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Physiological significance of forest tree defoliation: Results from a survey in a mixed forest in Tuscany (central Italy)

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ABSTRACT

A survey of tree crown defoliation and leaf physiological traits (chlorophyll *a* fluorescence, nitrogen content, and stable carbon isotope composition) was carried out in the thermophilous deciduous forests in Tuscany (central Italy). In contrast to large scale surveys, where variation in defoliation can be associated with the change in environmental conditions, in a limited homogenous area the defoliation of co-existing tree species may have different significance and depends on the interaction between the characteristics of each individual species with biotic stress and environmental conditions. The survey included measurements of structural and vegetational characteristics of the forest stands, such as Leaf Area Index (LAI), basal area and tree diversity, which is expressed as the Shannon diversity index. The five tree species studied (*Castanea sativa, Quercus cerris, Quercus ilex, Quercus petraea* and *Ostrya carpinifolia*) showed species-specific crown conditions and physiological features relative to stand structure and diversity. The shape of the crowns and their area (LAI) affected forest defoliation. Tree diversity reduced defoliation in *C. sativa*, which was the tree species most affected by defoliation, and likewise for *Q. ilex*. Chlorophyll *a* fluorescence parameters showed lower photosynthetic efficiency in defoliated *C. sativa*, *O. carpinifolia* and *Q. petraea* trees. Similarly, foliar nitrogen content decreased in defoliated *C. sativa* and *O. carpinifolia* trees, whereas $\delta^{13}C$ was higher in defoliated *C. sativa*. These responses may be related to the health status of *C. sativa*, since it was subjected to pathogen damages and insect attacks. In contrast, the mast year in *O. carpinifolia* may have diverted the nutrient resources from leaves to fruits, and consequently explaining the physiological effects on the tree crown. These results suggest that the combined analysis of defoliation with foliar features and stand characteristics can provide insights into tree health and vitality.

Abbreviations: BA, basal area ($m^2\ ha^{-1}$); CC, crown compression; ChlF, chlorophyll *a* fluorescence; C/N, carbon/nitrogen ratio; F_0, minimum (basal) fluorescence in dark adapted samples; F_M, maximal fluorescence in dark adapted samples; F_V, total variable fluorescence ($F_M - F_0$); $F_V/F_M = \varphi_{P0} = TR_0/ABS = [F_M - F_0]/F_M$, maximum quantum yield of PSII photochemistry of a dark adapted sample; LAI, Leaf Area Index ($m^2\ m^{-2}$); LI, light interception index; M_0, initial normalised slope of the fluorescence transient; OJIP, labels of the different time-steps of the fluorescence transient; PI_{ABS}, performance index on absorption basis. Index for energy conservation of photons absorbed by PSII, through the electron transport chain to the reduction of the electron acceptors in the intersystem between PSII and PSI; PI_{TOT}, performance index total. Potential capacity for energy conservation until the reduction of the final acceptors beyond the PSI; PSI, photosystem I; PSII, photosystem II; V_I, relative variable fluorescence at I step (30 ms); V_J, relative variable fluorescence at the J step (2 ms); $\delta^{13}C$, carbon isotope composition (‰); $\Delta V_{I\text{-}P} = 1 - V_I$ = I-P phase, relative contribution of the I-P phase to the fluorescence transient OJIP (it is regarded as a measure for the efficiency of the electron flux through PSI to reduce the final acceptors of the electron transport chain); $\Psi_{Eo} = 1 - V_J$ = Jstep = ET_0/TR_0, probability of an electron to move from reduced Q_A, the secondary PSII electron acceptor, into the electron transport chain.

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1. Introduction

Tree crown defoliation is the main parameter adopted in surveys (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests, ICP Forests programme, www.icp-forests.net) to assess the health of European forests (Eichhorn et al., 2010). Defoliation is a raw visual indicator of the relative amount of foliage on the tree crown compared to a reference standard tree, and is assessed visually by trained field teams (Ferretti et al., 1999). Defoliation is an unspecific parameter integrating intrinsic tree genetic variability, site effects (soil fertility, climatic features, structure and composition of a forest stand), and external factors such as abiotic and biotic stresses. Consequently, defoliation (as assessed according to the ICP Forests criteria) is not necessarily equivalent to damage and can be considered indicative of the plastic equilibrium of a tree in a given environment.

Crown defoliation has been assessed extensively in many European countries since the 1980s, and the trends recorded are assumed to correlate with the effects of environmental stress, such as air pollution and climate change (Van Leeuwen et al., 2000; Meining and Fischer, 2011; Bussotti et al., 2014, 2015). Recent papers examining these historical trends found relationships between the increasing defoliation levels and the change of climatic conditions, with special reference to drought and heat waves (Seidling, 2007; Carnicer et al., 2011; De la Cruz et al., 2014). To increase the effectiveness of the surveys, and to evaluate the overall conditions of the trees, visual assessment of defoliation and crown status could be combined with the analysis of the functional traits most likely linked to the responses of trees to environmental stress (Bussotti and Pollastrini, 2015).

