Pest insect populations in relation to climate change in forests of the Mediterranean basin

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Introduction

Forest trees are an important component of Mediterranean flora; the number of tree species is larger compared to Central Europe (100 vs. 30, respectively), with the genus *Quercus* alone having more than 20 species in the region (SCARASCIA-MUGNOZZA *et al.*, 2000). The Mediterranean forest biome — around 81 million hectares — accounts for about 1.5% of the planet forests (FABBIO *et al.*, 2003). In addition, some 80–90% of these unique types of forest are concentrated in the Mediterranean Region, the rest being split amongst small areas of Australia, South Africa, California and Chile.

The area is characterized by harsh and unpredictable Mediterranean-type climate, associated with recurrent disturbances related to fire and intense livestock grazing, major determinants of forest transformation into open woodland. The climate change is a recent, further large-scale disturbance increasing climatic extremes occurrence such as prolonged summer drought, high temperatures and rainfall variability (SOLOMON *et al.*, 2007).

Effects of climate change on forest pest insects

Climate change information has been used for modeling the future of the forests in the world (ALFARO *et al.*, 2010). Different types of consequences can be envisaged for the vegetation zones. In the Mediterranean there will be a loss of tree species, because the warmer conditions may cause the local extinction of taxa, associated with the simplification of the forest ecosystems. The higher frequency of drought may depress the growth, modify the tree physiology, and eventually lead to extended tree mortalities (ALLEN *et al.*, 2010).

Direct effects of climate change on insect species

The effects of global warming on living organisms have now been recognized from the level of individual species to communities, most notably in the form of temperature-related range shifts (WALTHER *et al.*, 2002; ROOT *et al.*, 2003). As the number of insects per unit area is inversely related to latitude and elevation (SPEIGHT *et al.*, 2008), we may assume that the increase of temperature would allow the spreading of insect species northward and upward, especially for those species that have wide ranges, as many forest pests have. PARMESAN & YOHE (2003) have provided a quantitative assessment of the biological impact of climatic change, using data from different types of organisms, including insects. This analysis concerned the spatial (range shift) and phenological (advancement of spring events) data, averaging 6.1 km/decade and 2.3 days/decade, respectively. Eighty percent of the studied species (n = 434) showed a consistent range shift and 87% an advancement of spring events, such as flowering or migration. Those insects developing without winter diapause, which are active during this season and are protected from the low temperature, are the best candidates for range expansion if the winter temperature maintains the current increasing trend (SINCLAIR *et al.*, 2003). A good example concerns the pine processionary moth *Thaumetopoea pityocampa*, which expanded considerably its range in southern Europe at higher latitude and altitude in the last three decades as a consequence of the increase of winter temperature (BATTISTI *et al.*, 2005). This expansion has been also detected with genetic markers of the population in the whole of the Mediterranean region (KERDELHUÉ *et al.*, 2009; ROUSSELET *et al.*, 2010).

It seems also reasonable to assume that an increase of temperature within the vital limits of a species will imply a faster development (WILLIAMS & LIEBHOLD, 1995; AYRES & LOMBARDERO, 2000; HARRINGTON *et al.*, 2001; BALE *et al.*, 2002). However, the response of insects to climate change is not always linear (BALE *et al.*, 2002; GASTON, 2003). For example, the developmental stages of the insects can be differentially affected by the climate change, i.e. the growth can be accelerated by higher temperature, but at the same time the length of diapause may be extended.

Little is known about the direct effect of drought on herbivorous insect physiology and development. It is assumed that low air humidity may increase insect mortality through dehydration (ROUAULT *et al.*, 2006). On the contrary during heavy rains many small insects living on stem bark or leaf surface, such as aphids, scales and adelgids can be washed away and thus may benefit from prolonged drought periods (WAINHOUSE, 2005). Reduced soil moisture may also favor the survival of several defoliating insect species that pupate in the upper layer of the soil, such as the pine processionary moth (JACTEL *et al.* 2009), the winter moth *Operophtera brumata* or sawflies like *Pristiphora abietina* (WAINHOUSE, 2005).

Indirect effects of climate through variation of tree quality and resistance

Changes induced by water stress

Drought can affect the nutritional quality of host trees for herbivorous insect via water content and carbohydrates, and via nitrogen.

In severely stressed trees, decreased water content leads to tougher foliage, resulting in lower herbivory by chewing insects such as defoliating Lepidoptera or Hymenoptera (ROUAULT *et al.*, 2006; NETHERER & SCHOPF, 2010). Sap feeding by forest aphids is also impaired in water stressed trees due to lower turgor pressure that limits extraction of nitrogen from elaborated sap (HUBERTY &

DENNO, 2004; ROUAULT *et al.*, 2006). Water supply is critical for primary metabolism of plant and thus greatly influences carbohydrate synthesis and then provision of sugars for herbivorous insects. As a consequence of drought, reduced concentration of carbohydrates in conifer bark tissues may then impair the development of bark beetles and of the fungi they carry into their gallery (WAINHOUSE, 2005).

