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The growth and nutrient uptake of invasive vines on contrasting riverbank soils

M. Harun Rashid*[1], Md Nazim Uddin[2], Animesh Sarkar[3,4], Mahfuza Parveen[5], and Takashi Asaeda[3]

[1]Department of Agronomy, Bangladesh Agricultural University, Mymensingh 2202, Bangladesh
[2]Institute for Sustainable Industries & Liveable Cities, Victoria University, Melbourne 8001, Australia
[3]Department of Environmental Science, Saitama University, 255 Shimo-okubo, Sakura-ku, Saitama 338-8570, Japan
[4]Department Food Engg. & Tea Technology, Shahjalal University of Science and Technology, Sylhet 3114, Bangladesh
[5]Department of Environmental Science and Disaster Management, Daffodil International University, Dhaka 1207, Bangladesh

Running head:
Growth and nutrient uptake of invasive vines

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*Corresponding author (mhrashid@bau.edu.bd)

Abstract

This study sought to investigate the research question as to whether the growth and nutrient uptake of two invasive vines, *Pueraria lobata* and *Sicyos angulatus*, are affected by the heterogeneity of soil characteristics of two riverbank sites with different flooding regimes. Soil, individual ramets of *P. lobata* and *S. angulatus* plants were sampled monthly from quadrats set on homogenous stands from two riparian sites along Tama River, Japan for over a year. Soil nutrients, above- and belowground biomass, tissue nutrient and non-structural carbohydrate contents were estimated and resource allocations to different organs were calculated. Flooding frequency directly affected the substrate characteristics of the sites; the frequently flooded site had coarser particle and less nutrient content. There were significant differences between the belowground biomass (BGB) and the aboveground biomass (AGB) of both *P. lobata* and *S. angulatus* between the sites. However, the BGB:AGB ratio of these species were statistically similar regardless of the substrate conditions. While the biomass of *S. angulatus* were much reduced in coarse habitat, the total amount of nutrient uptake by *P. lobata* was not affected by habitat the condition. Concentrations of total nitrogen, total phosphorus and starch in root tissues of *S. angulatus* were less in frequently inundated soil. The results of this study suggest that inundation frequency directly affects the substrate condition of a riverbank habitat which in turn affects plant growth, and invasive plant species growing in such habitat respond differently to substrate condition in terms of growth and nutrient uptake.

keywords *Pueraria lobata*; *Sicyos angulatus*; resource allocation; riverbank soil; soil characteristics

1 Introduction

The performance of a plant species is governed by various interacting physico-chemical factors of the habitat. These factors include the availability of nutrients, moisture, light and other resources, physiological capabilities of that species in the given environment, and biotic factors such as herbivory or diseases. Biological diversity faces tremendous pressure throughout the world. Vitousek (1990) recognized biological invasion as the second most important factor that causes biodiversity loss. In addition, much other research (for example, McGeoch et al., 2010; Sala et al., 2000) has also agreed with the view of Vitousek (1990). Invasive species are believed to have special traits that enable those plants to utilize natural resources more efficiently than the native species, and these plants can modify the ecosystem to produce favorable conditions for their growth and development (Rao & Sagar, 2012; Vitousek, 1990).

Some research has concluded that the management of invasive plants depends on the understanding of the processes of their introduction and dispersal, and on other environmental factors that govern these processes (for example, Ramula, Knight, Burns, & Buckley, 2008; Reid, Morin, Downey, French, & Virtue, 2009). It has been established that in habitats with poor nutrients, the input of nutrients increases the chance of invasion by one or more species (James, 2012) over the native species. For example, it has been reported that the inclusion of nitrogen in slow-growing species dominating nutrient-deficit systems results in the colonization of the invasive species (Brooks, 2003). Due to the faster growth rates and capabilities of higher N use efficiency, fast-growing invasive species are thought to be more competitive than their slow-growing native counterparts in N rich soils (Perry, Blumenthal, Monaco, Paschke, & Redente, 2010). In contrast, slow-growing native species allocate much of their resources to belowground structures due to their ability to recycle and store N, and therefore these plants prefer to grow under low N conditions (Fargione & Tilman, 2002).

Although the triggers and underlying mechanisms of plant species invasion are not yet been fully understood, it is clear that disturbance of the habitat or fluctuation of resources promotes the process (Shackelford, Renton, Perring, & Hobbs, 2013). Researchers have noted that some invasive species are highly capable of invading a system irrespective of disturbance, and some invasives are able to modify the ecosystem structure, energy flows, and nutrient pools and fluxes. For example, Meyerson, Saltonstall, Windham, Kiviat, and Findlay (2000) reported that aboveground N stocks were found to be higher in plant communities dominated by *Phragmites australis* compared to sites without it.

Riparian floodplains under a natural flow regime are highly dynamic due to a large amount of flooding disturbance (Brunet & Astin, 2000). Therefore, riparian landscapes provide corridors for the dispersal of many invasive exotic species (Johansson, Nilsson, & Nilsson, 1996; Naiman & Décamps, 1997) invasion, and naturalization of exotic plants (Pyšek & Prach, 1993). Catford et al. (2012) reported that early stages of succession are more prone to exotic invasion due to the abundance of resources. However, on a riparian floodplain during a large flood, vegetation is often washed away and the succession starts afresh (Asaeda, Baniya, & Rashid, 2011). Therefore, the same mechanism of exotic invasion as in terrestrial ecosystem might not be applicable on a riparian floodplain.

Since the terrestrial ecosystem is more or less stable, an invasive plant species adapted to a nutrient-deficit terrestrial habitat will follow a nutrient acquisition or habitat modification strategy. The riparian ecosystem, on the other hand, is frequently disturbed and the nutrient and moisture regimes change abruptly (back and forth in positive and negative directions). Therefore, nutrient acquisition of an invasive plant species adapted to such habitat (frequently flooded) will be governed by the level of disturbance unlike to species adapted to a habitat with less disturbed (comparatively fertile) soil. To test this hypothesis, we observed the growth and tissue nutrient contents of two invasive vines, *Pueraria lobata* and *Sicyos angulatus*, on two sites (in terms of flooding disturbance and soil fertility) along the Tama River in Japan.

