Ecological significances of leaf trichomes in *Metrosideros polymorpha*

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Abstract

Metrosideros polymorpha Gaud. (Myrtaceae), an endemic dominant tree species on the Hawaiian Islands, shows enormous phenotypic variations across an exceptionally broad range of habitat environments. *Metrosideros polymorpha* is an ideal model species for studying adaptive evolutions of tree species because this species satisfies the criteria of adaptive radiation. However, the adaptive significance of leaf trichomes that characterizes the enormous phenotypic variation in *M. polymorpha* is still unclear. Pubescent individuals are more abundant in dryland, high-elevation or bog areas where plants may suffer from drought, low-temperature or anaerobic conditions whereas glabrous individuals are often abundant in moderately wet areas. In this thesis, I aim to elucidate the ecological significance of leaf trichomes in the evolutionary model plant *M. polymorpha* by examining the three possible functions in relation to the adaptation to drought and low-temperature conditions: (I) leaf trichomes increase diffusion resistance to save water and/or to enhance carbon gain, (II) leaf trichomes promote leaf wetness and foliar water uptake and consequently enhance carbon gain, and (III) leaf trichomes defend against insects especially specialist psyllids to avoid an extra water loss from their forming galls.

In Chapters 2 & 3, I examined the function I in relation to diffusion resistance. I quantified both direct and indirect effects of leaf trichomes on the gas-exchange rates: leaf trichomes in theory could directly decrease the gas fluxes through increased gas-diffusion resistance and also indirectly increase the gas fluxes through increasing leaf temperature. With detailed ecophysiological measurements, I found that the leaf-trichome resistance accounts for no more than 9% of total water-vapor diffusion resistance even in leaves with the largest amount of leaf trichomes (more than 30% of leaf mass), suggesting that the leaf trichomes in *M. polymorpha* had negligible effects on water-use efficiency (WUE) of gas exchanges through the direct effect on the gas diffusion resistance (Chapter 2). When I considered the effect of leaf trichomes on sensible-heat fluxes (increased by up to 45%) and on the gas-exchange rates through increasing leaf temperature, I found that this indirect effect was much greater than the direct effect. In the model simulation analyses using a set of the field-obtained physiological and morphological traits and the diurnal environmental data, I demonstrated that leaf-trichome resistance can increase the daily carbon gain through increasing leaf temperature only in the cold alpine area. The daily WUE, which is defined as the daily carbon gain per unit water loss, was lower with the presence of leaf trichomes at any elevational sites (Chapter 3). Thus, in relation to adaptive significance of leaf trichomes through increasing diffusion resistance, I concluded that the leaf trichomes of *M. polymorpha* can contribute to the adaptation to low-temperature environments but not to dry environments.

In Chapter 4, I examined the function II in relation to leaf wetness. I With monitoring leaf wetness in the field, I found that the leaf trichomes could prolong the duration of leaf wetness up to ca. 2 hours in the sites, and that this effect was significantly positively associated with the amount of leaf trichomes. The anatomical investigation

suggested that the leaf trichomes of *M. polymorpha* had thick cell walls and hydrophilic characteristics, which can contribute to the effect of leaf trichomes on the prolongation of leaf wetness. The capacity of foliar water uptake was greater in pubescent individuals inhabiting a dry cold site than in glabrous individuals inhabiting a wet warm site. Moreover, when nighttime leaf wetting was prevented in the field, the duration of high photosynthetic rates became shorter, suggesting that leaf wetness in the nighttime can contribute to keeping stomatal openness longer in the daytime probably through improving leaf water status via foliar water uptake. Thus, my results suggest that the leaf trichomes in *M. polymorpha* can contribute to the adaptation to drought stresses through promoting leaf wetness and foliar water uptake, and consequently enhancing photosynthesis in drought environments.

In Chapter 5, I examined the function III in relation to defense against gall makers. Three gall types were found on the island of Hawaii: the largest one is the 'cone' type, followed by 'flat' and 'pit' types. I found that leaf minimum conductance was significantly higher in leaves with a greater number of the cone- or flat-type galls but not pit-type galls. By the field census, I found that the amount of trichomes was negatively associated with the presence of cone- or flat-type galls but not pit-type galls, irrespective of environmental factors, suggesting that the leaf trichomes can impede formation of the large galls, i.e., cone and flat, increase the leaf water loss but not impede formation of the small pit galls that have negligible effects on leaf water status. Therefore, the leaf trichomes in *M. polymorpha* can contribute to the avoidance of extra water stress through interactions with the certain gall-making species, and potentially increase the fitness of plants under arid conditions.

Overall, this thesis demonstrates that the leaf trichomes of *M. polymorpha* have multiple functions depending on environmental conditions. Such multi-functionality can be responsible for the great variation in the amount of leaf trichomes in *M. polymorpha*. By combining the ecological significance of leaf trichomes clarified in this thesis as well as knowledge on the genetical background and spatial and temporal variations in climate conditions, we could better understood how the great intraspecific variation in the amount of leaf trichomes have been emerged in *M. polymorpha* over evolutionary timescales.