The Donaciines (Coleoptera Chrysomelidae Donaciinae) and the Gause Principle

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Summary

Based on bibliographical data, the author analyses the structure of guilds of multispecific donaciine populations that were studied by HOFFMAN (1939, 1940) in the United States (Michigan) and tries to find out if donaciine species living in the same site follow the principle of Gause or not. It appears that adults of almost half of the donaciine species observe allomonophagy, and this prevents them from entering into competition. In the case of tautophagous species, where two, or more, donaciine species may exploit the same food plants, and consequently could possibly enter into competition, it seems that there are always some segregative mechanisms (different phenologies; allotopy) that allow donaciine species to coexist on the same food plants. As far as the available data analysed here allow a conclusion, one can state that donaciine species obey the principle of Gause. It also appears that monophagy, for larvae as well as for imagines, is rather the rule than the exception amongst the donaciines.

Keywords : Coleoptera, Chrysomelidae, Donaciinae, guild structure, ecology, Gause principle, trophic selection.

Résumé

À partir de données bibliographiques, l'auteur analyse la structure des guildes d'un peuplement de donacies qui furent étudiées par HOFFMAN (1939, 1940) aux États-Unis d'Amérique (Michigan) et essaye de découvrir si les différentes espèces de donacies vivant dans un même site observent ou non le principe de Gause. Il apparaît que les adultes de près de la moitié des espèces de donacies suivent une allomonophagie, ce qui prévient la compétition entre elles. Dans le cas des espèces tautophages, où deux, ou davantage, espèces de donacies peuvent exploiter la (les) même(-s) plante(-s) nourricière(-s), et conséquemment pourraient entrer en compétition, il semble qu'il y ait toujours quelques mécanismes ségrégatifs (différentes phénologies, allotopie) qui autorisent les espèces de donacies à coexister sur la (les) même(-s) plante(-s) nourricière(-s). Pour autant que l'on puisse en juger à partir des données analysées ici, on peut en conclure que les donacies obéissent au principe de Gause. Il apparaît également que la monophagie, aussi bien pour les larves que pour les adultes, est plutôt la règle que l'exception parmi les donacies.

Introduction

The donaciines are a small group of semi-aquatic leaf beetles, of some 150 extant species, covering all biogeographic regions but the Neotropical, occurring more specially in the Nearctic and Palaearctic regions, with 32 and 49% of species respectively (BOROWIEC, 1984). The oldest fossil records of donaciines date from the Upper Paleocene (ASKEVOLD, 1990a; SANTIAGO-BLAY, 1994), but the existence of the subfamily should go back to, at least, the Jurassic era (ASKEVOLD, 1991a). The Donaciinae seem to derive from common ancestors shared with the Sagrinae, the Bruchinae, but also the Criocerinae and the Hispinae (ASKEVOLD, 1990b; REID, 1995, 2000; SCHMITT, 1985 a & b, 1988, 1989). The emergence of donaciines seems directly related to the appearance of the Nymphaeaceae during the end of the Jurassic era (SCHMITT, 1985 a & b).

Unlike most other subfamilies of Chryso-

melidae, of which members may occupy different ecosystems, the donaciines are rather stenoecious, being restricted to wetlands : rivers, lakes, ponds, marshes, etc., where they live intimately associated with the phytocoenosis of these humid zones. In order to realize a complete life cycle, the donaciines rely upon a large spectrum of aquatic or semi-aquatic food plants : water lilies, sedges, cattails, bulrushes, arrowheads, bur reeds, pond weeds, etc.

A very old association between the donaciines and their food plants has led the former to some noteworthy morphological and physiological adaptations. A fine hydrofuge pubescence entirely covers the lower face of donaciine imagoes (extremely fine and dense among *Macroplea* and *Neohaemonia* that spend most of their life under water) : such pubescence protects the beetles from drowning when falling on the water. When the donaciines have to go under water (for instance to lay their eggs or to escape danger), the pubescence creates a plastron, allowing them to breathe while under water. Donaciine larvae are even more adapted to aquatic life. In general, larvae feed on the roots or rhizomes, in a rather anaerobic environment (mud) (see HOULIHAN, 1969, 1970). However, these larvae are well armed to survive in a such environment : on the eighth abdominal segment one finds a pair of strongly sclerotized caudal spines. In inserting its hollow spiracular spurs in the aerenchymal tissue of the plant, the larva is able to take the necessary oxygen needed to assure its metabolism. It is also on the roots, or rhizomes, that the larva builds its cocoon where pupation takes place. A complete life cycle takes 2 to 3 years (BIENKOWSKI, 1996) (see LAYS, 1997 for a summary of the biology of donaciines). Larvae are known to be, mainly, radicivorous, but feed also on rhizomes, stems, culms, sheathing leaves and leaves. Adults depend on, principally, leaves, but also on flowers (pollen; nectar ?). This ancient association between the donaciines and their food plants has led to co-evolutions in some cases : in their study on the floral biology of the waterlily *Nuphar lutea macrophylla*, SCHNEIDER & MOORE (1977) conclude that : " *These observations suggest that the overall floral structure (i.e., the large number of stamens, masses of pollen, and the flat stigmatic surfaces), coupled with the sequence of floral development, odor and the timing of sepal movements are primary adaptations to assure pollination by beetles* [Donacia piscatrix] ".