2 Materials & methods

2.1 Site characteristics

Observations were conducted at two locations along the banks of the Tama River: (1) at Fuchu (35°39′46″N, 139°26′15″E), 34.6 km upstream, and (2) at Ohguri (35°38′59″N, 139°28′32″E), 33.6 km upstream from the river mouth (Figure 1). The locations have difference in elevation (0.3∼0.9 m at Fuchu and 3.0∼3.5 m at Ohguri) from the normal water level. The Fuchu site is inundated almost every year, whereas Ohguri is inundated if only there is a large flood. The soil of Fuchu is coarse and dry and that of Ohguri is finer, contains higher moisture and organic matter than Fuchu soil. There was a large flood (20 yr return period) in September 2007 in the Tama River system. Both of the study sites were inundated during this flood and all herbaceous vine colonies were washed away. Therefore, the colonies of *P. lobata* and *S. angulatus* colonies were relatively young during this study.

2.2 Study species

The study involved two invasive vines, viz. *Pueraria lobata* (Willd.) Ohwi, and *Sicyos angulatus*. *P. lobata* is a perennial plant and it has an extensive underground rhizome system (Parks, Tanner, & Prokop, 2002). It usually propagates through rhizome and flushes new shoots in early spring after overwintering (Bodner & Hymowitz, 2002). The growth of the *P. lobata* can be 30 cm a day and 18 to 30 m a season (van der Maesen, 2002). This species has been reported to have alleopathic potential (Rashid, Asaeda, & Uddin, 2010a, 2010b). *S. angulatus*, on the other hand, is an annual herbaceous vine. Its seedlings start growing in June, when the spring-flowering taxa are dying. It propagates through seeds that germinate sporadically throughout the growing season (Pheloung, Swarbrick, & Roberts, 1999). Smeda and Weller (2001) have recorded its stem length up to 7 m and growth rate up to 30 cm/day. *S. angulatus* has a very shallow and superficial root system (EPPO, 2010).

2.3 Soil and plant material collection

Homogenous areas of *Pueraria lobata* and *Sicyos angulatus* were located and three individual ramets or plants of each species were randomly selected from both sites. Four quadrats (2 m × 2 m) were randomly selected from each area and marked with poles and plastic rope. Soil and plant samples (*Pueraria lobata* and *Sicyos angulatus*) from these quadrats were collected during every month from April 2008 to April 2009. Samples were only collected on sunny days when there was no precipitation on the study sites. For estimation of the biomass, aboveground parts (stem, leaves etc.) of *P. lobata* and *S. angulatus* were collected. For the belowground biomass, soil was dug out to a depth of at least one meter and all underground tissues were collected. At the same time, four soil samples were collected from each quadrat (from the surface to a depth of 30 cm) with a soil-sampling auger. Before the senescence stage, all the pods (fruits) of the sampling plants were also collected separately for the purpose of nutrient uptake estimation.

For the analyses of plant tissue nutrients, carbohydrates, and chlorophyll concentrations, mature leaves (8-10), three stems and roots of both species were collected from plants which were close (<50 m) to the selected quadrats. For this, the month of peak vegetative growth (September) was chosen for the *P. lobata*; whereas the tissues of the *S. angulatus* were collected in October. The collected leaves were immediately put in a portable box and preserved with dry ice. The leaf chlorophyll contents from these leaves were measured immediately, on the same day when they were returned to the laboratory.

2.4 Laboratory analyses and estimation

All plant materials were washed thoroughly with tap water in the laboratory. Leaves, stems, and rhizomes or roots were sorted and were dried at 80°C in the oven for more than three days to a constant weight. The aboveground biomass (AGB) and belowground biomass (BGB) of each plant were measured. For each plant the leaf, stem, root/rhizome, and fruit/pod were oven-dried and ground with a Wiley mill. The ground materials were stored in sealed plastic vials until the chemical analyses were conducted. The total carbon (TC) and total nitrogen (TN) of the plant tissue was determined with a Yanaco MT5 CHN analyzer (Kyoto, Japan). The total phosphorus (TP) was determined by the molybdenum blue colorimetric method (Murphy & Riley, 1962) after digestion with H_2SO_4-$HClO_4$ (APHA, 1998). Sodium, copper and zinc were extracted using a Mehlich-3 extractant (Mehlich, 1984) from the ground plant tissue and by using the methods stipulated by Ziadi and Tran (2007). Then they were measured with an atomic absorption spectrophotometer (AA-6300 Shimadzu, Japan) at the respective wavelengths specified for the metals.

The total amount of all sugars (total non-structural carbohydrate, water soluble carbohydrate and starch) was measured using the phenol sulphuric acid method (Kabeya & Sakai, 2005). Acid extraction was carried out with a solution of 0.4 N H_2SO_4 for total non-structural carbohydrate (TNC). Each sample (∼6 mg) was placed in a 100 mL round-bottom flask with 50 mL of acid and refluxed for 1 h in a boiling water bath (Hot water-bath, Yamoto Scientific Co., Ltd., Kyoto, Japan). In the case of the water soluble carbohydrate estimation, only 50 mL of distilled water was used. The hot solution was filtered through Whatman No. 42 filter paper (Whatman International Ltd., Maistone, U.K). The filtrate was then cooled and diluted to a volume of 100 mL with distilled water. The carbohydrate content of the filtrate was determined spectrophotometrically (HACH-4800, Hach Company, Loveland, CO.) at 485 nm wavelength using the phenol-sulphuric acid method. A Glucose solution was used as a calibration standard. A correction factor of 0.9 was used to convert glucose equivalents to starch (Latt, Nair, & Kang, 2001). The results were expressed as a percentage on a dry weight basis.

Small fragments (5 mg) from the fresh leaves of the *Pueraria lobata* and *Sicyos angulatus* were taken by using scissors and the fresh weight of these segments was measured. Chlorophyll was extracted by 7 mL of N, N-dimethylformamide incubated in the dark for 24 h at 4°C (Moran & Porath, 1980). Extracted pigment was measured spectrophotometrically (HACH 4800; Hach Company, Loveland, CO, USA), following the equation proposed by Moran (1982), and expressing in micro grams chlorophyll per gram of the fresh weight (μg g^{-1} FW) of the leaf.

