



Natural Regeneration After Volcanic Eruptions: Resilience of the Non-legume Nitrogen-Fixing Tree *Parasponia rigida*

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Volcanic eruptions disturb vegetation at a time it is needed for preventing mudflows. A resilient indigenous non-legume nitrogen-fixing tree that is adapted to the ash and spreads rapidly protects areas downstream in a volcanic landscape in Indonesia. Within the volcanic ring of fire both the long-term benefits (including densely populated, fertile agricultural soils) and short-term ecological disturbance of volcanic ash deposition are clear. Mount Kelud in East Java has erupted on a 15–37-years cycle for the past centuries, most recently in 2014, causing damage to settlements, agricultural land, agroforestry, and watershed protection forests, as the ash deposits caused tree mortality, restricted infiltration, and led to ash flows. Rapid “restoration” or recovery of tree-based vegetation with planted Legume trees (such as *Calliandra* spp.) has been attempted but is not very effective. However, the non-legume nitrogen-fixing *Parasponia rigida*, symbiotic with rhizobium bacteria, contrasted to its non-symbiotic sibling (*Trema orientalis*) has been studied in laboratory conditions, but not in its native environment. We mapped and sampled *P. rigida* in various locations (upper, middle, and lower elevation positions in ridge-slope-valley toposequences) on the Kelud complex starting 1 year after the latest eruption, estimated biomass development, and quantified *P. rigida* root nodules in relation to N availability in the ash/soil mixtures in these locations. *P. rigida* was found as a pioneer tree at elevations between 600 and 1,700 m a.s.l. (above sea level) along ridges, in slope, and valley positions. At lower elevations *T. orientalis* dominated. Within 3 years of the eruption, stem diameters were 3–10 cm. Up to 93% of *P. rigida* root nodules were found to be effective, based on the hemoglobin color on cross-sections. *Rhizobium* bacteria were found in root nodule tissue at densities of two to a hundred times higher than in rhizosphere soil. Between a total soil N content from 0.01 to 0.04% the density of effective nodules decreased from 1,200 to 200 m⁻². *P. rigida* stands in the area, especially at ridges close to the crater deserve to be managed proactively as future seed sources, given the high frequency of eruption episodes, while recovery after eruptions on similar volcanoes can likely be facilitated by tactical assisted seed dispersal if effective seed collection and storage methods can be established.

Keywords: disaster preparedness, Indonesia, Mount Kelud, N₂-fixation, restoration, rhizobium, *trema orientalis*, volcanic ash

INTRODUCTION

Indonesia has more than 100 active volcanoes, and many more that are dormant, as it is part of the global ring of fire linked to tectonic plate subduction zones. Densely populated Java and Bali reflect both the long-term soil fertility benefits of volcanic ash and a large number of people at risk during fresh eruptions, ash deposition, and lahar flows (Van Ranst et al., 2004; Achmad and Hadi, 2015). Volcanoes are regularly resetting the clock on vegetation succession and create a need for “restoration” when downstream impacts such as mudflows of unconsolidated ash is to be controlled (van Noordwijk et al., 2020). Beyond scenic beauty, volcanoes are also home to a limited, but specialized flora, contributing to the overall biodiversity of the country. The short-term damage of eruptions involves settlements, access roads, agricultural lands, agroforestry, and watershed protection forests, and calls for remedial disaster responses. Human resilience is challenged by damaged infrastructure, loss of boundaries of land ownership, destruction of forests, disturbed water catchment areas, and springs (Rahayu et al., 2014). Can a resilient local tree, adapted to volcanic ash environments be of help? Current emergency preparedness documents in Indonesia are not aware of any such tree.

Atmospheric deposits after a volcanic eruption can consist of ash, sand, gravel, or stones with the lighter materials traveling further. Ash deposits change the physical, chemical, and biological properties of the soil surface (Achmad and Hadi, 2015). Thick layers of ash can cause a dense, cement-like soil surface after rainfall (Suriadikarta et al., 2010). Emergent hydrophobicity decreases infiltration below what is expected given the substrate's porosity and leads to a dry soil environment (Rudianto et al., 2017), with low levels of organic C and N and a soil pH that can be acidic, neutral, or alkaline depending on SiO₂ levels in the volcano's substrate (McGeary et al., 2002). Regrowth of vegetation is hindered by a challenging soil environment (Sinaga et al., 2015), but also by a lack of viable seed supply, an absence of biological dispersal agents and shelter for seedlings; regrowth from stumps is possible, however, outside of the primary deposition zones. Lack of vegetation regrowth leads to the high mobility of the ash within the landscape and accumulations in the riverbeds, causing further problems downstream, but also opportunities for collecting “volcanic sands” that are a preferred resource for the building industry and allow former farmers a temporary source of income. Rapid recovery of vegetation, especially on the higher slopes is desirable to support the recovery of the village economy, however.

The Kelud eruption (East Java, also commonly spelled as Kelut) on 13 February 2014 was one in a long series of recorded eruptions and ash deposits with return times of 15–37 years (with ash deposits in intervening years as well): 1826, 1848, 1864, 1901, 1919, 1951, 1966, 1990 (Thouret et al., 1998) and a relatively minor event in 2007. These relatively short return times may be part of the local selection of species that rapidly recover. In 2014 the top of the plume reached to a height of nearly 30 km and the umbrella cloud spread radially at 17–20 km high; ash was recorded up to Bogor, West Java; due to the prevailing wind, there were large deposits on the north and northeast area of the volcano