In contrast, during drought period, reduced water content leads to higher nitrogen concentration which can stimulate insect feeding (MATTSON & HAACK, 1987). Because nitrogen is generally limiting for many insects, increase in available plant nitrogen during water stress could result in improved growth and reproduction of phytophagous insects and thus promote outbreaks. For example defoliator performances are higher in moderately water stressed trees due to higher concentration of soluble nitrogen in foliage (LARSSON, 1989; LARSSON & BJÖRKMAN, 1993; MATTSON & HAACK, 1987; WHITE, 1984). Sap feeding insect may also benefit from this increase in nitrogen concentration.

Secondary metabolites (e.g. tannins – FORKNER *et al.*, 2004, in ROUAULT *et al.*, 2006), involved in tree resistance, are often in higher concentration in foliage of water stressed trees which was showed to affect larval performance of Lepidoptera such as *O. brumata* on *Quercus robur* (BUSE & GOOD 1996, in Rouault *et al.*, 2006). Leaf chewers such as moths, sawflies, and beetles, and some gall makers would be more susceptible to increased defense compounds in leaf tissues of water stressed trees than sap feeders (e.g. aphids), phloem and cambium feeders as vascular tissues contain lower amount of allelochemicals (MATTSON &HAACK, 1987; HUBERTY & DENNO, 2004; LARSSON, 1989; AWMACK & LEATHER, 2002, in ROUAULT *et al.*, 2006). However lower water supply not only affects sap flow but also oleoresin production and pressure. This results in lower constitutive resistance to primary attacks of many bark beetles (LIEUTIER, 2004; ROUAULT *et al.*, 2006).

Picture 1:
An example of a forest pest shifting its range in response to climate change is the pine processionary moth (*Thaumetopoea pityocampa*), an important pest of pine forests in southern Europe (in the picture is an egg mass on a twig of *Pinus sylvestris* in the expansion outbreak area, at 1450 m, Mont Avic, Aosta, Italy). This pest has expanded its range substantially (both northward latitudinally and upward altitudinally) during the last ten years, with high attack rates in previously unaffected areas (Battisti *et al.* 2005 and 2006, Stastny *et al.* 2006). This has been attributed to warmer winter temperatures that allow greater survival of overwintering larvae, and increased warm summer nights above a threshold temperature required for flight take-off and nocturnal dispersal of females (Battisti *et al.* 2006). If range shift and increased survival events such as this become a global trend, there may be serious consequences to silviculture worldwide.

Changes induced by elevated CO_2

As an indirect mechanism related to global change, an elevated concentration of CO_2 may affect the performance of phytophagous insects through the modification of the nutritional properties of the host plant (JONES *et al.*, 1998; HUNTER, 2001). As CO_2 is the main carbon source for photosynthesis, its increase could alter the carbon/nutrient balance of plants, increasing the C/N ratio and thus diluting the nitrogen content of the tissues.

The main reaction expected from herbivores to the increase of the C/N ratio is compensatory feeding, in other words they should eat more to accumulate enough nitrogen for their development. Thus, plant damage may increase, but the relative damage could remain stable if we assume that the plants exposed to high CO_2 grow more. In a FACE (Free Air Carbon Enrichment) experiment carried out in Wisconsin (PERCY *et al.*, 2002), the activity of all guilds of herbivores, combined with the effect of increased ozone, may be compensated by the beneficial consequences of enriched CO_2 on growth of *Populus tremuloides*. The response of herbivore insects to increased CO_2 may also differ among the feeding guilds, as suggested by BEZEMER & JONES (1998). Defoliators are generally expected to increase leaf consumption by about 30%, but leaf miners showed a much lower rate. Phloem-sucking insects appear to take the greatest advantage from increased CO_2, as they grow bigger and in a shorter time.

The effects of a modified atmosphere on herbivore insects could also involve the third trophic level, i.e. their parasitoids and predators. As we are expecting a delay in the developmental time of the herbivores after exposure to high CO_2 (FAJER *et al.*, 1989; LINDROTH *et al.*, 1993; SMITH & JONES, 1998), the probability of parasitism and predation should increase as well.

