

Control of Fruit Tree Pests through Manipulation of Tree Architecture

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ABSTRACT

Although chemical aspects of plant-insect relationships are largely studied, the effect of within-plant structure on insects is seldom investigated, especially in perennial crops. In fruit production, the manipulation of tree architecture is generally considered to be involved in pest development through considerations of “tree vigour” or branching density. However, both physiological and physical aspects of tree architecture (i.e., canopy height, width and shape, fruiting and vegetative shoot distribution, branching, connectivity, growth rhythmicity) affect the distribution and abundance of both phytophagous arthropods and natural enemies. Tree architecture can affect arthropod pests by modifying: (a) the attractiveness of the host-plant; (b) the within-plant life conditions including microclimate, availability and accessibility of resources and reproduction sites, and enemy-free spaces; (c) the efficiency of chemical or alternative pest control methods (including the use of pheromones). Despite seasonal effects and variability in species biology, modelling and experimental approaches have shown that a more complex architecture favours phytophagous insects and is detrimental to the foraging of most natural enemies. Orchards are permanent habitats, in which the manipulation of tree architecture is potentially a powerful tool for pest regulation, through the implementation of innovating training systems.

Keywords: arthropod pest, natural enemy, orchard, plant architecture, tree training

CONTENTS

INTRODUCTION.....	33
TREE ARCHITECTURE AND ORCHARD INFESTATIONS.....	34
Disentangling processes affecting tree arthropods.....	34
Attractiveness.....	34
Resources.....	34
Habitat conditions: microclimate and permanence.....	35
Efficiency of pest control methods.....	35
Results at the orchard level.....	35
CONCLUSION.....	36
ACKNOWLEDGEMENTS.....	36
REFERENCES.....	36

INTRODUCTION

Heterogeneous distribution of pests within the tree canopy is often reported (Chouinard *et al.* 1994; Blomefield *et al.* 1997; Piñero and Prokopy 2005). An alteration of the population dynamic of pests is thus expected from the manipulation of tree architecture. However, although pest control is a key point in fruit-tree production, most of the recent studies on tree architecture (Lauri and Laurens 2005; Whiting *et al.* 2005; Costes *et al.* 2006) mainly address the effects of tree training on fruit yield, fruit colour and quality, and return-bloom. Actually, the manipulations of tree architecture commonly used in orchards, such as pruning and training, are mainly dedicated to enhance fruit yield and quality and pay poor attention to pest control. Moreover, even though considerations of “vigour” are hypothesized to be involved in fruit-tree pest infestation, e.g. in relation to growth patterns induced by pruning (Koschier 1997; Holb *et al.* 2001), the processes involved in such plant-insect relationship are scarcely studied. They may be related to the

following two aspects:

First, within-plant physiological and chemical characteristics are heterogeneous: sectoriality in the allocation of resources (Marquis 1996) and induced plant defences (Jones *et al.* 1993) is widely documented. The complex process of within-plant sectoriality, mainly developed at plant level, is hypothesized to explain different patterns of herbivory and to affect a wide range of categories of arthropods: chewers, suckers, borers and gall-forming species (Orians and Jones 2001). The manipulation of tree architecture is likely to modify the sectoriality in resource availability, and therefore the interaction between plant and herbivores (Larson and Whitham 1997; Martinez and Wool 2003). However, such interactions are seldom demonstrated on a scientific basis, and resource availability as affected by tree manipulation is more commonly understood in a physical and structural meaning.

Second, orchard trees are permanent habitats in the agro-ecosystem. As functional perennial structures, they may shelter various arthropods, including orchard pests and

their natural enemies. Integrated pest management developed in orchards promotes and aims at favouring natural pest control, through non-disruptive agricultural practices, adjusted management of tree requirements, and conservation pest control. Although cultural practices such as pruning and training are poorly referred to as tools for pest management, manipulation of tree architecture is likely to affect both categories of arthropods (herbivores and natural enemies) and therefore to modify the natural enemy/arthropod pest ratio. Investigation on pest regulation through tree manipulation thus addresses the “plant-herbivores-natural enemies” tri-trophic system involved in pest control (Price *et al.* 1980). Research developed in forestry on the plant-herbivore-natural enemies system as affected by tree architecture (e.g. Riihimäki *et al.* 2006) strengthens the importance of a tri-trophic level approach in a context of arboreal permanence.