(Suzuki et al., 2014; Kristiansen et al., 2015). The 2014 eruption deposited about $50 \times 10^6 \text{ m}^3$ of material on the upper slope of Kelud Volcano. A considerable part of this was washed down by rainfall in mudflows along the rivers and deposited downstream where the riverbed widened (Dibiyosaputro et al., 2015). This was not the first time this happened, and part of the vegetation may be adapted to these circumstances. The German explorer Junghuhn had in 1,844 collected a tree specimen on Mt Kelud from which Miquel (1859) described the species as belonging to the genus *Parasponia*, as it closely resembled *Sponia*, now known as *Trema*. Local names confirm the close resemblance, with *Trema* known as “anggrung”, and *Parasponia* as its greener sibling “anggrung hijau”. Clason (1935) exploring the vegetation of the mountain slopes and valleys after the Mount Kelud eruption of 1919, reported *Parasponia* especially from the volcanic ash and lahar valley, while *Trema* grew more frequently in places where the original soil, “although probably more or less sterilized” had persisted after the eruption. Clason (1935) mentioned in passing that “*Parasponia* possesses root nodules, nitrogenous food being possibly obtained in this way so that *Parasponia* is thus adapted as a pioneer type to virgin soil.” However, it took another 40 years before this observation was noticed, although Smiet (1992) described *Parasponia* as a common part of Java's mountain flora. Trinick (1973), Akkermans et al. (1978), Trinick (1979), and Becking (1979) established the exception to the rule that only the *Leguminosae* can associate with rhizobium bacteria. The genus *Parasponia* (in the *Cannabaceae* family, formerly seen as part of the *Ulmaceae*) that is known from volcanic ash environments in Indonesia and the Philippines can form effective nodules with rhizobium bacteria (*Bradyrhizobium* species according to Trinick and Hadobas, 1989). Due to its more open canopy, *Parasponia* stands allow the development of a dense layer of the grass *Saccharum*, which in turns prevents other late-successional trees to establish. “It would seem that the *Parasponia*-socio has already attained its greatest development and that it does not hold its own; in any case, I saw very few young trees and on the other hand several old trees which had died off. It seems as if *Parasponia* became established before the edaphic conditions allowed the development of the *Saccharum*-socio.” This description suggests that *Parasponia* occupies the “regeneration niche” (Grubb, 1977; Pickett and White, 2013), being able to establish itself rapidly in the extreme conditions that prevail after a recent ash deposition event (given the short return period of eruptions), but by enriching the ash deposits with nitrogen, paves the way for grasses to take over, which in turn delay succession to other woody vegetation. A deeper understanding of these ecological relations in the field and aspects of the “regeneration niche” is warranted, as the unique volcanic ash environment in which *Parasponia* is evolving may account for its unique properties.

A productive line of research has explored the molecular biology of *Parasponia*-rhizobium interactions and the evolutionary interpretation of such interactions as either independently (re)discovered in multiple plant families or lost from a large number of plant families that are otherwise related to both rhizobium hosts (Geurts et al., 2012; van Velzen et al., 2018). While many *Leguminosae* are not only able to initiate

N₂-fixation by rhizobium but also down-regulate it when there is sufficient nitrogen in its internal circulation system, there still is debate about the ability of *Parasponia* to do the same in laboratory test conditions (Vassey et al., 2005; Op den Camp et al., 2012; Yulia, 2013). Dupin et al. (2020) recently showed that in lab conditions exogenous fixed-nitrogen inhibits nodulation on *P. andersonii*. Much less is known on the ecology of the species in its native environment. From the existing evidence and literature, it appears that *Parasponia* evolved in the specific “regeneration niche” of volcanic ash where access to a nitrogen source is essential for early establishment but may pave the way, by enriching the soil, for more competitive non-nodulating sibling (or unrelated) species.

The specific research questions for our exploration of vegetation on Mount Kelud after the 2014 eruption were:

- 1) Has the most recent eruption had different effects on the populations of *Trema* and *Parasponia*? We quantified the composition of the recovering vegetation across the slope, with specific attention to the relative share of the two sibling species.
- 2) Which aspects of landscape position were related to biomass recovery? We compared seedling, sapling, pole, tree populations and biomass estimates with soil properties in toposequences at three elevation zones
- 3) Is (effective) nodulation of *P. rigida* in the regrowth stage related to soil nitrogen levels? We tested the hypothesis that down-regulation of N₂ fixation is absent in this early stage of an evolving symbiosis with *Rhizobium*, leading to soil enrichment.

In relation to options for enhancing natural regeneration to restore landscapes, we will discuss the opportunities *Parasponia* provides to existing disaster preparedness plans for the area (and similar volcanoes elsewhere in Indonesia) to embrace a more pro-active vegetation management protecting seed sources in the highest zone.

MATERIALS AND METHODS

Study Area

The research focused on the northeast side of Mount Kelud (Figure 1), where most of the ash of the 2014 eruption was deposited. The satellite imagery for the area (Figure 1) compares the land cover before the eruption (peaking 14 Feb 2014, BNPB, 2014) that covered an area at 5–10 km from the crater with ash. Vegetation at a larger distance from the crater recovered, despite some tree mortality, while regrowth closer to the crater had to start from either seeds or stumps.

The main access to the mountain slopes we used was via the Kutut Pandansari village (7°54'35.74"S, 112°22'0189"E) in the area downstream of the Selorejo reservoir in Ngantang district (Malang Regency). A path toward the crater passes through three elevation zones: lower (700–800 m a.s.l.), middle (900–1,000 m a.s.l.), and upper (>1,000 m a.s.l.) (Figure 1). The steeper slopes of Mount Kelud are classified as “watershed protection” forest, with lower parts classified as production forest, both managed by the State Forest Company (Perum Perhutani).

The research activity was carried out in 2 stages: Phase 1 focused on vegetation analysis 1 year after the eruption (July–December 2015), and Phase 2 on *Parasponia* nodulation was carried out 2 years after the eruption (July–November 2017), with some follow-up observations at later dates.

Data Collection

Observation Plots for Vegetation Analysis

Observation plots were selected for exploring the distribution of pioneer plant vegetation in various landscape positions on the slopes of Mount Kelud starting from Mahogany plantations in the lower zone (700–800 m a.s.l.), mixed vegetation at the middle (900–1,000 m a.s.l.), and upper zones (>1,000 m a.s.l.) using a survey scheme of plants on the slopes of Kelud mountain (Smiet, 1992). In each toposequence an East-West transect was sampled, with ridge (8–15% slope), mid-slope (40–60% slope), and valley (0–3% slope) positions. Stand density was determined within patches of vegetation, not randomly sampling the landscape.

Starting 2 years after the eruption, stem diameter and tree biomass were measured for *P. rigida* in various landscape positions: zones (upper, middle, and lower) and for a toposequence of ridge, slope, and valley, as before.

Soil Analysis

In phase 1, soil samples were collected from each observation plot from soil depths of 0–10, 10–20, and 20–30 cm, respectively; soil samples per layer were composited from five points per plot. Dried soil samples were used for the analysis of total organic carbon (C_{org}) using the Walkley and Black (1934) method, total nitrogen (N_{tot}) with a Kjeldahl procedure (Bremner, 1960), pH(H₂O), and soil texture as standard at the Chemical Laboratory, Soil Science Department, Faculty of Agriculture, Brawijaya University, Malang. Separate samples were taken for the determination of the soil bulk density (Hairiah et al., 2011).

In phase 2, soil samples were taken at 50 cm distance from the main stem of *P. rigida* at a depth of 0–10, 10–20, and 20–30 cm were taken and analyzed for C_{org}, N_{tot} (Kjeldahl), and mineral NH₄ and NO₃ concentrations in extracted soil solution using a colorimetric flow-injection autoanalyzer.