In wetlands, several factors may determine the species richness of donaciines in a site; the most preponderant parameter, as one could logically expect from phytophagous insects, being the floristical diversity. Well preserved wetlands, with a rich phytocoenosis, may hold many donaciines in a given site, quantitatively as well as qualitatively. In some parts of Europe or North America, for instance, it is not uncommon to find sites where some 10-15 species coexist, and even up to 25 species as reported in Canada by ASKEVOLD (1988), some of them with very large populations, just in a single site.

How do all these species manage to coexist in a site ? How do they exploit their environment and is there a structure in the means they exploit the phytocoenosis ? Does interspecific competition occur amongst the donaciines ? Do the donaciines observe the Gause principle ?

In ecology, the Gause principle states that : " *No two species can coexist at the same locality if they have identical ecological requirements* " (MAYR, 1979); the supposed causes of the said principle, also known as the " competitive exclusion principle ", presume that in a such context of coexistence " *one or the other species will prove superior in the utilization of the resources. This will lead to an exclusion of the other species from the zone of potential ecological overlap. To avoid such fatal competition, the two species must utilize the resources of the environment in a somewhat different way* " (MAYR, 1979).

In order to be able to answer the above questions, one needs to rely on some thorough observations regarding the food plants exploited by the donaciines. Even if for many donaciine species one still does not know their food plants, some species have been recorded on many plants. To discover a phytophagous insect on a plant does not imply, *ipso facto*, that the former feeds on the latter and that, *a fortiori*, the insect can realize its complete life cycle on it.

The donaciines fly very well and may spread all over the vegetation of wetlands and, consequently, can be collected on plants on which they do not feed at all. This explains that some species have been reported from numerous different plants, for instance : *Plateumaris nitida* on *Arum, Caltha, Carex, Cornus, Eleocharis, Eriogonum, Iris, Juncus, Picea, Pinus, Ranunculus, Salix, Scirpus, Smilacina, Sparganium, Veratrum, Viburnum*; *Plateumaris pusilla* on : *Abies, Agropyrin, Alnus, Carex, Dulichium, Juncus, Eleocharis, Lepidium, Mentha, Poten-*

tilla, Rumex, Salix, Solidago, Scirpus, Spar-ganium; or *Plateumaris rufa* on : *Acer, Caltha, Carex, Lysitchitum, Prunus, Ranunculus* (ASKE-VOLD, 1991a). For the donaciine species just mentioned, it seems obvious that most of the cited genera are only adventitious (ASKEVOLD, 1991a). Even when one retains only the aquatic or semi-aquatic plants recorded, it remains doubtful that one given donaciine species could realize its vital cycle on numerous different plant genera.

Fortunately, some entomologists have paid special attention to the ecology of local multi-specific populations of donaciines and their observations allow us to better understand their coexistence.

Material & Methods

The data given hereafter, and analysed farther, have been entirely compiled from HOFFMAN's publications (1939, 1940). The studies conducted by HOFFMAN in the USA provide accurate and informative data for the problem considered here; this author followed the com-plete evolution of donaciine populations (phenology, food plants, etc.) of 12 species living in Douglas Lake, Cheboygan County, Michigan. His data have been summarized by the author in the form of tables given below.

The nomenclature used by HOFFMAN (1939, 1940) have been preserved. However, since his publications some nomenclatural changes have been carried out :

1 - *Haemonia nigricornis* KIRBY, 1837 has been transferred by ASKELVOLD (1988) to the genus *Neohaemonia*. ASKEVOLD (1988) can not substantiate the identification of the specimens reported as *Haemonia nigricornis* by HOFFMAN (that were in fact identified by H.S. BARBER), although the material (not HOFFMAN's specimens) reviewed by ASKEVOLD (1988) from Douglas Lake belongs to this species.

