



Plants colonizing volcanic deposits: root adaptations and effects on rhizosphere microorganisms

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Abstract

Background Volcanic activity alters earth surfaces creating environments where new ecosystems can be established. Just some plants are able to colonize this kind of environment. Low availability of nitrogen and phosphorus have been widely considered to restrict plant colonization on volcanic deposits worldwide. Root adaptations such as associations with mycorrhizal fungi, associations with nitrogen-fixing microorganisms, and root structures specialized to exude carboxylates, comprise mechanisms plants use to grow on low nutrient availability conditions, such as volcanic ash or tephra.

Scope Most of the studies carried out on volcanic deposit colonizing plants have been focused on above-ground features such as plant survival, growth, and plant-plant interactions. Belowground processes, involving root activity and the rhizosphere, have been less studied. Plants that colonize different volcanically

affected areas in the world, the effect on microorganisms associated mainly with the rhizosphere of these plants, microbe-microbe and microbe-plant interactions are reviewed here.

Conclusions Plant-to-plant interactions, involving the different kind of roots adaptations, may be complementary to facilitate each other and positively influence the ecosystem recovery of volcanic deposits. At rhizosphere level, particular microbial communities can be recruited with specific beneficial functions (nitrogen-fixing, plant promoting growth, etc.) that improve soil development and plant colonization of volcanic deposits. New aspects such as the ability of mycorrhizal fungi to recruit bacteria able to solubilize phosphorus, and the presence of endophytes and their role in promoting the growth of early plant colonizers of volcanic are also discussed.

Keywords Volcanic deposits · Colonizer plants · Mycorrhizae · N-fixing nodules · Cluster roots · Exuded carboxylates · Rhizosphere

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Introduction

Volcanic activity has a pronounced influence on ecosystems, affecting the natural history of earth through geological time by modifying the composition of the atmosphere, climate, and geochemistry of soils (Deligne and Sigurdsson 2015). The effects of volcanic eruptions on the regolith are quite variable, depending on the physicochemical nature and volume of the deposited material. Volcanic material may cover large areas, such

as hundreds of km² for pyroclastic flows or thousands of km² for tephra, and its depth varies depending on distance from volcanic sources, i.e. shallower at greater distances (centimeters to meters) (del Moral and Grishin 1999). The material from volcanic eruptions, such as lava flows and ash or tephra deposits, creates clean land surfaces on which ecosystem development processes such as plant colonization and soil formation begin (Fig. 1a; Fig. 2a). Such areas thus affected are referred to as “volcanic deserts” (Yoshitake et al. 2013).

Tephra is used to describe all materials released from volcanic eruptions, regardless of their type, size, and shape, however, strictly tephra corresponds to ashes that are less than 2 mm in diameter (Dahlgren et al. 2004). The type and abundance of primary minerals in tephra depends on the volcano, but usually includes silica, quartz, plagioclase, pyroxenes, hornblende, biotite, olivine (Dahlgren et al. 2004; Arnalds 2013). As it weathers, tephra develops into non-crystalline and poorly crystalline minerals and oxides, with a large specific surface area and high reactivity, which lead to the complexation, stabilization and physical protection of organic matter. In this way, volcanic eruptions lead to productive soils. In fact, soils derived from volcanic ash or tephra, denominated Andisols, have many distinctive properties that are rarely found in soils derived from other parent materials. Some unique properties of these volcanically derived soils include variable charge, high water and phosphate retention, low bulk density, high friability, highly stable soil aggregates, and excellent tilth. Andisols are recognized as fertile soils with a high capacity to accumulate carbon (Dahlgren et al. 2004; Arnalds 2013). Volcanic ash could severely affect the ecosystem development, which is critical for agricultural areas and farmers and is particularly important in areas such as Indonesia, Philippines, Japan, New Zealand, Hawaii and Pacific Islands, the Caribbean islands, Iceland, and South America. Tephra can store moisture, which enables blue-green algae to colonize the bare surface layer, which is followed by the development of layers of lichen, and finally, the colonization of vascular plants (Fiantis et al. 2019).

Both ecosystem development and recovery are influenced by several abiotic parameters such as drought, hydric conditions, soil toxicity, salinity, pH values, low temperatures, substrate stability, and air pollution, among other factors (del Moral et al. 2005). In this review we will focus on plant establishment, as it has been recognized as the most

critical phase in ecosystem recovery (Walker and del Moral 2003; del Moral et al. 2005), and the strategies they use to overcome nutrient limitation. The early colonizers, also called “founders” or “pioneer plant species”, generally have certain characteristics that allow them to grow and persist in harsh conditions (Fig. 1b, c and d; Fig. 2b and c). Some of these characteristics include seed dispersal, nutrient mobilization and acquisition traits, and the ability to obtain water in the heterogeneously sized pyroclastic materials. In contrast, late colonizer species are usually better at competing for space and resources than early colonizer plants (Walker and del Moral 2003). Initial colonization is usually limited by unfavorable local environmental conditions, seed availability, or lack of facilitating species (del Moral et al. 2005; Walker and del Moral 2003). Among the nutritional constraints, phosphorus (P) and nitrogen (N) limitations largely impede plant growth on volcanic deposits (Shoji and Takahashi 2002; Vitousek et al. 2010). As plant succession advances, abiotic conditions improve (Buma et al. 2017) and species interactions such as competition, increasingly influence further establishment (Walker and del Moral 2003). Since founders have a large effect on subsequent plant community development, the identification of processes involved in early colonization would allow for a better understanding of not only the nature of plant community assembly (Buma et al. 2017), but also how to best manage the recovery of ecosystems affected by volcanic activity (Walker and del Moral 2003).

