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Biomass distribution and material translocation in two herbaceous lianas in flood plain of a regulated river

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Abstract: Biomass distribution and materials (total nitrogen, total phosphorous and carbohydrates) translocation in two herbaceous lianas (*Pureria montana* and *Sicyos angulatus*) were studied in the floodplain of a regulated river, Tama in Central Japan over their life cycle from April 2008 to June 2009. They are very aggressive vines causing ecological imbalance by their resource allocation strategy, a high rate of net photosynthesis; and diurnal leaf movements that maximize exposure of lower canopy leaves and reduce overheating of upper canopy leaves. Few plants can survive once smothered by them. Plant and soil samples were collected and above- and below-ground biomass were measured from two locations with different soil characteristics along the Tama River. Total nitrogen (TN) and total phosphorus (TP) concentration in the soil of S. angulatus were higher than those of P. montana. High biomass of *S. angulatus* was recorded from soils with high nutrient contents. P. montana, though produced higher biomass in nutrient-rich soil, can even grow well on nutrient-limited soils. The dry and nutrient-poor habitats produced higher amount of belowground biomass in kudzu than habitats with more moisture and nutrient content. The dynamics of TN and TP in plant organs showed the highest accumulation in leaves, followed by roots and stems in both species. The total non-structural carbohydrates had consistent seasonal dynamics among different organs of P. montana but not in S. angulatus.

Key words: Biomass, Pureria Montana, Sicyos angulatus, nitrogen, phosphorous, total non-structural carbohydrate

Introduction

Most dominant species at first were *Phragmites japonica* and *Miscanthus sacchariflorus* which are pioneering species at stony floodplain in East Asia. However, they were gradually replaced by herbaceous lianas. The dominant lianas species in these days are exotic *Sicyos angulatus*, while frequently replaced by *Pueraria montana*, which is native in this area. This species colonizes generally at riparian area rather than inside the river channel. Both are herbaceous lianas and invasive, however, their life cycles are very different from each other. *P. montana* is a perennial leguminous characterized by possessing of large stolon and roots underground (Parks et al. 2002), therefore all leaves die off during winter, it is still alive and starts growing at the same spot in the next spring (Bodner and Hymowitz, 2002). *S. angulatus*, on the other hand, is annual. Its seedling starts growing in June, when spring flowering taxa are dying. However, it can germinate sporadically throughout the growing season (Jones, 1971; Pheloung et al., 1999), and then extend vines at an enormous speed. In contrast to *P. montana*, its tap root is extremely shallow and small (EPPO 2009). Besides the fundamental difference in their life-cycles, soil conditions of their habitats also seem to be enormously different.

P. montana shows a high adaptability to different habitat conditions and fast growth in different conditions but *S. angulatus* shows different attitudes from the *P. montana*. Although nutrient availability is a major determinant of plant distribution, little is known about adaptations that enable species to occupy nutritionally distinct sites. Possible adaptations to nutrient stress include (1) a low growth rate and consequently reduced nutrient requirement, (2) a high nutrient absorption capacity, (3) reduced nutrient loss, and (4) alterations in biochemistry of nutrient use. Most plants from low-nutrient sites have an inherently low growth rate and consequently a low nutrient requirement (Chapin and Kedrowski, 1983). Knowledge of the nutrient status of the various plant organ and their seasonal changes during their growing season is a necessary basis for a proper judgment of the effect of these changes on the functioning of the ecosystem (Tolsma et al. 1987). As well as storage is a characteristic feature of most plants, particularly perennials, and the subject has been thoroughly reviewed according to its chemistry and physiology (Smith, 1973). *P. montana* is able to allocate a significant portion of its carbon budget to root growth and the high allocation of carbon to roots is accompanied by an ability to root wherever stems touch the soil surface (Tsugawa et al., 1986). Quantitative studies that determine material budgets and resource allocation patterns across the growing season are of paramount importance (Asaeda et al., 2008). The lack of quantitative investigation on the ecological effects of *P. montana* and *S. angulatus* is a severe impediment to our understanding of its current and future effects on plant communities, forest ecosystems. Despite widespread anecdotal statements, little quantitative information is available about their eco-physiology and survival mechanisms. The major objectives of the study were to find out the adaptation mechanisms of theses species through the evaluation of biomass measurement; functions of nutrient cycles in ecosystem through seasonal changes of nutrient status in plant organs as well as seasonal allocation of TNC in plant organs as a control mechanism in two contrasting soil sites.