2 - *Donacia quadricollis* SAY, 1827 has been placed as a synonym of *Donacia subtilis* KUNZE, 1818 by ASKEVOLD (1987a). It would be useful to know which key or what material BARBER used to identify the specimens collected by HOFFMAN in Douglas Lake, this would probably help to solve some problems that arise from this new synonymy. The Douglas Lake specimens presented by HOFFMAN under the names of *Donacia subtilis* and *Donacia quadricollis* do not seem to refer to a single species if one

considers the imaginal phenologies, the ecology of imagoes and preimaginal stages, the descrip-tion of egg masses, eggs and larvae. So, we are probably in presence of two species and, conse-quently, will treat them in this paper as two separate taxa, whatever the name of the species they belong to.

3 - *Donacia aequalis* SAY, 1824 has been placed in synonymy with *Donacia caerulea* OLIVIER, 1795 by ASKEVOLD (1987b).

4 - *Donacia pubicollis* SUFFRIAN, 1872 has been transfered to the genus *Donaciella* by ASKEVOLD (1990b).

5 - The specimens reported as *Donacia flavipes* KIRBY, 1837, belong in fact to the genus *Plateumaris* (ASKEVOLD, 1991a), but the exact species name is uncertain. ASKEVOLD (1991a & b) states that : " *the taxon hitherto known as* P. flavipes *is thus correctly known as* P. shoe-makeri (SCHAEFFER, 1925) ". Nowhere in its revision ASKEVOLD (1991a) make allusion to the publications of HOFFMAN. *P. flavipes* has not been recorded from the State of Michigan (ASKEVOLD, 1991a); so, it is probable that HOFFMAN's Douglas Lake specimens belong indeed to *P. shoemakeri*. If so, there is a problem with regard to their food plants : ASKEVOLD (1991a) states that *P. shoemakeri*'s normal food plant is *Acorus calamus* L., adding, however, that in absence of the latter plant, this donaciine can use Cyperaceae (*Carex* and *Scirpus*), a fact reported by HOFFMAN for his " *Donacia flavipes* group B " on *Scirpus americanus*, but not for his " group A " of the same taxon, found only on *Typha latifolia* (see tables below).

It seems difficult to give an opinion on the exact taxonomic status of " groups A and B " of HOFFMAN created for *Donacia flavipes* and *Donacia subtilis*. Unfortunately, this author eluded that problem at the level of immature stages, as pointed out by MARX (1957).

Concerning *Donacia subtilis*, HOFFMAN (1940) thinks that " group B " could be a variety of " group A ". MARX (1957), who has examined donaciines collected in Douglas Lake (although he did not see HOFFMAN's material) thinks that one of the two " groups " of HOFFMAN could indeed refer to *Donacia fulgens* LECONTE, 1851, a very close species to *D. subtilis* KUNZE, 1818 (see BRIVIO & BALSBAUGH, 1984). As for the two " groups " of the taxon *flavipes*, HOFFMAN (1940b) assumes that, morphologically, they are similar and can only be separated on the base of their respective phenology and food plants; if the

specific status of these specimens is confirmed, we can consider them a couple of sibling species that came to exist through, perhaps, quasi-sympatric speciation. In his systematic revision of the Nearctic *Plateumaris*, ASKEVOLD (1991a) does not tackle this problem.

It is not the purpose of this paper to debate the taxonomic status of some of the American dona-ciines treated here and the aforesaid nomenclatural modifications made by ASKEVOLD are probably justified, but they have not yet undergone the test of time; in other respects, some of his nomenclatural changes – related to Palaearctic and Australian species – have been already suppressed : for instance, *Plateumaris discolor* (PANZER, 1795) was placed in synonymy with *P. sericea* (L., 1758) by ASKEVOLD (1991a), a position refuted by HANSEN, LILJE-HULT & PALM (1993); on the other hand, the American scholar (ASKEVOLD, 1990a) treated as distinct taxa *Donacia australasiae* BLACKBURN, 1892, *D. papuana* GRESSIT, 1971 and *D. inopinata* GOECKE, 1944, but they appear to be one species (REID, 1993).