Early colonizing plants can promote favorable conditions on bare volcanic substrate for the establishment of other species, allowing for primary succession (Titus and Tsuyuzaki 2003). In this regard, positive plant–plant interactions, or facilitation, drive community composition and biological diversity (McIntire and Fajardo 2014). Positive interactions are defined as interspecific relationships that increase the fitness of at least one species, and these kinds of interactions affect plant community composition, dynamics, and maintenance of diversity in many ecosystems (Titus and Tsuyuzaki 2003). Plant canopies improve microclimatic conditions that stimulate productivity and allow the recruitment of species that are less adapted to the adverse local conditions, increasing plant diversity (Cavieres et al. 2014). These kinds of interactions identify “facilitators” as early colonizing plants with a positive effect on

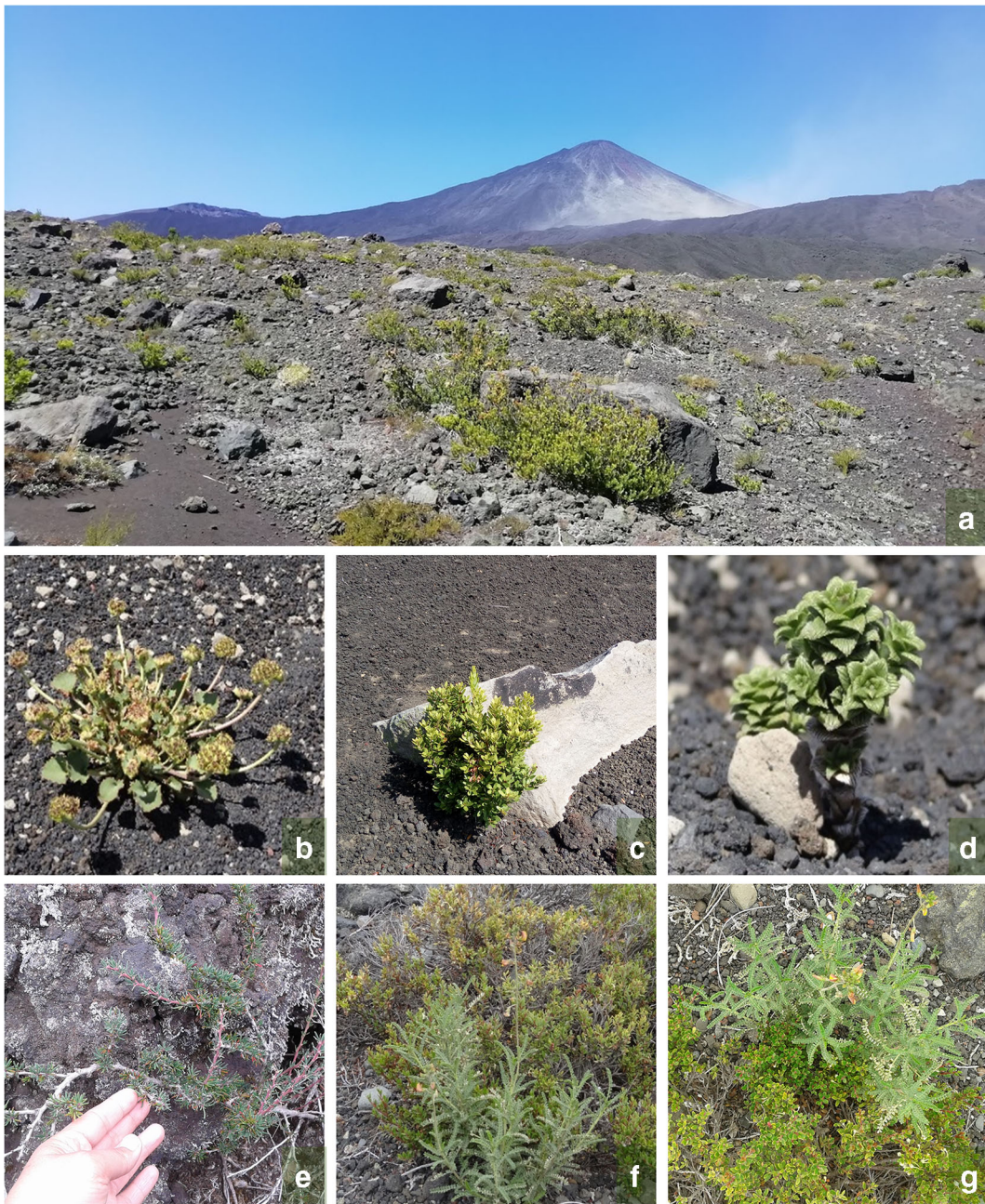


Fig. 1 Plant colonization of ecosystems on volcanic deposits. **(a)** General view of a volcanic desert in which early colonization is underway, near Antuco volcano, Chile (1200 m.a.s.l.), please note different sized pyroclastic andesites. Early plant colonizers or founders growing alone: **(b)** *Pozoa volcanica*. **(c)** *Orites*

myrtoidea. **(d)** *Nassauvia lagascae*. **(e)** *Berberis* sp.; or growing combined (probably in a positive interaction), **(f)** *Adesmia emarginata* and *Maytenus* sp. **(g)** *Adesmia emarginata* and *Gaultheria pumila*

neighboring plant species and promote the recruitment of other plants (i.e. beneficiaries) under their canopies (Cavieres et al. 2014). Facilitator species are also often referred to as “nurse plants,” “foundation species,”

“ecosystem engineers” or “ecosystem constructors”, as they can modulate environmental forces and change the habitat conditions to favor the establishment of other species (Fig. 1e, f and g; Fig. 2d) (Jones et al. 1997).

