

Cu and Zn, results in alterations in the photosynthetic process due to a single phenomenon or cumulative phenomena of: i) the direct interaction of heavy metals with the protein thioyl-, histidyl- and carboxyl-groups; ii) displacement of essential cations in protein-active centres; iii) formation of reactive oxygen species (ROS) (Nagajyoti et al., 2010; Prasad, 2013). Reduced photosynthetic pigment is another possibility by which heavy metals, particularly Hg, Cu, Cd, Ni or Zn, interfere with photosynthesis. These metals may indeed substitute the central Mg ion in chlorophyll molecule to form chlorophyll-metal complexes, and thus lower PSII quantum efficiency (Sharma & Dietz, 2009; Dietz & Pfanschmidt, 2011).

Of the different heavy metals, Cd is certainly one of the most toxic elements (Sanità di Toppi & Gabrielli, 1999; Lin & Aarts, 2012). Most plants show sensitivity to low Cd, which alters the chloroplast ultrastructure and the photosynthesis rate, and disturbs the Calvin cycle, antioxidant enzymes, and the uptake and distribution of macro- and micronutrients (Di Cagno et al., 1999, 2001; Mobin & Khan, 2007; Kahn et al., 2007; Anjum et al., 2008; Márquez-García et al., 2010; Degl'Innocenti et al., 2014). Photosynthetic pigment and Chl fluorescence responses of *Quercus suber* L. at high Cd concentrations are impaired F_v/F_m , F_{PSII} and q_p decrease, and when NPQ increases, which occur with a concomitant increase in the amount of the pigments involved in the xanthophyll cycle (Gogorcena et al., 2011). On the contrary, no alterations in the F_v/F_m ratio have been observed in sunflower plants subjected to Cd stress, even though q_p and F_{PSII} under steady-state conditions were significantly depressed and non-photochemical quenching increased (Di Cagno et al., 1999, 2001). In poplar and willow clones, the use of CFI has allowed areas inside leaves to be visualised, where Cd accumulates and corresponds to the dark area in which F_{PSII} comes close to zero (Pietrini et al., 2010). In general terms, Chl fluorescence has long since been utilised to detect the influence of heavy metal ions on plant species grown in heavy metals-contaminated soil. For example, Zurek et al. (2014) tested perennial grasses as potential phytoremediators, which they grew in contaminated soils. The F_v/F_m ratio lowered in these plants, which indicated reduced PSII efficiency strictly in relation to heavy metal uptake. It was noteworthy that no differences in the F_v/F_m parameter were found for the cultivars that limited ion uptake.

Other metals, like Cu or Zn, cause alterations to Chl fluorescence parameters. Wodala et al. (2012) investigated the effect of moderate Cu and Cd stress on *Pisum sativum* L. plants. Both metals slightly inhibited PSII photochemistry (decrease in Φ_{PSII}) and the electron transport rate. Redondo-Gómez et al. (2011) induced excess zinc in the C4 halophytic species *Spartina densiflora* Brogn. Zinc concentrations $> 1 \text{ mmol l}^{-1}$ stunted the growth of

S. densiflora through reduced CO_2 assimilation, and a marked overall effect on photochemical PSII efficiency was noted.

In the air pollutants context, tropospheric O_3 is one of the most relevant pollutants mainly in the Mediterranean climate (Ferretti et al., 2007; Paoletti, 2009). The first study on the relationship between O_3 stress and Chl fluorescence was published by Schreiber et al. in 1978. To date, much research has utilised Chl fluorescence to monitor changes in photosynthetic apparatus in plants subjected to O_3 (Guidi & Calatayud, 2014). Clearly the response of plants to O_3 differs among plants, and even among cultivars of the same species (Calatayud et al., 2002a, 2002b; Calatayud & Barreno, 2004; Guidi et al., 1997, 2009). Recently Bussotti et al. (2011) reported the overall reassessment of the results obtained from fluorescence transient and modulated fluorescence analyses on tree species subjected to treatment with O_3 . Their review aimed to identify the damage mechanisms and repair/avoidance strategies adopted by different plant species that have been reported in the existing literature. In another work, Gottardini et al. (2014) studied the concurrent measurements of Chl fluorescence transient parameters together with O_3 -specific visible foliar symptoms. They concluded that Chl fluorescence parameters provide a set of valuable diagnostic indicators for the early identification and assessment of O_3 effects on native vegetation and, potentially, for phenotyping ozone-sensitive individuals.

