Comparison of metal-sensitive *Acer pseudoplatanus* with metal-tolerant *Silene cucubalus* grown on the same mine dump.

	Zinc level (mg Zn/g d. wt)		Phytochelatin level (µMol Glu-Cys-units/g d. wt)	
	Root	Leaf	Root	Leaf
Acer pseudoplatanus	9.2	0.23	0.90	<0.008
Silene cucubalus	2.2	0.42	0.06	<0.008

There was, however, an interesting difference (table). The *Acer* plants produced substantial amounts of phytochelatins (0.9 µmole γ-Glu-Cys units per g (d. wt) root tissue) while the metal-tolerant *Silene* plant yielded a distinctly lower level of phytochelatins (0.06 µmoles γ-Glu-Cys) even in relation to the zinc content of the root system, which was about 4 times higher in *Acer*. In both extracts the glutathione content was comparable (ca 0.9 µmole/g d. wt). This finding could indicate that plants adapted to heavy metals have evolved additional mechanisms of tolerance[7] besides complexation of metal ions by phytochelatins. The fact that root tissue contains a much higher concentration of heavy metals as well as of phytochelatins than the leaf tissue points to the fact that metals are obviously immobilized to a far greater extent at the site of metal uptake. The question whether phytochelatin-metal complexes can be transported at all in plants is currently under investigation.

This study, however, demonstrates that plants grown on soils containing considerable amounts of heavy metals do contain phytochelatins.

This is the first report of the natural occurrence of phytochelatins in the ecosystem and emphasizes the role of phytochelatins in the detoxification of heavy metals in plants.

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Reproductive effort of short shoots in silver birch (*Betula pendula* Roth)

J. Tuomi[a], S. Nisula, T, Vuorisalo, P. Niemelä and V. Jormalainen[1]

[a] *Department of Ecology, Theoretical Ecology, University of Lund, Ecology Building, S-223 62 Lund (Sweden), and Department of Biology, University of Turku, SF-20500 Turku (Finland)*

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Summary. The degree of autonomy was estimated for generative short shoots of silver birch by defoliating them after leaf flush. Defoliation reduced both final length (4%) and weight (18%) of female inflorescences. Short shoots are thus reproductively semi-autonomous modules of silver birch.

Key words. Modularity; reproduction; birch; short shoot.

The modular structure of higher plants is a basic theoretical foundation of modern plant population biology[2,3]. Trees, for example, develop as a result of the births and deaths of their iterated structural elements, such as buds, shoots and branches[4,5]. The term 'module' originally referred to developmental products of single apical meristems[5,6], but it has since been used more loosely to denote all repeated units of 'multicellular structure, normally arranged in a branch system'[3]. Such morphological modules, however, may not always correspond to any appropriate physiological units. If modules are thus re-defined on a physiological basis, basic functional consequences of modular organization may become more apparent[7–10].

Functional modularity has two basic ecological consequences: 1) Functionally, modules can be defined as partially self-maintaining, repetitive, and multicellular parts of physically coherent 'structural individuals'[10]. 2) Reproductive effort in modular organisms is divided among a number of modular units which assimilate at least a part of the resources required for their own maintenance, growth and reproduction[7]. Consequently, the total reproductive output of functional modules in trees should depend both on their own photosynthetic activity, and on resources imported from other parts of the tree[11]; and the relative importance of these internal and external components of reproductive effort may be used to estimate the independence of modular units in their reproduction[12].

In the present study, we tested how the artificial defoliation of separate short shoots influences female catkins in the silver birch (*Betula pendula* Roth). Several (usually 2–3) leaves and a female catkin emerge from generative short shoot buds of the silver birch in early May[11]. Since reproductive organs do not generally have a positive net photosynthesis[13], we assume that the leaves of generative short shoots are the main sources for the internal component of reproductive effort that supports the growth of female catkins. We therefore studied how the removal of these leaves affects the final length and weight of female catkins on separate short shoots.

Materials and methods. The study was carried out at the Archipelago Research Institute of the University of Turku in SW Finland (60° 14′ N, 21° 59′ E). Eleven birch trees (*B. pendula*) were used which were, on average, 10.0 m in height (SD = 4.2 m) and 15.5 cm in diameter at 1.30 m above the ground (SD = 8.3 cm).

