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SEASONAL CHANGES IN RESERVE SUBSTANCES OF HERBACEOUS PERENNIALS IN THE ALPINE ZONE OF MT. FUJI

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Abstract: The seasonal changes in soluble carbohydrates in rhizomes were measured for six species of herbaceous perennials growing in the gravelly habitats immediately above the timberline of Mt. Fuji. *Arabis serrata* and *Polygonum weyrichii*, the first colonizing species on newly exposed soil, used skillfully the reserve substances to adapt to the severe environment. *Polygonum cuspidatum*, *Hedysarum vicioides* and *Astragalus membranaceus*, second appearing species, accumulated a large amount of reserve substances in autumn due to their longer growing season. For *Saussrea triptera*, growing on the forest floor, the shoot growth slightly depended upon the reserve substances. Thus the respective species had different manners of using reserve substances corresponding to their environments.

1. Introduction

In the alpine zone, snow covers the ground for long periods, and the season which is suitable for plant is very short. Moreover, the mean temperature during the growing season is far below that suitable for the growth of ordinary temperate-zone plants. For that reason, it is difficult for the plants growing on the alpine zone to survive depending upon only the current products. Therefore, the alpine zone is dominated primarily by perennials which have large reserve organs and utilize reserve substances for their growth (MIDORIKAWA, 1959; MOONEY and BILLINGS, 1960).

Mt. Fuji is the highest peak in Japan (3776 m above sea level). The timberline is located at 2400 to 2500 m above sea level. The area immediately above the timberline is bare volcanic gravel with herbaceous perennials growing sparsely. In this site, the primary succession after the Hoei eruption (1707) is advancing, and the seedlings of herbaceous perennials and woody plants are gradually invading into bare area (HAYATA, 1911; MASUZAWA, 1985).

PARKER (1963) suggested nine factors that affect timberlines: 1) Lack of soil, 2) Desiccation of leaves in cold weather, 3) Short growing season, 4) Lack of snow, exposing plants to winter drying, 5) Excessive snow lasting through the summer, 6) Mechanical aspects of high winds, 7) Rapid heat loss at night, 8) Excessive soil temperatures in the day, 9) Drought. On Mt. Fuji, the same factors characterize the vicinity of the timberline. For example, the growing season with the monthly mean air temperature near or above 10°C lasts about five months, from late May to early October (MASUZAWA, 1982, 1983). During this short cool growing season, the herbaceous perennials utilize not only current products but also reserve substances for their growth.

It is expected that the utilization of reserve substances corresponds to the order of invasion into a newly exposed ground surface and to the microclimate of habitat of each species.

In this study the seasonal changes in carbohydrates in rhizomes were investigated in six species which grow near the timberline of Mt. Fuji.

2. Study Site and Methods

The study site is a bare ground situated near the timberline on the southeastern side of Mt. Fuji at the elevation of 2400 m above sea level. All the species studied occur in this site. *Arabis serrata* and *Polygonum weyrichii* are typical pioneer perennials in the early stage of the volcanic desert succession on Mt. Fuji. They are subsequently followed by such species as *Polygonum cuspidatum*, *Hedysarum vicioides* and *Astragalus membranaceus*. *Saussrea triptera* grows both inside the patches of *Polygonum cuspidatum* and on the forest floor below the timberline.

The phenology was observed on each species. Rhizomes of each species were collected for laboratory analysis. Three separate samples were taken from the upper 10 cm of rhizomes in some instances during the growing season. After measuring their volume, the samples were dried at 100°C for 1 h and 80°C for 23 h to obtain the dry weights. Then they were ground to fine powder.

Each carbohydrate fraction from these powders was analyzed. The extraction was performed three times with 80% ethanol. The fraction was used for the determination of total sugar. The residual plant powder was extracted with boiling water for 1 h. The fraction which desolved into the water was hydrolyzed with 0.2M amiloglucosidase at 50°C for 10 h then analyzed for starch.

For the quantitative analysis of sugar, the phenol-sulfric acid method (Hewitt and Marrush, 1986) was used. All results are given as mean values, and are expressed as weight per unit volume.