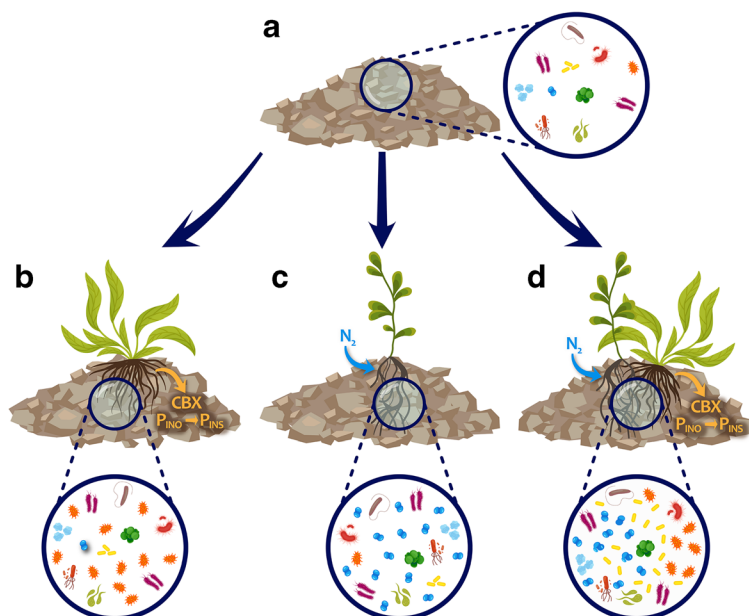


Fig. 2 Interactions between plant, microorganisms and soil during plant colonization on a recent volcanic deposit. The upper part (a) represents a “volcanic desert”, where volcanic deposits with heterogeneous granulometry provide a habitat for initial microbial populations, with low abundance but relatively high diversity (each colored symbol represents different microbial taxa in the soil). The bottom part shows three different scenarios able to develop over time. (b) and (c) represent pioneer or founder plants. In (b) a colonizing plant begins to grow in the volcanic substrate and through CBX exudation, possibly involving CR, selects for specific microbial populations (orange fimbriated taxon) in the rhizosphere. At the same time, CBX release the unavailable insoluble phosphorus (P_{INO}) from soil to a form that plant roots can absorb (P_{INS}). (c) shows another colonizing plant with N-fixing

structures and selecting for other specific microbial populations (light-blue diplococci) in their rhizosphere. (d) shows two plant species with different root adaptations able to complement their nutritional strategies when grown together, despite one of them acting as a nurse. Both plants could obtain benefits from the other in a belowground facilitation processes increasing access to forms of P and N suitable for root absorption. This facilitation could also be related to the microbial communities both plants select for in their rhizosphere. In addition to the bacteria that plants individually select, the new environment generated in the common rhizosphere selects a new type of microorganism (yellow bacilli). The selected microorganisms in the rhizosphere could promote plant growth

Most studies carried out on colonizer plants of volcanic substrates have focused on aboveground changes that improve survival, growth, and facilitation (Buma et al. 2017; Cavieres et al. 2014; del Moral and Lacher 2005; Walker and del Moral 2003). However, belowground processes that occur in the rhizospheres have received little attention. Nutritional constraints, mainly P and N availability, are major factors contributing to the low number of plant species that are able to successfully colonize and survive on volcanic substrates (Shoji and Takahashi 2002; Vitousek et al. 2010). Three root adaptations have been described in plants as mechanisms to obtain nutrients in volcanic deposits. These adaptations include two kinds of mutualistic associations with microorganisms such as mycorrhizal fungi (Genre et al. 2020) and the development of nodules with N_2 -fixing microorganisms (del Moral and Rozzell 2005). A third mechanism is the formation of root

structures that exude P-mobilizing carboxylates, named cluster roots (Zúñiga-Feest et al. 2014). All of these adaptations can modify the rhizosphere, recruiting not only other plants but also microorganisms, which in turn can benefit the plant or chemically modify the soil. Because these processes have been described in several ecosystems, in this review we will focus on these characteristics in a volcanic context.

The information reviewed here will focus on ecosystems affected by volcanic deposits, mainly ash or tephra, in places near volcanoes but not in the volcano itself. We present information related to mechanisms founder plants employ to overcome nutrient limitation as well as the interactions they establish with other plants and microorganisms. The ecosystems reviewed involve long-term studies of volcanic environments, such as those associated with Mount Saint Helens (USA), Fuji (Japan), and Hudson (Chile) volcanoes (Table 1), which

involve effusive depositions. These volcanoes are still active; although some of them haven't erupted recently. The plant communities we mention are far away from the crater and fumaroles, as these environments are characterized by extreme abiotic stress (Baillie et al. 2016). The colonizer plants mentioned in this review, their locations, and the mechanisms described to grow in volcanic deposits are listed in Table 1. This information is relevant for understanding soil development processes especially in volcanically derived soils, soil quality improvement to recover lands for agricultural purposes, plant conservation, and the design of restoration programs.

Root adaptations of colonizer plants of volcanic soils

Mycorrhization

Mycorrhizas are ubiquitous mutualistic symbioses established between plant roots and soil fungi. Across the intimate cellular contact between the two symbiotic partners, mycorrhizal fungi receive fixed carbon from their photosynthetic hosts in exchange for mineral nutrients, such as P & N, with a positive impact on plant growth (Genre et al. 2020; Jansa et al. 2013). Mycorrhization enables plants to acquire P, mainly from organic sources, in poor soils and is important for sustaining plant growth in harsh environments (Kikvidze et al. 2010).

