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SUCCESSION OF GROUND VASCULAR PLANT COMMUNITIES ON PYROCLASTIC DEPOSITS SEVEN YEARS AFTER A VOLCANIC ERUPTION ON MOUNT MERAPI

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Seven years after the eruption of Mount Merapi, there were substantial differences in the degree of recolonisation on barren landscape formed by pyroclastic flow. This study aimed to quantify the ground vascular plant communities represented through an investigation of plant cover, rock cover, species richness, diversity, and frequency in three different habitats, bare ground, herbaceous and tree patches. Tree patches were characterized by the presence of trees and shrubs ≥ 1 m height. Plant cover was less ($P < 0.001$) and rock cover more ($P < 0.001$) on bare ground than the two patches. Although tree patches had the highest plant and lowest rock cover, these were not significantly different to those in the herbaceous patches. Species richness and diversity were not different among habitats and species composition had a commonality of 55%. *Pytirogramma calomelanos, Imperata cylindrica* and *Eupatorium riparium* accounted for half the plant cover in all habitats. *Parasponia parviflora* was the most frequent tree species but *Acacia decurrens* had the greatest mean stand basal area in the tree patches. The earlier formation of tree canopies and more ground space for colonisation due to low rock cover is anticipated to promote the further development of vegetation cover and primary succession on Mount Merapi.

Keywords: Merapi's eruption, succession, patch, vegetation

INTRODUCTION

In 2010, Mount Merapi erupted and ejected pyroclastic flow containing *ca.* 130,000,000 m^3 of volcanic materials alongside the Gendol River that destroyed vegetation in the Mt. Merapi National Park (Idjudin et al. 2012). Forested land was buried deeply under these deposits which consisted of ash and a wide variety of solid materials, including pulverised rocks (Idjudin et al. 2012, del Moral & Grishin 1999). This extreme local disturbance turned complex natural forest into non-vegetated barren land of low nutrient availability and high surface dryness which with time triggers primary succession (Sutomo et al. 2011, del Moral & Walker 2011).

The trajectory of primary succession in ecosystems is closely associated with volcanic landscapes (Elias & Dias 2007). Plant colonisation rate and patterns can differ following volcanic eruptions which depend on abiotic factors such as climate and the chemistry and weatherability of the volcanic deposit as well as biotic factors such as proximity from sources of colonists, presence of survivor plants and inter- and intra-species competition for resources (Garcia-Romero et al. 2015, del Moral & Grishin 1999, del Moral et al. 2005). Following the great eruption on Krakatau in 1883, plant colonisation was slow as it occurred on an island isolated by sea, where there was a limited number of dispersal agents and the surrounding islands that could act as seed sources had also been damaged (Tagawa et al. 1985, Whittaker et al. 1989). By contrast, following less severe eruptions on Mt. Merapi, succession might be expected to proceed without delay owing to the proximity of propagules provided from undisturbed vegetation including forest and favorable climatic conditions (Gunawan et al. 2015, Sulfiantono 2012). Nevertheless, volcanic deposits that consist of a mix of pulverised volcanic rocks, sand, gravel and ash may still slow succession due to the absence of patches of pioneer species which can serve as nuclei for later colonisation if these have also been affected by the deposits (del Moral & Grishin 1999). The role of pioneer species is significant for vegetation restoration in a severely disturbed habitat such as bare ground. However, little is known about the role of tree pioneer species on the succession rate of ground vascular plant communities during primary succession.

This study examined the early development of tree canopies that shape current and determine future community vegetation within a decade of an eruption by comparing the ground vascular plant communities develop in three contrasting habitats, bare ground, and patches supporting either plants of < 1.0 m height or ≥ 1.0 m height with developing tree canopies. The observation had been classified from satellite imagery taken 7 years after the volcanic eruption. Given that dominance of a particular species limits the space for later colonists (Lawrence et al. 2006, del Moral & Walker 2011), the study hypothesised that ground vascular plants in the patches with tree canopies should show a higher cover rate and lower species richness and diversity than in the other habitats. Species composition and size of trees and shrubs ≥ 1 m height in tree patches were also assessed to understand their effects on ground vascular plant communities.