Heterogeneities in leaves by O_3 can be seen under CFI, which allows the identification of damaged (localized) areas and provides detailed information about leaf disturbance. An images analysis in *Lupinus albus* L. leaves fumigated with O_3 has shown spatial damage distribution (Guidi et al., 2007). In this study, the fluorescence yield was lower in leaf veins than in the interveinal area. This suggests that the leaf area close to the veins is more sensitive to the ozone. CFI has also been used for distinguishing between acute (high level of O_3 concentration $> 100 \text{ nL L}^{-1}$ for a short-period, i.e. hours; Guidi et al., 2007) and chronic effects (O_3 concentration $< 100 \text{ nL L}^{-1}$ over long-term exposure). Damage by an acute O_3 concentration (400 nL L^{-1} for 6 h) in *Glycine max* Merr. has been characterised by small local areas where photosynthesis decreases, most of which are located in the areas near major veins (Chen et al., 2009). In chronic O_3 treatment, the worst photosynthetic capacity has been found in the interveinal areas, associated with more variable sizes and shapes of the chlorotic/necrotic area (Chen et al., 2009).

Studies into watermelon (Calatayud et al., 2006a) have also shown that the interaction between O_3 and N fertiliser can occur. At a high O_3 concentration and with strong N fertilisation, a significant drop in the F_v/F_m ratio and in F_{PSII} , and an increase in NPQ, were observed.

In addition to the quantum yield of PSII photochemistry

under light conditions, Φ_{PSII} , other useful parameters have been represented by the quantum yield of regulated energy dissipation in PSII, Φ_{NPQ} , and the quantum yield of non-regulated energy dissipation in PSII, Φ_{NO} (Kramer et al., 2004). Two bean cultivars with different sensitivities to the ozone, i.e. O_3 -sensitive Cannellino and O_3 -tolerant Top Crop, have been exposed to acute O_3 -stress. The ability to dissipate excess energy via regulated Φ_{NPQ} , and unregulated non-photochemical quenching (Φ_{NO}) mechanisms, has been reported to be greater in Top Crop than in Cannellino. These physiological-traits have allowed the O_3 -tolerant cultivar to compensate for the light-induced declines in Φ_{PSII} , to preserve PSII from excitation-energy, and to likely prevent ROS generation to a lesser extent than the O_3 -sensitive cultivar (Guidi et al., 2010).

Nitrogen oxides (NOx) are the air pollutants precursors of O_3 , mainly at high light intensity (Chameides et al., 1992). NOx have been considered less toxic to plants, compared to SO_2 and O_3 , since exposure to NOx does not always lead to deleterious effects on plants (Capron & Mansfield, 1976). NO_2 inside leaves can form strong acids, such as HNO_2 and HNO_3 (Schmidt et al., 1990). Furthermore, cellular acidification causes nitrate reductase to lower (Padidam et al., 1991). The lower activity of this enzyme and the presence of HNO_3 and HNO_2 might enhance accumulation of nitrates, with negative effects on the photosynthetic process (Qiao & Murray, 1998). However, NO_2 exposure on rice has no effect on Chl fluorescence parameters, and only stomatal conductance reduction has been reported compared with the control plants (Maggs and Ashmore, 1998). van Hove et al. (1992) have reported a lower electron transport rate in Douglas firs subjected to chronic NO_2 treatment compared to the control shoots (filtered air).