In volcanic deserts, arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (ECM) are the most common fungal symbionts involved in colonization of pioneer plants (Kikvidze et al. 2010). In Japan, AMF and ECM were described in Mount Fuji and they may take part in primary succession depending on the taxa of the host pioneer plant (Table 1; Obase et al. 2007). Woody pioneer species are usually associated with AMF or ECM and some degree of host-specificity at the family level has been observed (Nara 2006; Obase et al. 2007). However, the role of AMF in the early stages of succession in volcanic areas is not clear. Some studies have demonstrated that AMF are dominant in volcanic deserts of Mount Fuji (Fujiyoshi et al. 2005), while ECM were dominant in Mount Usu, Japan (Obase et al. 2007). On Mount St. Helens (USA), AMF have not been found to be important for the growth of facultative mycorrhizal plants; however, in a greenhouse experiment, symbiosis with AMF improved the

competitive ability of these plants over nonmycorrhizal plants (Titus and del Moral 1998). Another discrepancy is whether or not non-woody pioneer species are mycorrhizal. In this regard, *Polygonum cuspidatum* and *P. weyrichii* (Polygonaceae), prominent pioneer species in volcanic deserts of Japan, have been reported as mycorrhizal, but with low frequency (<5% of fungal root colonization) (Fujiyoshi et al. 2005). However, in another study, only *P. cuspidatum* and not *P. weyrichii* was found to be mycorrhizal with high frequency (17–25%) (Table 1; Wu et al. 2004). Thus, it is not clear if these colonizing species are mycorrhiza-dependent or not, and whether environmental conditions could influence mycorrhization (Fujiyoshi et al. 2005; Wu et al. 2004). However, in Mount Fuji, AMF are more abundant and have greater species richness at lower altitudes where edaphic conditions improve, as soil becomes more fertile with the development of plant community structure and productivity during primary succession, leading to greater plant establishment, and additional habitats and more colonization opportunities for new AMF species (Wu et al. 2007). The same studies indicate that the plant community can influence the composition of AMF community (Wu et al. 2004, 2007). Host plant identity was also found to be the main factor driving AMF community composition in New Zealand during ecosystem development in a long-term soil chronosequence (Martínez-García et al. 2015).

Salix reinii (Salicaceae), alpine dwarf willow, is one of the first ECM plants to colonize volcanic substrates in the volcanic deserts of Mount Fuji (Table 1; Nara et al. 2003a) and Mount Koma (Tsuyuzaki et al. 2012), both in Japan. On Mount Fuji, pioneer *Salix* shrubs facilitate the subsequent establishment of conspecific seedlings by providing ECM fungal symbionts (Nara et al. 2003b). ECM fungi of established *Salix* may also aid in secondary colonization of tree species, and therefore could facilitate tree succession in the volcanic deserts of Mount Fuji (Nara and Hogetsu 2004) and Mount Koma (Kwon and Tsuyuzaki 2016). Despite these reports, *S. reinii* has not been claimed as an ecosystem engineer.

Mycorrhizal plants colonizing volcanic soils have been described in southern regions of South America. Among them, the “cushion plants” (a compact, low-growing, mat-forming plant) in the high Chilean Andes act as colonizers (Cavieres et al. 2006). Moreover, the favorable microclimatic conditions generated by cushion plants can have a nurse effect that benefits other plant species, but they also benefit from the well-

Table 1 Plant colonizers mentioned in this review and their mechanisms to grow in volcanic deposits

Mechanisms	Plant specie	Location	Details	References
<i>Mycorrhizas</i>				
Arbuscular Mycorrhiza	<i>Azorella madreponica</i> (Apiaceae)	Andes Mountains, Chile	a nurse cushion plant in an Andean alpine environment	Casanova-Katny et al. 2011.
	<i>Cirsium purpureum</i> (Asteraceae)	Mount Fuji, Japan	secondary dominant species with higher percentage of AM colonization	Wu et al. 2004.
	<i>Polygonum cuspidatum</i> (Polygonaceae)	Mount Fuji, Japan	pioneer species in volcanic deserts of Japan, low frequency of AM colonization	Wu et al. 2004.
Ectomycorrhiza	<i>Larix kaempferi</i> (Pinaceae)	Mount Koma, Japan	develop ECM relationships with host-specific <i>Suillus</i> fungal species	Nara 2006.
	<i>Salix reinii</i> (Salicaceae)	Mount Fuji, Japan	colonized by various non-host-specific, generalist ectomycorrhizal fungi	Nara et al. 2003.
<i>Nitrogen fixing</i>				
Actinorhizal nodulation	<i>Alnus viridis</i> (Betulaceae)	Mount St. Helen, USA	slow rate of spread from nearby seed sources explained by low densities of symbionts	Seeds and Bishop 2009.
Rhizobium nodulation	<i>Lupinus lepidus</i> (Fabaceae)	Mount St. Helen, USA	a legume able to establish on pyroclastic substrate and claimed as ecosystem engineer	Halvorson et al. 1991, del Moral and Rozzell 2005.
<i>Carboxylate exudation</i>				
Cluster root mediated exudation	<i>Embotrium coccineum</i> (Proteaceae)	Hudson Volcano and Torres del Paine, Chile	volcanic soil colonizer, claimed as ecosystem engineer	Zuñiga-Feest et al. 2014.
Root exudation	<i>Acacia integerrima</i> (Rosaceae)	Hudson Volcano, Chile	a nurse plant able to exudate carboxylic acids	Sanchez-Salazar, et al. in prep.
	<i>Tithonia diversicola</i> (Asteraceae)	Andes Mountains, Venezuela	the shrub exudate oxalate induced by aluminum on hydropony	Olivares et al. 2002.
<i>Microbial Endophyte</i>				
Fungal endophyte	<i>Laretia acutis</i> (Apiaceae)	Valle Nevado, Chile	fungal endophytes increase survival and growth of the plant and could be a mechanism for plant-plant facilitation	Molina-Montenegro et al. 2015.
Bacterial endophyte	<i>Zea nicaraguensis</i> (Poaceae)	San Cristobal Volcano, Nicaragua	organic acid released from roots when colonized with <i>Enterobacter asburiae</i>	Shehata et al. 2017

developed mycorrhizal networks present there. This was demonstrated for *Azorella madreporica* cushions at high-elevation sites in central Chile (Table 1; Casanova-Katny et al. 2011).