In HOFFMAN's papers, 12 species have been identified (including 1 unnamed *Donacia*); amongst these species, 2 of them were subdivided into two " groups " A and B (see above); so, waiting clarification on the exact taxonomic status of some of the donaciines observed by HOFFMAN, one can consider that 14 taxa were living at Douglas Lake.

Regarding the use of terms " host plant " and " food plant ". If a food plant is automatically a host plant, the reverse is not true : for instance, adults of some Coccinelidae or Symphyta occur on certain plants on which their prey feed; elsewhere, some Hymenoptera are associated with certain plants for nesting (*Anthidium, Dolichurus, Megachile, Osmia, Trypoxylon*). Although the term " host plant " possesses a larger meaning than the term " food plant ", both terms are often used indiscriminately in litera-ture. In the present case, for some donaciine species, their ova and pupae have been also found (aside from their normal plants) on plants different from those on which their respective larvae and imagoes feed (see below); these botanical species could be classified as host plants : they can host one or two stages (ova and/or pupae) of a donaciine species but, as far as one knows, are not exploited as food plants by the feeding stages (larvae and/or imagines). For instance pupation of *Haemonia nigricornis* may

occur on *Castalia odorata*, but neither larvae nor adults of this donaciine species have been recorded feeding on that plant, but only on *Potamogeton natans*. At the pupal stage, *H. nigricornis* is a commensal (not a parasite) of *Castalia odorata*. Therefore, *Castalia odorata* must be considered as a host plant for *H. nigricornis*, whereas *Potamogeton natans* is its food plant. Briefly, when donaciine eggs or pupae are found on a plant, it does not mean automatically that this plant can serve as food plant, although, most of the time, it actually does, but the rule is not absolute.

A last remark with regard to trophic selections observed in phytophagous beetles. As one will see, most of the donaciines presented here follow monophagy. Monophagy (including of first degree) in itself does not exclude coexistence or competition; in fact, five species can be mono-phagous, all of them depending on the same plant species or, on the other hand, each phytophagous beetle can be restricted to one plant species not shared with others. Wishing to introduce a distinction between species that share the same food plant species from those which do not, I refer to " tautophagy " as the trophic selec-tion observed by, at least, two species feeding on, at least, one common host species (food plant in this case, but could also be applied to animal parasitized); therefore " tautophagous species " refer to species that share the same food plants. If the species one refers to are monophagous, a subdivision can be made and one can talk of " tautomonophagy " and " tautomonophagous species ". On the other hand, one refers to " allo-phagy " as the trophic selection realized by, at least, two species living on, at least, one different host species (food plant; animal parasitized). Here too, if one considers monophagous species, a subdivision can be introduced and one can talk about " allomonophagy " and " allomono-phagous species ". These subdivisions can be extented to oligophagy and polyphagy.

Finally, amongst the tautophagous species, one has to differentiate between those sharing the same ecological niche, syntopic species, from those that occupy a different niche, allotopic species.

Terms related to trophic selection, aside from those defined here, come from JOLIVET (1954, 1983).

When one uses the term competition in the present text it always refers to interspecific competition.

Data

In the tables that follow below, ecological data (food plant, part occupied or eaten) regarding the different stages of the 14 donaciine taxa reported by HOFFMAN at Douglas Lake are provided.

Donacia aequalis	Food plant : *Sagittaria latifolia*
ova	above water surface; between tip of blade of one arrow-shaped leaf and surface of blade, tip turned back and attached to surface of blade
larvae	on the proximal portions of the roots; also on *Sagittaria arifolia*
pupae	on the proximal portions of the roots
imagines	+

Donacia cincticornis	Food plant : *Castalia odorata*
ova	/ under side of leaves
larvae	feed on the roots, rarely on the rhizome
pupae	on the roots
imagines	feed on the leaves (upper side)

Donacia flavipes group A	Food plant : *Typha latifolia*
ova	into the tissue of leaves or culms; above water surface
larvae	feed on the roots
pupae	on the roots
imagines	+; adults confined to this plant and observed *in copula*

Donacia flavipes group B	Food plant : *Scirpus americanus*
ova	into the tissue of leaves or culms; above water surface
larvae	feed on the roots; also on the roots of *Eleocharis palustris* var. *major*, growing close to *Scirpus americanus*
pupae	on the roots
imagines	+; adults confined to this plant and observed *in copula*