MATERIALS AND METHODS

Study area

The study was conducted on 48 ha of the most severely damaged area which had received frequent passage of lava, mud and pyroclastic flow and was covered by pyroclastic deposits. It was located within the Mount Merapi National Park. Its geographical position was from 7.569 °S–7.587 °S and 110.448 °E–110.453 °E (Figure 1a and 1b) and elevation ranged from 1,117–1,308 m above sea level.

Sampling method

ArcGIS software (version 10.6) and a greenness index based on RGB colour which measured a green chromatic coordinate (Naji 2015, Xue & Su 2017) were used to identify three habitat types in the study area such as bare ground characterised by surface exposure of ash, sand and rocks, herbaceous patches covered by ground vascular plant species such as herbs, grasses, forbs, ferns, vines and tree seedlings and tree patches represented by these same vascular plant species and the presence of tree canopies developing from tree species ≥ 1.0 m height

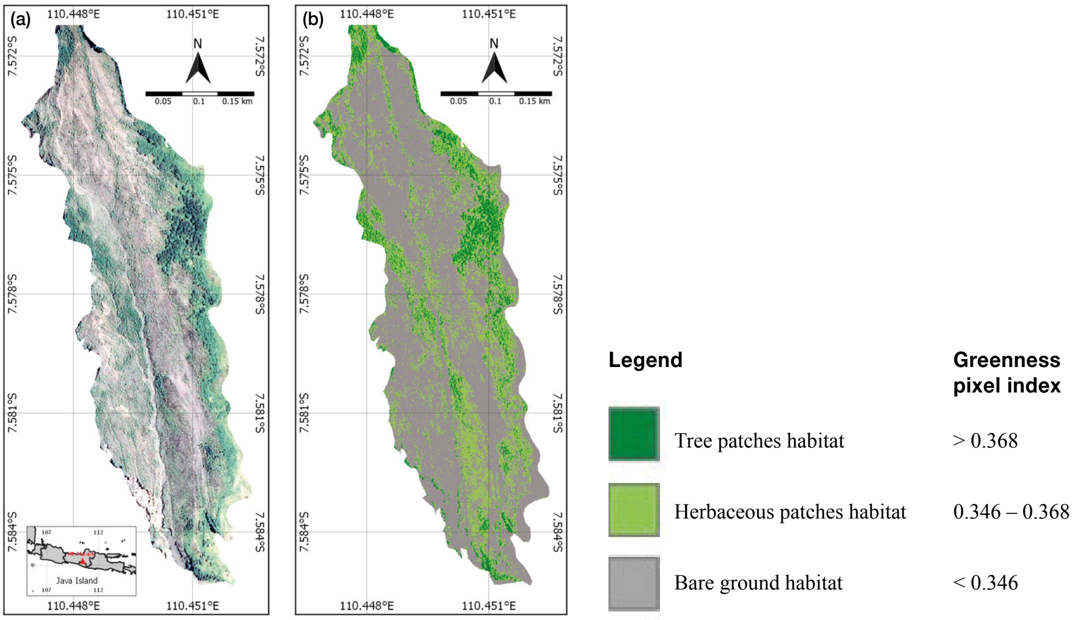


Figure 1 The 48-ha area of land affected by a pyroclastic deposit and damaged forest habitat after the Merapi eruption in 2010. (a) Enhanced resolution images captured from Google earth according to habitat distribution in 2017 and (b) An enhanced image based on a greenness vegetation index using ArcGIS software