Materials and methods

Observation was conducted at two locations: (1) near Fuchu Yotsuya bridge (35°39′46″N, 139°26′15″E) denoted by Fuchu and (2) at the flood plain of the downstream of Ohgurigawa river junction (35°38″59′N, 139°28′32″E), denoted by Ohguri. These sites are situated at 34.6 and 33.6 km up from the river mouth, respectively. All locations were relatively flat, although slightly inclined from the bank side to the channel (Fig. 1). However, these locations are different in height, such as 0.3–0.9 m at Fuchu and 3.0–3.5 m at Ohguri from the normal water level. Thus inundation frequency was different in the study sites. Fuchu was most frequently inundated, followed by Ohguri was rarely inundated even under high floods. The largest flood ever experienced in last 20 years occurred on September 7th 2007. During the flood all these area was washed and large colonies of lianas had disappeared. The river transports a large amount of sand or further finer washload and accumulates on the floodplain during floods. Thus soil properties differ among locations depending on the frequency of the inundation. Fuchu was most sandy and gravelly among these locations with relatively low in plant biomass. The higher part of

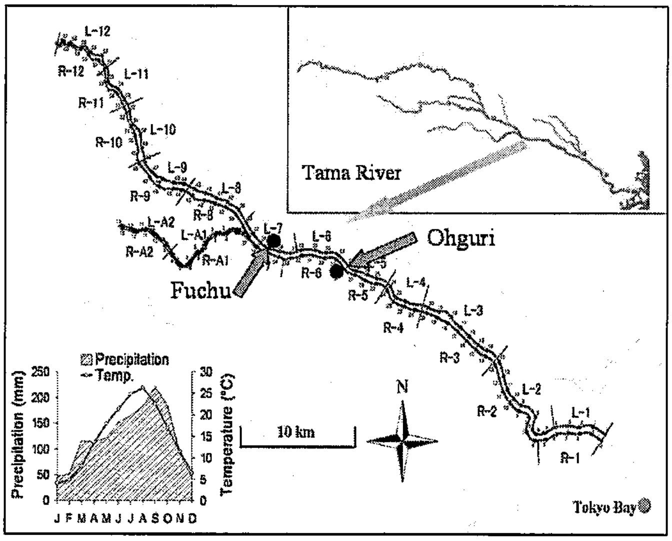

Fig. 1. Location of the study area (Fuchu and Ohguri)

Fuchu was gravelly with overlying thin sand layers. The lower part was composed of accumulated sand layer, which was finer and deeper in the layer. Although the area was covered widely with *M. sacchariflorus* before 2006, *S. angulatus* grew over *M. sacchariflorus* colony in 2006. After September 2007 flood, however, almost all *S. angulatus* colony disappeared from the area, then *M. sacchariflorus* stand widely recovered during the year. However, patchy colonies of *P. montana* and *S. angulatus* were also spotted. Ohguri was originally covered with *M. sacchariflorus*, which was, however, covered with *P. montana* invaded several years before, then by *S. angulatus*. The species competition was, therefore, extremely intensive with complex multi-stories structures, such that *S. angulatus* densely overlaid by *P. montana* which covered *M. sacchariflorus*. However, these two sites appear distinct soil characters shown in Fig. 2 & 3.

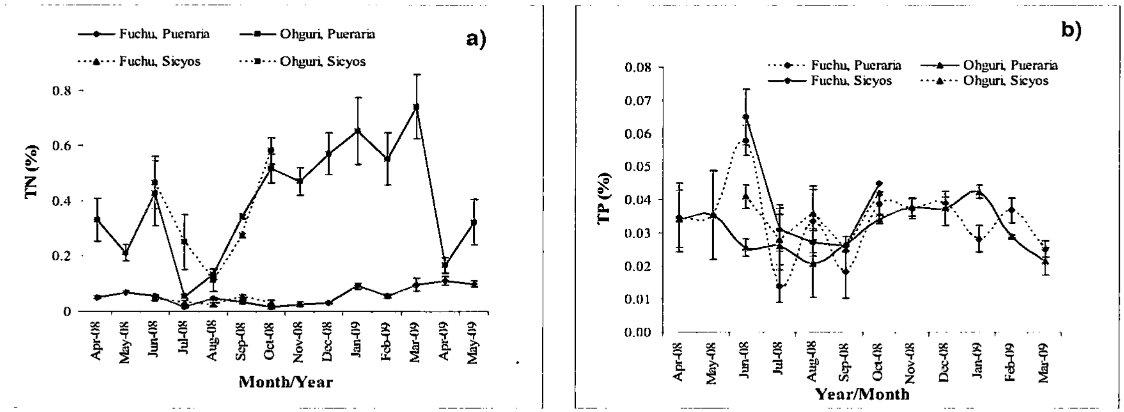

Fig. 2. Changes of (a) TN and (b) TP in soil over the season in two sites of *P. montana* and *S. angulatus*. Errors bars indicate standard deviations. When not visible, error bars were smaller than the symbols used.

