論文の内容の要旨

生圏システム学専攻
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論文題目：The effects of companion planting with Crassulacean Acid Metabolism (CAM) plants on the growth of nectar-producing plants for green roofs
（屋上緑化における CAM 植物の混植が蜜源植物の生育に及ぼす効果の解明）

Chapter 1: Introduction

Green roofs in urban areas have attracted a great deal of attention in recent years, primarily due to its range of ecosystem services, including cooling and pollination. Moreover, green roofing became widely popular since it requires lesser cost and maintenance, and due to their shallower substrate depths, it has relatively low weight and reduced requirements for watering. However, the shallow substrates often make the vegetation prone to drought, reducing the number of suitable plant species which can survive under water-stress condition. Many green roofs, therefore, rely on succulent plants such as *Sedum* species due to their superior drought tolerance. It is suggested that companion planting with *Sedums* can substitute for frequent watering on green roofs and can improve the health condition of the associated plants. The research hypothesized that companion planting with *Sedums* induce suppression of evapotranspiration due to their CAM photosynthesis and a mulching effect, which may lead to higher substrate water content. Hence, companion planting with CAM plants had positive effects on the growth conditions of nectar-producing plants on green roofs.

Previous studies, however, indicated that not all species combinations showed positive interactions in green roof system, and plant traits are important in determining the effects of companion planting with CAM plants. Particularly, physiological traits of plants, including photosynthetic type, could affect evapotranspiration and thus, impact substrate water condition. Additionally, morphological traits such as leaf shapes and growth forms would also affect the degree of

inter-specific interaction. Thus, the objectives of this study is to elucidate the relationship between effects of companion planting with CAM plants on health condition of nectar plants and their physiological and morphological traits. Specifically, this thesis had four objectives: (i) to reveal the relationship between physiological and morphological traits of leaves and evapotranspiration (Chapter 2), (ii) to reveal the effects of companion planting with *Sedums* on health condition of nectar-producing plants depending on physiological and morphological traits of the *Sedums* (Chapter 3), (iii) to reveal the effects of growth forms of nectar-producing plants on their health condition when *Sedums* were planted together (Chapter 4) and (iv) to reveal optimal substrate water condition when using CAM plants as companion plants (Chapter 5).

Chapter 2: Effects of leaf traits of *Sedum* on evapotranspiration

To elucidate the growth characteristics of *Sedums* species which has low evapotranspiration, I investigated evapotranspiration of three *Sedum* species (*S. album*, *S. kamtschaticum* and *S. reflexum*), focusing on their morphological and physiological traits. Companion planting with *Sedum* would positively affect neighboring plants by the increase of substrate water availability. CAM induction status in *Sedum* has a possibility to affect evapotranspiration, and it would be affected by its leaf trait. Hence, I measured chlorophyll fluorescence to evaluate CAM induction status non-destructively, which enables to measure evapotranspiration by weight changes of modules simultaneously.

CAM induction status differed by *Sedum* species, and suppression of evapotranspiration was accompanied by CAM induction. *S. kamtschaticum* and *S. album* showed gradual CAM induction, and might withstand drought stress without photoinhibition, presumably due to their leaf succulence. Particularly, *S. album* showed rapid CAM induction and suppressed evapotranspiration significantly, and thus it would have strong drought tolerance.

The results indicated that when CAM plants were used as companion plants on green roofs, *Sedums* with leaf succulence such as *S. kamtschaticum* and *S. album* would be suitable for drought resistance on green roofs. Additionally, *Sedums* with rapid CAM induction such as *S. album* would suppress evapotranspiration and contribute to increasing substrate moisture content, which could improve health condition of neighboring plants.

Chapter 3: Effects of companion planting with *Sedums* on health condition of nectar-producing plants depending on physiological and morphological traits of the *Sedums*

To elucidate the effects of differences in *Sedum* species as companion plants on health condition of neighboring nectar-producing plants, I cultivated *Sedums* and nectar-producing plants together in a greenhouse, and determined the optimal species combination. Companion planting with *Sedums*, which show low evapotranspiration, would affect positively on the growth of neighboring plants by increasing substrate water content. Thus, I tested two *Sedum* species that differ morphologically and physiologically as companion plants for nectar-producing plants in a greenhouse. I used two CAM species (*S. album* and *S. kamtschaticum*) and two species of nectar-producing plants (*Fagopyrum*

esculentum, *Trifolium repens*), and cultivated them by changing species combination and planting rate.