(Figure 1a and 1b). The field survey was conducted in August and September 2017 during the dry season, seven years after the eruption. A total of 90 1 m 1 m quadrats, 30 for each habitat were placed randomly by ArcGIS software and used to record all living ground layer plants (< 1 m) at species level. In order to measure species and rock cover percentage, a photographic image of each quadrat was processed with ImageJ software. A direct manual cover measurement with compacted transparent plastic was also used to crosscheck the vegetation cover rate from ImageJ software. In order to survey canopies of shrub and tree species ≥ 1 m height, 30 larger, circular quadrats of 3-m radius were centered on each of the square quadrats in the tree patches. Diameter at breast height of 1.3 m was measured if the plant height was > 2.6 m or at the half height if ≤ 2.6 m tall. As for multi-stemmed plants, all stems meeting these criteria were measured and the mean calculated.

Statistical analysis

Based on Marler & del Moral (2011), the number of species in a quadrat was recorded as species richness and diversity was measured using the Shannon-Wiener index (H'). The frequency, probability of species occurrence (ranging from 0–1), coverage of individual plants and rocks (% m^{-2}) at each quadrat and the mean basal area of tree species in the circular quadrats (cm^2 m^{-2}) were calculated. One-way ANOVA and a Tukey multiple comparison were used to evaluate for differences in these variables among the three habitats ($p \leq 0.05$). Commonality of species across the habitats was examined using Pearson's intercorrelation coefficients (*R*). The Non-Metric Multidimensional Scaling (NMDS) and the Bray-Curtis index (Krebs 2014) examined similarity across quadrats within and among habitats. R software version 4.0.3 (R Core Team 2020) was used for all statistical analyses.

RESULTS

Ground vascular plants in different habitats.

Mean ground vascular plant cover (< 1 m height) was significantly less, 23.8 % on bare ground than in herbaceous and tree patches at 45.5 and 59.0 %, respectively ($F = 17.982$, $P < 0.001$) (Figure 2a). A similar but inverse pattern was found for rock cover ($F = 12.324$, $P < 0.001$) (Figure 2b) that occupied 52.6 % of bare ground and in herbaceous and tree patches at 30.3 and 24.6 % respectively. There were no significant differences between patches in species richness (Figure 2c) and diversity (Figure 2d).

The three habitats exhibited similar species composition with 55% commonality (22 out of 40 of ground vascular plants < 1 m height). The commonality was also showed on the regression plots between habitats (Figure 3) where many species appeared in all habitats in terms of frequency and mean cover, and also from their distribution on the Non-Metric Multidimensional Scaling plot (Figure 4) where many quadrats of all habitats clustered together indicating that they were alike. The positive correlation of frequency and mean cover among habitats also indicated that they had similar patterns of species composition (Figure 3). The five dominant