3. Results

The seasonal changes in carbohydrates in the reserve organs of herbaceous perennials generally follow a regular pattern (Mooney and Billings, 1960; Masuzawa and Hogetsu, 1977). At the beginning of the growing season, the amount of carbohydrates decreases rapidly due to consumption for the early growth. Thereafter, the amount increases and reaches its maximum level at the end of the growing season. Although all six species studied were found to follow the general pattern of variation in carbohydrate level, there were differences in the timing of increase and in the amount of carbohydrate accumulated.

Figure 1 shows phenology and seasonal changes in the carbohydrate concentration in the rhizomes of *Arabis serrata*. *A. serrata* is characteristically evergreen. Since such evergreen leaves seem to begin photosynthesis as soon as snow melts, the decrease of carbohydrate at the beginning of the growing season might be slight. It is commonly known that accumulation of carbohydrate is primarily in the form of starch. In this species, however, the total sugar content was almost equal to the starch content

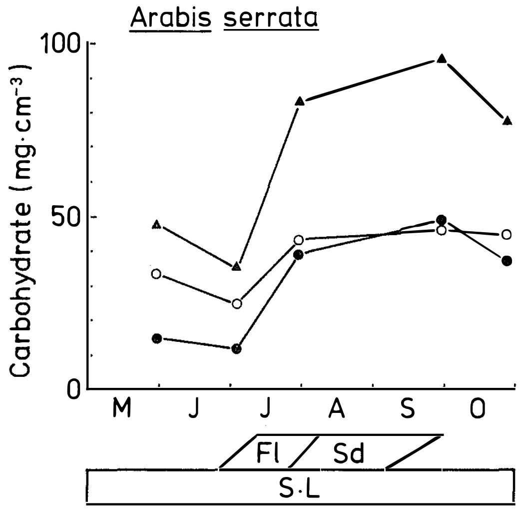

Fig. 1. *Phenology and seasonal changes in reserve substances of* Arabis serrata. *This species is characteristically evergreen. Total sugar content is almost equal to starch content from August to October.* ▲*: Total sugar and starch,* ○*: Total sugar,* ●*: Starch, Fl: Flowers, Sd: Seeds, S·L: Stems and leaves.*

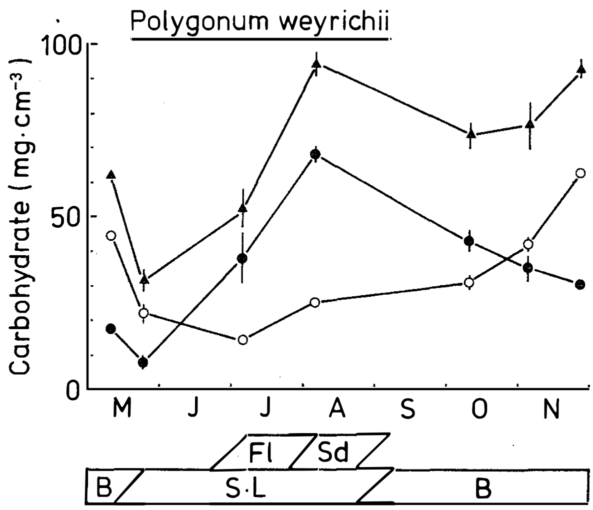

Fig. 2. *Phenology and seasonal changes in reserve substances of* Polygonum weyrichii. *Increase of carbohydrate occurs at the early stage (in May) and the growing season is short (about three months). B: Perennating buds. Other signs are the same as in Fig. 1.*

from August to October.

The shoots of *Polygonum weyrichii* sprouted in late May and died entirely by early September (Fig. 2). The end of growing season came earlier than that of the other species, and the growing season was about three months. In the rhizomes of this species, a decrease in concentration of carbohydrate occurred before elongation of the shoots which occurs in May, but the concentration increased in parallel with early growth of the shoots. The amount of carbohydrates reached the maximum at the beginning of August. The accumulation occurred mainly in form of starch. After the death of the shoots, the starch content decreased, and the total sugar content increased. In October, the total sugar content exceeded that of starch. The maximum value of carbohydrate concentration was 94 mg/cm^3 for *A. serrata* and 95 mg/cm^3 for *P. weyrichii.*

The shoots of *Polygonum cuspidatum*, *Hedysarum vicioides* and *Astragalus membranaceus* survived till the end of the favorable season (October) at this site, though the time of sprouting differed for each species (Figs. 3, 4, 5). Therefore, the growing season of these species was relatively long.