Sulphur dioxide is a primary product of fossil fuel combustion or from refining sulphur-containing minerals. SO_2 can easily penetrate chloroplast, which affects plant growth and development (Darrall, 1989; Surówka et al., 2007). It can react with water on the leaf surface to produce bisulphate and enter through the cuticle, where it is converted into sulphite in chloroplast (Laisk et al., 1988), and can be oxidised to sulphate. *Pinus sylvestris* L., a popular Mediterranean pine grown in an industrial polluted area, has shown a reduced F_v/F_m ratio compared to the control area (Pukacki, 2004). These results agree with those of Strand (1995), who showed a lower F_v/F_m ratio after exposing *P. sylvestris* to low concentrations of SO_2 and NO_2 for four consecutive years.

Temperature

The effect of high temperature on plants primarily affects photosynthetic functions, and the heat tolerance limit of

leaves coincides with the thermal sensitivity of primary photochemical reactions that occur in the thylakoid membrane system (Chen et al., 1982). High temperature modifies structure and damages PSII, and the oxygen evolving complex is particularly deactivated, even at slightly elevated temperatures (Yamane et al., 1998). Furthermore, the separation of LHCII from the core centre induces grana destacking (Gounaris et al., 1984) and induces the migration of LHCII to the non-appressed region.

Chl fluorescence has been used as a biomonitoring technique to test the effects of future warming events or sporadic hot waves on photosynthetic performance in several plant species (see Gorbe & Calatayud, 2012; Guidi & Calatayud, 2014). The optimal temperatures for maximum PSII quantum yields are generally broad and match the average daytime growth temperature (Larcher, 1995). For example, the leaves of *Phalaenopsis* Blume, *Deschampsia antarctica* E. Desv., *Larrea tridentate* (DC.) Coville, *Gossypium hirsutum* L. or *Nicotiana tabacum* L. maintain a constant F_v/F_m over a wide range of temperatures (Salvucci & Crafts-Brandner, 2004). A drop in F_v/F_m occurs at temperatures above those that inhibit a net photosynthetic rate (Georgieva et al., 2000), which indicates that the F_v/F_m ratio is quite a sensitive Chl fluorescence parameter. These results have been observed in barley (Oukarroum et al., 2009), strawberry (Kadir et al., 2006), tomato (Willits & Peet, 2001), grape (Kadir et al., 2007) and raspberry (Mochizuki et al., 2010; Molina-Bravo et al., 2011). In general, the tolerant varieties to heat temperature have shown a higher F_v/F_m , and have maintained higher rates of photosynthesis and F_{PSII} or zeaxanthin accumulation than sensitive varieties (Frachebound & Leipner, 2003).

However, plants that inhabit different environments have evolved mechanisms to optimise growth within defined temperature ranges. High temperature, in addition to a higher risk of heat damage, also enhances water shortage to plants. In fact, plants increase evaporation of water from stomata to cool leaves to minimise heat damage. Clearly in the era of global change, in which heat stress occurs contemporarily to drought, this event enhances the negative effects induced by water shortage (Allen et al., 2010).

Even low temperature or freezing can decrease, or even stop, biochemical activity in chloroplast. When comparing *Quercus ilex* L. and *Phyllirea latifolia* L. (Ogaya et al., 2011), the effect of cold temperature was stronger in *P. Latifolia*, and was associated with a lower F_v/F_m . High irradiance, along with low temperatures, spells overexcitation of the electron transport chain, which produces photo-chilling (Garcia-Plazaola et al., 1999). Photo-chilling occurs when a large amount of energy is trapped by Chls, but cannot be dissipated safely by heat. Consequently, carbon assimilation is limited and overproduction of oxygen free radicals takes place.