Recent research indicates that AMF can interact with bacteria to develop a highly-specialized microbial community on hyphal surfaces, and it is thought that these communities provide important functions such as accessing recalcitrant forms of nutrients, such glomalin, atmospheric N and P fixed in the soil (Jansa et al. 2013). In this regard, the bacterium belonging to the genus *Pseudomonas* in association with AMF *Rhizophagus irregularis* hyphae were reported to interact with each other and positively affect plant growth (Ordoñez et al. 2016). Recently, it was shown that fructose, exuded by *Rhizophagus irregularis*, stimulated the expression of phosphatase genes in the bacterium as well as the rate of phosphatase release into the growth medium by regulating its protein secretory system. Phosphatase activity subsequently increased, promoting the mineralization of organic phosphorus (i.e., phytate) into inorganic phosphorus, and the processes involved in phosphorus uptake by the AMF were simultaneously stimulated (Zhang et al. 2018). Because P is a limiting nutrient in volcanic deposits due to its sorption to minerals, it may be relevant to investigate the presence of phosphate solubilizing bacteria interactions with AMF associated with colonizing plants.

Nitrogen-fixing capability

Biological N-fixation (BNF) plays a key role in the onset of pedogenesis and ecosystem development after major disturbances or on denuded surfaces when soil C and N stocks are greatly depleted or exhausted and rock-derived elements may be available (Halvorson and Smith 2008; Walker and Syers 1976). BNF symbioses include two categories: (i) actinorhizal plants, corresponding to angiosperms in symbiosis with N-fixing actinobacteria of the genus *Frankia* (Schwencke and Carú 2001); and (ii) legumes, such as lupine species, which have the ability to fix N in a symbiosis with rhizobia (del Moral and Rozzell 2005). However, BNF is energetically expensive, and it has a high P demand associated with ribosomal RNA, which is mainly required for nitrogenase turnover (Raven 2012).

On Mount St. Helens (USA), large actinorhizal shrubs, such as alders (*Alnus* spp., Betulaceae), colonize pumice, a volcanic substrate. Sitka alder (*Alnus viridis*) and red alder (*Alnus rubra*) rapidly colonize pumice

(Dale et al. 2005), but further colonization is slow and limited to patches (Table 1; Seeds and Bishop 2009). The availability of *Frankia* and its compatibility with the host may limit the successful formation of rhizothamnia capable of N fixation (Markham and Chanway 1999), and in some cases *Frankia* forms rhizothamnia that do not fix N (Wolters et al. 1999). Moreover, N and P addition experiments and soil assays indicate that N rather than P limits the growth of most vascular plants on Mount St. Helens (Halvorson and Smith 2008). However, the extremely low densities of suitable symbionts in sparsely-vegetated primary successional areas on Mount St. Helens may explain the surprisingly slow spread of alders from nearby seed sources (Seeds and Bishop 2009). Interestingly, red alder roots are also colonized by AMF and ECM, both of which assist in P acquisition and often interact synergistically with the *Frankia*–alder symbiosis (Molina et al. 1994), serving as complementary mechanisms in volcanic deposit colonization. It is important to note that some actinorhizal species, such as alder, produce cluster roots (Hurd and Schwintzer 1996), and the effect of the carboxylate exudation through these structures was recently proposed to be especially important when plants are grown on bed rock (Lambers et al. 2019).

Lupins are major early plant colonizers of harsh environments, mainly due to their ability to fix N symbiotically and to generate large amounts of organic matter (del Moral and Rozzell 2005). They also release carboxylates, and many produce cluster roots, making them efficient P mobilizers (Lambers et al. 2013). In fact, *Lupinus lepidus* and *L. latifolius* (Fabaceae) were among the first plant colonizers on Mount St. Helens pyroclastic deposits (Table 1; del Moral et al. 2005). Lupins influence the rate and pattern of vegetative succession through physical and biological amelioration of bare sites and subsequent interactions with early colonizer plants. Lupins also affect plant succession belowground as they can ameliorate the chemical and nutrient constitution of soil, affecting the quantity and quality of substrates, which in turn can affect the diversity, activity and quantity of soil microbiota (Halvorson and Smith 2008; Ibekwe et al. 2007). *Lupinus lepidus* has been recognized as an ecosystem engineer because it is able to link above and belowground processes, influencing plant succession and ecosystem development, thus increasing fertility of the pyroclastic deposits (del Moral and Rozzell 2005). However, to our knowledge, rhizobacteria involved in nodulation and BNF have

not been identified in *Lupinus* species able to colonize volcanic deposits. Their characterization could allow identification of specific bacterial traits for survival and their ecological function in those environments.

Cluster roots and carboxylate exudation

Cluster roots (CR) are ephemeral structures developed on various lateral roots of the root system that exude carboxylates (CBX), *i.e.*, the conjugate base of a carboxylic acid derived from the tricarboxylic acid cycle (such as citric, malic, and oxalic acid), and enzymes with acid phosphomonoesterase (phosphatase) enzymes. Cluster roots are functionally linked with an efficient chemical mobilization of sparingly soluble soil P sources (Zúñiga-Feest et al. 2014). Cluster root formation has been widely reported in the Proteaceae family, but it is also present in some species of other families found around the world such as Fabaceae and Casuarinaceae (Shane and Lambers 2005). In all of the studied Proteaceae species, the development of CR occurs without intervention of microorganisms; in addition, most are nonmycorrhizal and naturally occur in soils with low P availability (Delgado et al. 2014).

