Fragm. Flor. Geobot. 45(1–2): 193–202, 2000

Compensation and induced defense in response to herbivory in Sedum maximum (Crassulaceae)

PAWEŁ ADAMSKI, KATARZYNA MARGIELEWSKA AND ZBIGNIEW WITKOWSKI

ADAMSKI, P., MARGIELEWSKA, K. AND WITKOWSKI, Z. 2000. Compensation and induced defense in response to herbivory in *Sedum maximum* (Crassulaceae). *Fragmenta Floristica et Geobotanica* 45(1–2): 193–202. Kraków. ISSN 0015–931x.

ABSTRACT. *Sedum maximum* (L.) Hoffm. often sprouts laterally after excision of the apex by herbivores. An experiment with apex removal showed that the compensatory mechanism involves principally the aboveground organs of a plant. It consists in a statistically significant increase of the assimilative surface and of the area of inflorescences in plants with excised apices, compared to control plants. In the field, browsing on leaves by *Parnassius apollo* (L.) caterpillars is of rather moderate intensity and does not exceed 3–7% of the leaf area. This suggests an induced chemical defense of leaves in response, which has been confirmed by other authors studying caterpillar browsing on mature leaves on this and a closely relative plant species (*Sedum album* L.). Investigations of the whole stonecrop plant (above- and underground organs) showed that the mass of underground organs is strongly negatively correlated with the total area of inflorescences. If so, the growth of inflorescence size after apical herbivory suggests energy trade-offs between the underground and generative organs in response to herbivory.

KEY WORDS: *Sedum maximum*, *Parnassius apollo*, herbivory, compensation response, shift of energy allocation, chemical defense

P. Adamski, K. Margielewska and Z. Witkowski, Institute of Nature Conservation, Polish Academy of Sciences, al. Mickiewicza 33, PL–31–120 Kraków, Poland; e-mail: nowitkow@cyf-kr.edu.pl

INTRODUCTION

Students of the effect of herbivory on plants have focused mainly on two issues: compensation of damage (Bergelson *et al.* 1996; Agrawal 2000) and defense against herbivores (Ohnmeiss & Baldwin 2000). Compensation of damage to plant fitness ranges from negative (net loss) to positive (net gain = overcompensation), forming a “compensatory continuum” depending on biotic and environmental factors (Mashinski & Whitham 1989; Mutikainen & Walls 1995); the costs are more evident in stressful conditions. Though the beneficial effects of herbivory on plant fitness have been questioned (Bergelson & Crawley 1992; Bergelson *et al.* 1996), one of the most common mechanisms of compensation (or overcompensation) in plants is an increase of branching following the destruction of apices (Verkaar *et al.* 1986; Paige & Whitham 1987; Maschinski & Whitham 1989; Aarsen & Irvin 1991; Aarsen 1996).

Stonecrop plants show adaptation to herbivory in two ways – by active defense and by compensation of damage. The concentration of alkaloids ranges from 0.03% to 0.06% of biomass, and polyphenolic compounds oscillate between 2.3 and 8.9% (Wolbiś 1989). Among other species, *Sedum maximum* (L.) Hoffm. is characterized by a high concentration of a specific compound, rohalkaloid (Frank & Hartmann 1963). Such compounds certainly serve plants as antiherbivore defense agents. Moser and Oertli (1980) described a strong defense against larval herbivory by the apollo butterfly *Parnassius apollo* (L.) in overwintering stolons of *Sedum album* L.

On the other hand, during a field inventory of *Sedum maximum* (Witkowski *et al.* 1993) we observed its robust ability to compensate apical excision by increased branching. In single cases we observed dense branching, which suggests even overcompensation after apex removal. The present paper concentrates on compensation process. The aims of our investigations were these:

– to identify the main herbivore taxa attacking stonecrop *Sedum maximum*,

– to describe the form of leaf and apex damage done by herbivores,

– to examine the plant’s reaction to herbivory (induced response),

– to excise apices experimentally, simulating one of the forms of herbivory, in order to determine whether apical destruction significantly influences the size of inflorescences.

