Ecological significance of the environmental heterogeneity between the upper and lower surfaces of a single leaf as a determinant of acarine predator–prey relationship

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Chapter 1

General introduction

Plants have evolved diverse topographies between adaxial and abaxial leaf surfaces, e.g., in possession of leaf domatia, hair density and shape, wax and cuticle layer thickness, and stomatal density. Such structures influence microclimates and cause differences in temperature and humidity. As a result, adaxial and abaxial leaf surfaces offer heterogeneous environments for plant-dwelling arthropods, affecting behavior of inhabitants and their (inter-specific) interactions.

The two surfaces of a plant leaf also correspond to the upper and the lower sides, which affects within-plant distribution and fecundity of spider mites. Additionally, leaves function as protective shields against solar ultraviolet (UV) radiation by accumulating phenolic compounds such as flavonoids. Living on an upper leaf surface have been considered to be harsh to mites in comparison with on a lower surface because of rainfall or submergence, which decreases survivability of spider mites. Recent studies have asserted that intra-leaf distribution in spider mites and phytoseiid mites is biased to the lower leaf surfaces to avoid solar ultraviolet-B (UVB, 280–320 nm wavelengths) radiation, which is harmful for both mite eggs and motile individuals. Nevertheless, potential impacts of the heterogeneous habitats between adaxial and abaxial (upper and lower) surfaces on the spatiotemporal structure and intra- and interspecific interactions have hardly been addressed on a foliar acarine community.

The habitat heterogeneity between upper and lower leaf surfaces may distinctively exert the effects on the leaf-surface utilization patterns of phytoseiid mites and their prey. As shelter (hairs and domatia) availability and food abundance promote the priority of the lower (abaxial) leaf surfaces as habitats for phytoseiids to the upper surfaces, prey mites possibly reduce predation risk if they can remain on the upper leaf surface. In this study, I investigated whether the environmental heterogeneity relevant to upper and lower leaf surfaces segregated the spatial distribution of acarine predator and prey within a single leaf and how the environmental and biological factors function in their interspecific interaction, possibly affecting the local population dynamics of the prey.

Prior to the present study, I surveyed the seasonal dynamics of foliar mite assembly on a deciduous shrub, *Viburnum erosum* Thunb. var. *punctatum* Franch. et Sav. (Adoxaceae; VEP), and other14 sympatric tree/shrub species of secondary forest on the outskirts of Kyoto. Leaves of VEP have stellate hairs on both of adaxial and abaxial surfaces and leaf domatia (hair tufts) on vein axils of abaxial surface. The VEP leaves maintain populations of fungivorous mites (Winterschmidtiidae and Tydeoidea) and predatory mites (phytoseiids) from May to November in each year. Therefore, VEP leaves are considered to be suitable substrata to investigate the leaf-surface utilization patterns relevant to various mite taxa and their seasonal fluctuations. On the other hand, the occurrence of herbivorous mites on VEP leaves was seasonally limited; a false spider mite, *Brevipalpus obovatus* Donnadieu (Acari: Tenuipalpidae), was observed only in autumn (September to October).

Chapter 2

Intra-leaf distribution of plant mites in temperate broadleaf forest

The two-year dataset obtained by the abovementioned field survey was re-analyzed. The adaxial–abaxial surface distributions of mites were compared among mite taxa, seasons, and morphology of host leaves (presence/absence of hairs and domatia). On VEP plants, seven of 11 distinguished mite taxa were significantly distributed in favor of abaxial leaf surfaces and the trend was seasonally stable, except for Eriophyoidea. Mite assemblages on 15 plant species were significantly biased towards the abaxial leaf surfaces, regardless of surface morphology. These results suggest many mite taxa commonly prefer to stay on abaxial leaf surfaces in wild vegetation. Oribatida displayed a relatively neutral distribution, and in *Brevipalpus obovatus*, the ratio of eggs collected from the adaxial versus the abaxial side was significantly higher than the ratio of the motile individuals, implying that some mite taxa exploit adaxial leaf surfaces as habitat.

Chapter 3

Protective effect of stellate hairs on leaves of VEP on *Brevipalpus obovatus* eggs from the predator *Phytoseius nipponicus*

The eggs of *Brevipalpus obovatus* have a longer incubation period than those of spider mites and are not protected by webs. At the same time, *B. obovatus* often lays its eggs in the gaps among the hairs on host leaves. Thus, I examined the protective effect of stellate hairs of VEP leaves on the survival of *B. obovatus* eggs. Adult *B. obovatus* and *Phytoseius nipponicus* were introduced to VEP leaf disks; each *B. obovatus* egg was inspected daily until hatching. More eggs (63 vs. 42 %) survived on the abaxial surfaces of VEP leaves, where the stellate hairs are more complicated, than on the adaxial surfaces. Predation hazard decreased rapidly with increasing egg age and a substantial portion of the eggs hatched. *Phytoseius nipponicus* preyed on eggs regardless of egg age when mixed-age eggs were provided. Manipulative experiments with bent stellate hairs showed that the normal hairs reduced the predation risk of *B. obovatus* eggs by *P. nipponicus*. Therefore, the predation hazard was considered to decrease since the stellate hairs hindered the search for *B. obovatus* eggs by the phytoseiid mite, and such a protective effect was more prominent on the abaxial than on the adaxial leaf surface of VEP.