The identification of architecture traits relevant to insect development proves to be extensive. Plant architecture includes physical structures and physiological functions of fruit trees, and is therefore related to space (three-dimensional (3D) design) and time (growth) aspects. The multi-level approach of the tree (whole-tree, branch, and eventually leaf) is stated and tree architecture is described by canopy height, width and shape; fruiting and vegetative shoot relative proportions and spatial distribution, branching, growth rhythmicity (Hallé *et al.* 1978; Godin *et al.* 1999; Costes *et al.* 2006). Other parameters describing the tree canopy are also considered: canopy porosity, which may be estimated by light interception (Willaume *et al.* 2004), connectedness and plant complexity (Hanan *et al.* 2002; Skirvin 2004) based on branching and/or spatial arrangements within 3D structures.

The aim of this review is to provide insight into the direct and indirect effects of tree architecture on the development of orchard pests and therefore pest control, and to present the mechanisms and hypotheses associated with such effects: plant attractiveness, resources and habitat conditions for arthropods. The development of both categories of arthropods (herbivores and natural enemies) is considered with both experimental and modelling approaches.

A literature search was carried out using the ISI Web of Science® from 1992 up to present. Most of older publications were cited in this selection. All the studies on insect behaviour or development as affected by tree architecture and/or tree training were first selected, excluding the cases related to the distribution of trees within orchards or within the landscape. Within this selection, the most relevant studies on fruit-tree or investigating the processes involved in the plant-insect relationship were then analysed. Last, root architecture and leaf morphology were not included in the study.

TREE ARCHITECTURE AND ORCHARD INFESTATIONS

How are tri-trophic relationships between fruit-tree, pest and natural enemies affected by tree architecture? The effect of tree architecture on the development of arthropod pests may be direct and related to attractiveness, resources (food, shelter) and habitat conditions (microclimate, permanence) provided by the host-plant, or indirect, due to the control by beneficial organisms. Among these natural enemies, arthropods only will be considered (as most common enemies of pests), and different groups will be distinguished: predators that feed upon preys, and parasitoids that develop upon or within a single host. The possibilities to improve classical pest control methods (chemical, mating disruption, trapping) by tree architecture are also presented.

Disentangling processes affecting tree arthropods

Attractiveness

The presence of a pest herbivore on a tree is due to the im-

migration of one or a few individuals, which is seldom done at random, but depends on various stimuli. Tree size has an effect on the trap efficiency of the apple maggot fly *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae) in the orchard perimeter apple trees (Prokopy *et al.* 2001): although larger trees have a greater visual appearance, insects have to forage for a longer time than in smaller trees to discover the stimulus (the synthetic fruit odour-baited trap). The testing of various models simulating within-tree movements of *R. pomonella* indicates that movements are influenced by tree architecture; flies tend to move upwards and towards the part of the tree with dense canopy (Casas and Aluja 1997). An effect of the tree size and canopy structure on the searching efficiency of this fly is thus expected. The benefit in the behavioural control of *R. pomonella* associated with small trees is however reduced by the fact that smaller trees are planted at higher densities in smaller blocks, resulting in a higher trap density (Prokopy *et al.* 2001). In apple orchards, an adverse effect is noted for the codling moth *Cydia pomonella* (L.) (Lepidoptera: Tortricidae). The performance of pheromone traps is higher in large spindle trees compared to small trees (Mani *et al.* 1995), with the hypothesis of a visual orientation of moths: large and high trees are likely to be more easily detected.