Carboxylates solubilize inorganic P forms, particularly those fractions chemically associated with oxides and hydroxides of aluminum or iron, and the capacity to dissolve P depends on the concentration and composition of the exudates in the soil close to the roots (Lambers et al. 2008). Additionally, CBX influence both nutrient availability and plant-microbe interactions, because microorganisms consume CBX as a source of energy (Bais et al. 2006; Sasse et al. 2018). However, as part of root exudation, CBX may play a profoundly important role in selecting and recruiting beneficial bacteria, beyond providing a carbon source. In fact, CBX, such as malate, have been postulated to act as recruitment signals for beneficial microorganisms (Rudrappa et al. 2008), as observed for *Arabidopsis thaliana* when malate recruited beneficial *Bacillus subtilis* to promote binding and biofilm formation on their roots (Chen et al. 2012). Several studies carried out on different rhizobacteria have identified plant signals that are central to colonization-relevant chemotaxis, as well as the cognate chemoreceptor. This was the case for chemoreceptors McpB, McpC, and TlpC, which mediated chemotaxis of the plant-associated strain *B. subtilis* to *A. thaliana* root exudates (Allard-Massicotte et al. 2016). In *Ralstonia pseudosolanacearum*, McpM-

mediated chemotaxis to L-malate, secreted by tomato roots, was essential for the infection process (Hida et al. 2015). Recently, it was demonstrated that chemotaxis to cucumber root exudates (such as malic, fumaric, acids) was essential for *Bacillus velezensis* SQR9 to efficiently colonize cucumber roots (Feng et al. 2018).

Proteaceae species are common colonizers of volcanic deposits in Chile and Argentina (Alberdi et al. 2009). For instance, *Embothrium coccineum* colonizes Hudson volcano ash deposits and grows on young metamorphic rocky substrates in Torres del Paine (Table 1; Piper et al. 2019; Zúñiga-Feest et al. 2014). Additionally, *Orites myrtoidea* is one of the few shrubs able to grow at high elevations on andesitic and dacitic lava flows in central Chile that are nearly devoid of soil (Pfanzelt et al. 2008). The prevalence of Proteaceae species in early successional stages has been related to their carboxylate exudation mediated by CR (Lambers et al. 2012; Piper et al. 2013; Zúñiga-Feest et al. 2015). The availability of soil nutrients influences CR formation and carboxylate exudation by roots of *E. coccineum* and *O. myrtoidea* seedlings. In fact, both species show CR formation more frequently in recent volcanic substrates than when growing in fertile, high-nutrient soil (Ávila-Valdés et al. 2019). Moreover, in *E. coccineum* seedlings, the ratio of CR to total plant biomass varies depending on the substrate (Zúñiga-Feest et al. 2010). Additionally, allocation to CR production increases when seedlings are grown in infertile natural conditions in Patagonia (Zúñiga-Feest et al. 2014).

It has been proposed that Proteaceae species act as ecosystem engineers due to their low remobilization of nutrients from senescing leaves which leads to a high nutrients concentration in leaf litter (Lambers et al. 2012); therefore, these plants may act as nurse species. Delgado et al. (2015) reported an increase in more labile P forms) in the rhizosphere soil around CR of *E. coccineum* compared with the P availability of bulk soil. Recently, *E. coccineum* and *O. myrtoidea* (Proteaceae), have been shown to increase P availability in the rhizosphere by at least 50% and up to 120%, respectively, when grow on volcanic deposits (Ávila-Valdés et al. 2019). Moreover, higher phosphatase activity was detected for *E. coccineum* grown on pumice than mixed organic substrate (Ávila-Valdés et al. 2019). The presence of CR-bearing species that can solubilize P may provide nutritional benefits to neighboring plants or soil microorganisms, as the root activity of these plants could increase available forms of P. A strategy

like this has been widely described for agricultural purposes, such as the intercropping between cereals and legumes (Li et al. 2014; Wang and Lambers 2020). Therefore, combining plants with different root adaptations could increase growth in volcanic deposits as a strategy to recover this kind of environment.

Some species of the genus *Lupinus* are also known to form CR and to exude carboxylates to solubilize P from soil (Lambers et al. 2013). This, along with their ability to symbiotically fix N, make individuals of this genus successful pioneers, invasive species, and suitable crops (Lambers et al. 2012, 2013). *Lupinus lepidus* does not form CR (Lambers et al. 2012), but the possibility that this species also enhances the availability of P in pyroclastic substrates through the release of carboxylates, directly from roots as in other plants (see below), has not yet been studied (Lambers et al. 2012, 2013). Moreover, in the case of white lupin, it has been described that CR also release flavonoids, which are involved in P acquisition both directly by mobilizing insoluble Fe-bound P and indirectly by reducing the microbial citrate mineralization and the activity of enzymes involved in organic P mineralization (Tomasi et al. 2008).

As far as we know, there are only two plant species without CR that are able to grow in volcanic substrates and to exude CBX. The first reported was *Tithonia diversifolia* (Asteraceae), Mexican sunflower, which is a very common shrub on roadsides in montane environments in the Andes with aluminum-rich soils (Table 1; Olivares et al. 2002). Volcanic soils are usually characterized by acidic pH, a chemical condition causing these soils to have high aluminum availability, which can be toxic for plants. The roots of young *T. diversifolia* were able to exude oxalate in hydroponic trials, and exudation was proportional to the aluminum concentration. Oxalate acts as an aluminum chelator in the soil and prevents aluminum toxicity (Olivares et al. 2002). The second is *Acaena integerrima* (Rosaceae), a cushion plant from Patagonia also recognized as a nurse plant (Table 1). Recently, citrate and oxalate exudation were measured for this species and found to be rapid compared to those of *E. coccineum* (Sanchez-Salazar et al. *in preparation*). To our knowledge, this is the first record of rapid CBX exudation in Rosaceae. It is unknown whether this phenomenon could occur in other cushion plants on volcanic deposits. Moreover, the exudation rate of CBX by the root system of *E. coccineum* increases when grown together with *A. integerrima* (Sanchez-Salazar et al. *in preparation*). It is as yet unknown whether this occurs in other colonizing Proteaceae.

Rhizosphere microbial communities associated with early colonizer plants on volcanic substrates

The rhizosphere is a zone with high levels of microbial activity, mainly due to the presence of a wide variety of substances secreted from root cells (known collectively as rhizodeposits) and may contain both low- and high-molecular-weight compounds such as amino acids, organic acids, phenolic compounds, simple sugars, mucilage and enzymes (Badri et al. 2009).