Cold-induced limitations on photosynthesis (i.e. reduced photochemical use of absorbed light energy, and an imbalance between the reducing equivalents produced in excess and the consumption capacity of photosynthesis) lead to photosynthesis photo-inhibition (Powles, 1984; Baker, 1994). Increased susceptibility to photo-inhibition has been well established during exposure of photosynthetic organisms to low temperatures in combination with even moderate photon flux density (Öquist & Martin, 1986; Osmond, 1994). It has been suggested that persistent photosynthetic efficiency depression in cold-acclimated maize may also result from the higher proportion of inactive PSII centres and the lesser capacity of repair and/or replacement of damaged PSII centres (Fryer et al., 1995).

Salinity

Salinity is one of the biggest limiting factors for agriculture in semi-arid environments. Nowadays saline soils cover more than 10 million ha only in the 22 countries that surround the Mediterranean Basin (Zdruli, 2014). Soils are classified as saline when electrical conductivity is 4 dS m^{-1} (about 40 mM of NaCl) or higher (USDA-ARS, 2008). This condition makes it harder for roots to extract water from soil, and can also cause hyperaccumulation of Na^+ and Cl^- in whole plants (Munns & Tester, 2008). Both these effects can reduce plant growth and photosynthesis (Long & Baker, 1986; Chaves et al., 2009).

Chl fluorescence has been widely utilised for two reasons: firstly, as an applicative tool for screening tolerant vs. salt-sensitive genotypes (a few exemplifiable works are: Penella et al., 2013; Hanachi et al., 2014; Khayyat et al., 2014; Sing & Sarkar, 2014); secondly, for more in-depth studies into plant physiology which aim to evaluate the effect of salt excess on photosynthetic machinery (Homann, 1969; Murata, 1969; Gross & Prasher, 1974; Mehta et al., 2010; Guidi et al., 2011; Penella et al., 2015).

For the first aim, simple F_v/F_m measurements suffice in some cases to distinguish salt-sensitive from salt-tolerant genotypes, particularly under severe salinity. For example, Singh and Sarkar (2014) used 12 rice cultivars to find a decline in F_v/F_m in the salt-sensitive, but not in the salt-tolerant, genotypes following 3-day exposure to 80 mM NaCl. Similarly, Khayyat et al. (2014) reported a good correlation between the decline in F_v/F_m and the salt concentration supplied to two pomegranate cultivars characterised by different salt sensitivity, where the decline for sensitive cultivar Shishe Kab was steeper. Conversely while screening pepper genotypes subjected to mild-prolonged salt stress (40 mM NaCl for 5 months),

Penella et al. (2013) evidenced that the widely used F_v/F_m ratio was not a useful parameter alone for assessing damage to photosynthetic apparatus, while gas exchange was more sensitive for this purpose. In addition, Netondo et al. (2004) observed no significant changes in F_v/F_m in response to salt stress between a sensitive and more tolerant cultivar of sorghum, but found a more marked increase in q_{NP} and a less decreased ETR in the salt-sensitive cultivar. The F_v/F_m ratio is a useful parameter, but its reduction can be attributed to regulated or damaged PSII units. Thus in some cases, using Chl fluorescence at the in-depth level (i.e., fast/slow kinetics and/or light curves) could provide a much more informative and detailed picture of PSII status and allow genotypes to be compared (Guidi et al., 1999).

For the second aim, Chl fluorescence has been used in particular to: (i) assess the direct effect of salt excess on photosynthetic apparatus and highlight the special localisation of salt-induced effects on whole leaf lamina; (ii) confirm that the species which adopt different mechanisms to cope with salt excess are healthier than the plant species that lack these mechanisms, or to evaluate the interaction of the factors that occur with salinity.