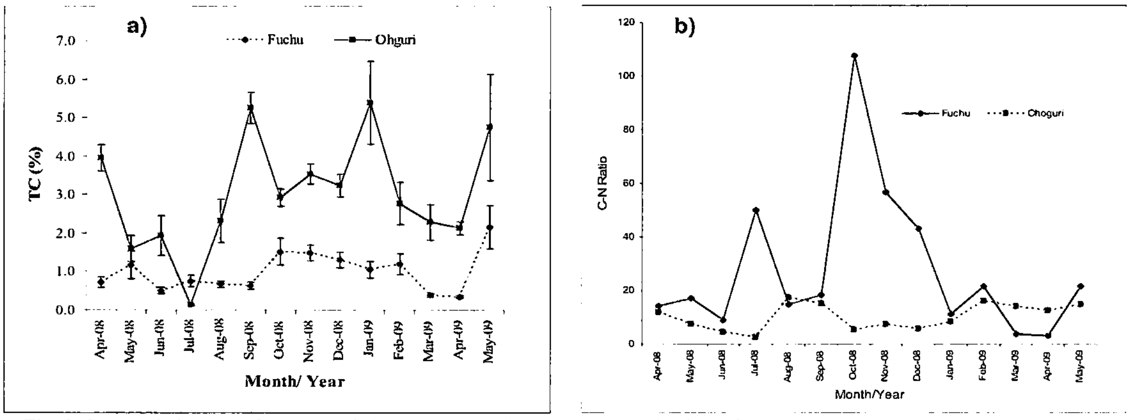

Fig. 3. Seasonal changes of (a) TC and (b) TC-TN ratio in soil in two study sites of *P. montana*. Errors bars indicate standard deviations. When not visible, error bars were smaller than the symbols used.

The study was carried out from April 2008 to June 2009 and sampling was carried out at monthly intervals in triplicate at each time from two sites. Three individuals were randomly selected in the apparently homogenous area. Ohguri was the highest between two sites and relatively homogeneous with dense herbs and the substrate is composed of mostly silt. At each observation, typical ramets were selected and then shoots, belowground organs and surrounding sediments were carefully dug out to a depth of at least 1 m to obtain all of the belowground tissues. The depth of *P. montana* roots was not much different at the same locations. Materials at the bottom of the hole were carefully sieved to ensure there was no remaining plant material. All of these samples were put into a plastic bag for transportation to the laboratory. At the same time, soil samples at the top and bottom of the rhizosphere were collected and were tightly sealed in a plastic vials.

In the laboratory, all plant samples were rinsed with pressurized water. Then they were sorted into leaves and stems for the aboveground tissues, and roots for the belowground tissues. These plant and soil samples were dried at 80°C in the oven for more than three days until the weight was constant. The dry weight was measured separately for each organ. Oven-dried samples were ground with a Wiley mill and were stored in sealed plastic vials until chemical analyses were conducted. For the plant biomass, total carbon (TC) and total nitrogen (TN) were determined by using Yanoco MT5 CHN analyzer (Kyoto, Japan). Total phosphorus (TP) was determined by ascorbic acid method (APHA 1998). For soil samples (particle size < 2 mm), TP and TN was determined by the same method as used for the plant biomass. Total non-structural carbohydrate (TNC) was measured using the phenol sulphuric acid method (Kabeya and Sakai 2005). All statistical analyses were performed using SPSS version 13.0 (SPSS Inc., Chicago, IL) and MS Excel. The t-test was adopted to compare means between two sites and p-values were considered significant at ≤ 0.05.