The soil pH was measured at a soil:water ratio of 1:2.5 (wt/wt). A 20 g portion of soil was extracted with 2 M KCl using a 1:5 soil: extractant ratio and 30 min shaking time. The moisture content of the soil samples was determined gravimetrically (Black, 1965). For this, a portion of each soil sample was separated before drying. All soil samples were then air-dried and the particle size distribution (in term of D25) was determined using the sieve method approved by the American Society for Testing and Materials protocol (ASTM, 2002). After the particle size analysis, all soils were passed through a sieve to obtain the $\leq$2 mm fraction. This fraction was used for the nutrient analyses. For the TC, TN and TP soil sample concentration analyses, the same methods were followed that were adopted for the plant tissue. When the soil samples were not used, they were kept in airtight polyethylene bags.

The annual biomass turnover of *Pueraria lobata* was calculated using the following equation:

$$BT_{net} = (AGB_{max} - AGB_{ow}) + (BGB_{max} - BGB_{ow}) \tag{1}$$

where BT_{net} = Annual biomass turnover (gDW/plant), AGB_{max} = Aboveground biomass in peak vegetative period (the maximum value) (gDW/plant), AGB_{ow} = Aboveground biomass at the onset of spring flushing (the minimum value) (gDW/plant), BGB_{max} = Belowground biomass at the end of senescence (the maximum value) (gDW/plant), BGB_{ow} = Belowground biomass at the onset of spring flushing (the minimum value) (gDW/plant).

In a similar way, the net annual production of the leaves, stem and underground rhizomes were calculated. The net storage of nutrients in the leaves, stem, fruits (pods), and underground rhizomes were calculated by multiplying the annual biomass of these organs with the respective average nutrient concentrations, and then all these components were summed to estimate the annual net nutrient uptake of a single *P. lobata* plant (Equation 2).

$$NU_x = \sum \left(BT_{net(i)} \times c_i\right) \tag{2}$$

where NU_x = Net annual uptake of a nutrient x (C, N, P, Cu, Zn and Na), $BT_{net(i)}$ = annual net mass of organ i (leaf, stem, rhizome, reproductive organs, etc.), c =

concentration of x in organ i.

2.5 Statistical analyses

All data were analyzed using R (R Core Team, 2013). Before conducting an analysis, raw data were checked for normal distribution with the one-sample Kolmogorov-Smirnov test as well as for homogeneity of the variances with the Levene's test. Arcsin data transformation was performed when the data did not follow normal distribution. A t-test was used to compare the means between the different sampling times. Two-dimensional Nonmetric Multidimensional Scaling (NMDS) of plant performance data (TN, TP, TC, Cu, Zn, Na, TNC and total biomass) were conducted using the function 'metaMDS', which is incorporated in the statistical package 'vegan' (Oksanen et al., 2010). The Bray-Curtis similarity was used as the pair-wise distance among samples.

3 Results

3.1 Site elevation and soil characteristics

The soil characteristics of the Ohguri and Fuchu sites were significantly different (Figure 2), and the size of D25 fraction of soil differed significantly between the sites ($p = 0.01$). It was found that the Ohguri soil was composed of fine sediments, whereas the D25 particle size of the Fuchu soil was more than twice as large as that of the Ohguri soil and the substrate was composed of coarse sand and gravels. The soil moisture content of the fine sediment (<2 mm) also differed significantly between the sites ($p = 0.02$) (Figure 2). Although the D25 fraction of soil was distinctly different between the sites, there was no significant correlation between the sediment moisture content and the D25 value ($R = -0.238$, $p = 0.072$). The Ohguri soil was slightly acidic ($pH = 6.29 \pm 0.21$) while the Fuchu soil was almost neural ($pH = 6.95 \pm 0.35$). Figure 2 also shows that the soil organic matter and nutrient levels significantly differed between the sites as all values were higher for the Ohguri. The N:P and C:N ratios were significantly different between the sites.

3.2 Biomass production

The aboveground biomass (AGB) of *P. lobata* increased sharply over the growing season and reached its peak values in September at both sites (Figure 3). It then gradually decreased until the beginning of the next growing season. Though the patterns of AGB production were similar at both study sites, the values were significantly different ($p < 0.05$). The maximum AGB values recorded were 750 g and 562 g of drymass per plant at Ohguri and Fuchu, respectively. There was significant difference of belowground biomass (BGB) production by *P. lobata* between Fuchu and Ohguri sites ($p < 0.05$) (Figure 3). The highest AGB of *P. lobata* at Fuchu site was recored in June, however, the seasonal variation of the same did not follow a conspicuous trend. The seasonal trend of *P. lobata* BGB was inverse to that of AGB at Ohguri site. AGB at Ohguri was recored higher during the early growth stage of *P. lobata* and then it inclined until August when it started to decline again. The mean ratio values of the belowground (BGB) and the aboveground (AGB) biomass (BGB:AGB ratio) of the *P. lobata* was 0.67 ± 0.23 and 0.59 ± 0.14 in Fuchu and Ohguri, respectively. There was no significant difference between these sites in terms of the BGB:AGB ratio ($p = 0.30$). The values were always <1.0 at Ohguri, but values >1.0 were sometimes recorded at Fuchu.

In *S. angulatus*, the drymass production was higher at Ohguri than at Fuchu (Figure 3).The BGB was very small compared to the AGB (Figure 3). The highest AGB was attained in August/September. At Fuchu, the *S. angulatus* density was very low and this species was rarely found on the lower riverbank, which contained comparatively more nutrients than the upper bank. At Ohguri, on the other hand, *S. angulatus* was evenly distributed on both the upper and lower banks thanks to the homogeneous soil moisture content and nutrient concentrations as well as the high contents of organic matter in the soil. The BGB:AGB ratio of this species did not differ significantly between the sites ($p = 0.59$). The average values of BGB:AGB in *S. angulatus* were 0.07 ± 0.02 and 0.066 ± 0.02 in Fuchu and Ohguri, respectively.

3.3 Nutrient uptake and plant tissue concentrations

There were no significant differences in nutrient (TN, TP and TC) concentrations in the *Pueraria lobata* tissues between the Fuchu and Ohguri sites (all $p>0.05$, Figure 4, Supplementary Table 1). However, TP and TC concentrations in leaf, stem, and root of *P. lobata* were slightly higher in Ohguri than those of Fuchu plants. TN, TP and TC concentrations in *Sicyos angulatus* did not change significantly due to the location, except for TN and TP in root tissues. *S. angulatus* in Ohguri had higher TN concentrations in the leaves and stems but the differences were not statistically significant. The phosphorus (TP) concentration of the *S. angulatus* root was significantly higher in Ohguri, whereas there were no differences in leaves and stems between the sites. Total carbon (TC) concentrations in the *S. angulatus* tissue were statistically similar at both sites. The dynamics of the TN, TP and TC concentrations in the *P. lobata* and the *S. angulatus* showed that the highest accumulation of these nutrients were in leaves at both sites. The leaf TN:TP value (at the vegetative stage) of the *P. lobata* was ∼20 at both sites, whereas this value for the *S. angulatus* was recorded ∼10 at both study sites (Table 1).