Pioneering works into the effect of salt excess on photosynthetic apparatus date back to late 1960s, when it was established that changes in Chl fluorescence in salt-treated thylakoids correlate with an energy spillover from PSII to PSI (Homann, 1969; Murata, 1969). It was suddenly demonstrated that excess cations induce conformation changes in the thylakoid structure (Barber, 1976) and staking (Gross & Prasher, 1974). More recently in detached wheat leaves exposed to high salt stress (0.1-0.5 M NaCl) for 1 h, it has been demonstrated that the number of inactive PSII reaction centres rose with increasing salt concentrations, and the damage caused by a high salt influx was more prominent on the donor side than on the acceptor side of PSII (Mehta et al., 2010). The effects of high salt stress are largely reversible as acceptor side damage completely recovered, while donor side recovery was below 85% (Mehta et al., 2010). As explained above, it has been revealed that F_v/F_m is not a useful indicator of salt stress in some plant species, while other parameters, such as Φ_{PSII} , q_p and NPQ, are more sensitive to salt stress (Bongi & Loreto, 1989; Zribi et al., 2009; Guidi et al., 2011). The latter parameters can also allow the spatial localisation of salt-induced symptoms to PSII centres on the leaf area to be distinguished. For example by CFI, Guidi et al. (2011) found that high salinity did not change the values of either F_v/F_m or NPQ in the whole leaves of tomato irrigated with a saline solution that contained 550 mg L^{-1} NaCl compared to the controls. Conversely, higher Φ_{PSII} values were found in salt stressed-leaves, and notably the Φ_{PSII} values in central area of leaves were higher than those found in the marginal area. This finding suggests heterogeneous salt-induced effects on whole leaf lamina.

The adaptive mechanisms adopted by plant species to cope with salinity stress, as well as the effect of the simultaneous concomitance of salinity to other stressors, have been intensively explored in recent years. As many publications on this matter exist, only a few key examples that highlight the versatility of Chl fluorescence are reported below. It has been found that, for example, Φ_{PSII} and carbon gains remain higher in *Pistacia lentiscus* L. than in *Myrtus communis* L. when exposed to mild-prolonged salt stress either alone or in combination with strong light (Tattini et al., 2006). The better performance of *P. lentiscus* derives from the better ability to use Na^+ and Cl^- for osmotic adjustment and by morpho-anatomical traits. Consequently, the biosynthesis of flavonoids and the incremented carotenoids/chlorophyll content ratio are likely adopted to compensate the inherent lower ability of *M. communis* to cope with salt accumulation in leaf tissues, especially when grown under full sunlight. Conversely, *Olea europea* L. leaves have been photo-inhibited; enhanced q_{NP} and reduced PSII efficiency have been reported only when plants were grown with 125 mM NaCl and in partial shade (15% full sunlight), while no differences in any Chl fluorescence parameters have been detected in plants grown in full sunlight (Melgar et al., 2009). In this species, changes in the $\text{Ca}^{2+}/\text{Na}^+$ ratios have been reported to take place in the root zone, a condition that usually occurs in calcareous soils where *O. europea* is largely cultivated, and which can further increase its salinity tolerance (Tattini et al., 2009).

CONCLUSION

Chl fluorescence represents a good useful technique to detect photosynthetic responses of plants grown under environmental stresses. It also provides useful information about the extent to which plant performance is limited by photochemical and non-photochemical processes. When utilised with other non-invasive techniques, such as gas exchange, it can provide insights into limitation to photosynthesis. Its use in plant physiology under environmental stresses has been widely reported. However, care must be taken because it is easy to make mistakes and obtain meaningless results, even though it is easy to utilise Chl fluorimeters and to obtain Chl fluorescence parameters (Murchie & Lawson, 2013).

In addition to the above-reported utilisation in plant ecophysiology, Chl fluorescence is widely utilised in other fields, such as studies into the physiology of algae (Roháček et al., 2014) cyanobacteria (Campbell et al., 1998) and lichens (Manrique et al., 1993).

