

CONTROVERSIAL COMPONENTS OF PLANT APPARENCY IN *ALLIARIA PETIOLATA* CAVARA & GRANDE (CRUCIFERAE)

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ABSTRACT

The importance of components of apparency for the two growth forms (rosette and stem) of *A. petiolata* is evaluated, and the term "intraspecific (developmental)" apparency is proposed.

Key words: rosette-plant, stem-plant, biennial cycle, *Pieris napi*, *P. brassicae*, *Anthocharis cardamines*, *Ceutorhynchus* spp., architectural complexity, herbivore load, plant distribution, intraspecific (developmental) apparency, herbivorous guilds, herbivore impact.

INTRODUCTION

The theory of plant apparency has had a stimulatory impact on the development of plant antiherbivore strategies, since the term was introduced by Feeny (1975, 1976), and by Rhoades and Cates (1976). The theory was further elaborated (Feeny, 1983), but at the same time also criticized (e.g. Fox, 1981; Crawley, 1983) both on theoretical and experimental grounds. As the theory is generally well-known and is also reviewed (Feeny, this volume), here only certain aspects are discussed.

In short, the term expresses the probability by which a plant species or individual is thought to be discovered by herbivores, which in turn is connected with a set of complex characters. In order "to go unnoticed", plant species may employ different strategies in space and time.

"Apparency", among others, depends on architectural complexity (Lawton and Schröder, 1977), leaf/flower colour, chemical constituents, neighbouring species' similar characters within the plant community, rate/speed of growth, "timing" of vital processes, such as flowering, etc. To treat such an all-inclusive term that combines each important attributes of a plant's life is the more difficult, as we still know very little about the stimuli guiding herbivorous insects to their host-plants.

From community ecological point of view, diversity of a phytophagous insect guild on any given plant species is supposed to be proportional to the available niches, what in turn to a large extent depends on plant structural characters, i.e. architectural complexity (Moran, 1980; Lawton, 1983). Furthermore, depending on the insect's body size the fractal dimensionality of a plant species may vary considerably (Morse

Table 1 Components of apparency contributing to differences in strategies followed by the two growth-forms of *Alliaria petiolata*.

Rosette-form (unapparent)	Stem-form (apparent)
Late, but durable (predictable)	Early, but ephemeral
Vegetative growth only	Vegetative and reproductive growth
Low apparency, low architectural complexity	High apparency, high architectural complexity
Slightly lower phytophage diversity, and lack of pollinators, nectarium-visitors, etc.	Slightly higher phytophage diversity, presence of flower and silique consumers
Low damage compensation ability	High damage compensation
Clumped occurrence	Random distribution
Defense against generalists ¹	Less defended against generalists

¹ Larvae of an extreme polyphagous noctuid, *Mamestra brassicae*, in preliminary experiments, consumed ca. three times more of the stem-plant leaves in comparison with those of rosette-plants

et al., 1985; Lawton, 1986). Apparency and its components, most likely, are temporary attributes of a plant species because of changes in the plant's chemistry, size, architecture, etc. as it grows. Therefore, only an average apparency of a species is probable [see another definition of average apparency with Fox (1981)].

The classical objects for apparency studies have been the cruciferous species (Feeny, 1977; Courtney, 1985; Chew, 1988, and others).

In order to study quantitative features of plant-insect interaction from the aspect of apparency, I have chosen a member of this family, the garlic mustard, *Alliaria petiolata*.

MATERIALS AND METHODS

The study area was a ca. 2 x 1 km size forest edge (main species: *Quercus cerris*, *Carpinus betulus*, *Sorbus* spp., *Prunus* spp., *Cornus mas*, *Crataegus* spp., all on limestone), located near Budapest at an elevation of ca. 300 m above sea level.

Populations of the two forms of *A. petiolata* were regularly censused, observed and sampled for herbivorous insects throughout several growing seasons.