Resources

The plant provides the herbivores but also the natural enemies with various resources: food, shelter, oviposition and overwintering sites, “enemy-free spaces”... that may be affected by tree architecture (Lawton 1983). Accessibility, availability and quality of the resource may also be considered. Fruit damage by *C. pomonella* is reported to be higher in the inner part of centrifugal trained apple trees compared to a more compact tree canopy (Simon *et al.* 2007). Here the porosity of tree canopy increases the availability of the resource, e.g. by favouring egg-laying by mated females within the inner part of the trees. In contrast, the same centrifugal training system with a lower branching density is favourable neither to the red spider mite *Panonychus ulmi* (Koch) (Acari: Tetranychidae), nor to the rosy apple aphid *Dysaphis plantaginea* (Passerini) (Homoptera: Aphididae), as though the shoot spacing along the branch slows down the colonisation rate within the canopy (Simon *et al.* 2006). For parasitoids, plant architecture adjacent to aphid colonies (leaf density, related to suitability and availability of oviposition sites) is reported to influence the oviposition of *Aphidius fumebris* Mackauer (Hymenoptera: Braconidae) (Weisser 1995). Growth rhythmicity modulated by tree training (PÉ Lauri, unpublished data) is likely to induce the presence or absence of resource-organs for foliar pests at various time in the growing season, and to affect the infestation level by the pest (i.e. growing shoots for aphids). Last, fast growing shoots may present a lower level of infestation by mites (Holb *et al.* 2001), as a result of a lower ratio of pest multiplication rate to newly grown leaves.

The relation between plant and herbivore may also depend on the nutrient status of the plant. This is illustrated by the “sink competition hypothesis” (Larson and Whitham 1997): the suppression of shoots (sinks) on resistant plants increases the availability and most probably the quality of resources and the sensitivity to galling insects. Moreover, it is not always clear whether abundance and richness of herbivores are favoured by the complexity of plant architecture or whether herbivores modulate the architecture of their host-plant, e.g. by destroying apical meristems and therefore increasing the branching and the structural complexity of the infested plant (Araújo *et al.* 2006).

“Enemy-free spaces” (e.g. possibilities to escape from natural enemies and, the case may be, cannibalism) are among the resources provided by the plant (Lawton 1983). Although the abundance of natural enemies is generally favoured by habitats presenting a high structural complexity, the effect is slight at the within-plant scale, and the herbivore density is reported to be not affected by this factor

(Langellotto and Denno 2004): abundance and foraging efficacy of natural enemies seem therefore to be disconnected within complex plants. The effect of plant architecture on host finding by the parasitoid *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae) is demonstrated on artificial plants of different structures, showing that the mean rate of parasitism decreases with an increase in complexity of the host plant structure (Gingras and Boivin 2002). The height of trees may be involved: parasitism by the Encyrtidae *Leptomastix dactylopii* (Howard) (Hymenoptera) is negatively correlated with tree height (Cloyd and Sadof 2000).

At the canopy level, models simulating arthropod movements in virtual complex 3D-plants (Skirvin 2004) are generic methods and powerful tools to investigate the foraging success of predators in relation to canopy connectivity and architecture complexity. Most of these models are based on a dynamic open plant model (Lindenmayer systems) providing virtual developing 3D plant structures in which movement patterns of one or more virtual arthropods are integrated (Hanan *et al.* 2002; Skirvin 2004). More precisely, the availability of resources for herbivores may be simulated by plant susceptibility (e.g. through plant component age), and modulated by damages and plant responses to damages (Hanan *et al.* 2002). Results from modelling approach are consistent with the conclusions of most experimental studies, namely that the probability of predators to explore large volumes and therefore to locate preys is reduced in complex spatial structures.

Habitat conditions: microclimate and permanence

Temperature and to a less extent humidity are involved in the development and multiplication rate of arthropod species. Within-tree microclimate therefore participates in the development of pests. As tree training significantly affects canopy porosity and light interception (Willaume *et al.* 2004), it is likely that within-tree microclimate may be modulated by tree manipulation. Surprisingly, Holb (2005) denoted difference neither in temperature nor in relative humidity between strongly pruned and unpruned apple trees, in contradiction with biological evidence (different development of a fungal disease). In contrast, Kührt *et al.* (2006) measured higher temperature in the habitat provided by dwarf apple trees than in the one of standard trees, with an earlier simulated emergence of codling moth as a result. Discrepancies between results may be due to the difficulties to measure the within-tree microclimate, especially in the leaf boundary layer which is maybe the most relevant site to monitor the habitat microclimate of foliar arthropods. Last, the combination of developmental rates of arthropod pests and models of within-tree microclimate would represent another aspect of a modelling approach of plant-insect relationships.

