Photosynthesis of fern species having different habitats and frond morphologies

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Introduction
Ferns are known to live in various habitats. Many species live in the shady and humid sites under tree canopy but some species live in the open or xeric sites. Their sporophyte fronds have quite different morphologies between species. The morphology of fern frond is considered to reflect the adaptation strategies to their environments. To understand the evolution of ferns and their adaptation to the various habitats, the information of morphological and ecophysiological trait of ferns are needed. Recent studies showed the relationship between habitats and morphological traits or photosynthetic traits separately. The integration of frond morphological traits, photosynthetic traits and their habitats or life forms are essential, since the frond morphology of ferns reflects the adaptation for effective photosynthesis and water relations.

The aim of this study is to integrate the frond morphological traits and photosynthesis for understanding the adaptation strategy of ferns to the various habitats.

Materials and Methods
4 species of temperate fern such as shady terrestrial deciduous, Adiantum pedatum (kujyakushida), Open terrestrial deciduous, Pteridium aquilinum (warabi), shady terrestrial evergreen, Dryopteris erythrosora (benishida) and Epiphyte evergreen, Lepisorus thunbergianus (nokishinobu) in sporophyte stage were grown in a glasshouse. Leaf mass per area (LMA), stomatal density (SD), leaf water content (LWC), relative water content (RWC)) and photosynthetic potentials ($V_{max}$ and $J_{max}$) were measured before stress treatment, and then they were subjected to drought stress to investigate the photosynthetic response.

Result
Stomata were on the abaxial side of fronds only in the all the ferns investigated. SD of the Open site fern, P. aquilinum was twice of the other ferns. Evergreen fern had significantly higher LMA than the deciduous ferns. Epiphytic fern, L. thunbergianus showed the highest LMA among the ferns. Photosynthetic potentials ($V_{max}$ and $J_{max}$) of D. erythrosora, L. thunbergianus and P. aquilinum were similar. However, their photosynthetic rate ($A_{max}$) and stomatal conductance ($g_s$) were lower than P. aquilinum.

Some fronds of the deciduous ferns under drought stress were dead. Tip of fronds were withered partly in D. erythrosora. In L. thunbergianus, all of the fronds were withered, but they were recovered after reirrigation. In all ferns, $A_{max}$ and $g_s$ decreased concurrently under drought stress. There were positive correlations between $A_{max}$ and $g_s$. Epiphyte fern, L. thunbergianus showed negative transpiration in severe drought stress. The rubisco content of each ferns were not affected by drought stress.

Discussion
In well watered condition, open site fern, P. aquilinum, have similar photosynthetic potentials ($V_{max}$ and $J_{max}$) to D. erythrosora and L. thunbergianus, but showed the highest $A_{max}$ among the fern species. High SD and gs of P. aquilinum may cause their high $A_{max}$ in the open sites.

The evergreen ferns showed higher WC than the deciduous ferns. The higher construction cost may be higher for water storage structure in the evergreen ferns. In stress conditions, some fronds of deciduous ferns were dead, but evergreen ferns maintained the frond.

All ferns decreased photosynthetic rate and $g_s$ concurrently but maintained the similar rubisco content in drought stress compared to the control. These results suggest that low stomatal conductivity may be a major factor reducing the photosynthetic rate in drought stress.

L. thunbergianus did not dead below 40% of RWC and showed negative transpiration in drought stress. These results suggest that L. thunbergianus is poikilohydry. Additionally, L. thunbergianus has the extremely higher LMA and WC than the other ferns, indicating that L. thunbergianus has succulent. L. thunbergianus live on the tree, where water resources may be limited. In such a prolonged drought environment, poikilohydry as well as succulent type morphology may be favorable.

Keywords: fern, pteridophyte, photosynthesis, adaptation, evolution, habitat

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