The physiological consequences of defoliation have not been thoroughly explored. Defoliation implies reduction of the leaf area, light absorbing area and the whole tree photosynthetic apparatus, and is commonly assumed that defoliated trees have reduced growth. This assumption, though supported by observational evidence (Augustatis and Bytnerowicz, 2008), does not take into account the so-called *compensatory photosynthesis*, i.e. the capacity to compensate the loss of leaves with higher photosynthetic rates in the remaining foliage (Nowak and Caldwell, 1984; Desotgiu et al., 2012a). Eyles et al. (2011) observed compensatory photosynthesis in aphid-defoliated *Pinus radiata* D.Don, and attributed this effect to the enhanced exploitation of sunlight by leaves in the inner layers of the crown. It is likely that there is a threshold of defoliation whereby the remaining foliage is no longer able to restore the full photosynthetic activity. The altered light regime within a thinned crown affects photosynthetic function (Lavigne et al., 2001; Turnbull et al., 2007) and leaf nitrogen content that is directly related to the protein composition of the photosynthetic apparatus (Ellsworth and Reich, 1995; Wright et al., 2004). Moreover, foliar transpiration can be either enhanced or suppressed by the altered microclimate inside the canopy (Quentin et al., 2011). It is reasonable to assume that the altered physiological functions in defoliated trees may be reflected by an array of leaf features detectable with foliar analysis (Bussotti and Pollastrini, 2015).

Among stand features, tree species composition and diversity are thought to be important. Mixed forests are assumed to be more productive (Jucker et al., 2014) and more resilient to environmental stress (Grossiord et al., 2014a,b) than monospecific ones that result from positive interactions among tree species and the ability to exploit resources more efficiently (Bengtsson et al., 2000; Balvanera et al., 2006; Knoke et al., 2008). Eichhorn et al. (2005) identified tree diversity as a relevant factor that positively influences the crown conditions (i.e. reduced defoliation) at the stand level in mixed oak – beech forests in Germany.

The present research was part of a project on the functional significance of forest biodiversity in Europe (FunDivEUROPE, Baeten et al., 2013), and was carried out in mixed broadleaved forests in central Italy (Tuscany). Defoliation and crown conditions, assessed according to the guidelines of the ICP Forests manual (Eichhorn et al., 2010), were studied in the context of stand characteristics and foliar features. Stand characteristics provide information on the possible detrimental (or beneficial) effects of forest structure and composition (basal area, Leaf Area Index, tree species mixture) on crown condition. Foliar features are relevant to investigation of the cause and/or consequences of defoliation on tree health and relative physiological functions. In contrast to large scale surveys, where variation in defoliation can be associated with the change in environmental conditions, for example drought or elevation gradients (Michel and Seidling, 2014) in a local homogenous area, with uniform climatic and soil conditions, defoliation may have contrasting significance to different tree species and depends on the interaction between the characteristics of each individual species with biotic stress and environmental conditions.

Within the hypothesis that defoliation may have different ecological and physiological meanings in tree species sharing the same environment, the present survey is aimed at exploring the effectiveness of comprehensive foliar analysis, combined with the structure and composition of the forest stands, to analyse species-specific responses connected to defoliation.

2. Materials and methods

2.1. Site description

This study was carried out in the Italian forests (Tuscany, Colline Metallifere) of the exploratory platform of the FunDivEUROPE project (www.fundiveurope.eu, Baeten et al., 2013). The study design of the survey in Tuscany has been described by Bussotti et al. (2012). The sites were located at 43.27°N, 11.26°E, mainly at 350–450 m asl (for detailed characteristics of the plots see Table S1). The mean annual precipitation in the plots is 733 ± 42 mm and the mean annual temperature is 13.35 ± 0.38 °C (data from WorldClim-Global Climate Data, www.worldclim.org, with spatial resolution of 1×1 km). The bedrock is predominantly siliceous (sandstones and various conglomerates) and the soil is Cambisol (FAO classification), with a mean soil depth of 68 cm. Almost all of the plots have northern exposure and mean slope <50%. Thirty-six plots (30×30 m) with five focal tree species (*Quercus ilex* L.; *Quercus cerris* L.; *Quercus petraea* (Matt.) Liebl.; *Ostrya carpinifolia* Scop.; and *Castanea sativa* Mill.) were selected. Forest stands are around 50–70 years old and originate from old coppices (the cutting of the stumps was suspended after the World War II). The trees of *C. sativa* are 60 year-old-stumps sprouted from the oldest trees cultivated in the past for fruits and then abandoned. At present, the forests considered in this study are public and managed as natural reserves.

In this survey thirty-two plots were used (four plots were discarded because data were biased by uncontrolled conditions). The plots had different levels of tree species diversity, ranging from monocultures to a maximum of four species. The level of tree diversity was calculated as the Shannon diversity index (Staddon et al., 1997; Spellerberg and Fedor, 2003), taking into account tree basal area, for each plot.

2.2. Leaf Area Index and light interception index

Canopy closure of the forest stands was assessed by means of Leaf Area Index (total one-side area of leaf tissue per unit ground