RESULTS AND DISCUSSION

A. petiolata, a biennial nitrophilous weed, is frequent at humid forest edges. Its two forms: rosette- and stem-form strikingly differ in architectural complexity, but in other characters, too (Fig. 1). The seeds germinate in mid-April, the young plant sprouts 1-4 leaves (rosette-form) and develops a strong root-system of which the probable function is storage. The rosette-form is present throughout the year, growing even during mild winters. The stem-form, starts to produce stems and leaves as early as in February, but usually in March. It grows fast, flowering is terminated by the end of May and siliques are ripe at the end of June. Seeds are spread continuously

during summer. Table 1 lists qualitative differences between the two forms from the point of view of plant apparency theory. The seasonal durabilities of the two forms differ, and this explains differential predictability and availability. While architectural complexity and visibility of stem-form is much higher, the rosette-form has a longer seasonal durability, therefore, is more predictable for herbivores. This trait may counterbalance the supposed unapparent character of the latter.

Quantitative differences are summarized in Table 2. While the rosette-form shows a purely vegetative growth and produces a large root of which wet-mass ratio to above-ground plant parts is slowly increasing, the presence of generative organs on the stem-form dramatically changes the architectural complexity of the latter. Also, microsite differences (e.g. edaphic conditions, duration of exposure to sun) may strongly alter size, number of leaves, etc. of plants. For example, at a sunny place the sum of leaf surface/stem-plant (average of 11 plants) was $48 \pm 17 \text{ cm}^2$, while the

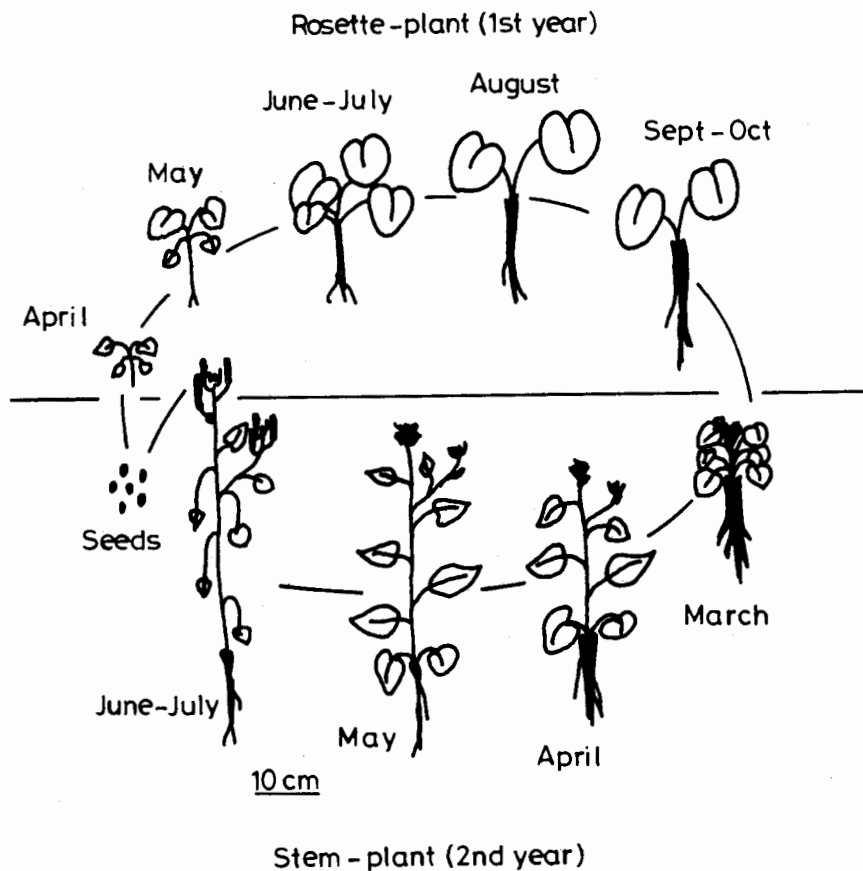


Fig. 1 Schematic drawing of the developmental cycle of *A. petiolata*.

Table 2 Generalized quantitative differences, as elements of architectural complexity and apparency between rosette- and stem-form of *A. petiolata*.

Characters	Rosette-form	Stem-form
Plant height (cm)	3-10	20-100
No. of stalks	none	1-5
No. of leaves	1-4	6-20
Size of leaves (cm ²)	1-80	1-100
No. of ramifications	none	1-5
Above-ground: root wet-mass ratio (root = 1)	1:3.5 ¹	max. 1:10
Wet mass (g)	0.5-1	>5-6
No. of inflorescence/plant	none	3-8
No. of siliques	none	1-30

¹ It drops from 1:40 (germination) to 1:3.5 by July.

same character at a shady surrounding was $390 \pm 115 \text{ cm}^2$. Rosette-plants have a leaf surface/plant of $63 \pm 21 \text{ cm}^2$ (mean \pm S.D.).