This study is part of research on the host plant of the apollo butterfly, whose population is now recovering in Pieniny National Park, Polish Carpathians (Witkowski & Adamski 1996).

MATERIAL AND METHODS

The investigations were carried out in the Pieniny Mts, a narrow limestone mountain range situated in the central part of the West Carpathians, crossed by the frontier between Poland and Slovakia. The range lies almost entirely in the lower montane forest belt (fir-beech forests). Now the central part of the mountains is included in the Pieniny National Park covering about 2700 ha, far less than 0.01% of the territory of Poland. Such a small area harbors about 1100 vascular plant species, which makes up about 50% of Poland’s native flora. Among them are two local endemics and many relict and rare species (Zarzycki 1991).

In the Pieniny Mts the stonecrop (*Sedum maximum*) is quite common, particularly on the southern slopes covered by xerothermic grasslands (*Festucetum pallentis* and *Origano-Brachypodietum* plant associations) and thin bushes, and also on stone debris and rocks (Łaskawiec 1988; Witkowski *et al.* 1993).

The stonecrop is a perennial succulent rhizocarp with characteristic roots of an elongated bulb type (Fig. 1). It spreads vegetatively by branching the root bulbs and also by seed. In early spring the rhizocarp gives off one or a few buds forming a 15–60 cm unbranched stem. Two elliptic or round succulent serrate leaves are located on each node, where dormant lateral buds are also located. The total number of leaves depends on the height of the plant. The inflorescence is formed in July and flowering is observed in August and September. Its cream-colored flowers form dense umbels. The 0.5 mm long seeds mature in October and November. The phenology of development of the aboveground organs of *Sedum maximum* and the intensity of leaf herbivory are presented in Fig. 1 (Wala 1995; Łaskawiec 1988).

The observed morphological effects of herbivory on leaves were internal or external removal of leaf tissue, varying in size (see Figs 2 & 5). Apex destruction resulted in lateral branching. Lateral shoot length and inflorescence formation were dependent on time of destruction and on how much shoot was removed.

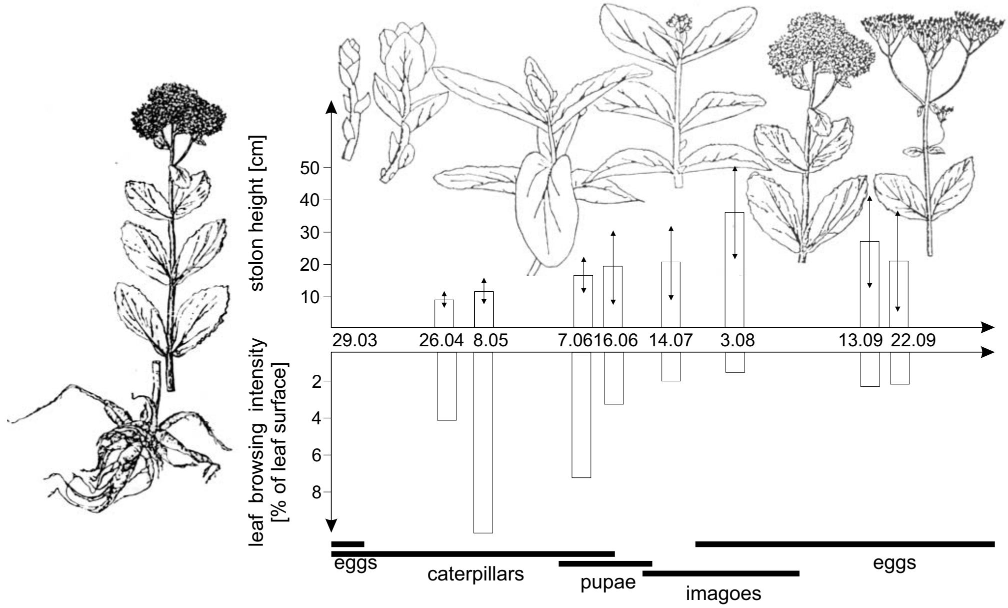

Fig. 1. Scheme of phenological development of stonecrop *Sedum maximum* (L.) Hoffm. (upper part) and of phenology of apollo butterfly *Parnassius apollo* (L.) (lower part). Upper diagram shows phenology of stonecrop and average height of plant shoot (cm); arrows indicate SD. Lower part shows intensity of browsing (percent of leaf removed) and phenology of apollo butterfly (after Wala 1995).