Copper concentrations in the leaf and root tissues of *P. lobata* differed significantly due to the locations (Figure 5), Supplementary Table 1). The Ohguri plants had a higher concentration of Cu in stem and root tissues. Significant differences of Zn between the two locations were found in stem and tissues only whereas Na concentration differed in leaf and stem. In the *S. angulatus*, no significant differences of Zn and Na concentrations in leaf, stem and root tissues were observed between the locations. However, significantly higher concentration of Cu were found in leaf and root tissues of Ohguri plants (Supplementary Table 1).

Table 1 presents the total amount of nutrient uptake from the soil by these plants from the soils of the study sites. There was not much difference in the amount of macro- (TN and TC) and micronutrients (Cu and Zn) absorbed by the *P. lobata* from the nutrient-rich Ohguri and nutrient-poor Fuchu sites. However, the difference was striking in the case of *S. angulatus*. The amount of nutrient (TN, TP, TC, Cu, Zn, and

Na) uptake from the Fuchu soil was much smaller than the values of Ohguri (Table 1).

3.4 Structural and non-structural carbohydrates

Non-structural carbohydrates (total non-structural carbohydrate (TNC), water soluble carbohydrate (WSC), and starch) in the *P. lobata* leaf, root and stem tissues did not differ significantly between the Fuchu and Ohguri sites (all $p<0.5$, Figure 6, Supplementary Table 1). For all non-structural carbohydrates, in the *P. lobata*, the highest concentration was found in the root, followed by the stem and the leaf, respectively. The same concentrations in the *S. angulatus* tissue was much lower than those in the *P. lobata*. In the *S. angulatus*, the order of accumulation in the tissue had no specific pattern. However, the concentrations of carbohydrates did not differ between the sites.

3.5 Chlorophyll concentrations in leaves

No significant difference in the *P. lobata* leaf chlorophyll concentration was found between the study sites (t-test $p = 0.054$, Supplementary Table 1). However, the values were always higher in Ohguri. Figure 7 shows the chlorophyll concentration was slightly lower in the early growth stage of the *P. lobata*; then the values increased slightly and remained the same until the senescence (November). In the *S. angulatus*, the leaf chlorophyll concentration was significantly higher in Ohguri (t-test $p = 0.01$, Supplementary Table 1, Figure 7).

4 Discussion

4.1 Flooding frequency and soil fertility

There were distinct differences in the soil particle size and nutrient contents of Fuchu and Ohguri. The Fuchu site is frequently inundated, whereas Ohguri is inundated only during large floods. The sampling sites of Fuchu were composed of large particles. In Ohguri, the undisturbed vegetation contributed to high organic matter incorporation into the soil and as a result the particle size became fine, and the nutrient content became higher. In a separate study, Asaeda, Rashid, and Ohta (2016) conducted a one-dimensional hydraulic simulation to estimate the frequency of inundation of study quadrats from its elevation and attributed the soil characteristics of these sites to the flooding regimes. They recognized that the inundation frequency was nearly inversely proportional to the elevation of the site. Since our observations were conducted on the same quadrats, we used the elevation to correspond the inundation frequency of the sampling points.

4.2 Plant performance comparison

The *Sicyos angulatus* produced a high dry mass at Ohguri, whereas its growth was very limited at Fuchu in comparison to the other site. This difference of biomass production between the sites might be the direct effect of washing away by floods, or the scouring of the nutrient-rich top layer sediment (Bayley & Guimond, 2009). The *Pueraria lobata*, although able to grow vigorously in wet areas, also grew in relatively dry areas. The total biomass and ratio of belowground biomass (BGB) and aboveground biomass (AGB) (BGB:AGB ratio or root:shoot ratio) was often considered to be the index of the conditions of the substrate especially on nitrogen and moisture content (Bonifas, Walters, Cassman, & Lindquist, 2009; Van Hees & Clerkx, 2003). Although the ratio depends on the trait, most plant species respond to altered substrate conditions by changing their BGB:AGB ratio.

The biomass partitioning of the *P. lobata* followed a similar pattern in nutrient-rich and nutrient-poor soils. Although the BGB:AGB ratio of the *P. lobata* was recorded >1.0 during the leaf flushing (in early spring) at the nutrient-deficit Fuchu site, in Ohguri it was always <1.0. The average value at both sites was also <1.0. No statistical significant difference in the values signifies that the *P. lobata* does not partition its resources due to the substrate conditions. Rather it follows the optimal partitioning theory (Gedroc, McConnaughay, & Coleman, 1996). Maintaining an optimal BGB:AGB ratio of this species can be explained by its nitrogen-fixing capability which enables this plant to grow well in nutrient-deficit substrates (Markham & Zekveld, 2007). Asaeda et al. (2016) reported that the nitrogen-fixing capacity of *P. lobata* increases when the availability of inorganic nitrogen in soil decreases and vice versa. Therefore, it can be assumed that this plant compensated the low soil TN by increasing its nitrogen-fixing capability in Fuchu and thus the BGB:AGB did not change. *P. lobata* accumulates its resources in the underground rhizome system before senescence and uses stored resources for flushing shoots in early spring. This phenology can explain the higher BGB:AGB ratio at the early and later growth stages.

In comparison to *Pueraria lobata*, *Sicyos angulatus* has much less biomass turnover. This is an annual vine and propagates though seeds. Therefore, it does not accumulate its resources in underground organs or roots. It has a very shallow and superficial root system and cannot move effectively through the Fuchu hard soil to forage nutrients and moisture. Therefore, at the Fuchu sites, its biomass drastically reduced in comparison to the Ohguri site. Since this species does not adjust the BGB:AGB ratio depending on the nutrient availability, its biomass production is greatly affected by the soil conditions.