The establishment of interactions between plants and rhizosphere microorganisms is a highly coordinated event influenced by the host plant and the given soil characteristics. Multiple studies show that the host plant and its developmental stage significantly shape the rhizosphere microbial community (Badri et al. 2009). Microorganisms mainly perceive differences in plant host species via detection of differences in the secretory exudates of the roots (el Zahar-Haichar et al. 2014). Therefore, root exudates act as a crucial driving force for multitrophic interactions involving microorganisms and neighboring plants (Badri et al. 2009; el Zahar-Haichar et al. 2014). Moreover, soil microorganisms provide essential ecosystem services such as nutrient cycling, carbon sequestration, and soil fertility (Bardgett and van der Putten 2014). The rhizosphere bacterial community composition largely depends on the bacterial community composition of the bulk soil and the colonizer plant *Carex arenaria* (sand sedge; Cyperaceae; de Ridder-Duine et al. 2005), acts selecting a fraction from them. Additionally, soil microbes also strongly influence plant fitness, also known as plant growth-promoting rhizobacteria or PGPR, as well as the composition and diversity of plant communities (Lozano et al. 2014). Rhizosphere communities associated with nurse species can have strong facilitatory effects through a variety of mechanisms including improved nutrient mobilization and uptake, direct molecular signaling, plant defense, soil stabilization and functional complementarity of microbial symbionts (Rodríguez-Echeverría et al. 2016).

Nowadays, it is well known that root activity affects soil microbial communities, but this aspect has been scarcely studied in volcanic deserts. Because the particularities of this environment, it is important to understand these processes in order to improve soil recovery. On Mount Fuji (Japan), a substantial shift in microbial community composition has been described as the result of initial colonization by the pioneer herb *Polygonum*

cuspidatum (Polygonaceae) and subsequent colonization by *Larix kaempferi* (Pinaceae) (Yoshitake et al. 2013). Colonization by the first herbaceous pioneer plant (*P. cuspidatum*) changes the soil environment. Both the amount and quality of organic matter increase, affecting the microbial community in terms of biomass and the community-level carbon-source utilization profiles. The bacterial community composition is then altered by a subsequent invasion of the “island” by shrubs such as *L. kaempferi*. This study also shows that changes in the soil microbial community are closely related with the development of island-like plant communities and the quality of organic matter thus generated (Yoshitake et al. 2013). Along the same lines, Ibekwe et al. (2007) assessed microbial community composition and structure in pyroclastic deposits with living, dead, and no plant material on Mount St. Helens (USA). In soil, smaller and less diverse microbial communities were found compared with those in soil associated with plants. Moreover, microbial community composition was affected by (i) the proximity to lupine plants, and (ii) possibly by different plant types. Living and dead plant materials have a direct and profound impact on microbial development. A high number of *Proteobacteria* in the soils, especially in those with live lupine, indicates a dominance of this phylum near the rhizosphere and also suggest that this group may contribute most to the pioneering communities of the pyroclastic soils. *Proteobacteria* can colonize plant roots both because of its r-strategy and copiotrophic characteristics and nutrients provided through exudates (Ibekwe et al. 2007).

Even though differences can occur due to mineral composition and the degree of soil development, high-mountain ecosystems, due to their oligotrophic and harsh environmental conditions, can be considered homologous to volcanic ecosystems, especially for the volcanos we mention in this review which are located in highlands (Table 1). In the French South-Western Alps, it was found that the beta diversity of microbial communities (archaea, bacteria and fungi) was associated with the species composition of several vascular plants (Zinger et al. 2011). Also in the French Alps, the cushion pioneer plant *Silene acaulis* (Caryophyllaceae) affects microbial community structure through modifying the calcareous and siliceous bedrock soil properties, specifically by buffering soil pH and enhancing soil nutrient availability, thus acting as a selective force that counteracts the influence of the

bedrock and the resource limitations of bacterial and fungal communities (Roy et al. 2013). Similar results were found for *S. acaulis* and eleven other pioneer plant species, during early primary succession in the inner central Alps, South Tyrol (Ciccazzo et al. 2014). Thus, these studies show that in the rhizosphere of pioneer plants in high-mountain ecosystems, specific microbial communities are selected.

There are few studies focused on the diversity and function of soil microbial communities associated with CR. Specific bacterial communities associated with CR in *Leucospermum truncatum* and *Leucadendron xanthoconus* (Proteaceae) were described for The Cape region, South Africa, where three bacterial species were specifically identified in CR (Stafford et al. 2005). Acidophilous *Burkholderia* was reported as the major genus present in the rhizosphere of *L. albus* CR, able to produce siderophores and to consume carboxylates (Weisskopf et al. 2011). More recently, an abundance of Burkholderiales in the rhizosphere of P-deficient plants was described in the rhizosphere of *L. albus* CR, and a role in the degradation of different organic P fractions, such as phytate, was suggested (Wasaki et al. 2018). Under N deficiency, a high abundance of Rhizobiales and Rhodospirillales was found in the rhizosphere of CR, indicating an importance of N-fixing microorganisms (Wasaki et al. 2018). There is just one study where CR formation is linked to the presence of plant growth-promoting bacteria in the soil, for the Australian species *Viminaria juncea* (Fabaceae) and *Hakea laurina* (Proteaceae) by *Bradyrhizobium elkanii* and *Bacillus mageratum* (Lamont et al. 2015). The occurrence of phosphobacteria (phytate-mineralizing bacteria and phosphate-solubilizing bacteria) in the rhizosphere of different crops in volcanic soil (Andisol) were evaluated in southern Chile (Jorquera et al. 2008). Phosphobacteria were reduced in the rhizosphere of *Lupinus luteus* (a CR-forming species) compared to that of *Lolium perenne*, *Trifolium repens*, *Triticum aestivum*, and *Avena sativa*. This might be related to the ability of lupins to exude carboxylates in order to obtain the fixed P from soil (Lambers et al. 2013).