Donacia hirticollis	Food plants : *Potamogeton natans*	*Sparganium angustifolium*
ova	between the stipules and the stem	between the submerged portions of two leaves
larvae	/ roots Also occurred on *Sagittaria latifolia*	/ roots
pupae	on the roots	[6]
imagines (remain under water most of their life)	+	+

Donacia piscatrix	Food plant : *Nymphaea advena*
ova	/ the submerged part of the flower pedoncule
larvae	feed on the roots, rarely on the rhizome
pupae	on the roots
imagines	feed on the flowers

Donacia proxima	Food plant : *Nymphaea advena*
ova	/ under side of leaves
larvae	/ basal portion of leaf petioles; sometimes / rhizomes [3]
pupae	on the rhizomes
imagines	feed on the leaves (upper side)

Donacia pubescens	Food plant : *Scripus occidentalis*
ova	on inner sides of the outer culm sheaths
larvae	feed on the roots
pupae	on the roots
imagines	+ on the culm; feed on the newly formed flowers

Donacia pubicollis	Food plant : *Phragmites communis*
ova	on the inner side of the leaf or on the part of the culm coverved by the leaf
larvae	first beneath the leaves, then feed on the proximal portions of the roots
pupae	on the culms, just above the roots
imagines	eat the leaves; hide between the leaves and the culm

Donacia quadricollis	Food plant : *Scirpus occidentalis*
ova	between the sheath and the culm; / inner sides of inner culm sheaths
larvae	beneath the sheathing leaves; between the sheathing leaves and the culm; some may feed on the roots
pupae	on the culm, just above the roots
imagines	+ on the culm

Donacia subtilis group A	Food plant : *Sparganium eurycarpum*
ova	+between two floating leaves; may deposit its eggs on other plants [1] [2], but growing near *Sparganium*
larvae	sheathing leaves; larva found also on other plants [4]
pupae	on the outside of the inner leaves
imagines	feed on the leaves

Donacia subtilis group B	Food plants : *Sparganium angustifolium;S. diversifolium*
ova	+ between two floating leaves; may deposit its eggs on other plants [1] , but growing near *Sparganium*
larvae	sheathing leaves; larva found also on other plants [4]
pupae	on the roots [5]
imagines	feed on the leaves

Donacia sp.	Food plants : *Potamogeton natans*; *Sparganium angustifolium*
ova	0
larvae	+
pupae	+
imagines	+

Haemonia nigricornis	Food plant : *Potamogeton natans*
ova	between the stipules and the stem; inner sides of submerged stipules
larvae	between stipules and stem, few on the lower stem and roots; feeding on the stem
pupae	on the stem, close to the root [7]
imagines (remain under water most of their life)	feed on the leaves

remarks :

+ : recorded on that plant, but no other information given

0 : no information given by HOFFMAN

[1] : *Polygonum amphibium* and *Polygonum hydropiperoides*, also chosen for oviposition, but adults never feed on them.

[2] : *Nymphaea advena* : according to HOFFMAN (1940), although *Donacia subtilis* depends on *Sparganium* for its food, the donaciine may deposit its eggs on other plants; females choose plants for egg laying in which two floating leaves are in close proximity, something seldom observed in *Sparganium eurycarpum*, unless the leaves are broken and floating; this explains why this donaciine may deposit its eggs on any close plants different from the adult food plant.

[3] : in one case, 1 last-instar larva has been found on *Castalia odorata*.

[4] : on the roots of : *Sagittaria latifolia, Typha latifolia, Pontederia cordata*; larvae are more numerous on *Sparganium* than on these latter plants.

[5] : cocoons of this species were also found on the roots of : *Sagittaria latifolia, Typha latifolia, Pontederia cordata*.

[6] : cocoons of this species were also found in *Sparganium diversifolium, Sagittaria latifolia, Glyceria borealis, Myriophyllum spicatum, Potamogeton richardsonii, Potamogeton amplifolius*. HOFFMAN (1940 : 272) remarks that 1- the larvae have never been observed on these plants; 2- that the cocoons were never abundant on these plants.

[7] : one observation only of a cocoon on *Castalia odorata*.

Discussion

The reality of the Gause principle has been debated; a debate that is not yet closed. It is not the aim of this article to " preach " for or against this principle. One must remain open to any fact or theory. Life is undoubtedly too diverse and complex just to be ruled by only a few laws and it is certainly an illusion to believe one can reduce its mechanisms to some mathematical equations. Future ecological data on the donaciines may confirm or refute, partially or totally, the conclusions made here. One just attempts to test a theory with reliable field data.