It appeared that *P. lobata*, due to its nitrogen fixing property and the capability to extend root to the deeper zone of the soil, could grow on soil with varying range of D25, moisture and nutrients. The *S. angulatus*, however, grew only on fine soils. Therefore, we are unclear whether it's similar resource partitioning behavior in nutrient-poor and rich soils was due to its trait or succession mechanism, which has been studied elsewhere (Asaeda, Rashid, Kotagiri, & Uchida, 2011). Many invasive plants have increased rates of decomposition and nutrient cycling and thereby improve the habitat by incorporating organic matter into the substrate (Allison & Vitousek, 2004; Dassonville et al., 2008).

The nutrients and carbohydrate concentrations in the *Pueraria lobata* tissues (leaf, stem and root) did not vary between the Fuchu and Ohguri sites, except for the micronutrients (Cu, Zn and Na). Although the micronutrient concentrations varied between Fuchu and Ohguri, the pattern did not match the soil nutrient variations of the sites. This results were also reflected in the NMDS analyses of plant performance data for two sites (Fuchu and Ohguri) (Figure 8). *Pueraria lobata* biplot (stress=0.13) had much overlapping than that of *Sicyos angulatus* (stress=0.07). Some authors (for example, Dassonville et al., 2008; Vanderhoeven, Dassonville, & Meerts, 2005) have reported that many invasive plants grown in nutrient-deficit soil uptake higher amount of nutrients than those grown in comparatively more fertile soil and thus contribute to enriching the top soil upon degradation, while others argue that invasive plants bring about soil improvement by incorporating a large amount of organic matter.

The findings of this study suggest that flooding frequency in a riparian habitat governs soil characteristics and affects plant growth. However, all invasive plants growing on frequently disturbed riverbanks do not follow the similar pattern of nutrient acquisition and allocation, and growth. Rather their performance in such habitat is mostly dependent on their phenological and physiological traits.

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Data Availability Statement (DAS)

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Figure captions

Figure 1: Location of study area (Fuchu and Ohguri). The rectangle on the inset map shows the position of the study locations in Japan.
File Name:fig1

Figure 2: Soil characteristics of the study sites. The top, middle and bottom margins of the box represent third quartile, median and first quartile, respectively (n=21). The whiskers represent data range while the black dots are data outliers. Double asterisk (**) in a plot indicates that the respective soil characteristic differs significantly ($p<0.01$) between Fuchu and Ohguri sites. OM, TC, TP and TN designate organic matter, total carbon, total phosphorus and total nitrogen, respectively.
File Name:fig2

Figure 3: Seasonal variation of above and below-ground biomass production of *Pueraria lobata* and *Sicyos angulatus* at the study sites. Error bars indicate standard deviation (n = 3). 'Pue', 'Sic', AGB and BGB stand for *P. lobata*, *S. angulatus*, above ground biomass, and below ground biomass, respectively. BGB/AGB designates the ratio of BGB and AGB.
File Name:fig3

Figure 4: Total nitrogen (TN), total phosphorus (TP) and total carbon (TC) concentrations of *Pueraria lobata* and *Sicyos angulatus* tissues collected from study sites. Error bars indicate standard deviation (n = 9). Double asterisk (**) in a plot indicates that the values differ significantly ($p<0.01$) between Fuchu and Ohguri sites.
File Name:fig4

Figure 5: Micronutrient (copper (Cu), zinc (Zn) and sodium (Na)) concentrations of *Pueraria lobata* and *Sicyos angulatus* tissues collected from study sites. Error bars indicate standard deviation (n = 9). Single (*) and double asterisks (**) in a plot indicate that the values differ significantly at $p<0.05$ and $p<0.01$, respectively between Fuchu and Ohguri sites.
File Name:fig5

Figure 6: Concentrations of carbohydrate fractions (starch, total non-structural carbohydrate (TNC) and water soluble carbohydrate (WSC)) in *Pueraria lobata* and *Sicyos angulatus* tissues collected from study sites. Error bars indicate standard deviation (n = 9). Single asterisk (*) in a plot indicate that the values differ significantly at $p<0.05$ between Fuchu and Ohguri sites.
File Name:fig6

Figure 7: Total chlorophyll concentration (chl) in *Pueraria lobata* and *Sicyos angulatus* leaves collected from study sites. Error bars indicate standard deviation (n = 9). The bars in April and November are missing because no *S. angulatus* plant grew in these months. Single asterisk (*) in a plot indicate that the values differ significantly at $p<0.05$ between Fuchu and Ohguri sites.
File Name:fig7

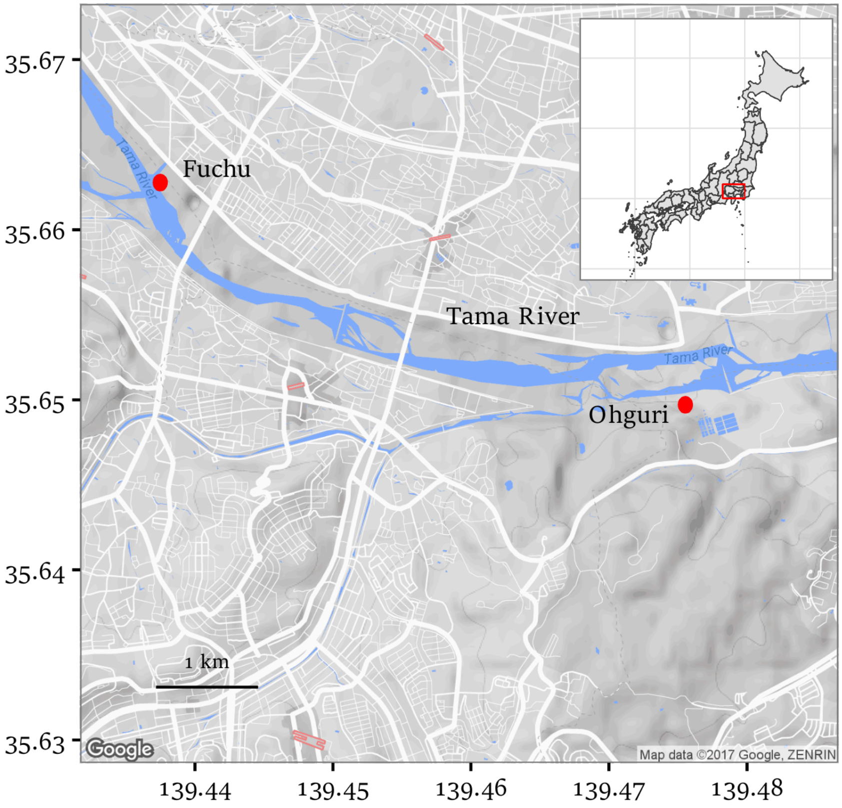
Figure 8: Nonmetric Multidimensional Scaling (NMDS) based on average values of tissue nutrient and carbohydrate contents, and biomass data of *Pueraria lobata* and *Sicyos angulatus* of two study sites. Bray-Curtis similarity as the pair wise distances among samples was used for grouping. The label is situated at the centroid of each convex hull grouping the sites. Study sites are connected to the cluster centroids by a line using the functions 'ordispider' and 'ordihull' (statistical package 'Vegan').
File Name:fig8

