, 169–191. [CrossRef]
57. Beesigamukama, D.; Subramanian, S.; Tanga, C.M. Nutrient quality and maturity status of frass fertilizer from nine edible insects. *Sci. Rep.* **2022**, *12*, 7182. [CrossRef]
58. Surendra, K.; Tomberlin, J.K.; van Huis, A.; Cammack, J.A.; Heckmann, L.-H.L.; Khanal, S.K. Rethinking organic wastes bioconversion: Evaluating the potential of the black soldier fly (*Hermetia illucens* (L.)) (Diptera: Stratiomyidae) (BSF). *Waste Manag.* **2020**, *117*, 58–80. [CrossRef]
59. Houben, D.; Daoulas, G.; Faucon, M.-P.; Dulaurent, A.-M. Potential use of mealworm frass as a fertilizer: Impact on crop growth and soil properties. *Sci. Rep.* **2020**, *10*, 4659. [CrossRef]
60. Chavez, M.; Uchanski, M. Insect left-over substrate as plant fertiliser. *J. Insects Food Feed.* **2021**, *7*, 683–694. [CrossRef]
61. Oonincx, D.G.; De Boer, I.J. Environmental impact of the production of mealworms as a protein source for humans—A life cycle assessment. *PLoS ONE* **2012**, *7*, e51145. [CrossRef] [PubMed]

62. Smetana, S.; Schmitt, E.; Mathys, A. Sustainable use of *Hermetia illucens* insect biomass for feed and food: Attributional and consequential life cycle assessment. *Resour. Conserv. Recycl.* **2019**, *144*, 285–296. [CrossRef]
63. Schmitt, E.; de Vries, W. Potential benefits of using *Hermetia illucens* frass as a soil amendment on food production and for environmental impact reduction. *Curr. Opin. Green Sustain. Chem.* **2020**, *25*, 100335. [CrossRef]
64. Armson, K.A.; Sadreika, V. *Forest Tree Nursery Soil Management and Related Practices*; Ontario Ministry of Natural Resources: Toronto, ON, Canada, 1979.
65. Mexal, J.G.; South, D.B. Bareroot Seedling Culture. In *Forest Regeneration Manual*; Kluwer Academic Publishers: Dordrecht, The Netherlands, 1991; pp. 89–115.
66. Grossnickle, S.C. *Ecophysiology of Northern Spruce Species. The Performance of Planted Seedlings*; NRC ResearchPress: Ottawa, ON, Canada, 2000.
67. Thompson, B.E. Seedling morphological evaluation: What You Can Tell by Looking. In *Evaluating Seedling Quality: Principles, Procedures, and Predictive Abilities of Major Tests*; Forest Research Laboratory, Oregon State University: Corvallis, OR, USA, 1985; pp. 59–72.
68. Grossnickle, S.C. Importance of root growth in overcoming planting stress. *New For.* **2005**, *30*, 273–294. [CrossRef]

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