In general, species may enter into competition for several reasons : they depend on the same food (for instance, the same plant species or the same animal parasitized and exploit the same part of it; the same prey); they may use the same material for the building of their tests, nests, cases, etc.; they may use identical sites for nesting or for their courtship rituals; etc.

What are the means of avoiding coexistence and its possible consequence : competition ?

Segregative spacial factors : the most effective way is to occupy an other area, different from potential competing species : allopatry and vicariance.

Otherwise, when sympatry occurs, species may avoid competition through ecological segregative factors : where related species live in different ecosystems, biotopes or occupy different ecological niches (allotopy). If two species share the same ecological niche (syntopy), it remains possible to avoid niche overlap through 1- segregative phenological factors : adults of species are active at different seasons of the year (seasonal segregation), or at different moments of the day or the night, or day versus night (nycthemeral segregation); or through 2- segregative mating factors : all mechanisms put in place in order to avoid sterile matings with other species (courtship rituals, sites for mating, colours, pheromones, etc.). A last theoretical case can be considered : here sympatric and syntopic species, with synchronous phenologies, come to coexist, in a given site, in occupying different individuals of the same species of food plant (or parasite) : there would be a kind of priority of seniority of occupancy for a niche; if one specimen of a β species comes to visit a plant and notes that the niche is already exploited by a α species, the β specimen would just move away to an other vacant plant specimen, or possibly occupied by conspecific individuals. In that case symparasitism does not occur. Finally, one can extend that case to the station level : where, in a site, species sharing a similar niche would coexist in dominating (numerically) at the level of the station : 1 species per station.

Amongst the four stages, one will mainly focus on the larval and imaginal stages : ova and pupae are static, do not realize any trophic selection and therefore are assigned to " neutral " or " passive " stages in the context of competition (which does not mean, of course, that these stages could not interfere in interspecific competition [for instance through the space they occupy, that could be in itself a limiting factor for the settling of heterospecific individuals; or through the production of some unknown allomones than could inhibit the development or drive away heterospecific individuals]). On the other hand, larvae and adults are dynamic, operate trophic selections and therefore can be attributed the status of " active " stages in the process of coexistence and competition, if competition occurs.

The aforesaid compiled data show quite instructive facts about how donaciines deal with coexistence.

From the data given by HOFFMAN, it is interesting to note that : with respect to the adults of the 14 taxa, 12 are monophagous (11 of first degree; 1 of third degree); 2 are polyphagous (of first degree). If one considers the larvae of the same taxa, one finds : 9 monophagous (8 of first degree; 1 of third degree); 1 is oligophagous (of first degree); 4 are polyphagous (of first degree). From this figure, it seems that, in the case studied, monophagy, both amongst the larvae (9/14 taxa) and the imagoes (12/14 taxa), is rather the rule than the exception amongst the donaciines, as already underlined by HOFFMAN (loc. cit.); a fact which is rather in contradiction with some statements found in the literature (JOLIVET, 1954, 1977, 1988, 1995). An indirect way to be informed about the reality of the presumed polyphagy of donaciines would be through a survey of their mixed-function enzymes (located in gut microsomes), both in larvae and imagines : polyphagous insects' metabolism has to overcome the toxicity of numerous constitutive and inductive allelochemicals (alkaloids, polyphenols, terpenoids, etc.), a detoxification undertaken by a set of enzymes whose activities are higher in polyphagous species than in monophagous species (KRIEGER, FEENY &

WILKINSON, 1971); this could be done provided that donaciines do not sequester these plant poisons as sometimes insects do (EDWARDS & WRATTEN, 1980). Anyway, these biochemical approaches of polyphagy will not replace the indispensable field data with regard to trophic selection.

Let us see how allophagy and tautophagy is spread amongst larvae : allophagy concerns 4 taxa : *D. cincticornis*, *D. flavipes* group A and *D. pubicollis* for allomonophagy and *D. flavipes* group B for allo-oligophagy. 10 species demonstrated tautophagy, 6 under tautomonophagy : *D. aequalis*, *D. piscatrix*, *D. proxima*, *D. pubescens*, *D. quadricollis*, *H. nigricornis*; 4 under tauto-polyphagy : *D. hirticollis*, *D. subtilis* group A, *D. subtilis* group B, *D. sp*.