Last, the permanence of the habitat for overwintering stages may be affected by tree training. Koschier (1997) reported that winter pruning of apple trees resulted in a 50% reduction in winter egg densities of the pest mites *P. ulmi* and *Aculus schlechtendali* (Nalepa) (Acari: Eriophidae) compared to no pruning. Beside other hypotheses, Simon *et al.* (2006) proposed a “pest or inoculum removal hypothesis” to explain differences between two training systems in an apple orchard. For example, the selective removal of vegetative and fruiting shoots during the extinction procedure carried out at bloom in the centrifugal training system removes some shoots infested by the rosy aphid *D. plantaginea*, and is likely to explain a lower infestation level in this system compared to control (Simon *et al.* 2006).

Efficiency of pest control methods

Beside the direct effects of branch or shoot removal as a sanitation practice against borers and foliar pests, respectively, two main aspects of tree architecture are involved in the

success of direct control of pests in orchards: canopy porosity, and the orchard height and shape. Beyond a potential effect of the within-tree microclimate (especially through exposure to sunlight) on the persistence of chemical, microbiological insecticides, or of pheromone formulations (Waldstein and Gut 2004), both factors may affect spray quality and/or pheromone diffusion within the orchard and the canopy. Foliage porosity is the main factor affecting the diffusion of sprayed compounds within trees and most of the models on the subject are based on tree porosity (Endalew *et al.* 2006). The penetration of sprayed compounds in the orchard canopy (i.e. particle deposition on leaf and fruit) is reported to be different according to tree total leaf area and tree size (Cross *et al.* 2001); the deposit of the active ingredient on the target organs is greater in small and porous trees. This is consistent with Juste *et al.* (1990), who reported in *Citrus* orchards a higher spray penetration and a better pest control of *Lepidosaphes* sp. (Homoptera: Diaspididae) in the outer part than in the inner parts of the tree whatever the spraying machine.

Mating disruption is used in orchards to control various Lepidoptera species with massive pheromone release. Pheromone concentration gradually decreases towards a minimum shortly above the plane of the dispensers where the highest concentrations are measured (Suckling *et al.* 1999). In apple orchards where dispensers are hung by hand at two m high (i.e. in the upper third of the crown), top and water shoots reaching four to five m high after a few week growth are poorly protected (Witzgall *et al.* 1999). The vigour and architecture of the trees may also affect mating disruption efficiency. Calling codling moth females are mostly observed on exposed spots in the upper part of the apple tree crown, around which male moths are mostly flying or even walking in mating disruption orchards (Witzgall *et al.* 1999; Lösel *et al.* 2002). As visual stimuli play an important role in the mating behaviour of this species, irregular canopy surfaces with long top shoots as well as the presence of high unpruned (unmanaged) pollinator trees are expected to reduce the efficacy of pheromone-based control method. Mating disruption is thus expected to be less efficient in high and vigorous orchards.