Results and discussion

Seasonal biomass allocation

Primary production and the ratio between aboveground and belowground biomass characterize growth traits of plants as well as the conditions of the study sites. Most species respond to different conditions by changing their ratio between belowground (R) and aboveground (S) biomass (R/S ratio). The responses to changing condition observed as differences in the R/S ratio reflect the general ecological characteristics of the *Pueraria montana* species. The study conducted in two places with distinct soil characteristics- one place called Fuchu is sandy, frequently flooded and low nutrient content and another place called Ohguri is more organic, rarely flooded and high nutrient availability than the former one. These two places show the different biomass allocation (Fig.4a). Ohguri had the highest above ground biomass (AGB) and below ground biomass (BGB) biomass than Fuchu as this area is rich in nutrient and high moisture content.

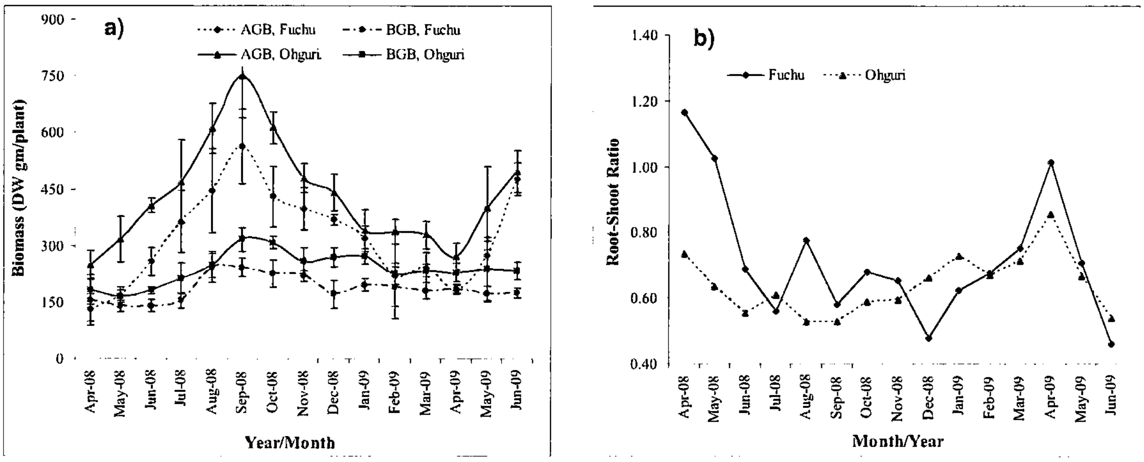

Fig. 4. Seasonal changes of (a) biomass and (b) root and shoot ratio in P. montana of two study sites. Errors bars indicate standard deviations. When not visible, error bars were smaller than the symbols used.

The highest biomass production was found in September in both places and then it decreased during autumn and winter. In growing period the maximum AGB was about 750±112 g DW plant^{-1} and 562±99 g DW plant^{-1} in Ohguri and Fuchu, respectively. AGB in Ohguri was significantly higher that of Fuchu (t-test, $p<0.05$) as well as there is significant difference between BGB in two sites (t-test, $p<0.05$). However, the root-shoot ratio (Fig. 4b) was higher .in Fuchu than Ohguri. As Fuchu soil contains less nutrient and low moisture so the plants form the extensive root system for arranging the required materials.

The root-shoot ratio was always lower than 1.0 in Ohguri but sometimes it is more than 1.0 in Fuchu. The R/S ratio was greater than 1.0 at the beginning of the growing season and it decreased during the growing period and again increased in the autumn and winter period. The root-shoot ratio showed the similar trend to those reported elsewhere (Lambers and Poorter, 1992). Dusek and Kvet (2006) reported that belowground biomass increases in dry and nutrient poor habitat, whereas more aboveground biomass allocation is in sufficient nutrients and water condition. This study supports the hypothesis because the result shows more or less similar pattern. The AGB (stems and leaves) showed a decreasing pattern after the summer but the BGB showed the reverse pattern.

