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Ecophysiological responses and vulnerability to other pathologies in European chestnut coppices, heavily infested by the Asian chestnut gall wasp

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ABSTRACT

Dryocosmus kuriphilus Yasumatsu, the Asian chestnut gall wasp (ACGW), is an invasive alien species, which is causing alarm in the chestnut stands of Italy and Europe. It has extensively colonised the *Castanea sativa* Miller range throughout the country and highly conspicuous, alarming symptoms have appeared on plants. In addition, chestnut trees growing in Mediterranean climates are more frequently subjected to stressful environmental conditions, such as hot-dry periods or extreme weather events, which compromise both yield and productivity. It will be useful, therefore, to gain further insights into the biotic and abiotic disturbances affecting chestnut and their interactions in order to develop management strategies to counteract the loss of productivity.

This study was aimed at investigating the effects of ACGW on European chestnut ecophysiology during warm, dry summer conditions, typical of Mediterranean environments. We studied the functional and structural responses of young chestnut sprouts in a coppice stand in the Apennines (Tuscany, Italy), focussing in particular on photosynthetic capacity, leaf morphology, shoot growth, and hydraulic architecture. We also assessed the vulnerability of sprouts to chestnut blight *Cryphonectria parasitica* (Murrill) Barr. ACGW is a gall-making insect with strong dispersal potential. It spends its larval stages inside the chestnut buds and grows to adult state inside galls, which are located mainly on the main leaf axis or petiole. In this study, we found a reduction of about 30% in CO_2 assimilation and stomatal conductance in the blades of galled leaves. PSII efficiency (Φ_{PO}) was not negatively affected by the presence of galls, although lower electron transport to PSI acceptors (ΔV_{IP}) was found in galled leaves, which could have negative consequences for $NADP^+$ production and carboxylation.

ACGW strongly affected the photosynthesizing leaf area, which was reduced by about 40% compared with a non-galled leaf. Carbohydrate concentration was higher in leaf blades while galls were richer in starch.

Shoot vigour was affected by a massive presence of ACGW, resulting in a smaller leaf area and biomass, and very low capacity for water transport through the wood xylem compared with vigorous shoots. In fact, compared with vigorous shoots, non-vigorous shoots had a higher percentage of impaired xylem conductive area (5.7% vs. 1.3%) and a higher number of obstructed vessels per mm^2 (31.2 vs. 7.4).

Assessment of shoot vulnerability to chestnut blight revealed a prevalence of hypovirulence in blight infections, probably not directly due to ACGW, but instead related to loss of vigour in the shoot. However, ACGW could play a role in the appearance and spread of *Gnomoniopsis* sp., which was the most common endophyte on vigorous and non-vigorous shoots and the main coloniser of old galls.

ACGW is opening up unpredictable scenarios in European chestnut forests, which are also susceptible to environmental stress factors. Therefore, the simultaneous study of disturbance dynamics and chestnut response, and advanced monitoring of insect spread and climate change would allow timely and effective implementation of adaptive forest management strategies.

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1. Introduction

Recently, increasing concern has been raised about the appearance and spread of new alien (or exotic) invasive pests and pathogens (Bale and Hayward, 2010). The number of immigrant species reported worldwide is increasing dramatically and almost 10% of them (Williamson, 1996) have become invasive, with implications at socio-economic (yield losses, increased production costs, changes in the landscape, endanger of human health), environmental and ecological levels (reduction of native biodiversity and genetic variability, impacts on ecosystem services) (Wheeler and Hoebeke, 2009).

Among invasive species, insect pests and diseases can have direct effects on their host plants. For example, feeding insects directly reduce leaf biomass by redirecting photosynthates from plant organs for their own benefit (Shorthouse et al., 2005), but they also induce physiological responses in the host plant, which affect the remaining tissue (Zangerl et al., 2002), or activate strategy for carbon-based defence mechanisms in plants (King and Caylor, 2010) with an increase of carbohydrate production.