Vegetation

Observation of vegetation was carried out on all types of vegetation in various growth stages (seedlings, saplings, poles, and trees). Sample observation plots were nested within a 100 × 20 m main plot (Kusmana, 1997), with five plots of 20 × 20 m used to measure trees (D > 10 cm; D = diameter at 1.3 m above the ground, also known as diameter at breast height) (trees), subplots of 10 m × 10 m used for poles (5 < D < 10 cm), sub-sub plots of 5 × 5 m for saplings (D < 5 cm, H > 2 m), and sub-sub-sub plots of 2 × 2 m for seedlings (H < 2 m).

Assessment of the Effectiveness of Root Nodules

Root nodules were sampled by sorting through all soil in a 50 × 50 × 10 cm depth sample adjacent to 10 trees that were considered representative of the stand (avoiding the largest and smallest 20% of the distribution as found in the stand). All root nodules were separated from the roots, counted, and

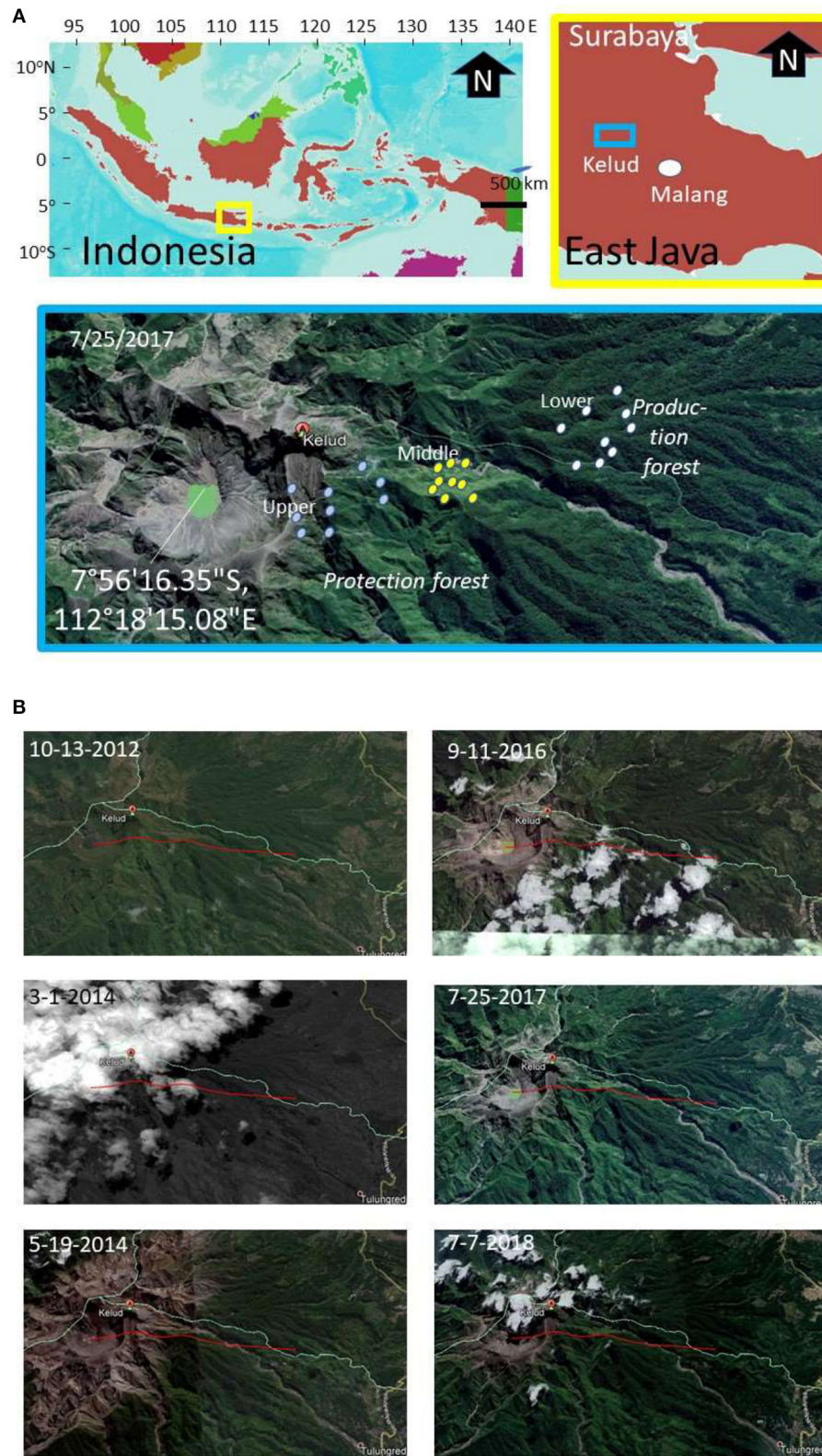


FIGURE 1 | (A) Location of Mount Kelud (East Java, Indonesia), **(B)** with satellite imagery before (2012), directly after (March 2014), and in recovery phase from the 2014 eruption and the position of sampling points in lower, middle and upper elevational zone; the red line indicates a 5 km transect.

stored in 70% alcohol. All nodules were observed under a dissecting microscope for hemoglobin color on a cross-section. Red hemoglobin was taken as an indicator of effectiveness, white nodules were classified as non-effective (Sarasawati, 2007).

Additional fresh nodule samples and rhizosphere soil adherent to roots was also collected for quantification of rhizobium density, via a dilution series and plating on petri dishes kept at room temperature (around 20°C) for 7 days to estimate the number of Colony Forming Units (CFU). Details of the method are described by Sarasawati (2007). The (autoclaved at 250°C) growth medium consisted of Potato Dextrose Agar (7.8 g), Mannitol (2 g), Yeast extract (0.2 g), K₂HPO₄ (0.1 g), MgSO₄ (0.04 g), NaCl (0.1 g) in 200 ml distilled water, with Congo Red (0.25 g) added as indicator. The highest dilution that still showed bacterial colony formation was taken as an indicator of the rhizobium concentration in the original sample, with calculations specified in Sarasawati (2007).

Parasponia's Taxonomic Position

The GlobalTreeSearch (Beech et al., 2017) mentions only one *Parasponia* species for Indonesia *P. rigida* Merr. & Perry (Hassler, 2019). In the Kew Garden plant list, all species in the genus *Parasponia* are indicated as “unresolved.” Part of the literature on Indonesia [including Ishaq et al. (2020) refers to *P. andersonii* Planch. which has been confirmed for islands in the Pacific. Part of recent taxonomic interpretation places the species into the genus *Trema* (which has *Sponia*, to which *Parasponia* refers, as a synonym), as *T. rigida* (Merr. & L.M. Perry) Byng & Christenh. Pending this taxonomic debate, we will here use *P. rigida* as the botanically correct name for the tree species found on Mount Kelud.