In the rhizomes of *P. cuspidatum*, the amount of carbohydrates decreased continuously for the period of about two months after the beginning of the shoot elongation (Fig. 3). Then, the amount increased to the maximum level (145 mg/cm^3) at the time of the death of the shoots. The increase was mainly due to accumulation of starch. Toward the end of the growing season, the total sugar content increased as in the rhi-

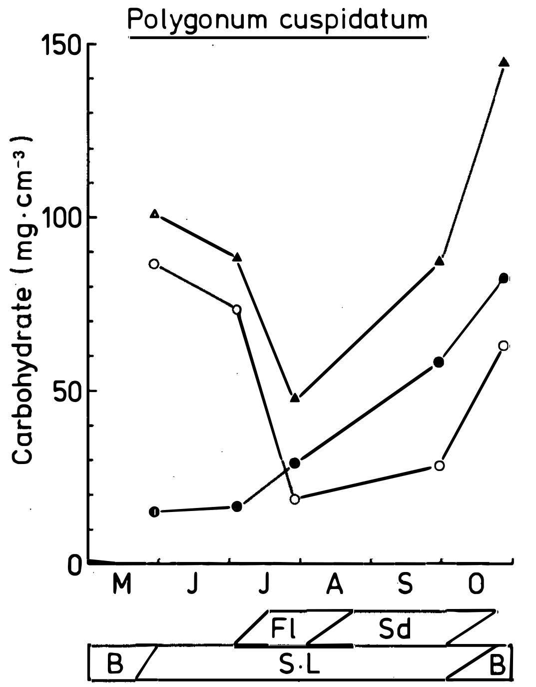

Fig. 3. Phenology and seasonal changes in reserve substances of Polygonum cuspidatum. *Increase of carbohydrate content begins in July and continues until the end of the growing season. Carbohydrate content at the end of growing season shows relatively high value (145 mg/cm^3). Signs are the same as in Figs. 1 and 2.*

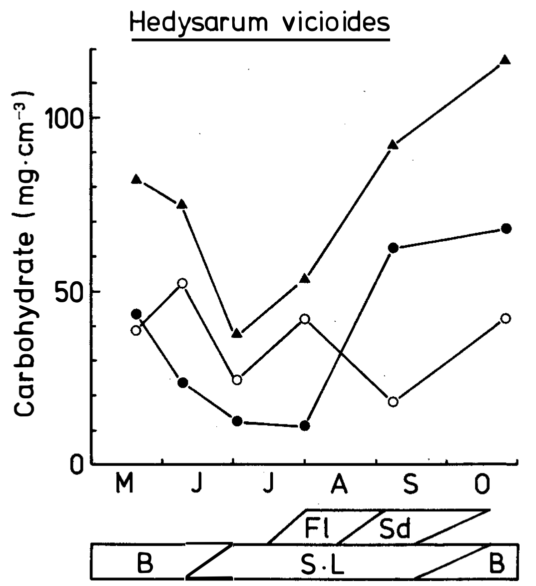

Fig. 4. Phenology and seasonal changes in reserve substances of Hedysarum vicioides. *The carbohydrate content changes in a pattern similar to that of* Polygonum cuspidatum. *Signs are the same as in Figs. 1 and 2.*

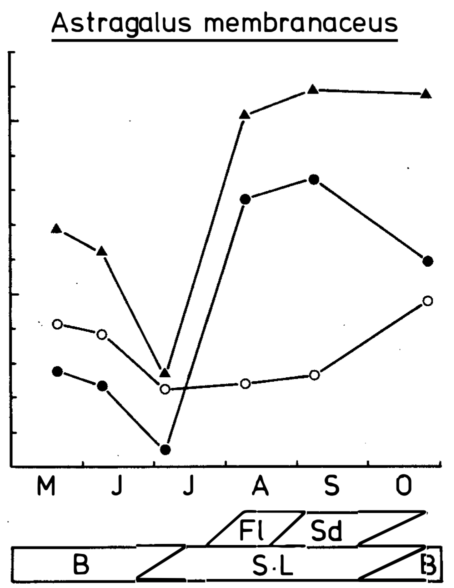

Fig. 5. Phenology and seasonal changes in reserve substances of Astragalus membranaceus. *The carbohydrate content changes in a pattern similar to that of* Polygonum cuspidatum. *Signs are the same as in Figs. 1 and 2.*

zomes of *P. weyrichii*. *H. vicioides* (Fig. 4) and *A. membranaceus* (Fig. 5) showed similar patterns of seasonal changes in carbohydrates to *P. cuspidatum*. The maximum value of the carbohydrate concentration was 117 mg/cm^3 in the rhizomes of *H.*

