SPATIO-TEMPORAL VARIATIONS IN ALLOCATION OF MACRONUTRIENTS IN *SMILAX EXCELSA* L. (LILIACEAE)

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Résumé. — *Variations spatio-temporelles de l'allocation des macronutriments chez* Smilax excelsa *L.* (Liliaceae). — L'allocation des nutriments (N, P et K) dans la liane *Smilax excelsa* a été étudiée dans divers habitats au long de la saison de croissance. Les concentrations de macronutriments (à l'exception de la concentration en K foliaire) différaient de manière significative selon la saison. De même, des différences significatives des concentrations ont également été observées entre les stations échantillonnées, sauf pour N des tiges et rhizomes et K des rhizomes. Les concentrations de macronutriments du sol différaient significativement selon les stations mais pas selon les saisons. Les *S. excelsa* des canopées ouvertes et celles en position émergente allouaient davantage de macronutriments aux fruits que celles des canopées fermées ou en position de surcimées.

Summary. — Allocation patterns of macronutrients (N, P and K) of a liana species *Smilax excelsa* were investigated in different habitats and along growing season. Macronutrient concentrations significantly differed according to the season (except for leaf K concentration). Similarly, significant differences were also found among sampling stations except for stem and rhizome N and rhizome K% concentrations. Soil macronutrient concentrations were significantly different among studied stations, but not among seasons. *S. excelsa* individuals occurring in open canopies and overstory positions allocated more macronutrients to fruits as compared to those occurring in closed canopies and understory positions.

Allocation implies that resources internal to the plant are subdivided and used for different functions, then it is of fundamental importance to determine how a plant's total pool of resources vary and how it is allocated over the growing season. Allocation patterns of macronutrients indicate seasonal development of different component organs that have specific tissue element concentrations. Plants use nutrient allocation for maximizing resources for next generations (Ohlson & Malmer, 1990; Reekie & Bazzaz, 2005).

Plant allocation patterns are affected by both internal factors like genetical traits (Scheible *et al.*, 2004; Gibson, 2005; Hermans *et al.*, 2006), reproduction modes (sexual or clonal) (Méndez, 1999), plant size (Méndez & Karlsson, 2004), plant age (Niinemets, 2004; Asaeda *et al.*, 2006), phenological period (Korkmaz *et al.*, 2006), sexual dimorphism (Ramula & Mutikainen, 2003) and life form (Kaneko & Homma, 2006); and external factors like canopy structure (open vs. closed / exposed vs. shaded) (Pagès & Michalet, 2006), soil nutrient concentration (Renzhong *et al.*, 2001; Tateno *et al.*, 2004; Hermans *et al.*, 2006), successional stage of vegetation (Gleason & Tilman, 1990), plant density (Maliakal *et al.*, 1999) and altitude (Fabbro & Körner, 2004).

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Allocation of nutrients between above- and below-ground plant parts differs widely in different populations of the same species (Cairns *et al*., 1997). For example, in forest ecosystems, allocation of nutrients may differ at a small spatial scale along a topographical gradient due to availability of soil nutrients (Garten *et al*., 1994; Enoki *et al*., 1996; Tateno *et al*., 2004). Allocation of macronutrients between above- and belowground plant parts has differentiated during the adaptation to a particular habitat or soil type (Müller *et al.,* 2000; Li *et al.*, 2005; Korkmaz *et al*., 2006). Allocation of macronutrients may be changed due to canopy openness (Salzer *et al.,* 2006). Similarly, it has been reported that allocation of nutrients between above- and below- ground plant parts varied owing to seasonally changing environmental factors (Routhier & Lapointe, 2002; Kutbay & Kılınç, 2002; Korkmaz *et al.*, 2006).

Lianas are often observed in the forest understory as shade-adapted species. They are also abundant in open habitats such as tree-fall gaps, forest edges, secondary forests and clearings (Zhu & Cao, 2010). Compared with self-supporting plants, lianas may allocate a smaller proportion of biomass to roots because they only have to produce fine roots for nutrient absorption (Leicht & Silander, 2006). Toledo-Aceves & Swaine (2008) reported that there is evidence for lianas possessing a wide physiological plasticity. Allocation patterns of nutrients in lianas have been scarcely studied (During *et al*., 1994; Toledo-Aceves & Swaine, 2008). *Smilax excelsa* is a characteristic liana species of circumboreal phytogeographical region in deciduous forests occurring along the Central Black Sea Region (Kilinç & Kutbay, 2007). We aimed to determine spatio-temporal allocation patterns of N, P and K between above- and below ground parts of *S. excelsa* individuals. In addition, we aimed to determine the differences in allocation patterns under open and closed forest canopies.