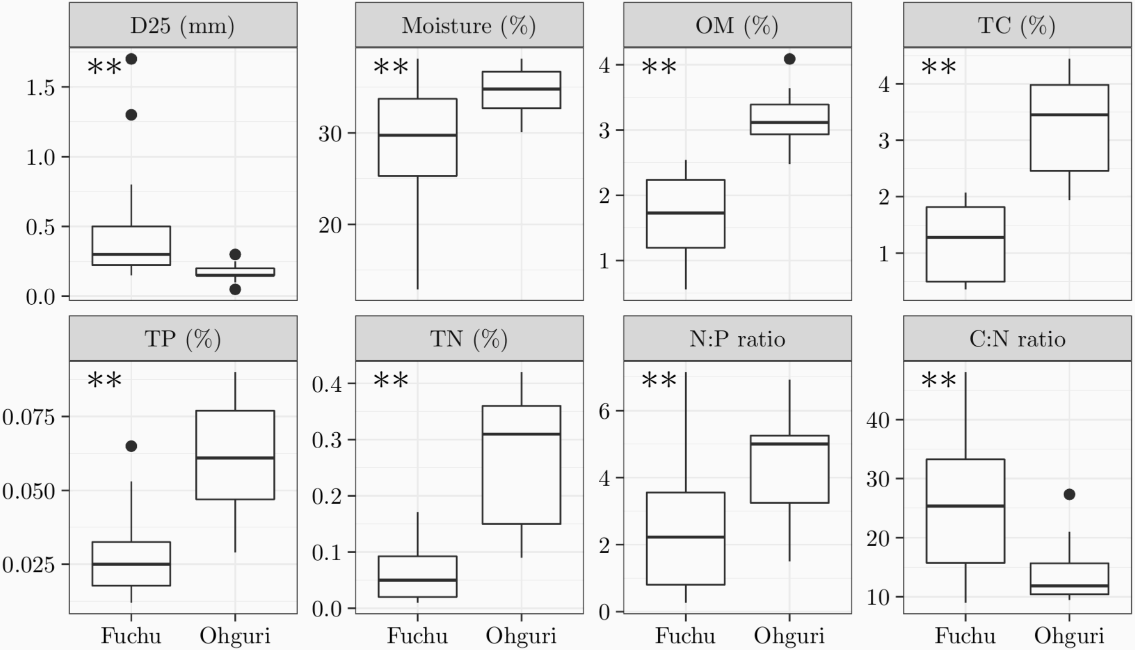
Table 1: Annual total nutrient uptake by individual *Pueraria lobata* and *Sicyos angulatus* plants from soil (n=3).[†]

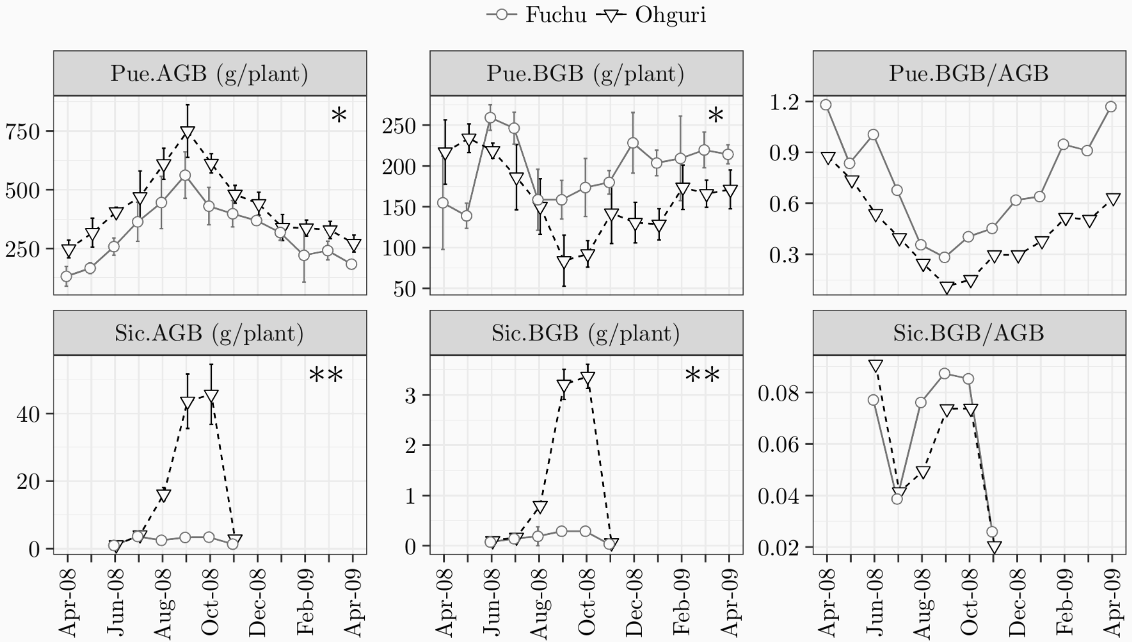
		TN (g)	TP (g)	TC (g)	Cu (mg)	Zn (mg)	Na (mg)	TN:TP[‡]
Pueraria	Fuchu	23.36±31.9	1.63±0.22	315.6±53.6	0.10±0.02	0.30±0.23	2.76±0.33	18.99±2.92
	Ohguri	28.46±4.06	2.09±0.13	378.3±52.1	0.12±0.02	0.44±0.53	4.32±0.69	18.43±8.74
Sig. level		p=0.80	p=0.04*	p=0.22	p=0.29	p=0.70	p=0.02*	p=0.92
Sicyos	Fuchu	0.42±0.05	0.05±0.001	6.33±0.93	0.002±0.0	0.004±0.0	0.063±0.0	9.59±1.99
	Ohguri	79.77±13.2	8.47±2.32	875.9±209.1	0.31±0.05	0.71±0.08	9.15±1.73	11.56±1.16
Sig. level		p<0.01**	p<0.01**	p<0.01**	p<0.01**	p<0.01**	p<0.01**	p=0.21