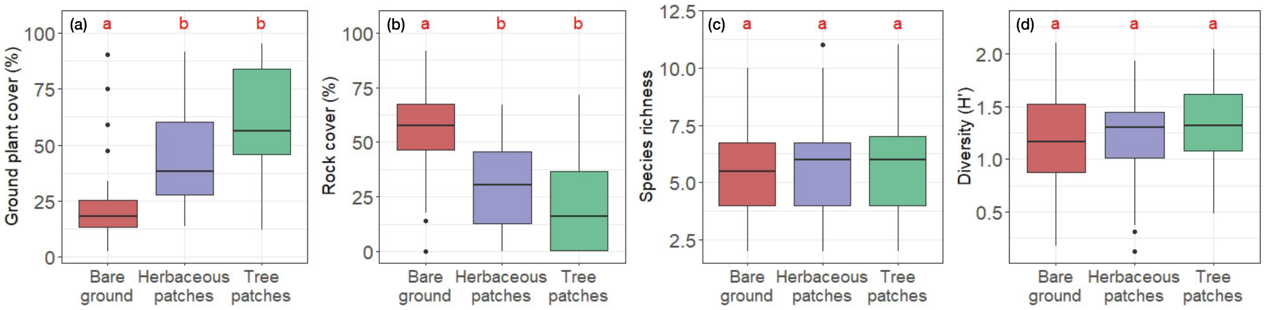
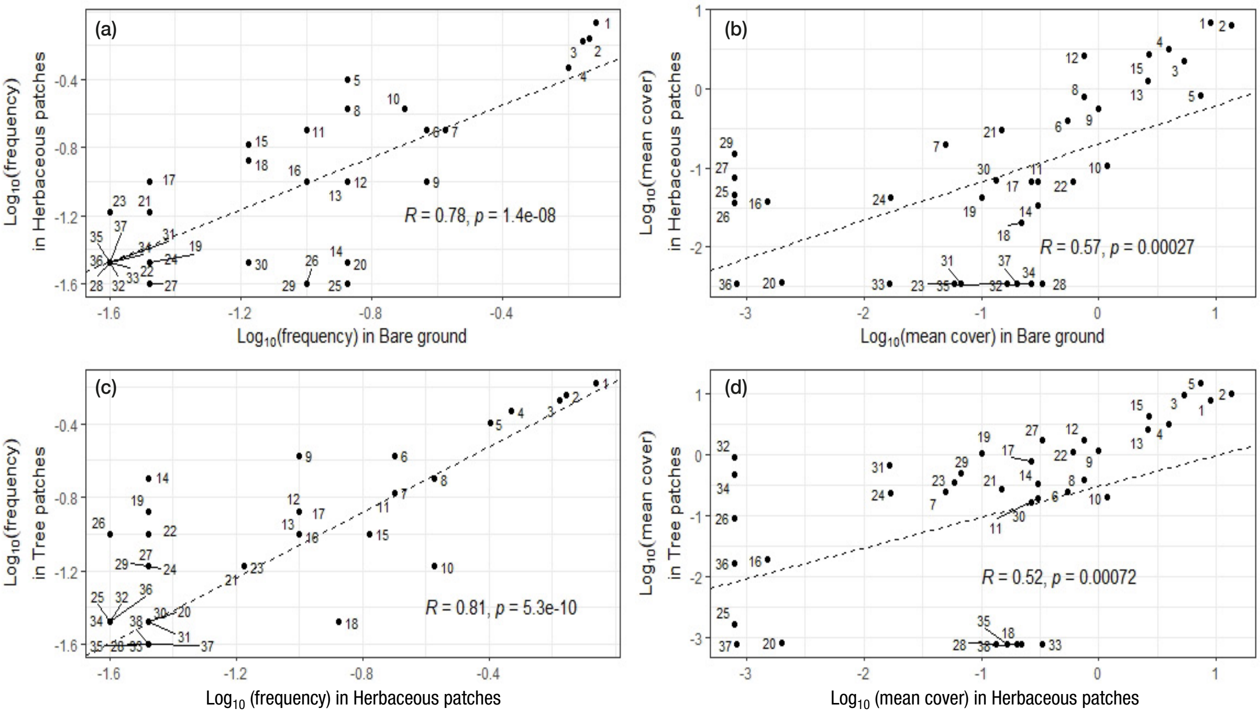


Figure 2 Comparison among three different habitats in the most severely damaged forest area on (a) vascular plant cover, (b) rock cover, (c) species richness and (d) diversity. The red letters, a and b, indicate presence or lack of significant differences based on a post hoc analysis of Tukey HSD