At the beginning of the experiment (12–15 May, 1986), 20–40 generative short shoots were selected from each tree. Short shoots were selected in pairs so that control and defoliated short shoots were located at similar positions on the

Table 1. Means and standard deviations of final catkin length and weight in July for control and defoliated short shoots on eleven trees of *Betula pendula*.

	Control shoots			Defoliated shoots		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD
Length (mm)	153	23.0	4.8	156	22.1	4.6
Weight (mg)	153	120.9	48.6	156	100.1	41.4

n = number of female catkins.

Table 2. Two-way analysis of variance for mean contrast in catkin length and weight between 144 pairs of control and defoliated short shoots on eleven trees of *Betula pendula*.

Contrast	Counts	Mean	Source	df	F	p
Length (mm)	144	0.82	Mean	1	5.94	<0.05
			Trees	10	1.18	0.313
Weight (mg)	144	21.01	Mean	1	29.31	<0.001
			Trees	10	1.81	0.064

same branches and on the lower parts of the trees. Short shoots were defoliated by carefully removing leaf blades from leaf stalks. The initial lengths of leaf blades ($\bar{x} = 20.4$, SD = 4.0 mm, n = 222) and of female catkins were measured for the experimental trees from samples of 20 leaves and 10 catkins per tree. The final catkin length (mm) and weight (dry wt mg, 24 h at 60 °C) were estimated at the end of the experiment (17 July, 1986) for control and defoliated short shoots. A part of the material had to be omitted from the final analysis since on some short shoots seeds had begun to fall off before the end of the experiment.

The effects of defoliation on final catkin length and weight were analyzed by calculating pairwise contrasts between control and defoliated short shoots, and by testing the statistical significance of the mean contrasts by two-way analysis of variance[14].

Results and discussion. Female catkins were on average 12.5 mm (SD = 2.1 mm, n = 109) in length just before the time of defoliation. This was about 54.3 % of the mean final catkin length of control short shoots (table 1). When control and defoliated short shoots are compared, it is evident that defoliation affected both the final length and weight of female catkins (table 1). Female catkins were on average 3.9 % shorter and 17.8 % lighter on defoliated short shoots as compared to control shoots. Both effects were statistically significant, and there was no statistically significant variation between trees in the effects of short shoot defoliations (table 2).

Since the removal of the leaves from generative short shoots thus reduced the final weight of female catkins, short shoots can evidently be considered as semi-autonomous modules. This is consistent with the functional criteria of modularity. That is, modules are multicellular units which a) are iterated during the growth of the plant[2,3,6], b) supply at least a part of the resources required of their own maintenance, growth and reproduction[7,8], and c) are physically interconnected to build up a higher-level functional unit, the structural individual[10].

Although short shoots can be considered as semi-autonomous birch modules, the present results emphasize their integration into higher functional levels. A major part (up to 82 %) of the reproductive effort of short shoots is supported by other parts of the birch tree. Also in white birch, we have found that the defoliation of all generative short shoots from single branches can reduce the final weight of female catkins by about 13 %[12]. Thus short shoots on both silver birch and white birch are semi-autonomous modules which are structurally and functionally integrated within individual birch trees.

The higher functional levels involved may include 1) old long shoots, as short shoots usually develop from proximal axillary buds of long shoots[15,16], 2) branches consisting of physically interconnected short and long shoots, 3) shoot-root sub-systems forming integrated physiological units[8] and finally, 4) entire birch trees (i.e. structural individuals)[10]. Short shoots, long shoots and branches as well as root-shoot sub-units can thus be understood as semi-autonomous modular units of individual birch trees. Consequently, one could also expect an increasing degree of autonomy from short shoots to higher levels of modularity.

Physically separate ramets would naturally show the highest degree of physiological independence[9]. Ramets are also frequently considered as modules that build up the genetic individual or the genet in clonal plants[2,3]. However, according to the present functional criteria of modularity, such ramets have the status of the independent structural individuals rather than that of modules. Therefore, we suggest that the criteria of modularity concerning the internal organization of structural individuals and, on the other hand, those of clonality concerning the modes of reproduction should be conceptually distinguished from each other in plant population biology.

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