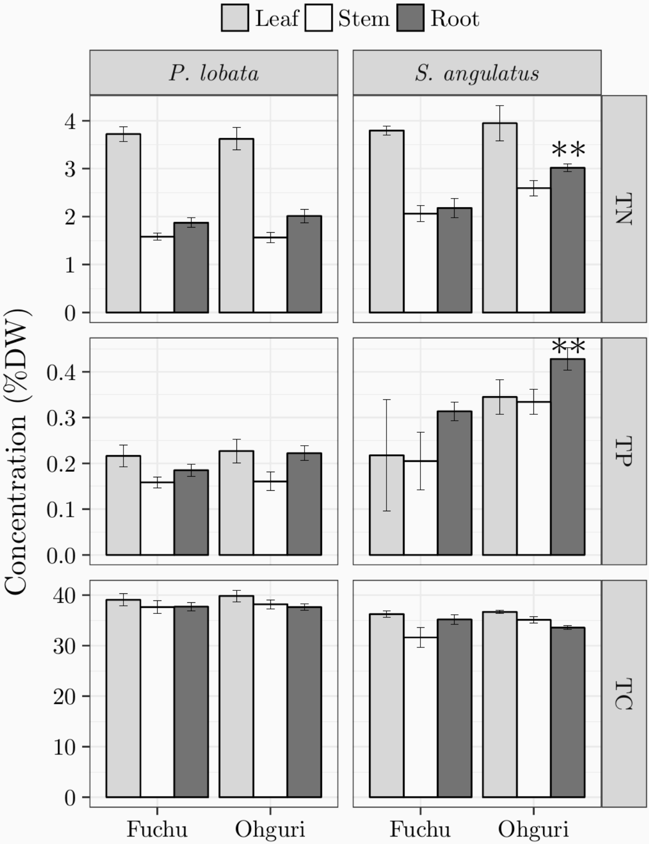
[†] Asterisk (*) and double asterisk (**) associated with p-value of a indicate that the mean difference is statistically significant at 95% and 99% level of significance, respectively, as per t-test.

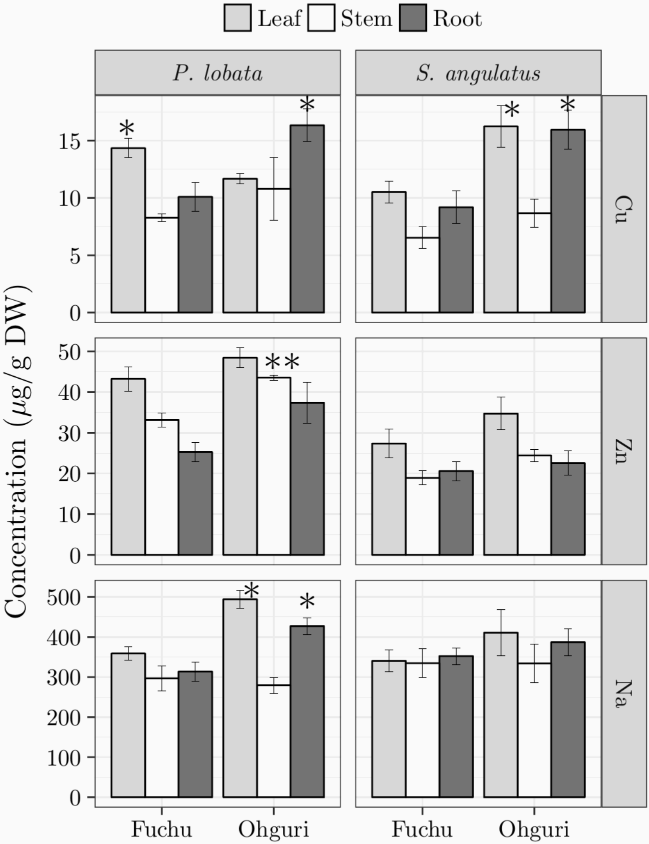
[‡] TN = total nitrogen, TP = total phosphorus, TC = total carbon, TN:TP= leaf TN:TP ratio


35.67
35.66
35.65
35.64
35.63
139.44
139.45
139.46
139.47
139.48
Fuchu
Tama River
Tama River
Tama River
Ohguri
1 km
Google
Map data ©2017 Google, ZENRIN

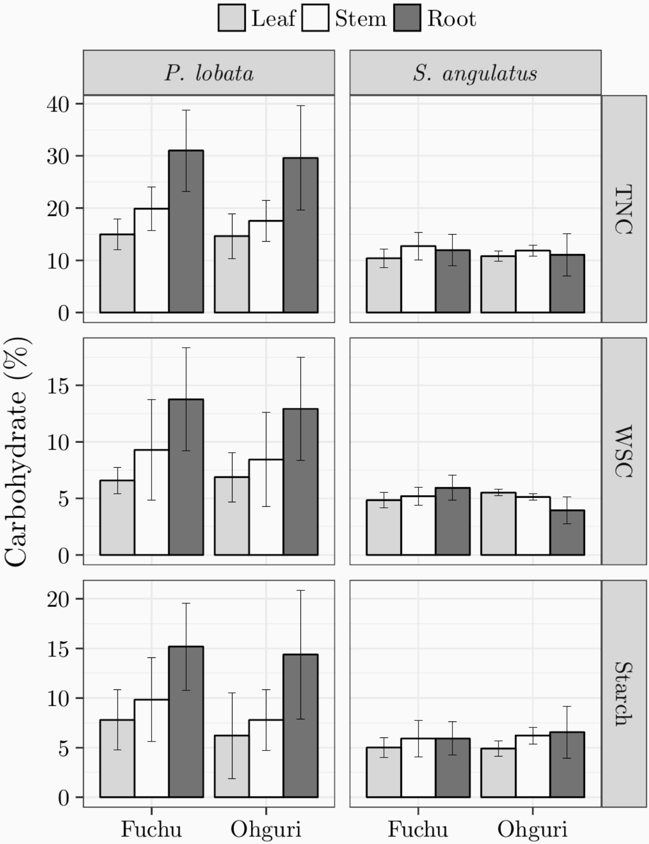

D25 (mm)
Moisture (%)
OM (%)
TC (%)
TP (%)
TN (%)
N:P ratio
C:N ratio
**
0.0
0.5
1.0
1.5
20
30
1
2
3
4
0.025
0.050
0.075
0.0
0.1
0.2
0.3
0.4
0
2
4
6
10
20
30
40
Fuchu
Ohguri