Our working group has found evidence suggesting that Proteaceae species influence the activity and composition of soil microbial communities in recent volcanic substrates in southern Chile. First, the metabolic diversity (based on the capacity to use several C sources) of the microbial community associated with the rhizosphere soil of *E. coccineum* was found to differ

significantly along successive developmental stages of CR (Renderos et al. *in preparation*). In this regard, higher β -glucosidase activity and fluorescein diacetate hydrolysis (both indicative of microbial activity) were detected in the rhizosphere of senescent CR of *E. coccineum*, growing under natural conditions on soils of volcanic origin, when compared with the microbial activity of bulk soil (Delgado et al. 2015). Second, in the rhizosphere of *E. coccineum* seedlings grown on pumice for two years, the abundance of oxalate-consuming bacteria (determined as unit colony forming counts in an oxalate-containing medium) was higher compared to that of malate- or citrate-consuming bacteria. This is in agreement with the rapid rate of oxalate exudation by *E. coccineum* seedlings through their CR detected during this experiment (Delgado et al. *in preparation*). Third, a recent study evaluating the bidirectional positive relationship between the native legume *Sophora cassioides* (Fabaceae) a N_2 -fixing species, and *E. coccineum* showed that the root activity of the Proteaceae species positively affected the abundance of total soil bacteria (determined as unit colony forming counts in glucose-containing medium), but not that of *Rhizobium* (determined as unit colony forming counts in a maltose-containing medium), in the rhizosphere of the legume when the two plants were grown together in an organic substrate (Zúñiga-Feest et al. 2018).

Moreover, soil microorganisms can be also involved in weathering of volcanic deposits. In the absence of plants, autotrophic microbes are the first colonizers, starting the biological weathering by oxidizing redox-sensitive elements, fixing CO_2 into biomass (King 2007) and providing C for colonization by heterotrophic organisms (Fig. 2a). Biofilms dominated by fungi, algae, cyanobacteria and heterotrophic bacteria could occur on mineral surfaces and induce chemical and physical changes contributing to weathering (Seiffert et al. 2014). Moreover, organic acids produced by plant roots, fungi and bacteria contribute to proton-driven weathering, and when deprotonated, they contribute to this process by complexing with metals such as Al^{3+} . Therefore, it is difficult to separately quantify the contributions of plants and associated microorganisms to weathering of volcanic deposits (Finlay et al. 2019).

It must be noted that there are no studies about interactions between CBX and volcanic deposit components, i.e. how mineral components in volcanic ash affect mobilization, stability, retention, and degradation of exuded CBX.

Microbial endophytes. The last frontier to explore?

Microbial endophytes promote plant growth through nitrogen fixation, phytohormone production, nutrient acquisition, and by conferring tolerance to abiotic and biotic stresses (Kandel et al. 2017). Fungal endophytes were associated with roots of *Laretia acaulis* (Apiaceae), a nurse cushion species found at 3200 m in the Andes of Central Chile (Table 1; Molina-Montenegro et al. 2015). This plant plays a fundamental role in the establishment, performance and survival of both native and exotic plant seedlings associated with the cushion plant. The study suggests that there are indirect effects mediated by the fungal endophytes that may also help explain the successful establishment of native and invasive species in alpine ecosystems (Molina-Montenegro et al. 2015). Another case involves a bacterial endophyte isolated from *Zea nicaraguensis* (Poaceae), a wild corn discovered in a swamp above rock lava from the San Cristobal volcano, Nicaragua (Table 1; Shehata et al. 2017). This endophyte, similar to *Enterobacter asburiae*, promotes root hair growth and the secretion of organic acids by the plant; thus, *Zea nicaraguensis* solubilizes and uptakes P from rocks with its large root hair surface. The authors hypothesized that organic acids could be acting to solubilize P, as described in other *Enterobacter* species (Shehata et al. 2017). Because of their impact on plant physiology, and the scarcity of studies on this issue in volcanic deposit colonizing plants, endophytes could be considered as the last frontier to discover and to study.

Concluding remarks

Volcanic deposits represent an ecosystem with several particularities at the biotic level, mainly substrate characteristics (physical and chemical), which strongly affect biotic development. Because P and N are the main nutrients limiting plant growth in volcanic deposits, colonizer plants display root adaptations including microbial associations as mechanisms to obtain these nutrients. While N is obtained through symbiosis with actinobacteria and rhizobacteria, P can be obtained through more pathways, such as fungal symbiosis with AMF and ECM and root modifications such as cluster root formation and consequent CBX exudation. The performance and impact of bacterial and fungal symbioses depend on the ability of plants to recruit these microorganisms, as well as their

specificity of establish symbiosis with plants and their abundance in the environment. These mechanisms are restricted to certain plant species, of which just a few are able to colonize volcanic environments (see Fig. 2). Some colonizer plants display more than one mechanism, such as lupin, which is able to fix N through rhizobacteria nodulation and obtain P through CR formation. Other colonizers, such as red alder, is able to establish symbioses with *Frankia* to obtain N, while P is obtained through association with AMF and ECM as well as CR formation. It is also possible that plant colonizers could display complementary nutrient acquisition mechanisms, when plants are grown close together in volcanic deposit. If this kind of positive interactions are or not belowground extended and affecting the success of plant colonization, should be studied in the near future. Moreover, through roots exudates, plant colonizers are able to attract or to repel microorganisms, influencing the rhizosphere as a whole, recruiting and shaping particular microbial communities with specific functions on volcanic deposits (nitrogen-fixing, PGPR among others, Fig. 2). These microorganisms act as intermediaries between plants and soil. In this regard, three points should be considered in future studies: (i) determine how commonly mycorrhizal fungi recruit P solubilizing bacteria, (ii) whether endophytes are present and if they promote early colonizer plant growth, and (iii) the community composition of soil microorganisms and their contributions to successful plant colonization of volcanic substrates.

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