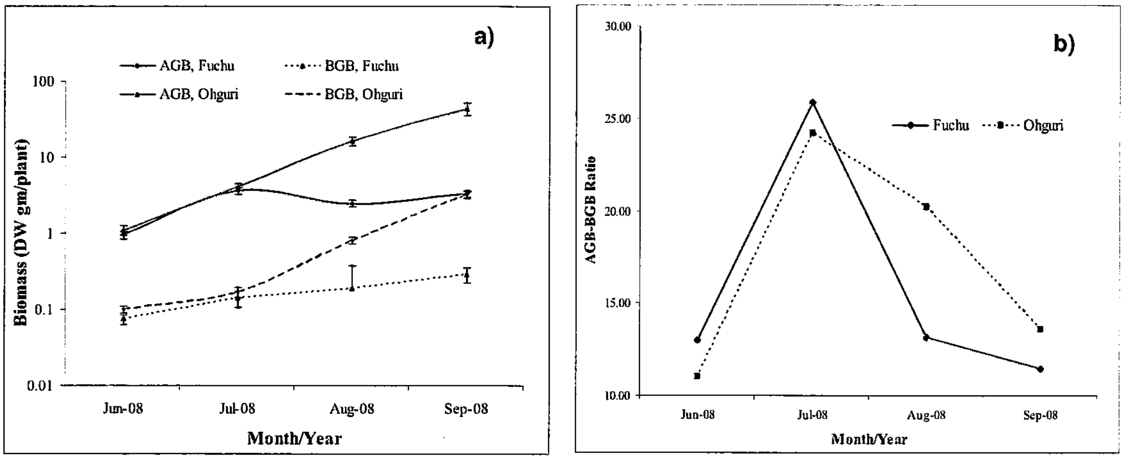

Fig. 5. Seasonal changes of (a) biomass and (b) AGB and BGB ratio of *S. angulatus* in two sites. Errors bars indicate standard deviations. When not visible, error bars were smaller than the symbols used.

In case of *S. angulatus*, the biomass allocation showed higher in Ohguri than Fuchu because it does not grow well in nutrient poor soil (Fig. 5a). The BGB was very small in comparison to AGB (Fig. 5b). The highest AGB biomass was attained in August- September. In Fuchu the plant density was very low, it was rarely found in the bank of river which contained comparatively more nutrients than the upper side whereas in Ohguri it was evenly distributed in the upper and lower bank of the river due to homogeneity in soil moisture and nutrient content as well as high organic matter presence in the soil.

Sometimes *S. angulatus* was found inside the *P. montana* stands but sometimes outside of the stands. Though they are both aggressive lianas but due to higher amount BGB biomass and hard wood root system in *Pueraria montana* it grows strongly in any soil type than *Sicyos angulatus* because it has small and sof wood root systems. Besides, the AGB-BGB ratio of *Sicyos angulatus* was many times higher than *Pueraria montana.* The *Pueraria montana* can grow any place with or without nutrients and other necessities but *Sicyos angulatus* can not grow without nitrogen rich small particle soil. Infertile habitats, which can support only a slow growth rate, are dominated by perennial rather than by annual species (Grime and Hunt, 1975). As Fuchu soil contains lower amount of TN and larger particle size, it attained low density annual species like *S. angulatus* as well as low biomass than Ohguri.

Seasonal changes of nutrient concentrations in plant organs

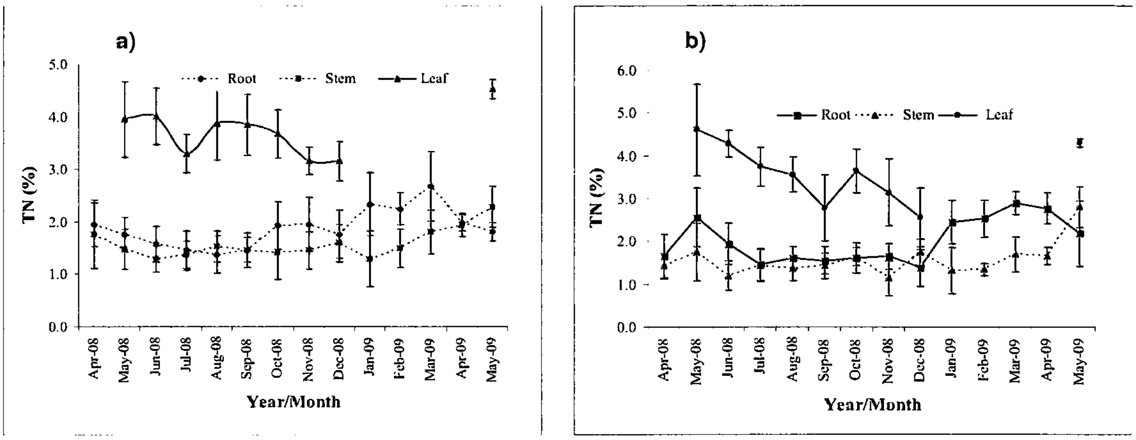

Fig. 6. Seasonal concentrations of TN in *P. montana* organ in (a) Fuchu and (b) Ohguri. Errors bars indicate standard deviations. When not visible, error bars were smaller than the symbols used.