Health condition of *F. esculentum* was improved by companion planting with certain *Sedum* species, though health condition was not improved in *T. repens*. Health condition of *F. esculentum* was strongly dependent on substrate water content during the experimental periods, and it was better in the modules with *S. album* than with *S. kamtschaticum*. These results indicated that lower evapotranspiration in *S. album* compared to *S. kamtschaticum* would increase substrate moisture content, resulting in improvement of health condition of neighbors.

The results also showed that health condition and substrate water content of *F. esculentum* and *T. repens* were negatively affected by the increase of individuals in pot, and there was a likely intra-specific competition. Thus, companion planting with *S. album* seems to be superior to conspecific treatments in *F. esculentum*, in terms of the avoidance of negative interactions due to substrate water deficit. Moreover, the decrease of conspecific density might also prevent growth inhibition by intra-specific competition.

The results suggest that evapotranspiration of neighboring *Sedums* would be key factor to improve health condition in companion planting, and evapotranspiration would be altered by morphological and physiological traits of *Sedums* which differs between *S.* album and *S. kamtschaticum.* Additionally, the degree of intra-/inter-specific competition depending on growth characteristics of plants would also affect health condition of companion plants. The reason why there was little effect of companion planting in *T. repens* would be inter-specific competition. Dry weight of *S. album* was significantly lower than that of *S. kamtschaticum* only when *T. repens* was planted together. However, I evaluated only two species of nectar-producing plants here, thus it is still difficult to recommend combinations of plant species which induce positive interactions. Therefore, more research is required to find effective species combinations on green roofs, focused on plant growth forms.

Chapter 4: Effects of growth forms of nectar-producing plants on their health condition when they were planted

Plant traits are important in determining the degree of competition for reproducing and space. Particularly, growth form seems to crucial factors to determine the effects of companion planting (Chapter 3). Therefore, to test the effects of inter-specific interactions due to companion planting with CAM plants in different growth forms, I cultivated each nectar-producing species with and without CAM plants.

I evaluated eight species of nectar-producing plant classified into three growth forms: prostrate ascending (*Mimosa pudica, Rosmarinus officinalis* 'Prostratus'), prostrate carpet (*Phyla canescens, Trifolium repens, Thymus serpyllum*) and erect (*Calamintha nepeta, Lavandula officinalis, Rosmarinus officinalis* 'Erectus'). In terms of neighboring CAM plants, I used *S. album* as companion CAM plants which showed significant positive effects on neighboring plants (Chapter 3).

Health condition of nectar-producing plants showed obvious differences among each growth form in response to companion planting with *S. album*. Health condition was improved only when prostrate ascending species were planted together with *S. album*, and substrate water content was also increased accompanied by the suppression of evapotranspiration. Prostrate ascending species grow upright during initial stages of their growth, and then grow horizontally, but did not show carpet-like growth. In these cases, there would be no spatial competition with *S. album*, which forms carpet-like stands.

On the other hands, health condition of prostrate carpet species was not improved by companion planting with *S. album*. Additionally, shoot and root biomass of neighboring *Sedum* planted together with prostrate carpet species was significantly lower than that with other growth forms. The growth form of prostrate carpet species was similar to that of *S. album*, suggesting that there could be interspecific competition for space, and positive effects of companion planting with *Sedum* would not be induced.

In the case of erect species, health condition was not improved by companion planting with *S. album* either. There could be no net inter-specific competition for space, because they growth upright. Previous studies indicated that effects of companion planting using erect species were observed only in relatively mature stages of community development. Thus, growth conditions of erect species planted together with *Sedum* may be improved in a long term experiment, though further studies should examine the detailed relationships between companion planting timing of experimental drought periods.

The results suggest that effects of companion planting with CAM species were determined by growth form. Particularly, spatially complementary growth forms may be important for selecting effective combinations to improve growth conditions on green roofs: companion planting with *S. album* and prostrate ascending species could avoid inter-specific competition; and prostrate carpet species induced inter-specific competition for space; and erect species could not cover substrate in short term experiment.

Chapter 5: Synthesis and outlook

Companion planting with CAM plants has positive effects on health condition of neighboring nectar-producing plants for green roofs. However, these positive effects are dependent on physiological and morphological traits of *Sedums* and growth forms of nectar-producing plants and were shown only under drought conditions. Additionally, increasing plant density induced intra-specific competition prevented growth inhibition by intra-specific competition. This study is imperative to understand the appropriate species selection of combination based on their growth characteristic, and can support cultivating nectar-producing plants on green roof without frequent watering though the aid of companion planting with CAM plants.