Chapter 4

Habitat segregation caused by opposite geotaxis and leaf-surface preferences mitigates negative effects of *Phytoseius nipponicus* on *Brevipalpus obovatus*

Reproductive success and population growth of an herbivorous mite are limited by activities of phytoseiid predators. However, occurrences on upper versus lower leaf surfaces may sometimes mismatch between these prey and predators. The mismatch potentially mitigates predation risk for the prey species. In this chapter, I assessed factors that affect mite distributions on leaf surfaces, testing whether the presence of *Phytoseius nipponicus* alters the leaf-surface distribution and reproductive success of *Brevipalpus obovatus* on VEP leaves. Leaves were set in natural and reversed (upside down) orientations using experimental devices. Both surfaces were accessible to mites. I detected lower and abaxial leaf-surface preferences in *P. nipponicus*. In contrast, upper and adaxial surfaces were preferred by *B. obovatus*. Thus, prey and predatory mites accumulated on different sides of leaves. Presence of the predator also indirectly decreased egg production in *B. obovatus*. *Brevipalpus obovatus* females actively avoided leaf surfaces with elevated predator numbers; these females shifted their distributions and changed oviposition sites to leaf surfaces with fewer predators. In consequence, *B. obovatus* eggs on the upper sides of leaves were less frequently preyed upon than were those on lower sides. It is suggested that upper leaf-surface exploitation in this particular herbivorous mite species mitigates predation risk from phytoseiid mites, which prefer lower leaf surfaces.

Chapter 5

Solar radiation as a restring factor of the seasonal fluctuation in the availability of an upper leaf surface as an oviposition site of *Brevipalpus obovatus*

Seasonal population dynamics of an herbivorous mite has been documented in terms of the relationship between thermoresponses and temporal biological factors such as resource availability or predation risk. Although recent studies emphasize the deleterious effects of solar ultraviolet-B (UVB; 280–320 nm wavelengths) radiation on plant-dwelling mites, how UVB affects mite population remains largely unknown. On VEP shrubs in Kyoto, *Brevipalpus obovatus* occurs only in autumn. Their females lay one-third of their eggs on upper leaf surfaces (Chapter 2). As I showed in Chapter 4, oviposition on upper surfaces is beneficial for avoiding predation by phytoseiids, but exposes eggs to solar UVB and heat stress. To test the hypothesis that the seasonal occurrence of this mite is determined by interactions between solar UVB radiation and temperature, I examined variation in egg hatching success under near-ambient and UV-attenuated sunlight conditions from spring to autumn. The UV-attenuation significantly improved hatching success. However, most eggs died under heat stress regardless of UV treatments in July and August. I established a deterministic heat stress–cumulative UVB dose–egg hatching success response model, which I applied to meteorological data. The model analyses illustrated lower and higher survivability peaks in late May and October, respectively, which partly corresponded to data for annual field occurrence, indicating the importance of solar UVB radiation and heat stress as determinants of the seasonal occurrence of this mite.

Chapter 6

General discussion

As for the herbivorous mite *Brevipalpus obovatus*, the nutritional value of the upper (adaxial) leaf surface of VEP was not inferior to the lower (abaxial) leaf surface; their fecundity on VEP leaves did not significantly differ between the adaxial and abaxial surfaces if phytoseiid mites were absent (Chapter 3). The predator *Phytoseius nipponicus* showed the positive geotaxis and the preference for the surface architecture on the abaxial surface of a VEP leaf (Chapter 4), and the intra-leaf distribution of phytoseiid mites on wild woody plants concentrated on the lower surfaces regardless of seasons and daytime/night (Chapter 2). Thus, oviposition of *B. obovatus* on the leaf upper surface is advantageous in avoiding phytoseiid predators throughout the seasons.

On the other hand, the upper-surface utilization increases the risk of environmental stress injury in eggs. *Brevipalpus obovatus* eggs are more protected against UVB and high temperature (radiant heat) than ones of the lower surface users (e.g., *Tetranychus urticae*) (Chapter 5). However, both solar UVB and high-temperature stress are considered to reduce *B. obovatus* egg hatchability less than half in the seasons except for autumn (Chapter 5). The seasonal effects in the availability of upper leaf surface would be responsible for the seasonal population dynamics of *B. obovatus*. As a conclusion, this study demonstrated the heterogeneity in physical environment between the upper and the lower surfaces of a VEP leaf segregated the within-leaf distribution of *P. nipponicus* and the *B. obovatus*, thereby mitigating their interspecific interaction and making the upper leaf surface an ‘enemy-free space’ for the prey mite in autumn.