1. *Imperata cylindrica* (g)
2. *Pytirogramma calomelanos* (fe)
3. *Pogonatetherum paniceum* (g)
4. *Anaphalis margaritacea* (fo)
5. *Eupatorium riparium* (h)
6. *Gynura* sp. (h)
7. *Polygala paniculate* (h)
8. *Paederia foetida* (v)
9. *Debregreasia hypoleuca* (s)
10. *Trema orientalis* (t)
11. *Ageratum conyzoides* (h)
12. *Paspalum commersonii* (g)
13. *Andropogon acicularis* (g)
14. *Parasponia parviflora* (t)
15. *Setaria italica* (g)
16. *Ermeleria sonchyfolia* (fe)
17. *Nephrolepis exaltata* (fe)
18. *Lycopodium cernuum* (fe)
19. *Brachiaria mutica* (v)
20. *Porophyllum ruderale* (h)
21. *Saccharum spontaneum* (g)
22. *Desmodium triflorum* (v)
23. *Acacia decurrens* (t)
24. *Blumea klarkei* (h)
25. *Pennisetum setacium* (g)
26. *Spermacoce latifolia* (h)
27. *Cyperus pumitus* (g)
28. *Imperata* sp. (g)
29. *Melastoma affine* (s)
30. *Sida acutifolia* (s)
31. *Eupatorium inulifolium* (s)
32. *Mikania micantra* (v)
33. *Panicum muticum* (g)
34. *Passiflora foetida* (v)
35. *Clotaria* sp. (h)
36. *Polygonum polystachium* (v)
37. *Paederia scandens* (v)
38. *Baccharis salicifolia* (h)
39. *Erigeron sumatrensis* (h)
40. *Eupatorium multiflorum* (h)

Figure 3 For vascular plant species of < 1 m height, the correlation of (a) log10-transformed frequency between bare ground and herbaceous patches, (b) log10-transformed per cent mean cover between bare ground and herbaceous patches, (c) log10-transformed frequency between herbaceous patches and tree patches, and (d) log10-transformed per cent mean cover between herbaceous patches and tree patches. Each point number represents a different species. Plant types are indicated by letters: herbs (h), grasses (g), forbs (fo), ferns (fe), vines (v), shrub seedlings (s) and tree seedlings (t)

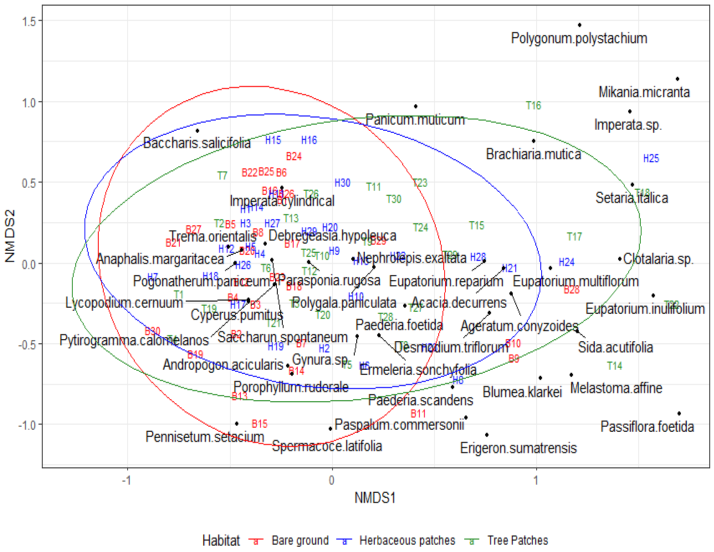


Figure 4 Non-Metric Multidimensional Scaling (NMDS) of the three habitats for ground vascular plant species with < 1 m height. B1–B30 are bare ground quadrats, H1–H30 are herbaceous quadrats and T1–T30 are tree patches quadrats

species in term of frequency and mean cover were *Pytirogramma calomelanos*, *Imperata cylindrica*, *Eupatorium riparium*, *Pogonatherum paniceum* and *Anaphalis margaritacea*. *P. calomelanos*, a fern species had the highest total mean cover among all species at 20.4 % and *I. cylindrica* and *E. riparium*, a grass and forb species for the second at 16.2 % and third at 15.9 % highest mean cover, respectively. Thus, just three species represented over half the mean vegetation cover (52.4 %) from all ground vascular plant species found in the three habitats.