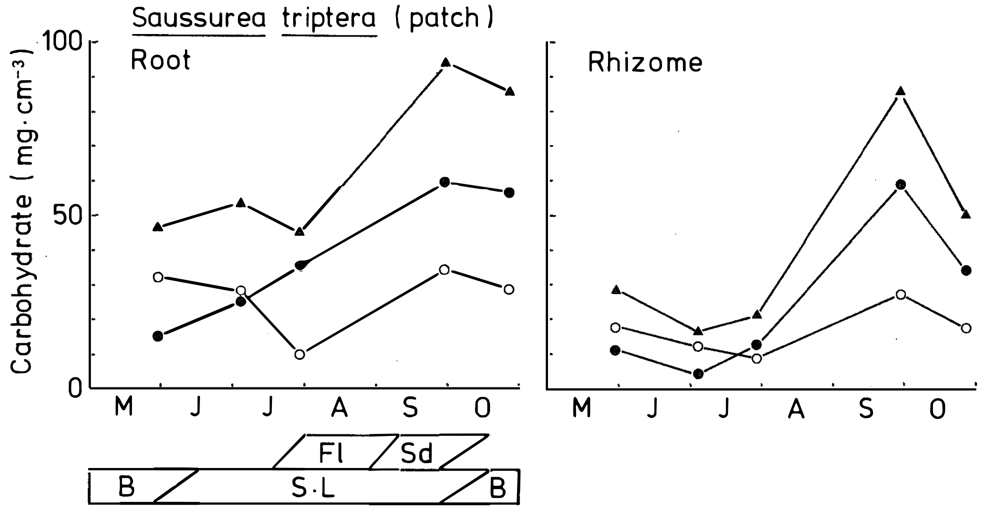

Fig. 6. Phenology and seasonal changes in reserve substances of Saussurea triptera *growing inside the patches of* Polygonum cuspidatum. *Both roots and rhizomes are used as reserve organs. At the early growth stage, decrease of carbohydrate is not distinctive. Signs are the same as in Figs. 1 and 2.*

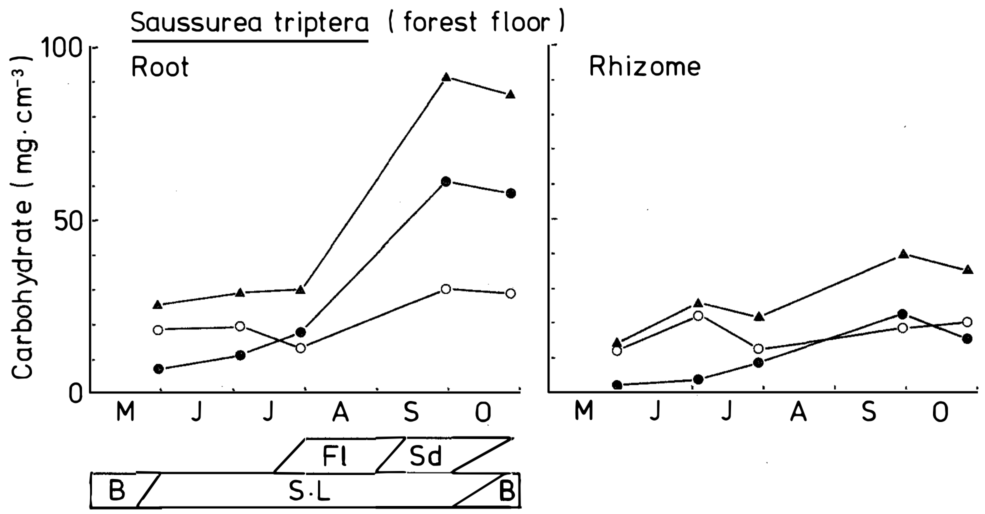

Fig. 7. Phenology and seasonal changes in reserve substances of Saussurea triptera *growing on the forest floor just below the timberline. A small amount of carbohydrate is reserved in the rhizomes. Signs are the same as in Figs. 1 and 2.*

vicioides and 110 mg/cm^3 in those of *A. membranaceus*. These three species had a long growing season and stored a large quantity of carbohydrates.