Field studies were carried out in four vegetative seasons in 1992–1995. We investigated *(1)* the maximum height of undamaged and damaged (apex excision) shoots, *(2)* the number of leaves on each shoot, *(3)* the number and height of lateral sprouts on damaged shoots, and *(4)* the diameters of each inflorescence (on damaged shoots there were sometimes more than one umbel). The last parameters ware used to calculate the total area of inflorescences on the stolon.

In 1994, two groups of 20–30 stolons of the stonecrop growing in the neighborhood were selected for the experiment. One group was treated as the control, and the other was cut in April and in May. The effects of cutting were identified and described, and stolons with excised apices were compared with the control group in respect of the characters investigated earlier (1–4).

In late autumn 1995, 20 plants were dug out and washed, and the four characters mentioned above were measured on each plant. Eleven plants were weighed, the aboveground and underground parts of the plant separately**.** This procedure enabled us to analyze the allometry of whole stonecrop individuals.

During data processing the following analyses were carried out:

– relations between the characteristics of different organs of the plant were checked by regression analysis. The correlations were accepted as significant when $p < 0.05$;

– differences in stolon characters (height and number of leaves) between years were analyzed by one-way ANOVA;

– the frequency of lateral branching between damaged and undamaged stolons were compared with the chi-square test;

– the differences in the maximum height and number of leaves between generative and vegetative shoots were analyzed with Student’s *t*-test for two independent samples. The same test was applied to the differences between the experimental (apex excision) and control groups.

All statistical tests presented here were based on the standardized computer procedures of the Statistica 4.0 program.

Results

The investigations of the whole stonecrop plant gave three relationships (Fig. 2): *(1)* the mass of the underground parts was directly proportional to the number of leaves on all stolons of the plant, *(2)* the inflorescence area was also positively correlated with the number of leaves on all stolons, and *(3)* the mass of underground parts was strongly negatively correlated with inflorescence width.