MATERIALS AND METHODS

STUDY AREA

This study has been carried out in four different localities situated in the central part of Northern Anatolia (Elifli: 41° 30' N; 35°57' E; Kurupelit 41°22' N, 36°12' E; Haci Osman: 41°15'N; 36°31'E; Çatkaya: 41°14'N, 36°12'E). Stands differed in elevation, climate, soil traits, plant cover and successional stage. Sampling areas of 10 x 10 m stands under closed and open canopies were selected to be as homogeneous as possible.

Elifli is located at 20 m a. s. l., on grey-brown podsolic soils, which is a plain area. This sampling station is characterized by a 3 m high shrub vegetation dominated by *Carpinus orientalis* subsp. *orientalis,* with an open canopy (5%) due to the fact that it has been exposed to heavy disturbance and that it is at secondary climax stage. *Pyracantha coccinea, Acer campestre* subsp. *campestre*, *Cornus mas*, *Mespilus germanica*, *Ruscus aculeatus* var. *angustifolius, Rosa canina* and *Rubus discolor* are the co-dominant species. *S. excelsa* individuals form open canopies. Mean annual temperature and the mean rainfall in Elifli are 13.5°C and 672.4 mm, respectively. The duration of arid period is 3 months (from June to August) and Mediterranean climate is seen (Turkish State of Meteorological Service, 2009).

Kurupelit is located at 120 m a. s. l. on 20% inclination northern-facing slopes. This sampling station is characterized by 10 m high, closed canopy (65%) *Quercus cerris* var. *cerris* dominated forests on grey-brown podsolic soils. Codominant species in tree layer are *Quercus petraea* subsp. *iberica* and *Carpinus orientalis* subsp. *orientalis*. The characteristic species in shrub layer are *Crataegus monogyna* subsp. *monogyna*, *Ligustrum vulgare* and *Clematis vitalba*. *S. excelsa* individuals receive diffuse light because they grow in the understory. Mean annual temperature and mean rainfall are 14.2°C and 668.9 mm, respectively. Mediterranean climate is seen in this sampling station with a dry period of 2 months (July-August). This community is not heavily disturbed comparatively.

Haci Osman is located at 4 m a. s. l. and is characterized by a swamp forest on hydromorphic alluvial forests. The dominant species in this swamp forest is 30 m high *Fraxinus angustifolia* subsp. *oxycarpa*, and mean tree height is 30 m. Co-dominant tree species are *Fraxinus exelsior, Quercus hartwissiana, Carpinus orientalis* subsp. *orientalis* and *Alnus glutinosa* subsp. *barbata*. Shrub layer is characterized by *Euonymus europaeus*, *Pterocarya fraxinifolia*, *Cornus sanguinea* and *Ruscus aculeatus* var. *angustifolius*. This station is a nature protection area, and because of this Haci Osman forest has a rather closed canopy (90%). This forest constitutes the climax phase of hydrosere (Kutbay, 2001). *S. excelsa* individuals receive diffuse light. Mean annual temperature and the mean rainfall are 13.8°C and 895.2 mm, respectively. Mediterranean climate is seen, without an arid period.

Çatkaya is located at 540 m a. s. l. on grey-brown podsolic soils and 30% inclination northern-facing slopes. This station is characterized by a low disturbed, closed canopy (90%), and 15 m high *Fagus orientalis* forest. *Carpinus betulus* and *Sorbus torminalis* var. *torminalis* are the co-dominant species in tree layer. *Cornus mas*, *Daphne pontica*, *Crataegus monogyna* subsp. *monogyna*, *Mespilus germanica*, *Ligustrum vulgare* and *Clematis vitalba* are the dominant species in shrub layer. *S. excelsa* individuals receive diffuse light. The mean annual temperature and the mean rainfall are 11.6°C and 958.3 mm, respectively. The climate is Mediterranean without a dry period.

To determine the changes in N, P and K% concentrations depending on habitat and seasons plant samples were taken monthly from belowground (rhizome) and aboveground (stem, leaf and fruit) parts from March 2005 to February 2006 at three different localities from each station. Fruit specimens were only taken in October during fruit ripening. Soil samples were taken from 0-20 cm depth after litter was removed. They were air-dried, crushed and sieved using a 2 mm mesh, and soil traits were determined by standart methods (Bayrakli, 1987).