Let us see now how allophagy and tautophagy is spread amongst imagines : allophagy, that by definition prevents coexistence and therefore competition, plays an important part in the present case, since it concerns 6 taxa, all of them under the subcategory of allomonophagous taxa : *D. aequalis*, *D. cincticornis*, *D. flavipes* group A, *D. flavipes* group B, *D. pubicollis* and *D. subtilis* group A. As for tautophagy, 8 taxa are concerned : 6 following tautomonophagy : *D. piscatrix*, *D. proxima*, *D. pubescens*, *D. quadricollis*, *D. subtilis* group B and *H. nigricornis*; and 2 following tautopolyphagy : *D. hirticollis* and *D. sp*. Among taxa where tautophagy occurs, four groupings must be made :1- *D. hirticollis*, *D. sp*., *H. nigricornis*; 2- *D. hirticollis*, *D. sp*., *D. subtilis* group B; 3- *D. piscatrix*, *D. proxima*; 4- *D. pubescens*, *D. quadricollis*.

As one can perceive from these data, monophagy in itself does not better guarantee a phytophagous species to avoid competition with other species.

Let us consider now these aforesaid four groupings of tautophagous species.

First case of possible coexistence : *Donacia hirticollis*, *Donacia* sp. and *Haemonia nigricornis* on *Potamogeton natans*. Nothing is known in respect of the niche(s) of *Donacia* sp. Larvae of *Donacia hirticollis* and *Haemonia nigricornis* are allotopic : roots for the former and stems for the latter. Incomplete data do not allow comparison of adults' ecological niches of these two species. It would be however interesting to clarify it, since these species spend most of their life submerged. Note that even if the adults of *H. nigricornis* shared the same niche as *D. hirticollis*, this would be only for a

short period of time, a maximum of two weeks according to the phenology given in Table 1 by HOFFMAN (1940), where it is shown that at the time the imaginal population of the former species declines, around the first half of July, the adults of the latter species emerge; so there would be no niche overlap owing to this phenological segregation. Last but not least, these two species are not congeneric.

Second case of possible coexistence : *Donacia hirticollis*, *Donacia subtilis* group B, *Donacia sp*. have been recorded on *Sparganium angustifolium*. Nothing is known about the niche(s) of *Donacia* sp. While larvae of *D. hirticollis* exploit the roots of the above mentioned bur reed, *D. subtilis* group B exploit its leave sheaths. Incomplete data do not allow comparison of the adults' ecological niches in these two species. The imaginal phenologies of *D. hirticollis* and *D. subtilis* group B are almost the same, except that the latter appears one month earlier than the former. These two taxa are probably not syntopic since *D. hirticollis*, as previously stated and contrary to *D. subtilis* group B, spends most of its life under water.

Third case of possible coexistence on *Scirpus occidentalis* of *Donacia pubescens* and *Donacia quadricollis*. This is an interesting case where allotopy is observed, both at larval and imaginal stages. The larvae of the first donaciine feed on the roots of this bulrush whereas the larvae of the second exploit the leave sheaths (and culms ?). As for the imagoes of *Donacia pubescens* they feed on flowers while those of *Donacia quadricollis* depend on the culm.

Fourth case of possible coexistence of *Donacia piscatrix* and *Donacia proxima* on *Nymphaea advena*. Typical allotopic species, where, normally, the larvae of the former donaciine feed on the roots of the waterlily, whereas those of the latter feed on leaf petioles; for adults, the first donaciine feeds on the flowers and the second species eats the leaves.

In the four examples given above, the term " possible " coexistence is used because the data provided by HOFFMAN do not allow us to proclaim that they coexist. One knows that two donaciine species may exploit the same species of plant, but one does not know whether heterospecific individuals of donaciines can actually occur on the same plant specimen (see above : ways to avoid competition, last case); so, in a broad sense these species coexist (since they occur in a same site : a lake for instance) but may

not coexist at a smaller scale (*e.g.* : on the same plant specimen). In a word, one can not be sure of the occurrence of symparasitisms.

The fact that pupae of some donaciine species (*e.g.* : *Donacia hirticollis*, *Donacia subtilis* group B, *Haemonia nigricornis*) can also be found on host plants different from those on which the larvae feed on could be explained by the fact that at the pupal stage the choice of the plant does not really matter since trophic selection is interrupted; consequently the cocoons could be built, theorically, on any plant, provided pupae can get the necessary oxygen from the aerenchymal tissue of plants.