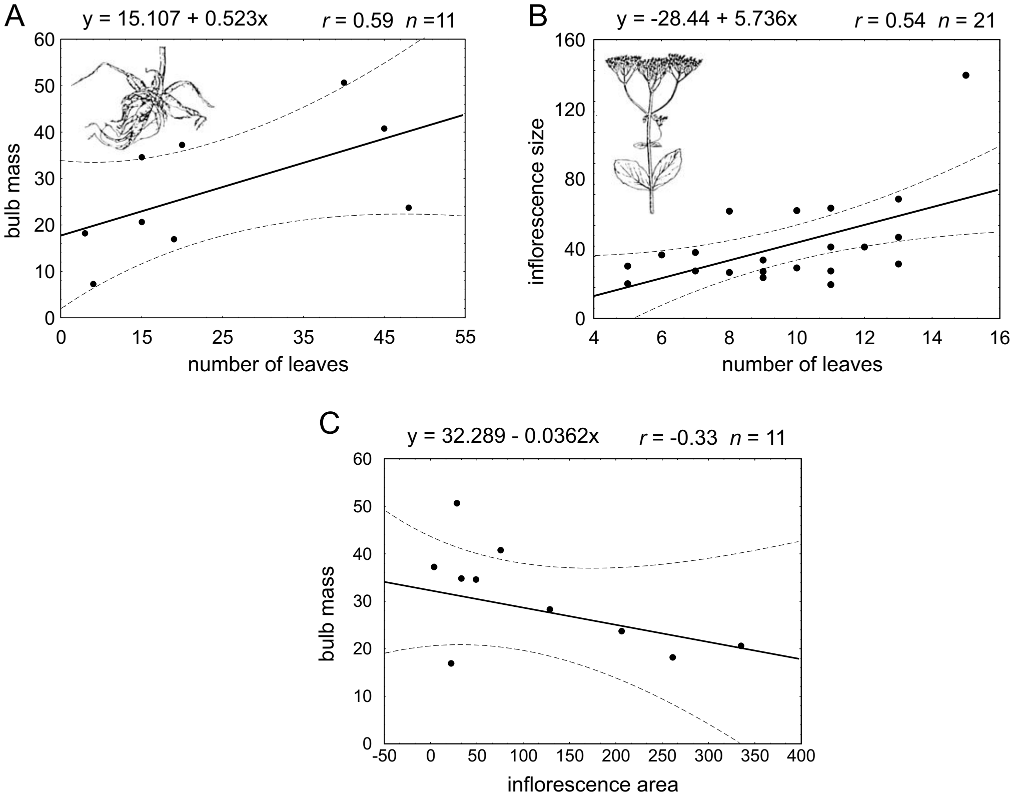

Fig. 2. Relationships between number of leaves and bulb mass (A), number of leaves and inflorescence size (B) and inflorescence size and bulb mass (C) in stonecrop *Sedum maximum* (L.) Hoffm.

There was no statistically significant variability in stolon size between particular years. Therefore it was accepted that the data for each year were a sample from the same population (Fig. 3). In this population, however, we found a significant difference in height between generative (with inflorescence) and vegetative stolons (Fig. 4).

Taking into account the term, intensity, site and features of damage (Figs 2 & 5) we distinguished three main groups among the herbivores (Fig. 5). The first included se-

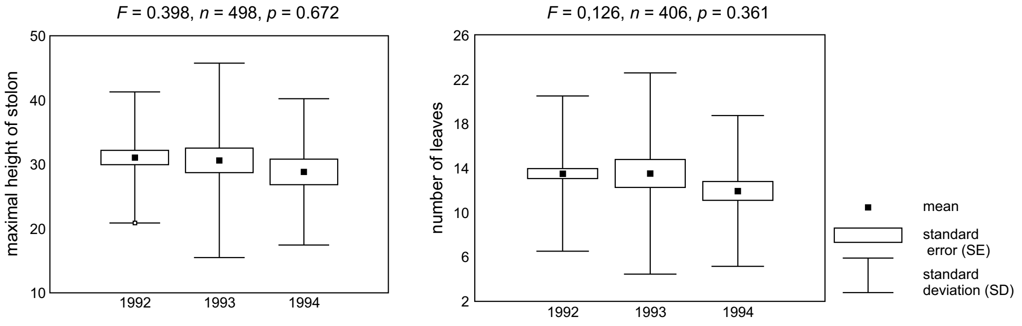

Fig 3. Comparison of stolon height (left figure) and number of leaves (right figure) of stonecrop *Sedum maximum* (L.) Hoffm. in investigation period (1992–1994).

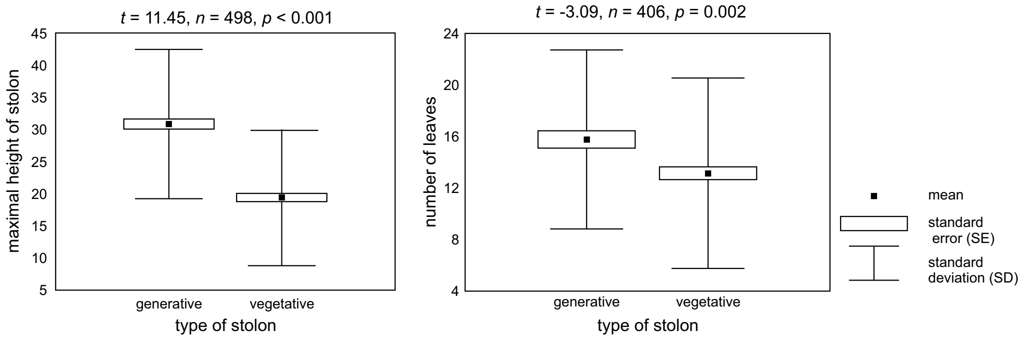

Fig. 4. Comparison of stolon height (left figure) and number of leaves (right figure) among generative (with inflorescence) and vegetative stolons of stonecrop *Sedum maximum* (L.) Hoffm.

