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Aphids as biological models and agricultural pests

Les pucerons : modèles biologiques et ravageurs des cultures

Aphids (*Hemiptera:Aphididae*) constitute a small group (about 4500 species in the world, around 600 in France) inside the immense cohort of the insect class (presumably several million species). They are distributed worldwide, but they are more common in the northern temperate zone. They appeared around 280 million years ago and, later, their diversification was concomitant with the radiation of Angiosperms. There is a non-stop increase of studies on these small insects for two main reasons.

1. Aphids as biological models

First, aphids can be considered as "experts" in probing and use phloem sap as their sole food source. These "mosquitoes of plants" are exquisitely adapted to their hosts. In contrast to the chewing herbivory insects, which macerate plant tissues and cause swift and extensive damage, aphids penetrate tissues by probing intercellularly through epidermal and mesophyll (or parenchyma) cell layers with slender stylets to reach the phloem. In addition, they puncture for a few seconds several cells along the stylet pathway [1] and, like chemists, they analyze the physicochemical properties of the apoplastic or symplastic microenvironment at the stylet tip. So, they can choose a phloem sieve-element among other cells. When the sieve-tubes of the phloem tissue do not exhibit the same properties, aphids are even able to select the most appropriate sieve-element in terms of transport ability and/or sap composition [2,3]. Whereas damaged sieve-elements are normally sealed immediately or almost immediately, mechanisms under the control of a complex salivation activity allow aphids (and other hemipterans) to feed for hours and even days [4,5].

Secondly, aphids supply other insects with a modified phloem sap. The phloem sap, which is a perfect diet for growing plant organs, poses, for aphids, two major nutritional problems called the "sugar barrier" and "nitrogen barrier" [6]. Aphids cope with the excess of sugar and the associated osmotic pressure several times higher than that of their haemolymph by converting sucrose into more complex molecules, which are expelled as honeydew from their anus. Besides the well-known mutualistic relationship between aphids and some species of ants (which protect them against predators and take care of their eggs during winter) many insect species (bees, beetles, flies, wasps, butterflies, moths) consume honeydew and thus phloem sap by proxy.

Thirdly, like various insects living on vertebrate blood, aphids bear symbiotic microorganisms. The nitrogen barrier of phloem sap for aphids consists in its low level in essential amino acids needed for protein synthesis. The aphids overcome this barrier through the nutritional contribution from these symbionts, especially *Buchnera aphidicola*, that is the primary obligate endosymbiotic bacteria of most aphid species. The association of aphids and *Buchnera* dates back about 150 million years and is one of the most popular models in symbiotic bacterial evolutionary research [7,8].

Fourthly, another intriguing trait of aphids is their mode of reproduction. They are among the few organisms capable of reproducing either sexually or asexually. The alternation of sexual (late summer or autumn) and asexual (spring and summer) phases is under the control of environmental parameters, especially photoperiod. Parthogenetic reproduction, which was in the past approached by de Réaumur and then evidenced by Bonnet [9] allows an explosive increase in aphid population under favorable environmental conditions, while sexual reproduction leads to frost resistant eggs. The mechanisms of the shift in the reproductive mode, which involve sensing and traduction of photoperiodic changes, as well as the loss of sexual reproduction observed in a few aphid species are intensively studied at the present time.

The recent sequencing of the genome of *Acyrthosiphon pisum* (Fig. 1) [10] now opens the way to go deeper in the understanding of aphid biological traits mentioned above and to search for the Achilles' heel of these pests.

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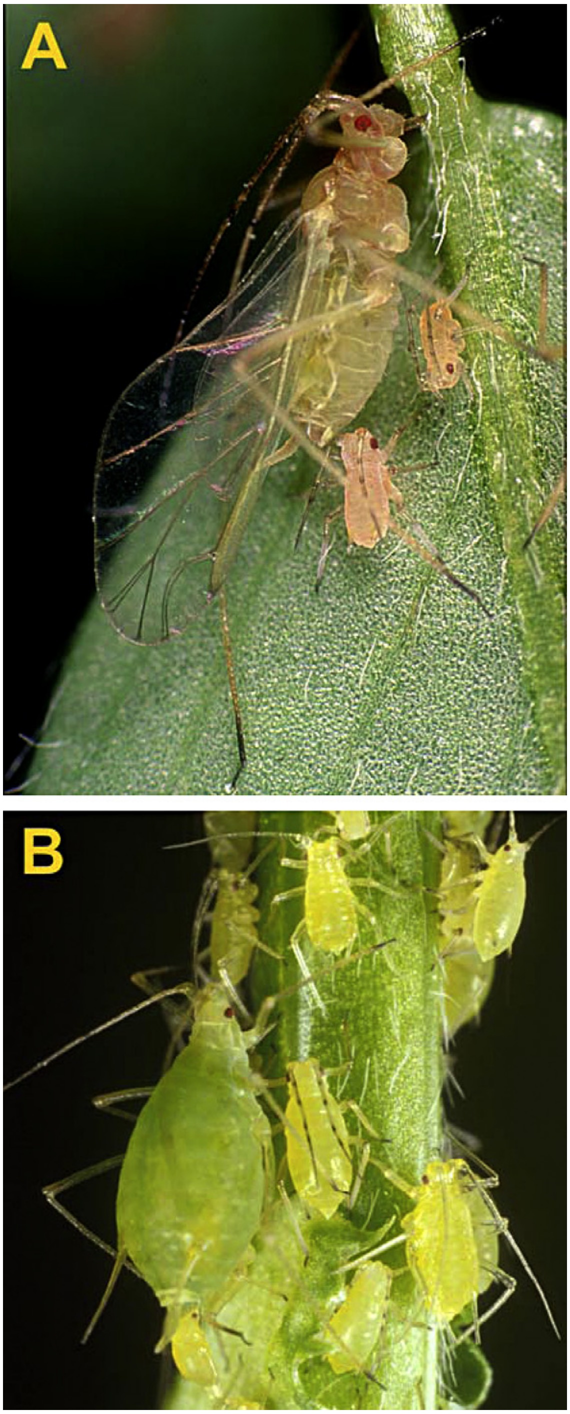