Pictures 2 and 3:
Defoliation by the pine processionary moth *Thaumetopoea pityocampa* in the Southern Alps and changing of forest composition. Pure plantations of *Pinus nigra* are completely defoliated for 2-3 times in the age of 15 to 30 years (A). Native broadleaf species (*Quercus pubescens, Ostrya carpinifolia, Fraxinus ornus*) fill the gaps left by the defoliation (B). The defoliation becomes then less important and concentrate on the most prominent pine trees. This is a mechanistic example about how a defoliating insect can modify the stand composition, with a negative feed-back on the insect itself. Foresters can accelerate the process and reduce defoliation damage by favoring broadleaf species in plantations.

Option for the future of forest pest control

Curative methods of pest management

When it comes to controlling pest insect populations, the first option that crosses to our mind is the application of insecticides. However the use of pesticides in forest has serious drawbacks such as the lack of effectiveness, the selection of resistance, the cost and the negative effects on non-target species. Other curative methods have thus been developed that aim at reducing pest population levels below the economic threshold (WAINHOUSE, 2005). They include mechanical, biological and biochemical methods. Mechanical control methods mainly consist in the pruning of attacked branches or the cutting and burning of individual trees during sanitary thinning. It mainly applies to the control of conifer bark beetles. In biological control, natural enemies such as predators, parasitoids or pathogens are manipulated to improve the natural regulation of pest populations. However few biological control methods have been successfully developed in European forests and they are almost exclusively used against exotic or invasive pests. For example, the release of specific predators to augment their density in newly infested areas proved to be effective to slow the spread of the invasive spruce bark beetle (*Dendroctonus micans*). The introduction of specific parasitoids from the native range of the introduced pest may also help to maintain the pest at low densities as was observed with the cedar aphid in Mediterranean French forests. Similar to chemical insecticides in the way of application, solutions of *Bacillus thuringiensis kurstaki* (Btk) spores can be sprayed to control forest Lepidoptera. The advantages of this biochemical method is that it is highly effective when applied in due time, easy to mass-produce, and some strains have a narrow spectrum thus limiting the detrimental effects on non-target species. In southern Europe Btk is widely used to control the pine processionary moth (*Thaumetopoea pityocampa*) in pine forests and the gypsy moth (*Lymantria dispar*) in oak forests for more than 100,000 ha every year. Several attempts have been made to use sex pheromones to control forest pest populations. While pheromone mass-trapping, which requires very high densities of traps, proved to be ineffective, mating-disruption sounds more promising. It consists in the introduction of many artificial sources of pheromone into the forest in order to prevent the mating of the target pests through the disruption of the between sexes communication. This method was successfully applied to control gypsy moth populations, at low levels, in isolated oakwoods in the US. More recently, the use of antiaggregation pheromones and repellents, such as verbenone, have been used to provide protection of pine trees during critical periods of bark beetle outbreaks. All these pest management methods are environmentally friendly but they remain difficult to implement due to the size of adult trees and they often have to be repeated across time which greatly increases their cost. They are therefore mainly restricted to the most valuable stands or individual trees at high risk of mortality or growth loss.

Preventive methods of pest management linked to stand management

Of much greater interest is the prevention of pest outbreaks, because it operates before severe damage is observed. It is basically a pest management strategy that relies on the ability of forest ecosystems to defend themselves. It is based on the main assumption that the use of good silvicultural practices would both reduce the likelihood of insect attacks and the susceptibility of trees to these infestations. A recent review of the scientific literature has shown that every single silvicultural operation may have a significant impact on forest stand vulnerability to pest insects (Jactel *et al.*, 2009). The decision to be made before starting any afforestation is to match the tree species to the right site conditions. Then soil preparation, including brash, stump and weed management may reduce the amount of breeding substrate for important pests such as bark beetles and weevils (*Hylobius abietis*), while fertilisation may either benefit some pests such as conifer aphids or increase tree resistance to other pest insects such as defoliators or bark feeders. The quality of the seedlings used in plantation and the initial planting density are two important drivers of pest damage during the first years of the forest cycle. The management of understorey vegetation may reduce the competition for light and water but on the other hand, nurse plants and shrubs may protect young trees against insect herbivores by providing habitat to their natural enemies. As thinning improves individual tree vigour it can reduce tree susceptibility to a number of secondary pests including bark beetles, but on the contrary it can favour primary pests such as several insect defoliators. Because overmature trees often show lower vitality it might be recommended to shorten the rotation age in order reduce the risk of damage. However precautions should be taken during harvesting. Logging operations with heavy machinery may result in soil compaction and bark injuries which can in turn trigger pest infections.

Felled trees, logging residues or stumps can also serve as breeding substrates for weevils (*H. abietis*) and many bark beetles in conifer (e.g. *Ips sexdentatus*) and broadleaved forests.