Results at the orchard level

The effect of tree architecture and/or tree manipulation on pest control in orchards may be diverse, depending on local conditions but also on the studied plant-prey-predator system. According to biology and behaviour, the effect of tree architecture on a range of orchard pests may lead to controversial results depending on pest species (Simon *et al.* 2006, 2007). Most of the studies in orchards are related to the intensity of pruning. Holb *et al.* (2001) found that strong pruning of apple trees resulted in less pest damage by the red spider mite *P. ulmi* compared to weak pruning techniques, especially in the organic growing system, and the underlying explanation was that the plant tissues of fast growing vigorous shoots induced by strong pruning were less sensitive to pests (and diseases) than those of weak pruned trees. This is consistent neither with the general plant vigour hypothesis (Price 1991) in which vigorously growing plants are more attractive for herbivores, nor with Koschier statement (1997) that strong winter pruning of apple trees encourages mite infestation despite a reduction in wintering egg density. Intensive pruning of peach trees also simultaneously increases shoot growth and aphid population, related to a modified shoot structure and to a greater infestation degree of growing shoots than of rosettes (Grechi *et al.* 2006). We may hypothesize from this result that the relative proportion of the different categories of shoots affects the level of pest infestation. The manipulation of tree architecture is thus likely to affect both the within-tree spatial distribution of the shoots and the shoot growth pattern through modification of the relative proportion of shoot categories. Although the mechanisms involved are not evoked, the study by Grafton-Cardwell and Ouyang (1995) is in fa-

our of such hypothesis: there is an effect of the part of the orange tree to be pruned (interior or exterior) on the densities of predacious mites and on fruit damage by thrips. Last, architectural response to similar browsing or pruning operations may differ in conspecific trees, resulting in contrasted plant resource availability and in different effects on colonisation levels of gall inducing species (Martinez and Wool 2003).

CONCLUSION

There is evidence that tree architecture has an effect on the development of pests, through various modifications of life conditions and by influencing the ability of natural enemies to prey upon pests. Surprisingly, the effect of plant architecture on pests is seldom investigated in orchards whereas it is far more studied in forestry or in annual crops. For example, we could not find any study related to pest infestation as affected by fruit tree architectural types or shapes. Whereas tree manipulation is scarcely used to improve pest control in orchards, basic research is needed to assess the potential benefit and the risks provided by tree training, according to pest and tree species.

At the orchard level, the integration of architectural types in the choice of cultivars is relevant for the modulation of growth patterns and related pest infestations. At tree level, differences of response according to arthropod / host plant species have also to be considered. As mentioned by Langellotto and Denno (2004), structural complexity (and all the related possibilities: enemy-free space, diversity of resources...) is the first factor affecting both herbivores (pest) and natural enemies (beneficial arthropods). As (1) the increase of complexity is generally reported to permit escaping predation or parasitism, and (2) the canopy porosity is an important factor for spray quality, the ideal tree designed to minimise pest and maximise natural enemies would be a simple porous architecture. But as porosity may, depending on architectural traits, favour codling moth (Simon *et al.* 2007), such a tree design is not adequate when the level of population of this major pest in apple orchards is high. No ideal design can be identified, it will rather depend on the (alternative) control methods available, and on the expected economic effect of each pest. A small size of the trees seems the only architectural trait favourable to both the use of control methods (chemical control, mating disruption) and the foraging success of natural enemies (Cloyd and Sadof 2000), with however poor information on the infestation level by pests in small trees compared to higher ones.

To promote tree manipulation as a control method of pests, research is needed on the within-tree spatial dynamics of colonisation by foliar pests in relation to growth patterns. Indeed, the level of infestation and the colonisation dynamics within the tree are of utmost importance to understand which categories of shoots, leaves or fruits are more susceptible to infestation during the growing season and are to be manipulated to decrease infestation rates. There is also a wide and inter-disciplinary field of research to investigate the relationship between architectural and chemical aspects of the plant and insect behaviour. Within-plant heterogeneity in morphology and chemistry is ubiquitous, and not only attributed to the variations in tissue age or plant microclimate but also to previous damage by herbivores. The sectoriality of nutrients transport and location generates heterogeneity in consumer presence (Orians and Jones 2001), as demonstrated in cotton where increased concentrations of secondary compounds related to plant resistance are predominantly found in top leaves (Anderson and Agrell 2005).

The manipulation of tree architecture dedicated to pest control is still in its first step despite empirical or descriptive reports. Complementary experimental and modelling research on the subject has to provide some bases to improve the knowledge on the benefits and risks of various manipulations of tree architecture in orchards. From the

current study, it seems that promising results may be expected from this approach, with undoubted benefit for orchard protection.

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