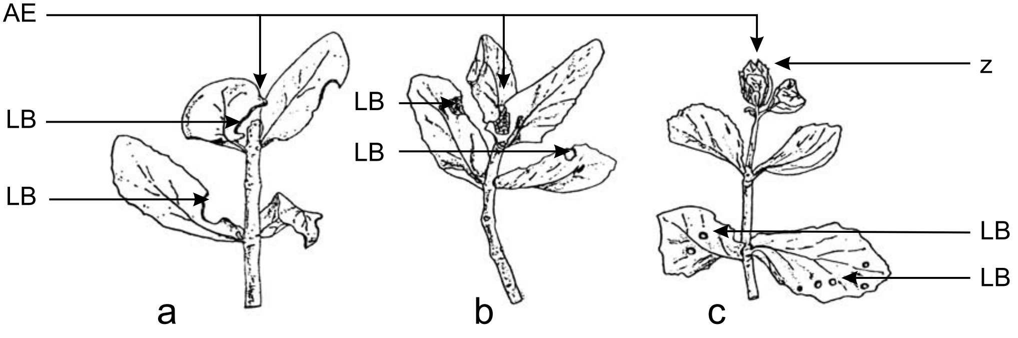

Fig. 5. Comparison of browsing characters of three groups of herbivores on stonecrop *Sedum maximum* (L.) Hoffm. a – apollo butterfly; b – snail; c – tortrix moth; AE – apex excision; LB – leaf browsing; z – cocoon of tortrix moth on top of *Sedum maximum* shoot.

lected species of land snails (mainly young individuals of *Helix pomatia, Perforatella umbrosa* and *Helicigona faustina*) and beetles (*Apion curtirostre* and *Polydrusus pilosus*) which attacked young shoots formed in late March to early May. Snails characteristically scratched leaves, and bigger specimens of *Helix pomatia* often ate all the apical part of a shoot. Beetles perforated the leaf surface.

Caterpillars of some moth species of the family *Tortricidae* and unidentified hymenopteran (*Symphyta*) larvae belonged to the second group, which attacked only the apical part of the stonecrop where they browsed inside a "cocoon" formed by a larva from rolled leaves. Such cocoons often dried and started to decay at the final phase of larval browsing.

The third distinctive group of herbivores included exclusively caterpillars of the apollo butterfly *Parnassius apollo*. When younger (instars 2 and 3), these caterpillars fed on the apical part of stolons. Grown larvae (instars 4 and 5) browsed mainly on leaves, but occasionally they also fed on the apical part of shoots or on the nodal part near the leaves (Fig. 5).

Other herbivores with distinctive browsings were deer, but their bites were rarely observed on the investigated plants.

The most often encountered damage to the aboveground parts of a plant were small losses of leaf tissues. The average damage to leaf blades from herbivory varied from 3% leaf removal in 1993 to 7% in 1994 (Fig. 2). Browsing of leaves did not cause visible changes in further growth and development of the aboveground parts of a plant.

The other kind of wound was removal of the apex with a larger or smaller part of a stem. Our field observations showed that this damage was always compensated by development of one or more lateral sprouts, some of which produced inflorescences.

As we did not find any morphological reaction of the stonecrop to browsing of leaves, our further reasoning will concern the response of the plant to apex removal. The experiment showed that breaking of a stolon resulted in the development of one or more lateral