Data Analyses

Pedotransfer as Reference Values for Soil Parameters

A reference value C_{ref} for the C_{org} concentration expected under long-term forest conditions for a soil of the same texture and pH at the same elevation (with additional factors for Andisol and Wetland conditions) was used, based on van Noordwijk et al. (1998) and Hairiah et al. (2020), including a depth correction for a soil layer from Z_H to Z_L cm depth:

$$C_{ref} = 0.9 * (Z_L^{0.705} - Z_H^{0.705}) / (0.705 * (Z_L - Z_H)) * EXP(1.333 \\ + 0.00994 * Clay\% + 0.00699 * Silt\% - 0.156 * pH(KCl) \\ + 0.000427 * Elevation + 0.834 * Andisol? + 0.363 * Wetland?)$$

with elevation expressed in m a.s.l. and “Andisol?” and “Wetland?” are zero unless the specific soil condition (with higher C_{org}) applies and the value is 1.

Vegetation Analysis

The diversity of vegetation was characterized by identifying all woody plants in the observation plots and calculating several indices from the results: density (number of individuals per unit area), frequency (fraction of plots in which a species was found), dominance (relative abundance) and the INP or Index

of Importance Values (Soerianegara and Indrawan, 1978).

$$\text{Density (PD)} = \frac{\text{number of individuals of a type}}{\text{sample plot area}}$$

$$\text{RelativeDensity (RD)} = \frac{\text{density of a type}}{\text{density of all types}} \times 100\%$$

$$\text{Frequency (F}_i\text{)} = \frac{\text{the number of sample plots containing type}(i)}{\text{total number of sample plots}}$$

$$\text{RelativeFrequency (FR)} = \frac{\text{frequency of a type}}{\text{frequency of all types}} \times 100\%$$

$$\text{Dominance (DM)} = \frac{\text{total basal area of a type}}{\text{sample plot area}}$$

with basal area (BA) derived as $\sum \pi DBH^2/4$ from measurements of DBH or stem diameter at breast height (1.3 m).

$$\text{RelativeDominance (DR)} = \frac{\text{Dominance of a type}}{\text{Dominance of all types}} \times 100\%$$

$$\text{Importance (INP)} = FR + RD + DM.$$

Diversity Index (Shannon and Wiener, 1949):

$$H' = - \sum_{i=1}^n \left(\frac{n_i}{N} \right) \ln \left(\frac{n_i}{N} \right)$$

where H' = Diversity index, N = Total number of individuals sampled, n_i = Number of species i .

Evenness index (with values between 0 and 1):

$$SEI = - \sum (P_i^* \ln(P_i)) / \ln(m)$$

where P_i are the frequencies of the m species observed.

Tree Biomass

Measured stem diameters of poles and trees (for $D > 5$ cm) were converted to aboveground biomass (AGB) estimates using allometric equations for wet tropics (average rainfall 1,500–4,000 mm y^{-1}) from Chave et al. (2005):

$$(AGB)_{est} = \rho * \exp(-1.499 + 2.148 \ln(D) \\ + 0.207(\ln(D))^2 - 0.0281(\ln(D))^3)$$

Where ρ = wood density ($g\ cm^{-3}$), derived from <http://db.worldagroforestry.org/wd>. A locally developed (Alfian, 2017) species-specific allometric equation was used: $AGB = 0.4992 D^{1.0012}$.

Statistical Analysis

The results of observations and measurements of biophysical data were analyzed by Analysis of Variance using Genstat (18th edition) software to test possible rejection of a null-hypothesis of no effects of toposequence and landscape positions as main factors, along with a simple interaction term. Where statistically significant differences ($p < 0.05$) were noted, a Duncan test was used to compare means at the combination of the two factors. Correlation and linear regression analysis (in the MS-Excel software) were used to describe relationships between response (Y) and explanatory (X) parameters, as $Y = b Y_m + (a Y_m / X_m)$ X , after normalizing or rescaling data sets relative to their means, Y_m and X_m , respectively.



FIGURE 2 | Soil profile on the ridge position at three elevations, with soil layers as identified in the field indicated by dashed lines and topsoil recent ash deposits of close to 20, 12, and 7 cm, respectively; the measuring tape indicates depth increments of 10 cm (Photo courtesy from Nugraha, 2015).

TABLE 1 | Soil properties for three soil layers in various landscape positions (BD, bulk density; C_{ref} , reference Corg concentration based on pedotransfer function; averages for three replicate plots).

Landscape position	Depth cm	BD g cm ⁻³	pH H ₂ O	C _{org} %	C _{ref} %	C _{org} /C _{ref}	Texture*, %		
							Sand	Silt	Clay
Upper (Shrub)	0–10	1.12	4.62	1.11	2.60	0.427	80	16	4
	10–20	0.90	4.78	0.18	1.43	0.126	95	2	3
	20–30	0.96	4.97	1.40	1.43	0.978	69	24	6
Middle (Shrub)	0–10	1.03	4.70	0.13	2.36	0.055	80	19	2
	10–20	0.88	4.80	0.57	1.41	0.404	84	14	2
	20–30	0.80	5.04	2.53	1.37	1.85	64	27	9
Lower (Production forest)	0–10	1.14	4.70	0.09	2.15	0.042	75	20	5
	10–20	1.14	4.88	0.74	1.33	0.555	72	26	2
	20–30	0.98	5.06	1.83	1.17	1.56	66	28	6
Lower (Annual plants)	0–10	1.07	4.69	0.31	2.20	0.141	67	25	8
	10–20	1.00	4.75	0.26	1.42	0.183	64	25	11
	20–30	0.96	4.97	0.45	1.22	0.369	59	28	13

*Data from Yunita (2016).

RESULTS

Vegetation and Soil Properties

Soil profiles in the area showed evidence of multiple ash deposition events, with topsoils buried by the 14 February 2014 and earlier Kelud eruptions at various depths (Figure 2). Soil analysis (Table 1) showed buried topsoil (with relatively high C_{org}) in the 20–30 cm depth layer, and slightly higher pH values. Lower elevations had higher silt content, but the sand fraction dominated in all samples.

Most of *P. rigida* plants were found in clusters on sites with a slope of 30–80%, spread over an altitude of 600–1,700 m a.s.l. at the lower, middle, and upper landscape positions, with sandy and relatively wet soil conditions. Usually, *P. rigida* was found in open shrubland, but it also developed well in the lava flow deposits (layers of sand and gravel) in the riverbeds (Figure 3D).