Fig. 1. *Acyrthosiphon pisum* feeding on *Medicago sativa.* Winged (A) and wingless (B) adult. In B, note the birth of a clonal larva and the high number of larvae around the parthenogenetic female
Photos: Serge Carré, INRA Lusignan.

2. Aphids as agricultural pests

Several aphid species can inflict considerable damage and fitness cost in many crops [11]. They affect plant growth and crop production either directly (removal of plant assimilates and systemic changes in nutrient allocation, leaf discoloration and necrosis, leaf and/or fruit deformation) or indirectly (development of sooty moulds on honeydew excretion and phytovirus transmission). Virus transmission is often the cause of major agricultural yield losses. The routes followed by many plant viruses within their respective vectors are now known in detail. Further progress in the molecular mechanisms of virus transmission by aphids would make possible development of strategies for controlling virus spread.

Fig. 2. Citrus-tree infested by the *Citrus tristeza* virus (CTV) (tristeza); CTV is transmitted by several aphid species, especially *Toxoptera citricida*. Photo: Pr Joseph Bové, INRA Bordeaux.

Under their winged form, aphids can be carried passively on long distance by wind. In addition, long-distance spread can occur through human activities and this can generate more or less sudden disasters in specific crops. For instance, Sharka, a serious disease of stone fruits, which spread throughout many European countries, probably from Bulgaria, during the last century, was recently discovered in North America. On the other hand, Tristeza (Fig. 2) caused by the *Citrus tristeza* virus, originated in China a long time ago, spread to most citrus production areas, devastating Citrus plantations in America several decades ago and then in many parts of the world, including Mediterranean countries such as Spain. The human transportation of infested plant materials also concern aphids and related insects inducing organ deformation and/or necrosis, such as the Russian wheat aphid and in the past, the grape phylloxera.

The first signs of infection of the European vines (*Vitis vinifera*) by the grape phylloxera appeared in the south of France one century and a half ago. This "aphid", which was introduced along with various species of American *Vitis*, tolerant to the insect, would destroy the French vineyard during the second half of the 19th century, and later go on to infect other European vineyards [12]. It is interesting to note that among the strategies initiated at that time to control phylloxera, those used presently to control the aphids were to be found: biological control, chemical control and plant resistance. The first, based on the use of ladybirds and acarids, was quickly abandoned because it could not reduce significantly the proliferation of phylloxera. The chemical control targeted the "radicicole" form of the insect, which is by far the most injurious one. It consisted in injecting carbon disulfide, a highly toxic molecule, into the ground. That treatment allowed the survival of the vineyard provided it was repeated regularly. Because of the high cost, however, this procedure was limited to a few prestigious vineyards in the Bordeaux and Burgundy regions. Eventually, the use of resistant American stocks enabled to reconstitute the French vineyard from the end of the 19th century onwards. Let us remember that this strategy, now obvious and elementary, met with fierce opposition although initiated from the very beginning of the invasion of the French vineyard by the "aphid" and supported by some French and American biologists. The American vineyards (and the hybrids produced by the colons) had a particularly bad reputation since they were the vectors for several diseases (oidium, phylloxera and then mildew). At the same time, the chemical control was strongly supported by other scientists since it brought about some hope for nearly two decades.

Nowadays, efficient insecticides such as pyrethroids and neonicotinoids (as seed treatments) are successfully used to control aphids in several annual crops, particularly cereals in temperate regions. For several decades, the general use of pesticides, insecticides included, have led to high yields and "clean zero-default" agricultural products. The side effects of this intensive chemical control are well-known: soil pollution, sometimes presence of xenobiotics in the food, development of resistances and, in the case of insecticides, negative impact on auxiliary insects among which aphid natural enemies. This last side effect may dramatically increase the harmfulness, initially of secondary importance, of various piercing-sucking insects [13]. This is why there is an increasing demand for alternative control strategies such as genetic resistance and biological control, in addition to a rational use of insecticides.

This volume presents a series of overviews about the main research areas on aphids, from their evolutionary history to control strategies of these pests.

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Jean-LouisBonnemain
Équipe « PhyMoTS », UMR 6503 LACCO,
bâtiment botanique, 40, avenue du Recteur-Pineau,
86022 Poitiers cedex, France
E-mail address: jl.bonnemain@voila.fr

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