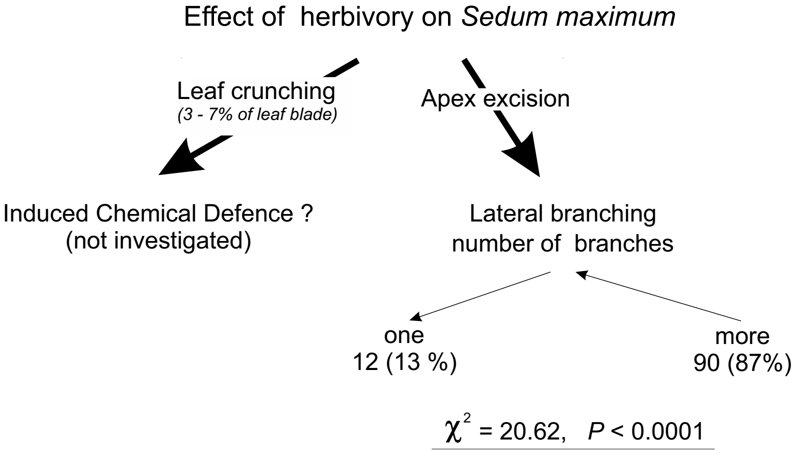

Fig. 6. Lateral branching statistics after apex removal in stonecrop *Sedum maximum* (L.) Hoffm.

shoots. Multi-shooted compensation of apex removal was significantly more frequent (80 cases) than single-shooted (12 cases) (Fig. 6); lateral shoots were more frequently generative than vegetative, but this difference was not statistically significant.

A comparison of treated stolons with the control group showed that the first group was not significantly higher than the control ones. In both groups (experimental and control) the width of inflorescences on generative shoots increased together with stolon height (Fig. 7). The rate of increase in inflorescence width per growth unit of stolon height (coefficient b of the equation $y = a + bx$) was higher (0.183) in stolons with apex removal than the controls (0.169). There were significant differences in the total number of leaves on treated stolons (sum of leaves at a base and on all lateral shoots) compared controls and in total area of inflorescences (all inflorescences developing from lateral shoots) between the compared groups. For both characters the values noted for treated stolons were significantly higher (Fig. 7).

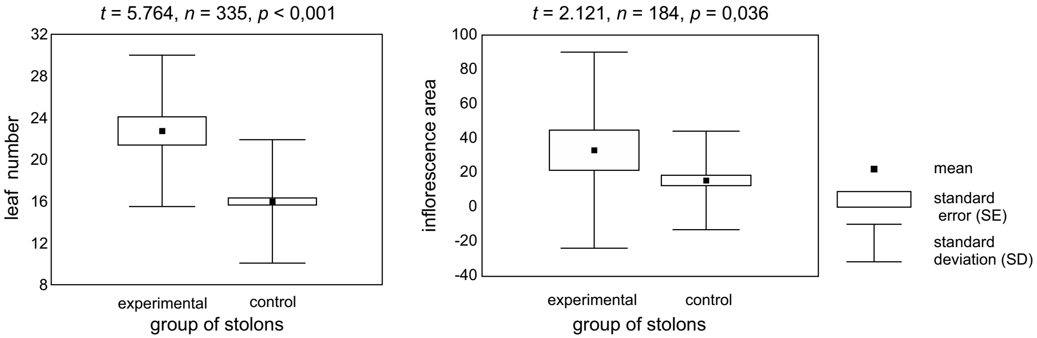

Fig 7. Comparison of number of leaves (left figure) and size of inflorescence (right figure) in broken (after apex excision) and control stolons of stonecrop *Sedum maximum* (L.) Hoffm.

DISCUSSION

Optimal defense theory predicts that the within-plant allocation of resources to defense against herbivory should be positively related to the relative fitness values of a plant tissue (organ) and its probability of being attacked (Rhoades 1979). Induced response, however, means not only the switch of energy allocation to any form of chemical or mechanical defense. In a considerable number of plant species the induced response to herbivory is also exhibited as an additional investment in the production of flowers and seeds, known as the compensatory mechanism (Mashinski & Whitham 1989; Mutikainen & Walls 1995).

The experiment with apex removal showed that simulated herbivore browsing on the apical part of a stem provoked compensatory lateral sprouting in the plant. In most cases (87%) the number of lateral shoots was significantly higher than one (Fig. 6). This mechanism compensates for losses caused by herbivory: the more shoots, the greater the number of leaves and total assimilative surface. (Fig. 7). Total area of inflorescences (including inflorescences on lateral schoots) in excised stems was greater

The results presented here confirm observations made in other species in the case of apex removal – the commonest mechanism of herbivory compensation is lateral sprouting (Aarssen 1995; Aarssen & Irvin 1991; Maschinski & Whitham 1989; Verkaar *et al.* 1986).