Although the two growth-forms differ considerably in the components of apparency the species compositions of herbivorous guilds turned out to be very similar on both (Table 3), only *Anthocharis cardamines* (Lep., Pieridae) and the aphids were restricted to one of them. This means that the apparency of the two growth-forms must be different for the two groups, but may be similar for the rest. Curculionid species most probably react to chemical plant characters. Living on and pupating under a rosette stand increases the probability of finding stem-plants at the same site next year. Herbivore populations, to some degree, do segregate in space and time in exploiting the two forms. Population levels of all species are generally low (Table 4).

Table 3 Herbivores on the two growth forms of *A. petiolata*.

Species/group	Rosette-plant	Stem-plant
Halticinae (<i>Phyllotreta</i> , <i>Aphona</i> , and <i>Longitarsus</i> spp.)	+ ¹	+
Curculionidae (at least 5 <i>Ceuthorhynchus</i> species)	+	+ ²
Lepidoptera	+	+
<i>Pieris napi</i>		
<i>Anthocharis cardamines</i>	-	+
<i>Evergestis forficalis</i>	+	(+)
Tenthredinidae	+	+
Aphids	+ ³	-
Slugs, snails	+	+

¹ + = present, - = absent.

² Some might have specialized to certain regions of the plant.

³ Seasonal, stem plant is not available when the aphids appear (from September on).

Table 4 Seasonal herbivore load on rosette- and stem-forms of *A. petiolata*. (50-100 plants examined per sample.) 1985.

	Census date	"Galls"		Halticinae		Curculionids		Pierid egg/larva		Others	
		R ¹	S ²	R	S	R	S	R	S	R	S
April	3	³	0	-	13	-	0	-	0	-	0
	10	-	11	-	37	-	0	-	0	-	0
	17	-	60	-	11	-	1	-	0	-	0
	24	16	89	0	17	0	5	0	0	0	3
May	7	18	140	2	6	0	0	0	0	0	1
	15	42	124	0	2	0	1	0	2	0	2
	22	97	161	0	0	0	2	0	1	3	0
	29	71	87	0	0	0	0	0	2	0	1
June	5	92	202	0	0	1	10	0	1	1	3
	12	99	131	0	0	2	4	1	2	0	6
	19	104	91	0	0	0	8	0	0	0	1
	26	87	105	0	4	0	8	0	2	0	2
July	3	123	59	0	2	7	3	0	0	3	3
	10	83	43	2	6	5	13	0	0	0	3
	17	82	65	1	12	9	29	1	1	0	3
	24	56	46	2	12	16	13	0	1	0	5
	31	48	⁴	4	-	12	-	2	-	0	-
August	9	33	-	1	-	1	-	4	-	1	-

¹ R=Rosette form.

² S=Stem-form.

³ -=No rosette-form was available yet that time.

⁴ -=No stem-form was available anymore from that time

Many attributes of crucifer life-history are assumed to serve as components of successful escape from herbivores (Chew, 1988). However, there are others that can increase the probability of host finding. Such a factor is, for instance, the spatial and timely coexistence of the two growth- (rosette- and stem-) forms. Still another factor is the patchy distribution of plants. Cain (1985) modelled plant density and herbivore damage relations and found that at high plant densities herbivore damage was low, while the opposite was expected at low plant densities. Cain's model was strengthened by the results of Auerbach and Shmida (1987) and data collected in a review by Antonovics and Levin (1980). My observations were also in agreement with the model in 1985: at 7 clumped plant stands the number of stem-plants was $29 \pm 12/m^2$ (mean \pm S.D.), and the number of gall-like tissue-proliferations caused by *Ceutorhynchus* species was approx. 1/plant, while at places where the density of plants dropped to $1.2/m^2$, the number of "galls" was 4.2/plant. The above data do not support the resource concentration hypothesis (Root, 1973).

Table 5 Quadrat-sized yearly and seasonal population fluctuations of the two forms of *A. petiolata* (means).