Basal area, biomass, and necromass of trees differed significantly between landscape positions (Table 2). Necromass was 34 and 26% of biomass at upper and middle landscape positions, indicative of eruption-related tree mortality, but no necromass was observed in the lower zone, while biomass there was highest. In the middle and upper zones, several trees had survived, as indicated by the biomass of trees above 30 cm diameter. Please note that the vegetation sampling referred to existing stands, not to their frequency within the wider landscape. The absence of necromass at lower elevation can be an indication of firewood collection by the neighboring village.

Tree population data (Table 3) matched the basal area (Table 2) data, with the high biomass but low tree diversity (and near-absence of internal regeneration) in the Mahogany stands in the lower zone). Tree diversity in the middle zone was significantly ($p < 0.01$) higher than that in the upper zone for trees ($D > 10$ cm) and poles ($5 < D < 10$ cm) but was not distinguishable between these two zones for the sapling and seedling stages. In the latter two categories, however, sapling and seedling diversity reflected that in poles and trees at the high landscape position.

For further analysis of the differences between the zones, the Importance Value Index combines relative density, relative frequency, and relative domination for the commonest species. In the middle zone the seedling and sapling stage was dominated

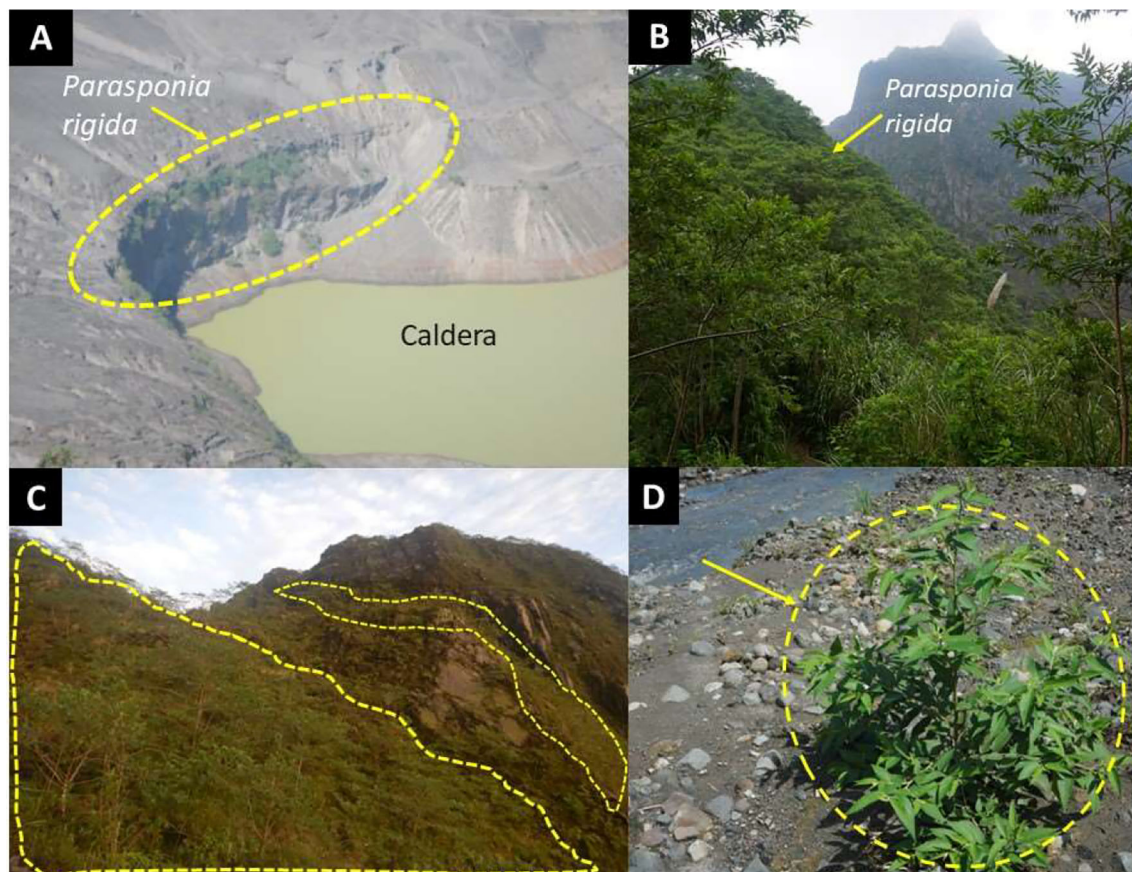


FIGURE 3 | *P. rigida* (dashed yellow lines) stands at various landscape locations: (A) Caldera, (B,C) high ridges, (D) Ash deposits in a river valley (Photo credits: first author).

TABLE 2 | Tree biomass and necromass differentiated by stem diameter in stands in three landscape positions (based on three replicates in each of three elevational zones).

Landscape position	Basal area (m ² ha ⁻¹)	Tree biomass (Mg ha ⁻¹)		Tree necromass (Mg ha ⁻¹)	
		5 < D < 30 cm	D > 30 cm	5 < D < 30 cm	D > 30 cm
Upper	8.93 a	13.41 c	60.77 a	13.49 a	12.04 b
Middle	8.21 a	7.74 b	58.71 a	13.44 a	3.56 ab
Lower	37.03 b	0 a	381 b	0 a	0 a
s.e.d	3.40**	1.76**	35.2**	9.02 ^{NS}	0.95**

Values followed by the same letter within a column were not statistically distinguishable; s.e.d, standard error difference, *significant difference ($P < 0.05$), **highly significant difference ($P < 0.01$), NS no significant difference.

by *Ageratum conyzoides* (babadotan, locally called “Tropos”) with INP = 177% and INP = 116%, respectively, and the pole stage by *T. orientalis* (INP = 61%). In the upper zone seedling and sapling, stages were dominated by *Begonia multangular* (“Mencok”) with INP = 100% and INP = 63%, respectively, while the pole stage was dominated *P. rigida* and *T. orientalis*, both?? with INP = 226%.

Biomass Production and Root Nodule Density of *P. rigida*

Results for the second survey showed that for each of the three elevational zones, the *P. rigida* population density, as well as average stem diameter, varied with position along the local toposequence (Figure 4). While population density was highest (80–200 trees/ha) in the valley positions in the upper and middle elevational zone, respectively. Tree diameter was highest in the ridge. Please note that in this second survey the lower zone toposequence did not include the Mahogany plantation, but *P. rigida* numbers were relatively low while other vegetation dominated.