Dominant tree species in the tree patch habitat

In the circular quadrats, the tree species *Parasponia parviflora* had the highest frequency followed by *Trema orientalis* and *Acacia decurrens* (Figure 5a) where *A. decurrens* had the largest though most variable total basal area (2.15 cm^2 m^{-2}) (Figure 5b). The shrub species *Debregeasia hypoleuca*, *Eupatorium inulifolium* and *Melastoma affine* had lower total basal area. Three tree species, *Trema tormensa*, *Falcataria mollucana* and *Vernonia amygdalina* were only found in the circular quadrats.

DISCUSSION

Ground vascular plant cover was least on bare ground. On a surface of pyroclastic deposits, the amount of rock cover inevitably regulated the available space for colonisation (Elias & Dias 2007). However, even on a bare surface there was usually a heterogeneity of microsites, some of which were favorable for and capable of supporting first colonists (Mori et al. 2008). In the most severely damaged area on Mount Merapi, rock cover occupied just over half the area and increasing rock cover was associated with strong abiotic filters that combined drought, extreme temperature and high wind speed and also poor nutrient availability were factors that inhibited seed germination

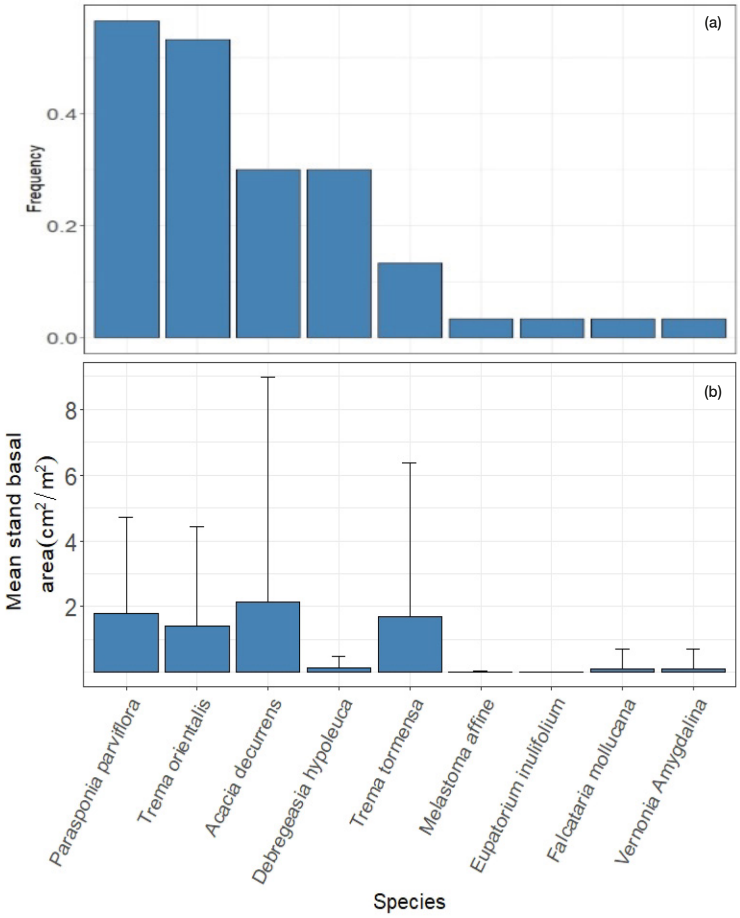


Figure 5 (a) frequency and (b) basal area among vascular plant species with ≥ 1 m height in circular quadrats of tree patches

and plant development (Lawrence et al. 2006, Tsuyuzaki et al. 1997). Nevertheless, out of the 50% of the area which remained free of rock cover, about half was now occupied by plant cover seven years after the eruption.