Year/month	Grid I ¹		Grid II ²		
	Rosette-	Stem Plants/1 m ²	Rosette-	Stem-	
1986	April	12.2	0	5.4	0
	May	12.3	0	6.4	0
1987	April	3	0.3	1.5	0.04
	May	4.7	0.1	4.8	0.04
	June	4.5	0.1	5.1	. ³
	July	2.7	. ³	2.8	
	Sept.	1.5		2.2	
	1988	April	1.3	0.1	0.6
	May	1.1	0	0.5	0.5
	June	0.7	0	0.25	0.37
	July	0.05	0	0.1	0.1
	August	-	-	0.04	. ³

¹ Grid I was a permanent census site. Size was 10 m², 5 quadrats had been seeded with 100 seeds each in 1984.

² Grid II was another permanent census site. Size was 24 m², no seeding occurred. They were 100 m apart, and had similar surrounding vegetations.

³ The stem-plants died by this time.

The above are partly the consequences of an alternating distribution pattern existing between the two forms. Stem-plants disperse the seeds in the immediate vicinity, therefore, the occurrence of a clumped rosette population at the same place next year is highly probable. Mortality factors decrease the number of rosette plants so that in the second year stem-plants will tend to show a random distribution. Yearly and seasonal large-amplitude (2 orders of magnitude) plant population fluctuations (Table 5) do serve as escape mechanisms. However, such fluctuations are frequently the consequence of abiotic factors (e.g. water shortage, low availability of microsites for germination, etc.), and additional herbivore impacts will only accelerate local extinction. Such is the case with rosette-plants, where the impact of summer water deficiency, further increased by the intensive curculionid feeding (peeling), eventually leads to the complete loss of photosynthetic surface and to mortality. While some seasonal fluctuations are compensated by the temporary coincidence of the two growth-forms, or compensatory regrowth, the total absence of one form locally in any one year or the senescing and dying off of the stem-form, may result in a disproportionate impact by herbivores, such as some curculionid (*Ceutorhynchus*) species living on both forms.

Visual components of apparency affect herbivore populations differentially. The orange tip, *A. cardamines* lays its eggs only during flowering of the plant, and avoids it outside this time period. A dense vegetation around a rosette-plant may hide it from phytophagous insects searching visually. Chew (1975, 1977) pointed out that

ovipositing butterflies confused plants either on the chemical basis or by the shape and size. Likewise, I observed that alighting response by *Pieris napi* (Lep., Pieridae) females on other plant species morphologically only rarely resembling the rosette-form of *A. petiolata*, was frequent in an area where they commonly occurred with the host-plant. Also in an open field experiment I noticed that a *P. rapae* (Lep., Pieridae) female alighted and oviposited on a *Galinsoga* species (family Compositae) in the abundant presence of the host-plant, *A. petiolata*.

Summarizing, the following may be outlined: 1) The herbivorous guilds of the two forms are *almost identical* which is the consequence of a) the similar host finding mechanisms employed in some insect groups (Halticinae, Curculionidae, Tenthredinidae) and by snails and slugs, and, b) the simultaneous presence of the two forms. 2) The *differences* existing between the rosette- and stem-forms means a difference also in apparency, e.g. for the possibly visually searching *A. cardamines*, while no such distinction is made by other two pierid butterflies, i.e. the apparency of the two plant forms seems to be similar for them. 3) Distribution patterns of plant forms regularly change and this has a bearing on the size and impact of the herbivorous guilds. 4) The composition of the herbivorous guilds on both plant forms are not influenced by the available niches. While the "leaf-chewing guild" comprises 7 members (species), there are no root consuming, seed predator, etc. guilds.

The two growth-forms of *Alliaria* possess two kinds of apparency that may result in different survival strategies, and the species as such, can be characterized by a mixture of these. During ontogenetic development the quality of apparency changes. Therefore, it may seem justifiable to make a distinction between inter- and intraspecific apparencies. Intraspecific (developmental) apparency comprises traits that explain plant strategies during ontogeny.

ACKNOWLEDGEMENTS

The author is grateful to Dr. Tibor Jermy and Prof. E. A. Bernays for critical comments, to Dr. Károly Vigh, Attila Podlussány and Csaba Szabóky for species identification work.

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