Data examined here show that donaciine imagines exhibit a rather stenotrophic regime compared to their respective eurytrophous larvae, a fact which rather goes against a general trend observed amongst insects where, usually, larvae are quite " rigid " ecologically speaking, and not only in respect of their trophic selection. Is the broader food plant range of donaciine larvae an archaic character compared with the regime of their adults ? If it is so, this trend should be probably more common than it is; furthermore, giving as examples the Eumolpinae, the Synetinae, the Galerucinae and the Alticinae, JOLIVET (1988) states that : " [*roots*] *feeding produces a larger phytophagy for the larva than the adult* ". Archaic or not, what is the reason that underlines a such choice ? A question not easy to answer for the moment : it is clear that polyphagy, or oligophagy, provides an adaptative advantage compared to monophagy; a poly-phagous species can better face a crisis situation than a monophagous species (when one or several of its food plants become rarer or vanish; in terms of colonization of other territories, etc.). However, as far as donaciines are concerned, it seems that polyphagy rather seldom occurs. As previously stated donaciines are confined to phytocoenosies of wet lands where they often live in great number (populations and number of species), so a generalized polyphagy would certainly lead to interspecific competition. Through other trophic selections, namely mono-phagy and oligophagy, such a competion is avoided or at least reduced. It seems clear that at the imaginal stage it certainly does matter, whenever possible, to be only in presence of conspecific individuals and thus to avoid sterile hybridization with other species (unless mating occurs in sites different from the food plants, but it does not seem to be the case); therefore, in limiting their regime to one or few plants, adults would reduce their chance to mate with hete-rospecific individuals.

Generally speaking, is the observed mono-phagy, oligophagy or polyphagy of a species the result of present or past competition (or its absence) (see CONNELL, 1980) or does it rather mirror past as well as present trophic selection put in place through both allopatric and sympatric speciation (provided that plants play a role in speciation, which seems more than probable amongst phytophagous insects) ? It can be expected that both are true, but for each species considered it will be difficult to attribute what respective part is due to each of these factors.

What do these data learn us regarding the structure of guilds of donaciines living in the lake studied by HOFFMAN ? In the case consi-dered here, the trophic selection – allomo-nophagy – observed by almost half of the species on one hand, and the allotopy and/or allochrony of tautophagous species on the other hand allow the donaciines to coexist in the same limno-logical phytocoenosis without entering into competition.

Of course, coexistence does not automatically imply competition; after all competition will only occur if an essential resource of two, or more, syntopic species starts to become too short to assure their survival. In the cases where aquatic plants have been reported to be exploited by more than one donaciine species, and where competition could be expected to be met, one notes that aldults of apparently syntopic species avoid competition through segregative pheno-logy (first case; allochronic species); that adults of species living on the same food plant will not enter into conflict through exploitation of diffe-rent niches (second, third and fourth cases; allotopic species).

From a purely theoretical point of view, one can not exclude that a phytophagous species may adopt several " trophic strategies " according to : 1- the geographic region in which it occurs (+ other ecological parameters); 2- the occurrence of potential food plants (+ the possibility of an allotrophy, not to confuse with allophagy; buffer species); 3- the density of populations of these food plants; 4- the occurrence and density of other sympatric, syntopic and synchronic phyto-phagous species. Depending on these parameters, a species could be monophagous here, but oligo-phagous there for instance; or could occupy

different ecological niches (see phenomena related to current competition and competitive release; fundamental niche vs realized niche).

When one wishes to assign a species to a certain trophic category, it is probably risky just to rely only on a simple list of plants on which the species has been observed all over its geographical area. In that list, aside from suppressing the adventitious species, one has also to distinguish the host plants from the food plants (see above), but, likewise, to take the occurrence of other syntopic phytophagous species as well as of other plants into account. All these parameters may – and probably do – interfere with each other in a dynamic equilibrium and may influence the trophic selection of the phytophagous species. Only comparative field studies will provide the key to these problems.

Concluding remarks

Even if precisions are still needed as to the exact niche of some species (or the exact niche used by some stages of some species), as far as available data allow, it seems that in multispecific donaciine populations the principle of Gause is followed.

In the study of phytophagous beetles, or plant-feeding insects in general, the study of their food plants is as important as our knowledge of the beetles themselves, since the latter are associated with the former from very ancient times, and considering only the first while neglecting the second would probably prevent us from understanding the evolution of both.

On the other hand, accurate knowlegde regarding the structure and functioning of donaciine guilds could teach us how food plants may have played or play a role, if any, in speciation.

Acknowledgments

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