There was no significant difference in plant cover between the herbaceous and tree patches. The reduction in rock cover in these patches compared to bare ground was by 40% and 50% in the herbaceous and tree patches respectively. The observation showed that there was more space for colonisation and plant development, greater facilitation of root development as well would have led to a reduction in plant mortality (del Moral & Bliss 1993). Other factors might also have contributed to the higher plant cover. Even with random seed dispersal, contrasting habitats within a discrete area did not necessarily receive seed rain evenly and a higher receipt of seed in these patches than on bare ground might have enhanced its rate of germination and site occupancy (Wood & del Moral 2000). Together these factors led to an approximate doubling to tripling of plant cover in the herbaceous and tree patches compared to bare ground.

Seven years after the eruption, species richness and diversity were the same in all three habitats. This suggested that in spite of the contrasting levels of rock cover, surface heterogeneity showed that that there were safe microsites and substrate available in each habitat to support the successful germination and development of the potential colonists. Similar species richness and diversity also indicated that the potential colonists were adapted to habitats with high rock cover (Wood & del Moral 2000). The physical amelioration of the pyroclastic materials was associated with the number of safe microsites increasing over time and happened faster in areas with a lower proportion of rock cover (del Moral & Walker 2011). Consequently, although there was commonality of species richness and diversity among habitats, the rate of plant development would have been able to increase as the level of rock cover decreased.

Twenty-two species were common to all habitats and three species such as *I. cylindrica*, *P. calomelanos* and *E. riparium* accounted for at least 48 % on bare ground and on average 52.4% of plant cover. *Imperata cylindrica* and *P. calomelanos* also had high frequency of 0.7 and 0.6, respectively and were considered well-adapted for growing in volcanic deposits and under low nutrient supply (Tagawa et al. 1985, van Steenis 2010, Mani 2011, Sutomo 2018) and to a wide range of temperature, humidity, altitude and slope (Afrianto et al. 2016). *Eupatorium riparium* was commonly found in older volcanic deposits in the Mount Merapi National Park dating back to 1997 (Afrianto et al. 2020, Susantyo 2011, Sutomo 2018) indicated that this species persisted into later successional phases (Sutomo 2018). In the tree patches, *E. riparium* had the highest mean cover, possibly associated with it having a positive association with *A. decurrens* (Afrianto et al. 2016), and its frequency increased from bare ground (0.13) to tree patches (0.4). Competition from and dominance by successful species could lead to later reductions in species richness and diversity as well as reducing space for later colonists (Garcia-Romero et al. 2015, Lawrence et al. 2006, del Moral & Walker 2011). Conversely, species richness and diversity could remain unchanged for long periods as happened for 10 years after an eruption of Mount Usu in Japan (Tsuyuzaki 1991). The eruption on Mount Merapi in the longer term remained to be investigated.

The mean species richness of around 6 and diversity of around 1.3 were low in all habitats. The relatively harsh environment associated with an extensive deposition of new volcanic deposits created conditions where the pyroclastic materials could easily erode. The rate of erodibility was around 0.6 and resulted in low surface stability and mud-flow during heavy rainfall (Faizah & Mardiatno 2012, Aisyah & Purnamawati 2012) on Mount Merapi. These conditions inhibited the development of root systems in many plant species while others such as *Eupatorium* spp. were well-adapted to erosive surfaces (van Steenis 2010). For similar reasons, low species richness of only four species with low diversity were also found on a pumice plain area dominated by pyroclastic materials six years after the eruption of Mount St. Helens (del Moral et al. 2005). In the case of Mout Merapi, there were some evidences that species richness and diversity could increase over time on highly erosive surfaces, indicating that the environment is becoming more stable (Sutomo et al. 2015). However, the relationships between ground stability and species richness and diversity and these changes with time remained unclear.