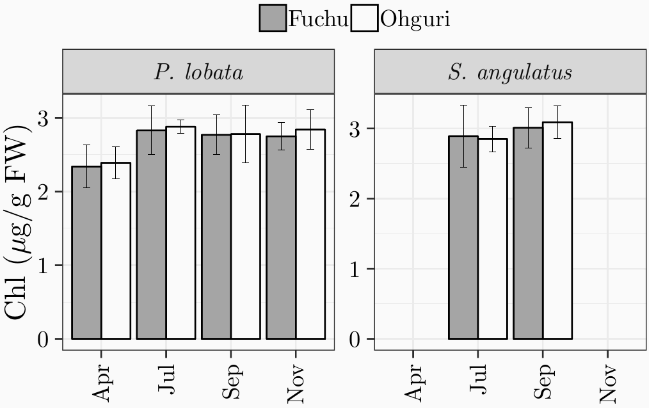

Fuchu
Ohguri
Pue.AGB (g/plant)
Pue.BGB (g/plant)
Pue.BGB/AGB
Sic.AGB (g/plant)
Sic.BGB (g/plant)
Sic.BGB/AGB
*
*
**
**
750
500
250
250
200
150
100
50
1.2
0.9
0.6
0.3
40
20
0
3
2
1
0
0.08
0.06
0.04
0.02
Apr-08
Jun-08
Aug-08
Oct-08
Dec-08
Feb-09
Apr-09

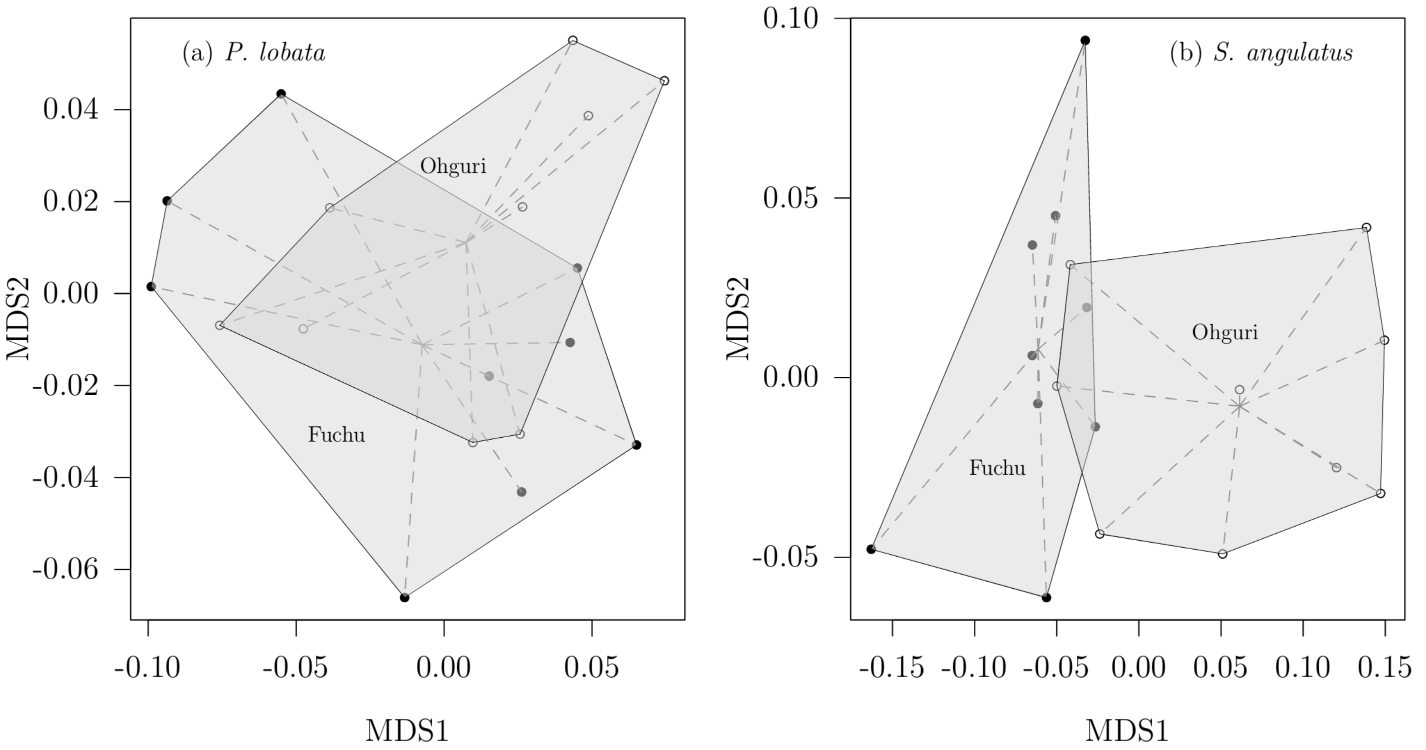

Leaf
Stem
Root
P. lobata
S. angulatus
TN
TP
TC
Concentration (%DW)
4
3
2
1
0
0.4
0.3
0.2
0.1
0.0
40
30
20
10
0
**
**
Fuchu
Ohguri
Fuchu
Ohguri



Leaf
Stem
Root
P. lobata
S. angulatus
Cu
Zn
Na
Concentration (μg/g DW)
15
10
5
0
50
40
30
20
10
0
500
400
300
200
100
0
*
**
Fuchu
Ohguri
Fuchu
Ohguri


Leaf
Stem
Root
P. lobata
S. angulatus
TNC
WSC
Starch
Carbohydrate (%)
0
10
20
30
40
0
5
10
15
0
5
10
15
20
Fuchu
Ohguri
Fuchu
Ohguri


Fuchu
Ohguri
P. lobata
S. angulatus
Chl (μg/g FW)
0
1
2
3
Apr
Jul
Sep
Nov


(a) *P. lobata*
Ohguri
Fuchu
MDS1
MDS2
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.10
-0.05
0.00
0.05
(b) *S. angulatus*
Ohguri
Fuchu
MDS1
MDS2
0.10
0.05
0.00
-0.05
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15