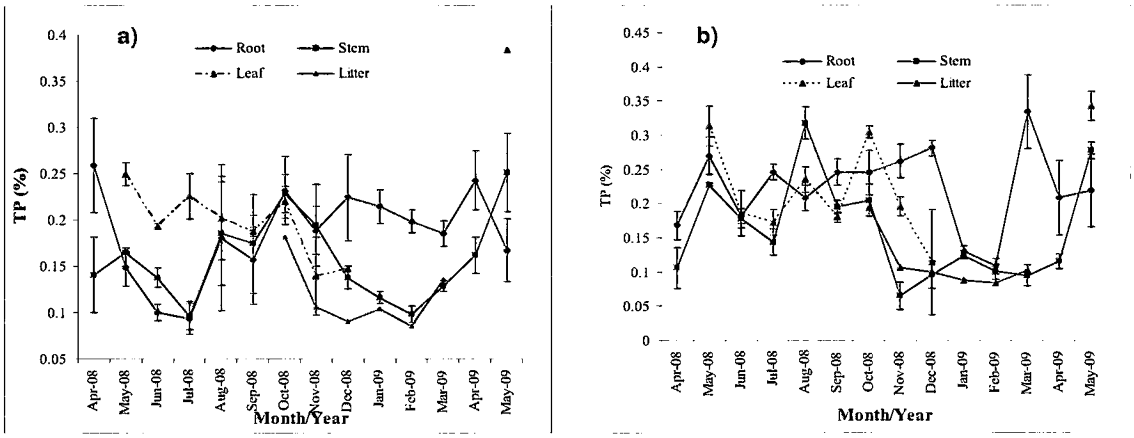

Fig. 7. Seasonal changes of TP in plant organ of *P. montana* in (a) Fuchu and (b) Ohguri. Errors bars indicate standard deviations. When not visible, error bars were smaller than the symbols used.

At the study site leaf emergence began at the middle of April, after that, leaves and shoots expanded from May to September. In October, leaves turned to yellow and began to shed. Leaf shedding ended by January. Fig. 6 a, b and 7a, b show seasonal changes in TN and TP in each plant organ of *P. montana* in Fuchu and Ohguri respectively. TN and TP concentrations were high in leaf in both places and the highest was in May but it decreased gradually during the leaf expansion period. The maximum TN concentration was 4.01 and 4.60% in Fuchu and Ohguri respectively whereas the maximum TP concentrations were 0.38 and 0.34% in Fuchu and Ohguri in leaf. Thereafter, leaf nutrient concentration showed little fluctuations until December. There was significant difference between two sites of TN content but no significant difference between plant organs (t-test, $p<0.05$). The concentrations of TN and TP in current stems decreased from May to June then showed little fluctuations until April. Again, the concentrations in roots decreased during the growing period and increased gradually after summer and showed the trend a little fluctuation until April. The dynamics of TN and TP concentrations showed the highest accumulation in leaf followed by roots and stems in both sites.

The results show that the largest portions of N and P were distributed in leaves throughout the growth period. The pattern of seasonal changes in leaf, stems and roots is similar to that of the other perennial plants reported previously (Grigal et al., 1976; Chapin et al., 1980; Ralhan and Singh, 1987; Saiko and Masuzawa 1992; Sasaki and Nakatsubo, 2007). The initial decline in concentrations of N and P in leaves coincided with leaf expansion and was probably due to dilution by increasing leaf material (Chapin and Tryon, 1983), although leaching loss of N and P by rain might also contribute to the decline (Sasaki and Nakatsubo, 2007). Many perennial plants resorb nutrients from leaves to organ (roots and stems) in the abscission period and use the stored nutrients for the next bud break and growth (Bollmark et al., 1999). So, the study supports that the *P. montana* species are prominent in nutrient storage because it shows the increment trend from the autumn period. Several authors have hypothesised that nutrients are stored in roots at the end of the vegetative cycle via retranslocation from shoots, allowing rapid regrowth in next spring season (Laclau et al., 2002).

