

論文の内容の要旨

論文題目 Ecophysiology of three Pyroleae species coexisting in subalpine forests on Mount Fuji: contrasting photosynthetic traits, root associated fungal communities, and trophic strategies

(富士山の亜高山帯林に生息するイチヤクソウ連植物3種の生理生態：光合成特性、共生菌群集、栄養戦略の違い)

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1. Introduction

The growth of autotrophic plants is directly affected by the intensity of light, which drives photosynthesis that produces virtually all of the carbon materials and energy of the plants. Thus, the light intensity is among the most critical environmental variables for plants to adapt. Light intensity on forest floor is very low, yet diverse plants adapt to such unfavorable environments. Most forest floor plants have a specifically optimized type of leaves, i.e. "shade leaves", that enable effective photosynthesis under low irradiance. Another mechanism of shade adaptation is "mycoheterotrophy (MH hereafter)", as achlorophyllous plants receive all carbon from root colonizing fungi. Recently, some green plants that perform photosynthesis also receive significant amounts of carbon from root colonizing fungi, known as "partial MH" plants. Previous studies have demonstrated that root colonizing fungi in these partial MH plants are ectomycorrhizal (ECM) fungi that can colonize surrounding trees. However, few studies have actually confirmed the mycorrhizal networks between partial MH plants and surrounding trees by common fungi. Moreover, we know very little about the effect of light environments on MH levels and leaf acclimation in partial MH plants. In this study, we investigated three Pyroleae species, which are regarded as a partial MH lineage, focusing on their mycorrhizal networks with surrounding trees, the effect of light on MH levels and leaf acclimation, and their interspecific difference.

2. Mycorrhizal networks of Pyroleae

We established three research sites on Mt Fuji and sampled soil cores including Pyroleae plants (*Orthilia secunda*, *Pyrola alpina*, an *Pyrola incarnata*). Mycorrhizal fungi colonizing Pyroleae roots and coexisting ECM roots in the same cores were identified based on

rDNA ITS sequences. Mycorrhizal fungi found in *O. secunda* were dominated by Ascomycetes species including *Wilcoxina*, which were rarely found in surrounding trees. Two *Pyrola* species were associated with various Basidiomycetes fungi, which were also detected in surrounding ECM roots. However, the number of confirmed networks between Pyroleae and surrounding ECM trees was significantly high in *P. incarnata*.

3. Light effect on mycoheterotrophy levels and leaf acclimation

ECM fungi usually have higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than autotrophic plants. Thus, when partial MH plants receive more C from root colonizing ECM fungi, their $\delta^{13}\text{C}$ values become higher. To estimate MH levels of the three Pyroleae species, we sampled their leaves as well as leaf samples of surrounding plants and fungal fruitbodies for stable isotope analyses. Light environments of the sampled Pyroleae plants were evaluated by canopy openness. We also measured their leaf traits, including leaf mass per area (LMA), nitrogen per area (N_{area}), and maximum photosynthetic rates (A_{max}). Mean $\delta^{13}\text{C}$ of *O. secunda* was not different from that of autotrophic reference plants. Moreover, its $\delta^{13}\text{C}$ values increased with canopy openness, representing a typical pattern of autotrophic plants. In contrast, mean $\delta^{13}\text{C}$ values of the other two *Pyrola* species were significantly higher than that of the autotrophic reference plants. Two source linear model estimated that 18.0% and 33.5% of C in *P. alpina* and *P. incarnata*, respectively, were derived from the fungi. $\delta^{13}\text{C}$ values of *P. alpina* were negatively correlated with canopy openness, indicating its higher C dependence on fungi in low light environments but higher autotrophy under high irradiance. $\delta^{13}\text{C}$ values of *P. incarnata* were constantly high and not effected by light environments, indicating its MH level is high irrespective of light environments. Light acclimation of leaf traits, e.g. positive correlation between LMA, N_{area} , or A_{max} with the light environment, was observed in *O. secunda*. Leaf traits of the two *Pyrola* species showed no sign of light acclimation except A_{max} of *P. alpina*, indicating their poor abilities for optimizing leaves to adapt different light environments.

4. Discussion

We found different strategies of shade adaptation in the three Pyroleae species. Our results suggest that *O. secunda* is autotrophic and adapts to shade environments solely by leaf acclimation, as in other autotrophic plants. In contrast, both *P. alpina* and *P. incarnata* exhibited almost no leaf acclimation. These two *Pyrola* species may adapt to dark forest floor environments mainly by carbon supplements from root colonizing fungi. MH levels of *P. alpina* increased with shade, indicating the plasticity of fungal C dependence. *P. incarnata* kept higher MH levels even under high irradiance, suggesting its advanced evolutionary state towards full MH. Because the mean MH levels of the three Pyroleae species corresponded with the

abundance of mycorrhizal networks confirmed, the number of fungal-plant interface in partial MH plants could partly account for the amount of C supply from the fungi. Partial MH plants include many threatened species. Given the different ecophysiological strategies confirmed in Pyroleae, we may need to clarify MH levels and compatible fungi, as well as the suitable host trees that support the fungi, to conserve putative partial MH plants.