In the circular quadrats on the tree patch habitat, there were nine species with heights >1 m and four tree species had the highest mean basal areas around 2 cm^2 m^{-2}. *Acacia decurrens*, an exotic and invasive species was commonly found on Mt. Merapi (Afrianto et al. 2017, Gunawan et al. 2015, Sulfiantono 2012). However, in the 1 m^2 habitat patches, *P. parviflora* a native species was present at lower frequency and this species was also highly dominant six years after the eruption on Mount Kelud, East Java in 1966 (van Steenis 2010). The allelopathic properties of *A. decurrens* (Sinung 2016) might have contributed to its lower frequency (Sinung et al. 2016). Other *Acacias* species such as *Acacia mangium*, *A. auriculiformis* and *A. nilotica* also inhibited the germination and growth of several herbaceous species and crops (Ismail & Metali 2014) while other herbaceous species which were insensitive to allelopathic substances (Strandberg & Strandberg 2000). Although abiotic filters were considered to have a greater effect than biotic filters on frequency during primary succession (Lawrence et al. 2006), it appeared that allelopathy had contributed to the low frequency of *A. decurrens* seedlings compared to other potential tree colonists.

Although the frequency of *P. parviflora* and *T. orientalis* was about double that of *A. decurrens* across the study area, *A. decurrens* had the greater mean total basal area in the circular quadrats, where a very high level of variation in this landscape which might be related to the heterogeneity of its topography. Quadrats on the eastern side were better protected from pyroclastic flow. The protection resulted in fewer rocks and boulders and accelerated successional growth of early colonists (Elias & Dias 2007) and these quadrats were associated with larger clumps of *A. decurrens*. Conversely, *P. parviflora* and *T. orientalis* were more evenly distributed and well-represented on the western and northern side which proportionately had more rocks and boulders. Both species were considered as drought-tolerant pioneer species in lava deposits, solidified lava flow and bare denuded mountain soils (Goodale et al. 2012, Setyawati & Ashari 2017). Interestingly, *P. parviflora* was also a non-leguminous species forming symbiotic relationship with nitrogen-fixing bacteria (Dommergues & Diem 1982). Two of three tree seedling species, *T. tormensa* and *V. amygdalina*, were not recorded in the 1 m^2 quadrats were found only as trees in circular quadrats on the eastern side where their relatively high basal area and low frequency suggest that they had survived the eruption. This study provided supporting evidence that the degree of shelter from pyroclastic impacts needed to be carefully considered when examining succession process following a volcanic eruption.

CONCLUSION

Mount Merapi area was most severely damaged by pyroclastic deposits in 2010, our results did not support the hypothesis that the presence of tree canopies would promote a higher cover rate of ground vascular plants and tree canopies were also not associated with lower species richness. However, the tree patches did have the highest mean ground plant cover and suggested that these developing canopies might be responsible for promoting the highest plant cover in the longer term. As other studies had shown that developing tree canopies following a volcanic event, species associated with higher rates of establishment were of *Salix reinii* in Japan (Endo et al. 2001) and *A. decurrens* on Mt Merapi (Ramadhan et al. 2020) while the survival and growth of *Larix kaempferi* and *Schima wallichii* were both moderate shade-tolerant species, respectively (Lawson & Michler 2014). Seven years after the eruption, the development rate of the primary succession was such that opportunities for potential colonists were similar across the study area. In the longer term, conditions might also change where each habitat was dominated by five species; *I. cylindrica*, *P. calomelanos*, *E. riparium*, *P. paniceum* and *A. margaricacea* which the first three species were dominant in half the plant cover in all habitats. Dominance by *A. decurrens* was previously found on Mount Merapi (Afrianto et al. 2020, Afrianto et al. 2017, Gunawan et al. 2015, Sulfiantono 2012) did not apply to our study site. *Acacia decurrens* currently had lower frequency than two other tree species, *P. palviflora* and *T. orientalis* where both genus were actually often found in disturbed and open habitats (Mangopang 2016, Marler & del Moral 2011, Widiyatno et al. 2017). In summary, this study could provide the first insights during primary succession and points out on future happenings. However, careful recording of environment dictating successional stages needed further investigation.

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