When a *P. cuspidatum* patch attains a large size of about 3 m in diameter, the biomass in the central area decreases and other species invade in the central area (MASUZAWA and SUZUKI, 1991). *P. cuspidatum* patches seem to provide a more favorable environment for other species to survive. Although *Saussurea triptera* grows mainly on the forest floor below the timberline, it is also one of the species which invade these patches. Therefore, the plants growing inside the patches were investigated separately from those on the forest floor. The shoots on the forest floor sprouted in late May, while those inside the patches appeared slightly later, in early June (Figs. 6, 7). In both habitats, the growing season lasted until October. Carbohydrates in both roots and rhizomes were measured. In all cases, there were very little decrease of carbohydrates at the beginning of the growing season. Inside the patches, both roots and rhizomes were used as reserve organs (Fig. 6), while on the forest floor, accumulation of carbohydrates was found only in the roots (Fig. 7). Carbohydrates accumulated mainly in the form of the starch. The maximum values of carbohydrates were about 90 mg/cm^3 in the roots and rhizomes of individuals inside the patches and in the roots of those on the forest floor. In the rhizomes on the forest floor, the concentration of carbohydrates reached only 40 mg/cm^3.

4. Discussion

A. serrata is one of the pioneer species which invade a newly exposed ground in the early stage of succession on the alpine zone of Mt. Fuji. The characteristics of reserving carbohydrates seem to be adaptive to the severe environment. *A. serrata* reserves sugar in a large amount, which can be readily used due to a lower molecular carbohydrate than starch. Moreover, it has been suggested that evergreen leaves play a very important role as reserve organs (YAMAZAKI, 1986). Larger amounts of carbohydrates are stored not only in rhizomes, but also in leaves.

Although *P. weyrichii* is also a pioneer species, it is thought to be adapted to severe environments in a manner different from *A. serrata*. The growing season of *P. weyrichii* was short. The shoots died by early September before the beginning of unfavorable season. This suggests that even if the season suitable for growth is unusually short due to early occurrence of unfavorable weather conditions, *P. weyrichii* may be able to reserve as much carbohydrate as in a favorable season.

P. cuspidatum, *H. vicioides* and *A. membranaceus* grow in slightly stabilized habitats by establishment of *A. serrata* and *P. weyrichii*. The growing season of these species was long, and the amount of carbohydrates stored was larger than those of *A. serrata* and *P. weyrichii*. Most reserve substances were utilized in the early growth of the following growing season. The rapid growth and establishment of shoots using not only current products but also the large amount of reserve substances in early stage of growth may be advantageous in the competition with other species. These three species which appear secondarily in succesional stage seem to have the ability to compete favorably with previously dominating species.

The sugar content in the rhizomes of *P. weyrichii*, *P. cuspidatum* and *A. membranaceus* increased at the end of growing season. It has been suggested by RUSSELL (1940, 1948), in his report of *Oxyria digyna* and *Polygonum viviparum*, that a high level of soluble carbohydrates in rhizomes may be necessary for resistance to cold winter in the arctic. The same conclusion has also been reported concerning alpine plants (ZACHHUBER and LARCHER, 1978).

S. triptera grows in habitats where the microclimate may be milder than the bare ground, for example, the forest floor and the inside of patches. *S. triptera* had lower dependence upon the reserve substances than species which grow above the timberline. In addition, differences within the species existed depending on the microclimate of the habitats. The microclimate inside the patches has been found to be severer than that of forest floors with respect to the force of wind and soil nutrients. In such conditions, more parts of underground organs may be used for strage, and a larger amount of reserve substances may be utilized for the growth. But it is possible that the differences depending upon the habitats are due to the differences in photosynthetic activity resulting from the differences in exposure to sunlight. Further research concerning photosynthetic activity and illuminance may be necessary.

Thus each species used reserve substances in a different manner corresponding to the environment of their habitats.

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