As well as *S. angulatus* starts to grow from June in the natural condition and less than 25% (generally less than 5%) of seed carbon comes from stores. The remaining carbon comes from concurrent photosynthesis. The reproductive structures themselves contribute as much as 30-65% of their carbon requirement through photosynthesis. In contrast, 50-90% of the nitrogen and phosphorus in seeds of annual plants is recycled from vegetative tissues rather than taken from

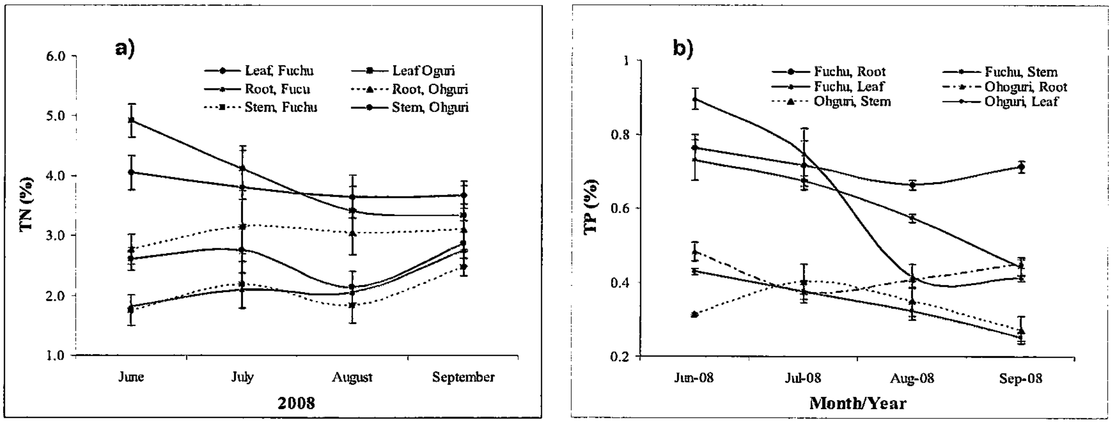

Fig. 8. Seasonal changes of (a) TN and (b) TP in plant organ of S. *angulatus* in Fuchu and Ohguri. Errors bars indicate standard deviations. When not visible, error bars were smaller than the symbols used.

concurrent uptake. Thus, as with autumn leaf senescence, recycling is a much more important source of nutrients than of carbon to support reproduction. There is remarkably little evidence on the extent to which wild plants draw on nutrient stores to support reproduction (Chapin et al. 1990). The Fig. 8a, b show that leaf contains higher accumulation of TN and TP than root and shoots in both places. In June, leaf attained the highest TN and TP and it gradually decreased with time. The maximum TN concentration of leaf was 4.92 and 4.05 % in Ohguri and Fuchu, respectively followed by root and stems. TN content in root showed a significant difference between two sites but stem and leaf had no significant difference (t-test, $p<0.05$).Whereas the maximum concentration of TP in leaf was 0.76 and 0.48% in Fuchu and Ohguri respectively followed by roots and stems. There was a significant difference TP concentration in root and stems between the two sites but leaf had no significant difference. The overall results of two species show that no major differences in patterns of TN and TP concentrations among plant organs in nutritionally distinct sites.

Seasonal variations of carbohydrates

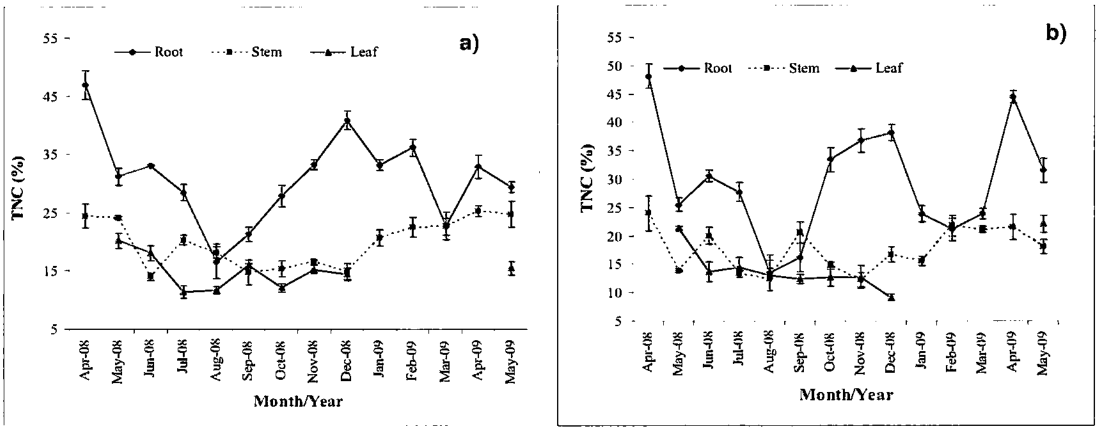

Fig. 9. Seasonal changes of TNC in plant organ of *P. montana* in (a) Fuchu and (b) Ohguri. Errors bars indicate standard deviations. When not visible, error bars were smaller than the symbols used.