Three *S. excelsa* individuals were selected in each sampling station per month. At least 10 leaves per plant were used. Leaves were dried at 60°C for 24 hours, whilst rhizomes, stems and fruits were dried at 70°C for 72 hours to constant weight. After grinding and sieving, plant nutrient concentrations were determined by standard methods (Bayrakli, 1987). Seasonal nutrient concentrations were expressed as aritmethic means of three months (i.e. December, January and February for winter).

The data were subjected to statistical analysis by using a SPSS (15.0) software. To determine the differences among seasons and sample stations with respect to N, P and K% concentrations of plant (rhizome, stem and leaf) and soil samples, two-way factorial-ANOVA test was used. Season, sampling station, and season x sampling station interaction were considered between subjects factors. For fruit samples the differences among sampling stations were evaluated by one-way ANOVA test (SPSS Incorporation, 2006).

RESULTS

There were significant differences among sampling stations with respect to soil macronutrient concentrations. However, no significant differences were found in soil macronutrient concentrations over the growing season. Similarly, season x station interaction was not significant with respect to soil macronutrient concentrations (Tab. I).

Statistically significant differences were found among seasons with respect to N, P and K% concentrations in rhizomes, stems and leaves except for leaf K% concentration. Similarly, significant differences were also found among sampling stations except for stem and rhizome N and rhizome K% concentrations, respectively. Season x station interaction was usually not significant, except for rhizome and stem P concentrations, and stem K concentrations, respectively (Tab. I).

The highest soil N concentrations were found in Haci Osman forest, whereas the highest soil P and K concentrations were found in Kurupelit sampling station (Tab. II).

While leaf, stem and rhizome N% concentrations were rather high in summer in all sampling stations, they decreased in other seasons. The highest leaf P% concentration was found in spring. The highest rhizome and stem K% concentrations were found in autumn similar to that of rhizome and stem P% concentrations. The highest leaf K% concentration was found in summer. The highest N, P and K% concentrations were found in Haci Osman sampling station. Fruit N% concentrations were higher in Elifli than that of the other sampling stations. However, fruit P and K% concentrations were highest in Haci Osman and Elifli sampling stations, respectively (Tab. II).

Fruit N and K% concentrations were significantly different among sampling stations (P ≤ 0.05, P ≤ 0.01), while P% concentrations were not significantly different with respect to sampling stations (Tab. III).

DISCUSSION

N/P ratios in sampling stations ranged between 4.05 to 4.44 which indicates N-limitation in studied sampling stations (Koerselman & Meuleman, 1996). In low-nutrient environments plants resort to using component nutrients of the leaves to supply reproductive needs, and they usually resorbed most of their nutrients to leaves (Reekie *et al.*, 1997). P and K concentrations of leaves were higher compared to rhizomes and stems over the growing season.

It has been pointed out that belowground resources (e.g., soil nitrogen and phosphorus concentration) can colimit growth, and the degree of colimitation may vary with shade tolerance (Walters & Reich, 1996). The lowest soil N, P and K concentrations were found in Çatkaya sampling station, which had the lowest soil macronutrient concentrations. The lowest leaf, stem and rhizome P% concentrations were also found in *S. excelsa* individuals in Çatkaya. Liana communities appear to be more influenced by edaphic conditions than by the abundance or species composition of canopy trees. However, there does not appear to be a simple, general rule that explains liana abundance along edaphic gradients (Malizia *et al.,* 2010; Asaeda *et al.,* 2011).

TABLE I

Two-way factorial ANOVA results of plant and soil traits (df - degrees of freedom, MS - mean square, F – F- value, P - probability P≤0.05*, P≤0.01**, P≤0.001***)