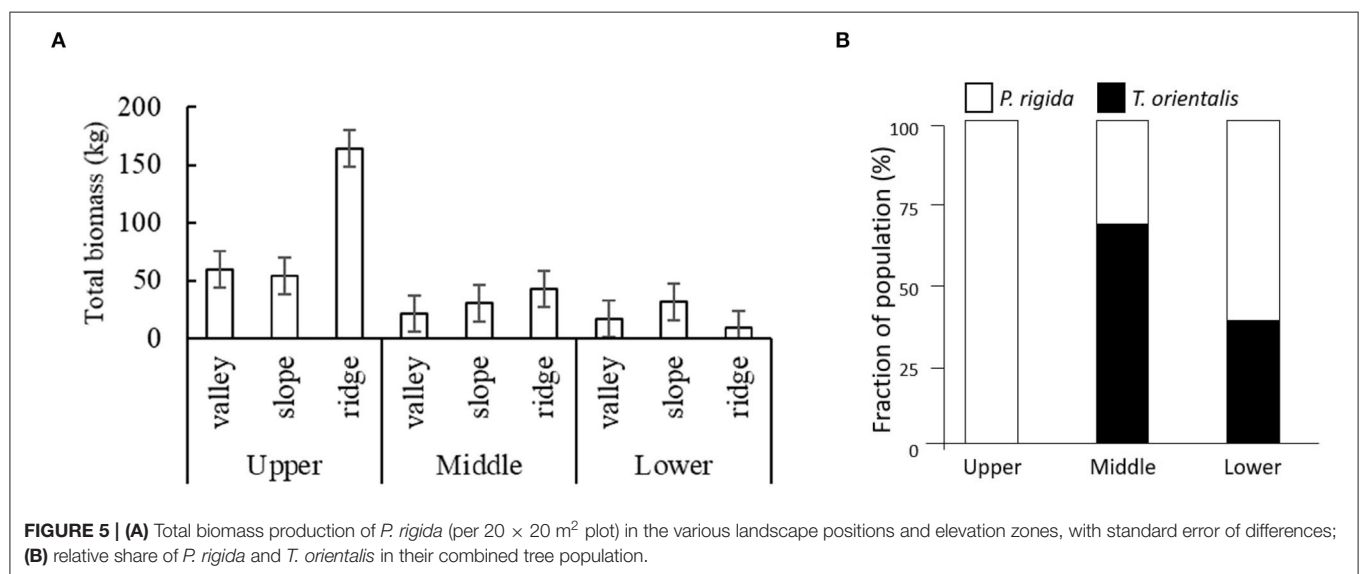
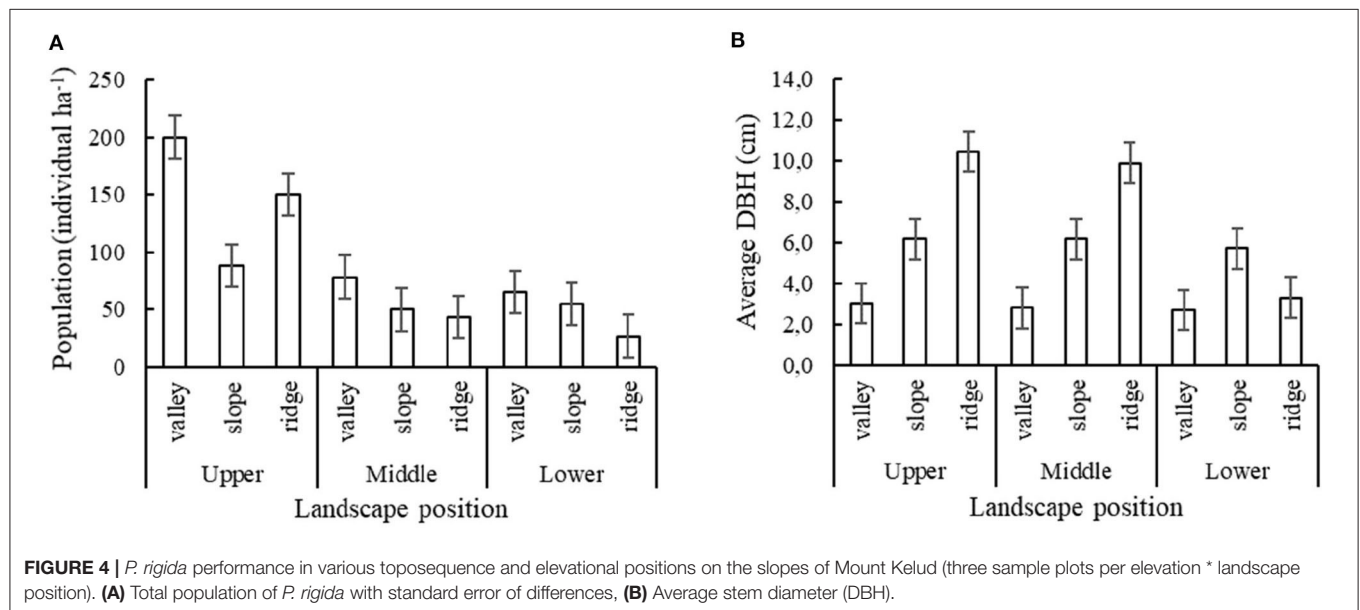
Plot-level biomass estimates (Figure 5A) show by far the highest *P. rigida* biomass (164 kg plot⁻¹) on the ridges in the upper zone. The relative share of *P. rigida* and *T. orientalis* in their combined tree population showed that *T. orientalis* was absent at the highest elevation and dominated at the middle elevation (Figure 5B).

Soil samples of the rhizosphere soil in existing *P. rigida* stands (Table 4) showed domination by the sand-sized fraction (fresh ash), with silt and clay at slope and ridge positions in the middle

TABLE 3 | Tree populations in various growth stages and biodiversity indices in three landscape positions (based on three replicates in each of three elevational zones).

Landscape position	Population (Indiv.ha ⁻¹)	Diversity Index (H')				Evenness Index (E)			
		Seed-ling	Sap-ling	Pole	Tree	Seed-ling	Sap-Ling	Pole	Tree
Upper	114 a	0.68 a	1.18 b	0.87 b	1.30 b	0.67 a	0.63 b	0.60 b	0.66 ab
Middle	119 a	0.97 a	1.58 b	1.64 c	2.36 c	0.65 a	0.72 b	0.80 c	0.95 b
Lower	394 b	0 a	0 a	0 a	0.19 a	0 a	0 a	0 a	0.27 a
s.e.d	39.6**	0.44 ^{NS}	0.45*	0.17**	0.39*	0.28 ^{NS}	0.19*	0.07**	0.22*

Seedling: $H < 2$ m, Sapling: $H > 2$ m, $D < 5$ cm, Pole: $5 < D < 10$ cm, Tree: $D > 10$ cm, with D = stem diameter and H = height; values followed by the same letter within a column were not statistically distinguishable; s.e.d, standard error difference, *significant difference ($P < 0.05$), **highly significant difference ($P < 0.01$), NS, no significant difference.



and lower zone. Bulk density was high (1.2 g cm^{-3} to 1.6 g cm^{-3} , N_{tot} (0.012–0.040%), and C_{org} (0.13 to 0.26%) concentrations very low in all stands.