The question arises, why doesn't *Sedum maximum* respond in the same way (through compensative mechanisms) to browsing of its leaves by different herbivores. It seems that the mature leaves (unlike the apical part of a stem) produce chemical defense agents.

Two observations point to this suggestion. Field data on leaf browsings show that in 1993–1994 the average fraction of damaged leaf blade in the stonecrop varied from 3% to 7% (Wala 1995). This observation accords with the prediction of Haukioja and Neuvonen (1985) that leaf damage exceeding on average a few percent of its blade induces the plant to activate a chemical defense mechanism.

Observations of the foraging behavior of grown (instars 4 and 5) apollo caterpillars showed that they often changed shoots during feeding even when the leaves were almost untouched. This suggestion was confirmed in experimental breeding of *Parnassius apollo* larvae on another stonecrop species, *Sedum album* (Moser & Oertli 1980), and on *Sedum maximum* (Zawisza 1998), where in captivity caterpillars foraged only on a limited number of stolons with mature leaves. Both experiments produced higher mortality rates and much less effective energy assimilation in comparison to the control group browsing on much younger stolons.

The above observations and experiments correspond to data on high concentrations of alkaloids and polyphenolic compounds in aboveground tissues of *Sedum maximum* (Frank & Hartmann 1963; Wolbiś 1989). These imply that mature leaves of the stonecrop have mechanisms of chemical defense at their disposal which effectively limit the intensity of browsing.

Correlations concerning the whole stonecrop plant (Fig. 2) show that the assimilative surface of leaves is positively correlated with the mass of underground organs and with the total area of inflorescence. At the same time, the negative correlation between the total area of inflorescence and the mass of underground organs suggests competition between the roots and inflorescences for assimilated energy, and a switch of energy allocation as an induced response to herbivory. However, the results of our experiment with apical excision demonstrate only the existence of a compensation mechanism in Sedum maximum and we are unable to correlate the range of compensation to the degree of lifetime fitness.

REFERENCES

AARSSEN L. W. 1995. Hypotheses for the evolution of apical dominance in plants: implications for the interpretation of overcompensation. – Oikos **74**: 149–156.

AARSSEN L. W. & IRVIN D. L. 1991. What selection: herbivory or competition? – Oikos **60**: 261–262.

AGRAWAL A. A. 2000. Benefits and costs of induced plant defense for *Lepidium virginicum* (Brassicaceae). – Ecology **81**: 1804–1813.

BERGELSON J. & CRAWLEY M. J. 1992. Herbivory and *Ipomopis aggregata:* the disadvantages of being eaten. – Am. Nat. **139**: 870–882.

BERGELSON J., JUENGER T. & CRAWLEY M. J. 1996. Regrowth following herbivory in *Ipomopsis aggregata*: compensation but not overcompensation. – Am. Nat. **148**: 744–755.

FRANK B. & HARTMANN W. 1963. *Sedum*-Alkaloide. – Abh. Deut. Acad. Wiess. Berl., Kl. Chem. Geol., Biol. **44**: 111–119.

HAUKIOJA E. & NEUVONEN S. 1985. Induced long-term resistance of birch foliage against defoliators: defensive or incidental? – Ecology **66**: 1303–1308.

ŁASKAWIEC A. 1988. Rozmieszczenie i zasoby *Sedum maximum* Sut. w Pienińskim Parku Narodowym (Distribution and resources of *Sedum maximum* Sut. in the Pieniny National Park). Mscr. of M. Sc. thesis, Institute of Botany, Jagiellonian University, Kraków.

MASCHINSKI J. & WHITHAM T. G. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability and timing. – Am. Nat. 134: 1–19.

MOSER H. A. & OERTLI J. J. 1980. Evidence of a biochemical interaction between insect and specific foodplant in the system *P. apollo – S. album*. – Rev. Suisse Zool. **87**: 341–357.