Trait		df	N (%)			P (%)			K (%)		
			MS	F	P	MS	F	P	MS	F	P
Soil	Season	3	0.016	2.517	0.061	21.423	2.657	0.051	0.038	0.777	0.509
	Sampling station	3	0.093	14.955	0.000***	235.290	29.178	0.000***	0.522	10.594	0.000***
	Season x Sampling station	9	0.009	1.514	0.149	9.167	1.137	0.342	0.038	0.779	0.636
	Corrected Total	143									
Rhizome	Season	3	0.036	16.072	0.000***	0.001	12.860	0.000***	2.343	35.416	0.000***
	Sampling station	3	0.002	0.715	0.545	0.001	10.154	0.000***	0.117	1.771	0.156
	Season x Sampling station	9	0.004	1.682	0.100	0.000	1.980	0.047*	0.078	1.187	0.309
	Corrected Total	143									
Stem	Season	3	0.140	85.237	0.000***	0.000	20.156	0.000***	0.830	47.327	0.000***
	Sampling station	3	0.003	1.616	0.189	0.000	28.890	0.000***	0.303	17.255	0.000***
	Season x Sampling station	9	0.002	1.237	0.278	5.51E-005	3.239	0.001**	0.054	3.095	0.002**
	Corrected Total	143									
Leaf	Season	3	0.028	17.922	0.000***	0.002	27.574	0.000***	0.110	2.166	0.095
	Sampling station	3	0.016	10.412	0.000***	0.001	10.672	0.000***	0.626	12.347	0.000***
	Season x Sampling station	9	0.001	0.840	0.581	0.000	1.679	0.100	0.078	1.534	0.143
	Corrected Total	143									
Plant parts	Season	3	0.173	95.710	0.000***	0.001	22.017	0.000***	2.242	50.040	0.000***
	Sampling station	3	0.011	6.125	0.000***	0.002	34.664	0.000***	0.896	19.999	0.000***
	Season x Sampling station	9	0.002	1.058	0.393	0.000	1.683	0.091	0.118	0.684	0.724
	Season x Plant parts	6	0.015	8.381	0.000***	0.001	18.633	0.000***	0.520	11.619	0.000***
	Sampling station x Plant parts	6	0.005	2.632	0.016*	5.63E-005	0.968	0.447	0.075	1.672	0.127
	Season x Sampling station x Plant parts	18	0.002	1.349	0.154	7.84E-005	1.349	0.154	0.046	1.031	0.423
	Corrected Total	431									

TABLE II

The comparison of Tukey's (HSD) results of soil and plant macronutrient concentrations over the growing season and sampling stations. Means followed by the same letter are not significantly different at the 0.05 level using Tukey's HSD test

	Trait	Season				Sampling station			
		Spring	Summer	Autumn	Winter	Elifli	Kurupelit	Hacı Osman	Çatkaya
Soil	N	0.300a	0.313a	0.349a	0.328a	0.313b	0.329b	0.386a	0.263c
	P	5.655a	5.907a	6.825a	4.959a	4.438c	9.160a	6.417b	3.332c
	K	0.423a	0.448a	0.460a	0.386a	0.379bc	0.575a	0.469ab	0.294c
Rhizome	N	0.082b	0.134a	0.063b	0.075b	0.092a	0.079a	0.093a	0.091a
	P	0.015a	0.012a	0.017a	0.005b	0.009bc	0.014ab	0.018a	0.007c
	K	0.606b	0.541b	0.812a	0.198c	0.469a	0.540a	0.609a	0.538a
Stem	N	0.053b	0.183a	0.053b	0.073b	0.083a	0.086a	0.102a	0.092a
	P	0.009a	0.010a	0.011a	0.004b	0.006b	0.011a	0.012a	0.005b
	K	0.273b	0.361a	0.411a	0.067c	0.205b	0.285b	0.406a	0.218b
Leaf	N	0.083b	0.138a	0.087b	0.078b	0.080b	0.098b	0.126a	0.081b
	P	0.033a	0.022b	0.014c	0.022b	0.018c	0.024ab	0.029a	0.020bc
	K	1.131a	1.150a	1.075a	1.028a	0.937c	1.083b	1.259a	1.105b
Fruit	N	-	-	-	-	0.036a	0.016b	0.020b	0.013b
	P	-	-	-	-	0.012a	0.012a	0.017a	0.012a
	K	-	-	-	-	1.096a	0.920a	1.076a	0.0713a

TABLE III

The comparison of fruit N, P, K (%) traits by one-way ANOVA

	Trait		S.S	df	MS	F	P
Fruit	N	Between Groups	9.67E-04	3	3.22E-04	12.889	0.002**
		Within Groups	2.00E-04	8	2.50E-05		
		Total	1.17E-03	11			
	P	Between Groups	4.47E-05	3	1.49E-05	0.662	0.598
		Within Groups	1.80E-04	8	2.25E-05		
		Total	2.25E-04	11			
	K	Between Groups	0.283	3	9.45E-02	4.152	0.048*
		Within Groups	0.182	8	2.28E-02		
		Total	0.465	11			

S.S: Sum of squares; df: degrees of freedom; MS: mean square; F: F- value; P - probability P≤0.05*, P≤0.01**