Based on the hemoglobin color assessment 79–93% of nodules were classified as “effective,” while nodule densities per m² of soil surface were highest in the valley positions at low and

TABLE 4 | Characteristics of soil physico-chemical properties in the *P. rigida* rhizosphere (three replicates).

Elevation	Position	Bulk density	pH H ₂ O	Texture			N-Tot C-Org C/N		
		g cm ⁻³		%Sand	%Silt	%Clay	---	---	---
Upper	Valley	1.6	5.1	95	5	0	0.029	0.15	5
	Slope	1.28	5.6	93	6	1	0.023	0.18	8
	Ridge	1.32	5.1	94	4	2	0.021	0.13	6
Middle	Valley	1.55	5.2	93	5	2	0.018	0.14	8
	Slope	1.41	5.4	87	10	3	0.023	0.21	9
	Ridge	1.45	5.1	75	20	5	0.030	0.25	8
Lower	Valley	1.32	5.0	90	10	0	0.012	0.16	13
	Slope	1.2	5.3	85	10	5	0.027	0.19	7
	Ridge	1.35	5.2	65	25	10	0.040	0.23	6

TABLE 5 | Root nodules of *P. rigida* in various locations, distinguished by effectiveness (hemoglobin color) (averages for three replicates).

Elevation	Position	Root nodules, m ⁻²			Effectiveness
		Effective	Non-effective	Total	%
Upper	Ridge	472 d	61 e	533 e	89
	Slope	348 c	50 d	398 d	87
	Valley	127 a	34 bc	161 b	79
Middle	Ridge	348 c	48 d	396 d	88
	Slope	364 c	32 ab	396 d	92
	Valley	526 e	62 e	588 f	89
Lower	Ridge	112 a	22 a	134 a	84
	Slope	314 b	44 cd	358 c	88
	Valley	610 f	44 cd	654 g	93
s.e.d.		8.71**	4.72*	8.93**	-

Values followed by the same letter within a column were not statistically distinguishable; s.e.d., standard error difference, *significant difference ($P < 0.05$), **highly significant difference ($P < 0.01$).

middle zone, and in the ridge position in the upper zone (Table 5).

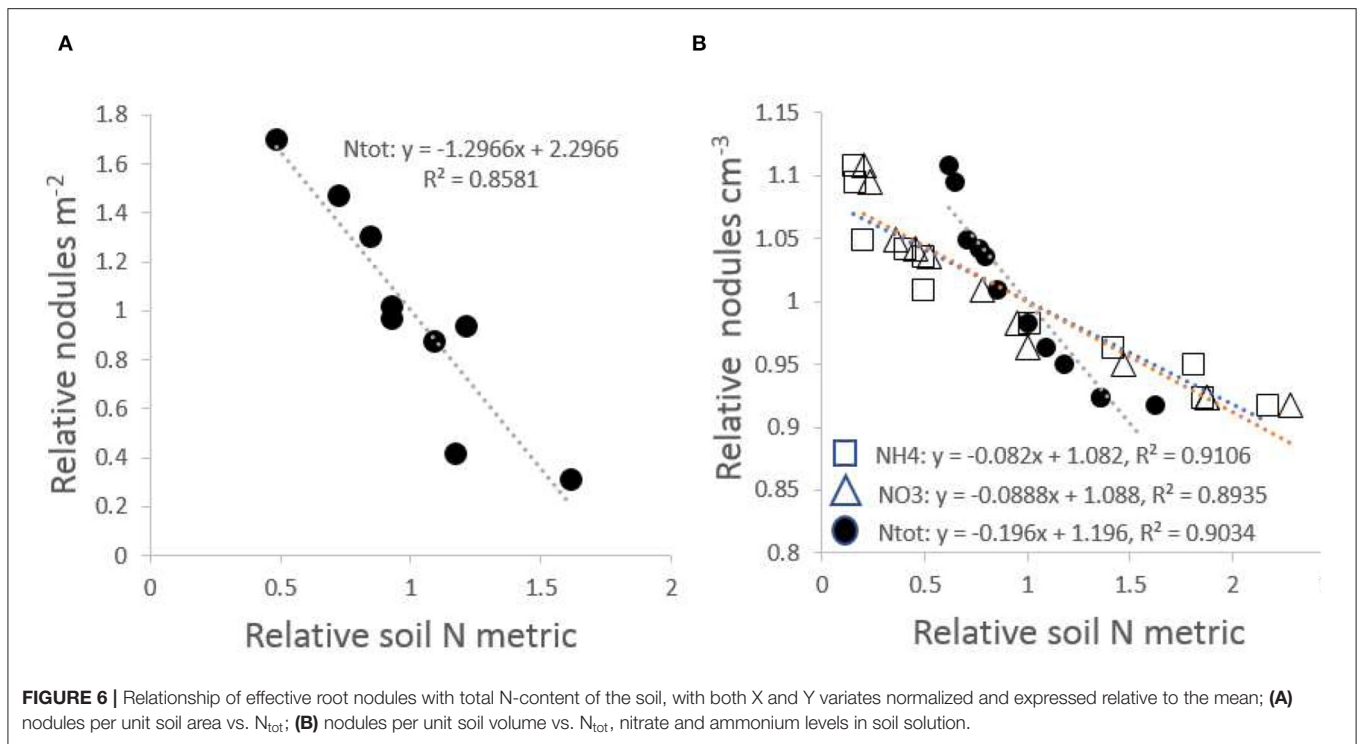
Regression analysis of nodules on the three indicators of soil nitrogen supply in *P. rigida* stands, N_{tot} , mineral NO_3^- and NH_4^+ , was based on normalized parameters to allow direct comparison between these indicators. The regression of the density of effective nodules on soil nitrogen indicators accounted for at least 85% of the observed variation (Figure 6). Nodulation was most abundant and effective on the poorest sites.