MUTIKAINEN P. & WALLS M. 1995. Growth, reproduction and defence in nettles: responses to herbivory modified by competition and fertilization. – Oecologia **104**: 487–495.

OHNMEISS T. E. & BALDWIN I. T. 2000. Optimal defense theory predicts the ontogeny of an induced nicotine defense. – Ecology **81**: 1765–1783.

PAIGE K. N. & WHITHAM T. G. 1987. Overcompensation in response to mammalian herbivory: the advantages of being eaten. – Am. Nat. **129**: 407–416.

RHOADES D. F. 1979. Evolution of plant chemical defense against herbivores. – In: G. A. ROSENTHAL & D. H. JANZEN (eds), Herbivores: their interaction with secondary plant metabolites, pp. 4–54. Academic Press, New York.

VERKAAR H. J. E., MEIJDEN VAN DER E. & BREEBART L. 1986. The responses of *Cynoglossum officinale* L. and *Verbascum thapsus* L. to defoliation in relation to nitrogen supply. – New. Phytol. **104**: 121–129.

WALA K. 1995. Rozchodnik wielki *Sedum maximum* – roślina żywicielska gąsienic niepylaka apollo *Parnassius apollo* [*Sedum maximum* – the host plant of apollo butterfly caterpillars]. Chrońmy Przyr. Ojcz. **51**(3): 44–55 (in Polish with English summary).

WITKOWSKI Z. & ADAMSKI P. 1996. Decline and rehabilitation of the apollo butterfly *Parnassius apollo* (Linnaeus, 1758) in the Pieniny National Park (Polish Carpathians). – In: J. SETTELE, C. MARGULES, P. POSCHLOD & K. HEINLE (eds), Species survival in fragmented landscapes, pp. 7–14. Kluwer Academic Publ., Dordrecht.

WITKOWSKI Z., PŁONKA P. & BUDZIK J. 1993. Vanishing of the local race of the apollo butterfly, *Parnassius apollo frankenbergeri* Slaby 1955 in the Pieniny Mountains (Polish West Carpathians) and measures taken to restitute its population. (in Polish). – In: A. BIDERMAN & B. WIŚNIEWSKI (eds), Utrzymanie i restytucja ginących gatunków roślin i zwierząt w parkach narodowych i rezerwatach przyrody [Preservation and restitution of declining species in natural parks and nature reserves]. – Prądnik (Suppl. 1993): 103–119.

WITKOWSKI Z. & ADAMSKI P. 1997. Decline and rehabilitation of apollo butterfly *Parnassius apollo* (Linnaeus 1758) in the Pieniny National Park (Polish Carpathians): 7–14. – In: J. SETTELE, C. MARGULES, P. POSCHLOD & K. HEINLE (eds), Species Survival in fragmented landscapes, pp. 7–14. Kluwer Academic Publ., Dordrecht.

WOLBIŚ M. 1989. Badania związków fenolowych w niektórych gatunkach rodzaju *Sedum* L. ["Studies of phenolic compounds in some species of the genus *Sedum* L."]. 112 pp. Habilitation Thesis, Medical Academy of Łódź, Łódź (in Polish).

ZARZYCKI K. (ed.). 1991. Przyroda Pienin w obliczu zmian [The nature of the Pieniny Mts. (West Carpathians) in face of the coming changes]. 578 pp. Państwowe Wydawnictwo Naukowe, Warszawa (in Polish).

ZAWISZA A. 1998. Pochodzenie linii hodowlanej niepylaka apollo, *Parnassius apollo* L. ssp. *frankenbergeri* Slaby (Lepidoptera: Papilionidae) a tempo metabolizmu i budżet energetyczny w końcowych etapach ontogenezy (Origin of breeding line of apollo butterfly, *Parnassius apollo* L., ssp. *frankenbergeri* Slaby (Lepidoptera: Papilionidae) and metabolism rate and energy budget in the final phase of ontogenesis). Mscr. of M. Sc. thesis, Chair of Physiology of Man and Animals, Silesian University, Katowice.