We found that the changes in N, P and K% concentrations were strongly seasonal, and such differences may be due to the canopy openness. Seasonal macronutrient especially nitrogen allocation, leads to a better assignment towards light harvesting, especially in shade (Salzer *et al.*, 2006). The highest rhizome, stem and leaf macronutrient concentrations were found in Haci Osman sampling station. Forest vegetation in Haci Osman sampling station is at climax stage (Kutbay, 2001) and soil N concentrations were high. Tree height is rather high (35 m) in Haci Osman sampling station, and trees form a closed canopy. So competition for light is more severe, and *S. excelsa* individuals in Haci Osman have longer stems, which provides them an advantage for competition. However, tree height in the other studied stations ranged between 3 (Elifli) and 15 m (Kurupelit). Plant individuals under closed forest canopies and productive soils allocate their macronutrients to their stems and compete with each other for light (Hunt *et al.*, 2002; Tateno *et al.*, 2004). However, plant individuals under open canopies allocate their macronutrients to foliage and/or reproductive organs because of the minimum investment in supporting tissues (i.e. stems) (Kaneko & Homma 2006; Hermans *et al.*, 2006). Reproductive plant parts need more light than vegetative plant parts (Kilinç & Kutbay, 2008).

Leaf nutrient concentrations of *S. excelsa* individuals were higher during spring and summer compared to autumn and winter. At the onset of autumn, macronutrients were allocated to long-lived plant parts (i.e stems) from leaves, and as a result of this, leaf nutrient concentrations were decreased (Kutbay, 1999; Kutbay & Kilinç, 2002).

Leaves emerged during summer, and as a result of this, stressfull conditions occurred for understory plants due to low light conditions and leaf senescence (Routhier & Lapointe, 2002). During leaf emergence plants usually resorbed their macronutrients especially nitrogen to their rhizomes and stems for growth in next spring (Kutbay & Kilinç, 2002; Routhier & Lapointe, 2002). Rhizome and stem N concentrations were found to be high in summer. Macronutrients in rhizomes are largely used for carbohydrate and water storage, and they promote vegetative growth at the onset of next year's spring (Ruiters, 1995; Routhier & Lapointe, 2002; Kutbay & Kilinç, 2002; Korkmaz *et al.*, 2006).

It has been found that allocation of macronutrients to reproductive plant parts under open canopies were considerably higher than that of closed canopies (Ruiters, 1995). N and K concentrations in fruits of *S. excelsa* individuals in Elifli, characterized by an open canopy, were higher compared to other sampling stations. Because light often limits plant growth in understory environments, small variations in light conditions may have a large impact on photosynthesis, growth and regeneration of understory species (Chazdon & Pearcy, 1991). In the present study, only *S. excelsa* individuals in Elifli sampling station occurred under open canopy. Therefore *S. excelsa* individuals have different ecological niches (overstory versus understory).

Higher nutrient concentrations were found in leaves and reproductive structures of *S. excelsa* compared to stem nutrient concentrations, except for Elifli and Çatkaya sampling stations, in which stem N concentrations were higher, compared to leaves and fruits. It has been reported that lianas re-use macronutrients in developing tissues (such as leaves or reproductive structures) (Cai & Bongers, 2007). In addition to this, leaf and fruit K% concentrations were higher compared to stem and rhizome K% concentrations. Higher leaf K% concentrations in lianas indicates a better ability to control the water regime through K involvement in osmotic and stomatal regulation (Marschner, 1995; Kazda *et al.*, 2009).

CONCLUSIONS

Macronutrient allocation patterns of *S. excelsa,* a characteristic liana species of circumboreal phytogeographical region, were investigated. N-limitation occurred in studied sampling stations. Soil macronutrient concentrations were significantly different among studied sampling stations, but not changed over the growing season. The changes in N, P and K% concentrations in rhizome, stem and leaf were strongly seasonal, and such differences may be due to the canopy openness. Similarly, significant differences were also found among sampling stations

except for stem and rhizome N and rhizome K% concentrations. Allocation of macronutrients to reproductive plant parts under open canopies were considerably higher than that of closed canopies in the studied sampling stations. The lowest leaf, stem and rhizome P% concentrations were also found in *S. excelsa* individuals in Çatkaya sampling station, which had the lowest soil macronutrient concentrations. This probably indicates that liana communities appear to be more influenced by edaphic conditions. Leaf and fruit K% concentrations of *S. excelsa* were found to be higher compared to stem and rhizome K% concentrations. Finally, macronutrient allocation patterns of *S. excelsa* were affected by both spatial and seasonal changes.

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