Gall-inducing insects cause in their host plants tumour-like structures that provide a warmer microenvironment for the pest insect. These galls may also have the ability to photosynthesize (Fernandes et al., 2010), thus serving as either a shelter or a source of food for the larval instars of the insect. There is controversy over the effects of leaf gall-inducing insects on the physiological behaviour of leaves. Galls have been found to have either negative (Gailite et al., 2005; Aldea et al., 2006; Fernandes et al., 2010) or positive effects on photosynthesis (Fay et al., 1993; Bogatto et al., 1996), including mechanical damage and/or arthropod-derived chemical signals, which affect endogenous plant signals and, consequently, the physiology of the host plant (Raman, 2007). The feeding strategies of gall-inducing insects may alter several parameters associated with leaf energy balance, such as stomatal conductance and absorbance of solar radiation (Pincebourde et al., 2005). Gall infestation might, therefore, produce effects at the macroscopic level; for example, an induced change in leaf coloration could alter the leaf microclimate and amplify the effects of environmental variations on the transpiration rate (Pincebourde and Woods, 2012); more generally, it might affect canopy processes and ecosystem functions.

One of the most prolific invasive gall-inducing insects is *Dryocosmus kuriphilus* Yasumatsu, the Asian chestnut gall wasp (ACGW) (Hymenoptera: Cynipidae). Native to China, this pest has rapidly spread out across chestnut woods and orchards of Europe, USA and Asia (Fig. 1).

Fig. 1. ACGW galls on new leaves of European chestnut trees.

The gall wasp was first recorded in northern Italy in the early years of this century (Brussino et al., 2002) and since then it has established extensively throughout the country. ACGW has now colonised almost the whole European chestnut (*Castanea sativa* Miller) range in Italy, which covers a conspicuous and contiguous surface area of 788,408 ha (INFC, 2008) and is present in the whole peninsula and in Sardinia and Sicily islands.

Aside from the absence of natural limiting factors, such as parasitoids and predators, this formidable colonisation rate can be ascribed to the high reproductive potential of this hymenoptera. ACGW is a parthenogenetic species and its populations are entirely constituted by female individuals, which are able to lay 10–150 eggs in chestnut buds (EPPO, 2005). Moreover, the absence of evident symptoms in scions and seedlings between July and April, owing to the long asymptomatic growth phase from egg to the second larval stage, has resulted in the diffusion of infected commercial material, that has triggered the insurgence of new foci. Finally, the ability of ACGW to move with prevailing winds has probably been underestimated and has concurred in its massive invasion (Graziosi and Rieske, 2012). These factors have frustrated eradication attempts and prompted an immediate and extensive programme of biological control, which involved the release of the specific parasitoid *Torymus sinensis* Kamijo in the areas of chestnut cultivation (Quacchia et al., 2008).

Until now, only scattered evidence has been gathered on the impact of ACGW on fruit and wood production and on chestnut vitality. Bosio et al. (2010, 2013) reported a reduction in the fruit harvest in the north-western Italy, while Battisti et al. (in press) found a clear correlation between the number of galls and the decrease in fruit production in the northeast. Maltoni et al. (2012a, 2012b) analysed and classified different kinds of damage on leaves, shoots and buds in chestnut sprouts, confirming the observations carried out in Japan by Kato and Hijii (1997) on *C. crenata* Siebold and Zucc.

Moreover, there have been warnings of a possible negative interaction between ACGW and *Cryphonectria parasitica* (Murrill) Barr, the fungal agent of chestnut blight. Hypovirulent strains of *C. parasitica* are well established in Italian chestnut woodlands and the disease can be considered as endemic but not hazardous (Turchetti et al., 2008). Recently, new virulent chestnut blight infections following ACGW colonisation were reported by Turchetti et al. (2010a) in Italy and by Prospero and Forster (2011) in Switzerland. The latter authors suggested that abandoned galls might facilitate penetration and infection by *C. parasitica* in twigs.

However, plants are not subjected only to biological diseases. Environmental conditions and changes in climate conditions are additional factors exacerbating the host functionality and consequently insect outbreaks, even though no clear trends have been found yet (e.g., Raffa et al., 2008; Büntgen et al., 2009). In plants, changes in climatic variables can affect leaf gas exchange, productivity and phenology, and potentially also the frequency and degree of insect damage. Given that extreme climate events (such as summer drought) are increasing in frequency and/or intensity (Brunetti et al., 2004; Nanni et al., 2007), they should not be mistreated and further knowledge of how these diverse factors interact may be useful in order to develop strategic proactive management plans to counteract adverse effects.

Therefore, the aim of this study was to investigate the effects of ACGW on European chestnut physiology during warm, dry summer conditions, typical of Mediterranean environments. To this purpose, we studied the functional and structural responses of young chestnut sprouts in a coppice stand in the Tuscan Apennines (Italy) colonised by ACGW. The study focused on physiological responses to environmental stresses, by measuring gas exchange, chlorophyll fluorescence, leaf morphology, stomatal density, stem