Fig. 9a, b presents the annual patterns of TNC concentrations in plant organs of *P. montana* where decreasing concentration in roots were observed in May-August and again it started to increase from August to December i.e. during autumnal it reached the highest accumulation and August was the lowest concentration. It seems a very clear trend in the case of roots whereas the stems and leaf did not show consistent pattern. Roots contain the highest amount of TNC among the plant organs. The maximum level (47%) was observed in roots and 24 and 20% was in stem and leaf respectively. The aboveground biomass production reflected the pattern of TNC in the belowground. Current stems had low TNC concentration in early stage of growing and increased a little bit with fluctuations during the growing period. In contrast, TNC concentration in roots declined in growing period, then gradually increased through the remainder of the time. Seasonal pattern of TNC concentration in the various plant parts of Fuchu were similar to those of the Ohguri populations (Fig. 9a, b). All roots show a decrease in TNC concentration in spring and summer followed by an increase in autumn until winter indicating the role in storing carbohydrates to support spring growth (Chapin et al., 1986). High levels of root TNC are believed necessary for legume plant survival when they are defoliated or exposed to environmental stress (Jung and Smith 1961; Smith 1973). Leaf TNC concentration remained stable from June to November and then declined, whereas in current stems it continued to rise or remained stable, reflecting loss of carbohydrate from leaves and accumulation in stems. TNC in plant organs of *P. montana* had no significant difference between two sites (t-test, $p<0.05$).

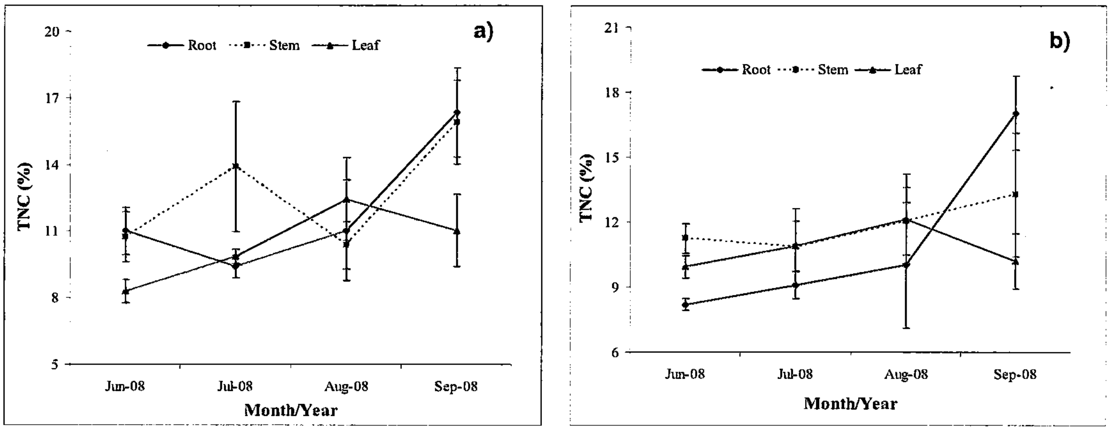

Fig. 10. Seasonal changes of TNC in plant organ of *S. angulatus* in (a) Fuchu and (b) Ohguri. Errors bars indicate standard deviations. When not visible, error bars were smaller than the symbols used.

Whereas *S. angulatus* as an annual allocates relatively little of their acquired resources to storage which contributes to their high growth rate (Schulze & Chapin, 1987). Annuals are generally short-lived, and the rapid formation of a large seed biomass ensures survival of the population and avoids periods of low resource supply. During seed filling, carbohydrate reserves in stems are depleted. As *S. angulatus* is an annual herb, it did not show any significant difference of TNC among root, stem and leaf concentration. Fig. 10a, b shows TNC concentration in roots, leaf and stem in Fuchu and Ohguri respectively. The concentration in plant fractions is very low compared to perennial one. The highest concentration was found in roots (16%) followed by stem (15%) in

September and at that time leaf experienced a decrease level from 13 to 11% in Fuchu whereas in Ohguri stem contained the highest in quantities (17%) and gradually increased from June to September. TNC had no significant difference between two sites among plant organs (t-test, $p<0.05$) of *S. angulatus*. As *P. Montana* is a perennial, the fall translocation of TNC to the tuberous roots is important to the establishment of the next plant growth. So, grazing or cutting prior i.e. in August to this translocation weakens plant growth the next year.

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