DISCUSSION

We found *P. rigida* populations over a considerable elevational range, from 600 to 1,700 m a.s.l., on around Mount Kelud after the recent eruption. A comparison of satellite imagery before (2013) and after (2014) the eruption (Nuzulah, 2016) indicated a decrease in vegetation density up to a radius of 10 km from the caldera, with a vegetation density index decreasing from

0.64 to 0.34 in 2013 to 0.52–0.01 in 2014; despite a partial recovery in 2016, vegetation was affected until a radius of 5 km. The observations of dominance by *P. rigida* in the highest zone (>1,000 m a.s.l.) demonstrate the remarkable adaptation of this species to the extreme environment of frequently erupting volcanoes and abundant ash deposition. Similar observations in 2018 in about 2 km from the active crater of Mount Merapi (Central Java) after an eruption in 2010 showed low levels of plant diversity, but *P. rigida* was observed in dense monospecific stands with some patches of *Acacia decurrens* (Dr. Subekti Rahayu, pers. comm. 2020). According to local informants on Mount Merapi *P. rigida* only occurred on the ridge and along riverbanks before the recent eruption, but it spread out throughout the landscape after the eruption. The literature on the vegetation of Mount Kelud in the past and the high frequency of eruptions match an interpretation that the species combines the effective colonization of *T. orientalis* (Mangopang, 2016) a pantropical pioneer species with the ability to thrive on soils of very low nitrogen content. The distribution of *P. rigida* observed suggests that its seeds may be carried by overland and river flows from trees on higher ridges, including the slopes of the caldera itself. *P. rigida* appeared to develop well in nutrient-poor and open soil conditions where the plants produce root nodules and the fresh green of leaves (Figure 3).

Our observations suggest that the stands on ridges in the highest zone (with populations of around 150 trees ha⁻¹) had the highest biomass and were the likely seed source for abundant regeneration in the valley positions at the middle and lower elevation. Seeds can be produced within 1 year of a regrowing stand. The trees also contribute to soil formation, with a half-life time of litter of around 20 weeks (Ishaq et al., 2020). The sibling species *T. orientalis* and *P. rigida* co-occurred at lower and middle elevation, while only *P. rigida* was found in the highest zone. These findings suggest that the selective advantage of the nodulated *P. rigida* over its non-nodulated sibling species *T. orientalis* is most pronounced in the most extreme and N-poor parts of the landscape. In the lush vegetation at lower elevations, *T. orientalis* can maintain a presence among grasses and other trees, *P. rigida* is abundant as a pioneer on the ash deposits in the valley but appears to lose out from other vegetation later in the succession. From the absence, at this stage of the recovery after the most recent eruption, of *T. orientalis* in the highest zone we cannot distinguish between lack of seed sources or lack of ability to grow as direct explanation, while *P. rigida* clearly meets both requirements for restoration success. Successful seed sources that can reach the rest of the landscape, however, do depend on the ability of pioneer plants to grow in the relatively harsh and nitrogen-poor soil conditions. The reduced role of *P. rigida* beyond the pioneer zone may suggest that the ability of *Parasponia* species to nodulate has had negative consequences, relative to their *Trema* siblings, for competitiveness under less extreme soil conditions. From these observations, it appears that explanations of the distributions of *P. rigida* and *T.* on the slopes of Mount Kelud will consist of the position of seed sources that survive the eruption, supported by the successful colonization of N-poor substrates by *P. rigida*. In more sheltered and N-rich landscape positions, *T. orientalis*



appears to have an edge in growth rates—but a direct test of competitive ability across levels of soil N availability has yet to be performed. Styger et al. (2009) reported from secondary forest regeneration sites in Madagascar that 3-years old *T. orientalis* had a biomass of 8.5 Mg ha^{-1} and 5-years old stands 24.7 Mg ha^{-1} . These biomass data, in a less extreme environment, are higher than what *T. orientalis* and *P. rigida* achieved on Mt Kelud, but effective soil cover was achieved and ash deposits along the riverbed were stabilized by *P. rigida* seedlings.

Our findings of a negative response of nodule formation to external nitrogen supply in the field match the laboratory results reported recently by Dupin et al. (2020). The density of effective nodules per unit soil surface area was associated with below-average soil nitrogen indicators, with rhizobium populations in the nodules (153×10^4 to $112 \times 10^6 \text{ CFU g}^{-1}$) up to a 100-fold increase above their concentrations in rhizosphere soil (average $82 \times 10^4 \text{ CFU g}^{-1}$). For comparison, Widawati (2015) reported a rhizobium density in the legume kaliandra (*Calliandra tetragona*) nodules of $2.2 \times 10^6 \text{ CFU g}^{-1}$.

Current emergency management plans for active volcanoes like Mount Kelud rely on nursery-produced legume trees as planting material to stabilize ash and reduce downstream mudflow risks. Three years after the eruption of Mount Kelud other surveys in the restoration area (Tanjungarsi et al., 2018) found the introduced legume tree *Calliandra* [both the red (*C. tetragona calothyrsus*) and white (*C. tetragona*) species to have been planted, along with naturally dispersed mahang (*Macaranga hispida*), and anggrung (*T. orientalis*)]. Relative to such plans and practice, our findings of a key role for *P. rigida* stands on the ridges at high elevation

are highly relevant. These trees can recover rapidly after an eruption and probably are the main seed source for successful natural regeneration of tree-based vegetation in the post-eruption landscape. *P. rigida* is not only a very interesting biological object of study, suggesting the conditions under which association between higher plants and rhizobium bacteria can evolve, it also deserves a key role in emergency preparedness plans for the area. Some investment in securing local *P. rigida* seed sources for assisted seed rains could likely speed up the recovery process in next steps of the eruption cycle.

CONCLUSIONS

1. *P. rigida* populations survived the recent eruption of Mount Kelud at an elevation of 600–1,700 m a.s.l. The sibling species *T. orientalis* and *P. rigida* (differing in their ability to nodulate) co-occurred at lower and middle elevation, while only *P. rigida* was found in the highest zone.
2. The rate of biomass recovery was related to landscape position: Stands on ridges in the highest zone (around $150 \text{ trees ha}^{-1}$) had the highest biomass and were the likely seed source for abundant regeneration in the valley positions at middle and lower elevation.
3. The density of effective nodules per unit soil surface area was associated with below-average soil nitrogen indicators.
4. A practical implication of these findings is that existing *P. rigida* stands on the ridges at high elevation are key to the successful natural regeneration of tree-based vegetation in the

post-eruption landscape and deserve protection and a key role in emergency preparedness plans for the area.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

The field and laboratory research was carried out by RM and IA as part of their Master of Science program at Brawijaya University, under direct supervision of KH. RM and IA collected and analyzed the data. RM, KH, and MN designed the research and drafted the manuscript, for which all authors agree to be accountable for the content of the work. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer RG declared a shared affiliation, with no collaboration, with one of the authors, MN, to the handling editor.

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