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学 位 論 文 内 容 の 要 旨

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学 位 論 文 題 名

Interaction between plant colonizers and ectomycorrhizal fungi through nitrogen transfer in the early stages of volcanic succession
（火山遷移初期段階における窒素移動を介した定着植物と菌根菌の相互作用）

Plant successional patterns are often dependent on plant strategy to acquire nutrients. Nitrogen (N) is poor in stressful and harsh habitats after catastrophic disturbances represented by volcanic eruptions. In addition, biological invasions often occur in such harsh ecosystems. Characterizing N uptake of plants is prerequisite to predict and conserve unstable ecosystems. Since N uptake by vascular plants has two pathways, directly from the soil substrates and from mycorrhizal fungi, the dependence of the respective plants on mycorrhizal fungi should be altered with progressing succession. To clarify spatial changes in the N acquisition of early and late plant colonizer, therefore, N status in plants and soil substrates was investigated with mycorrhizal fungi on Mount Koma (1,131 m elevation), northern Japan, that erupted in 1929. The early colonizer is a native shrub, *Salix reinii*, and the late colonizer is *Larix kaempferi* that is biologically invasive. The seedling growth of *L. kaempferi* was also monitored in a greenhouse.

The effects of *S. reinii* and mycorrhizal fungi on the seed germination and seedling growth of *L. kaempferi* were examined in the greenhouse (chapter 1). The N transfer between the soil substrates, mycorrhizal fungi and woody plants were evaluated in two elevations (ridge at 890m m and hillslope at 680m) with different successional stages on Mount Koma using stable N isotope ratio ($\delta^{15}N$) in plants, mycorrhizal fungi and tephra (chapter 2). Non-mycorrhizal *Carex oxyandra* was used to evaluate inherent plant $\delta^{15}N$. The study was extended to six woody plants, *Gaultheria miqueliana*, *Betula ermanii*, *Betula platyphylla*, *Populus sieboldii, Alnus maximowiczii*, and *Quercus mongolica*, at five elevations ranging from 920 m to 380 m (chapter 3).

In the greenhouse experiment, the seedlings of *L. kaempferi* had 2-3 times higher shoot/root biomass ratio (S/R ratio) when grown with *S. reinii* shrub than when grown on bareground. The S/R ratios of *L. kaempferi* were unchanged with changing light intensity when the seedlings grew with *S. reinii* patches, although shade by *S. reinii* decreased the seedling growth. Foliar N% of *L. kaempferi* seedlings was 42% higher with mycorrhizal fungi and *S. reinii* shrub than with less mycorrhizae. Therefore, the seedling growth of *L. kaempferi* was promoted by mycorrhizal fungi

that increased the N acquisition of plants.

N in the substrates was higher in *S. reinii* patches than on bareground on Mount Koma, suggesting that the N was mostly provided by *S. reinii* litter. On the ridge which contains higher N in substrate than that on the hillslope, less than 5% of N in *L. kaempferi* leaves originated from mycorrhizal fungi. *L. kaempferi* showed over 56% of N dependence on mycorrhizal fungi on the hillslope where N in the substrates was low. In contrast, *S. reinii* on the ridge developed mycorrhizae well and obtained over 45% of N from mycorrhizal fungi. Despite increased accumulation of *L. kaempferi* litter, decreased N in tephra and partial shade cast by *L. kaempferi* overstory on the hillslope (680 m), compared to the ridge (890 m), *S. reinii* did not vary mycorrhizal relation for N acquisition between the two elevations. Therefore, the dependence of N uptake on mycorrhizal fungi was more plastic on *L. kaempferi* than *S. reinii* and this flexible response of *L. kaempferi* to N in substrate was considered to partly explain the invasiveness of *L. kaempferi*.

The ground surface below 480m elevation was covered mostly with thick *L. kaempferi* litter. *G. miqueliana* was predominant on shrub layer in the area (480 m – 380 m) but did not contribute greatly to the N accumulation in the tephra though *G. miqueliana* considerably increased N in tephra at the higher elevations (> 680 m) where the amount of *L. kaempferi* litter was not significant. Three tall pioneer trees, *B. ermanii*, *B. platyphylla*, and *P. sieboldii* showed over 25% of N dependence on mycorrhizal fungi. The clear changes in N dependence among the elevations were not observed for the three species. Late successional species, *Q. mongolica*, started to recruit at 380 m with over 62% N dependence on mycorrhizal fungi. *Alnus maximowiczii* is known to develop N-fixing actinobacteria (*Frankia* spp.) that promote N acquisition. That is probably why foliar $\delta^{15}N$ of *Alnus maximowiczii* was highest among surveyed woody plants. Along a N fertility gradient in the tephra with elevations, *L. kaempferi* showed most flexible responses to the environments, including interactions with *S. reinii* and mycorrhizal fungi, and therefore, this species showed high invasiveness on various disturbed habitats.

Based on these results, I concluded that *L. kaempferi* successfully recruits to the forefront of the primary successional sere as dominant invasive species by exerting the favorable and flexible response to both early beneficent colonizers and mycorrhizal fungi in resource allocation and N acquisition along the gradient of N availability, suppressing the survival of other woody species including pioneer species by thick recalcitrant litter accumulation and/or shade of *L. kaempferi* overstory.