It has been also widely recommended that weakened and dying trees should be removed in order to avoid the breeding of insects which could later attack living trees (Wainhouse, 2005).

Preventive methods of pest management based on biodiversity conservation

Reviews of the international scientific literature (Jactel *et al.*, 2005; Jactel & Brockerhoff, 2007, Jactel *et al.*, 2008) generally show that mixed forests are more resistant than pure forest to forest insect. For example the scale insect *Matsucoccus feytaudi,* which is specific to the maritime pine (*Pinus pinaster*), showed significantly higher infestations in pure stands of maritime pine than in mixed stands with the Corsican pine (*Pinus nigra* laricio) (Jactel *et al.*, 2006). The pine processionary moth, *Thaumetopoea pityocampa*, mainly feeding on *Pinus* and *Cedrus*, caused lower defoliation to the Corsican pine when mixed with the common beech *Fagus sylvatica* (Géri, 1980). Recently it has been shown that broadleaved hedgerows may reduce the level of processionary moth infestation in pine stands located behind this physical barrier (Dulaurent *et al.*, 2010) and that odours emitted by birch trees may also result in lower damage in neighbouring pine stands (Jactel *et al.*, 2010).

The first reasons that explain that mixed forests are less sensitive to pests and disease agents is the diminished accessibility to host trees since the admixture of other species is expected to raise several physical or chemical barriers that may reduce its localization and colonization by insect pests (JACTEL *et al.*, 2005). The second main reason for explaining why mixed stands would be less prone to pest and pathogen damage than pure stands is the enhancement of their control by natural enemies (ROOT, 1973; JACTEL *et al.*, 2005). Generalist predators and parasitoids would benefit from more alternative preys or host in more diverse tree communities as the later provide habitat for more herbivorous species (SIEMANN *et al.*, 1998).

However the effect of tree species diversity varied with the host specificity of pest insects. Herbivory by oligophagous insect, feeding within a genus or a family of tree species was almost always reduced in mixed stands (93% of the cases, JACTEL & BROCKERHOFF 2007). In contrast, the effect of tree diversity on polyphagous pest insects, feeding on several tree families, was more variable with a reduction of damage in mixed stands in only 60% of the cases. Polyphagous herbivores may have a different response to a diverse tree community, called "diversion" and "contagion" effects. The diversion effect is explained by the association with a more palatable secondary tree species which would be infested first, reducing the damage on the most represented tree species. As shown previously for herbaceous communities (COUPE & CAHILL, 2003), the benefit from growing mixed stands will depend whether the total ecosystem or the single species production are considered. If the diversion effect is present, one should argue that the preservation of production of the main host will be compensated by a loss for the secondary host. The contagion effect occurs when an association of several host species leads to an increase of forest pest damage in tree mixtures, and it is also called associational susceptibility (WHITE & WHITHAM, 2000). Typical example here is given by both gypsy and nun moth (*Lymantria dispar* and *L. monacha*), when the neonate larvae develop on high quality food (young leaves of broadleaved trees and conifer male cones, respectively) and mature larvae feed on poor quality conifer needles (GOTTSCHALK & TWERY, 1989; JENSEN, 1991). Finally what determines the degree of exposure of mixed forests to the risk of disease would be the quantitative and qualitative composition of the mixture of forest species rather than their species-richness.

Conclusions

The material presented in this paper allows drawing two main conclusions.

1. There is little doubt that insect species range and performance are affected by the climate change, but the main objective is to understand the direction of the change. If the direct effect of the temperature or drought on insects can be included in predictive models, the indirect effects due to the modification of the host plant quality by the climate change are more difficult to find and to predict. A further complication is given by the interaction of temperature and host plant quality, and by the response of the third trophic level or natural enemies to the changes occurring in the herbivores and their host plants.

2. Forest sustainability and conversion of pure into mixed forests seems to be compatible with reducing the risk of insect damage, at least for monophagous species which are notably the most important. This may have a cost in term of yield of a given species, even if at the ecosystem level the loss of growth of one species can be compensated by higher growth of the unaffected species. However recent studies have shown that tree species diversity may also result in higher forest stand productivity (PIOTTO, 2008, POTVIN & GOTELLI 2008, PAQUETTE & MESSIER, 2010), notably in Mediterranean forests (VILA *et al.*, 2007).

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Summary

The paper presents the consequences of the climate change on the forests of the Mediterranean basin, in relation to the ecology and management of populations of insect herbivores. Climate warming may have consequences on forest tree composition, modifying the structure of the ecosystems and then the susceptibility to monophagous/polyphagous herbivores, as well as on the tree quality, affecting indirectly the performance of the insect populations. Several options are given for the future of pest management in Mediterranean forests.