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From Forest Nursery Notes, Winter 2010

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Low *Frankia* inoculation potentials in primary successional sites at Mount St. Helens, Washington, USA

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Received: 1 December 2008 / Accepted: 7 February 2009 / Published online: 24 February 2009
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Abstract The ability of 23 year old volcanic soils from Mount St. Helens, USA, to nodulate actinorhizal Sitka alder (*Alnus viridis* ssp. *sinuata*) was studied by estimating *Frankia* Inoculation Unit density (FIU) in four types of primary successional communities using a host-plant bioassay. Rhizospheric Mycelial Inoculation Unit (MIU) density and the effects of inoculation with alder soil and phosphorus (P) on seedling growth were also examined. FIU and MIU were highest in alder thickets, lower in lupin patch and riparian zone sites, and lowest, with no FIUs, in bare areas. Seedling dry mass was higher in treatments inoculated with alder soil but not with P addition, while root: shoot mass ratios decreased with both inoculation and P. The extremely low densities of suitable symbionts in sparsely vegetated primary successional areas at Mount St. Helens may explain the surprisingly slow rate of spread of alder from nearby seed sources.

Keywords *Alnus viridis* · Colonization · Mycorrhizae · *Frankia* · Mount St. Helens · Nitrogen fixation · Phosphorus · Primary succession

Responsible Editor: Juha Mikola.

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Introduction

For many plant species, colonization of primary successional substrates is expected to be limited by factors related to lack of soil development, such as low levels of nutrients and poor water-holding capacity. The absence of soil-borne mutualists, such as mycorrhizae or nitrogen- (N-) fixing symbionts, is also likely to be an important factor affecting colonization. The uncertainty of encountering mycorrhizal mutualists is thought to favor facultatively mycotrophic and non-host colonists in primary successional habitats (Allen 1991), and early successional communities often feature low levels of mycorrhizal inoculum and species diversity (Allen et al. 2005; Titus et al. 2007). Although N₂-fixing vascular plant species are often prominent in primary succession, at least 20% of primary successions lack them, for reasons that are unclear (Walker 1993). Because there are many examples in which nodulated N₂-fixing plants are present surprisingly early in primary succession, or are prominent invaders, lack of suitable mutualists has not been viewed as a limiting factor to colonization by these plants (Burleigh and Dawson 1994; Parker 2001; Sprent 1993; Walker 1993). On the other hand, these bacterial mutualists are not transmitted within seeds, host-specificity of the bacteria is sometimes high, and there are numerous cases in which introduced legumes have failed to nodulate (Parker 2001; Parker et al. 2006). In fact, there appear to be few investigations of the extent to which the range expansion by invading native or non-native N₂-