Some Chl fluorescence applications have even focused on the quality, chemistry and physical characteristics of fruits (Nedbal & Withmarsh, 2004; Gorbe & Calatayud, 2012). Indeed Chl fluorescence has been utilised to detect the vitality and healthy of flesh kiwi fruits upon storage as fresh-cut produce (Figure 2). Chl fluorescence has also been employed to detect cut flower quality under different storage conditions (Gorbe & Calatayud, 2012).

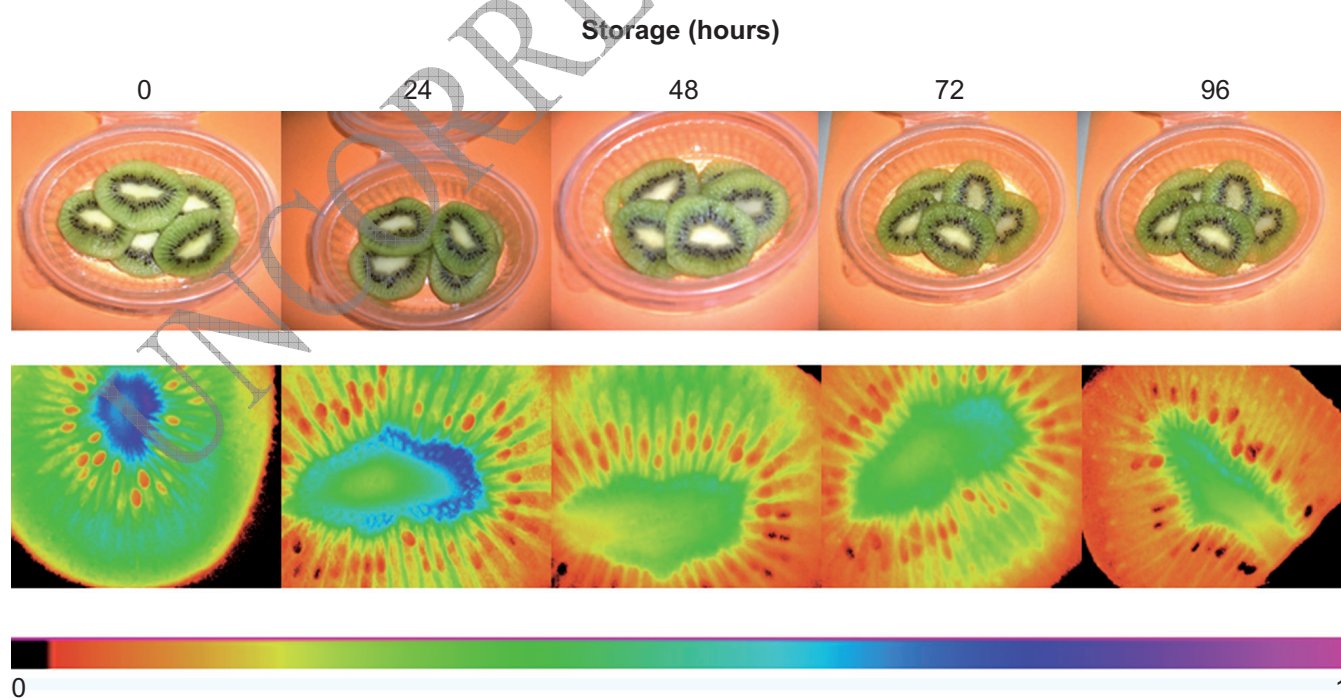


Figure 2. Flesh kiwi fruit upon storage as fresh-cut produce (top) and Chl fluorescence imaging of F_{PSII} recorded on fruit slices (bottom). Bar ranges from 0 to 1, and indicates the false colour palette.

Another recent Chl fluorescence application has been to provide information on the (in-)compatibility between rootstocks and scions in herbaceous plants, such as grafted melon plants (Calatayud et al., 2013) and pepper grafted

plants. Figure 3 depicts the greater compatibility between pepper plants grafted onto pepper (compatible union) or onto tomato rootstocks (incompatible combination) measured as an F_v/F_m ratio.

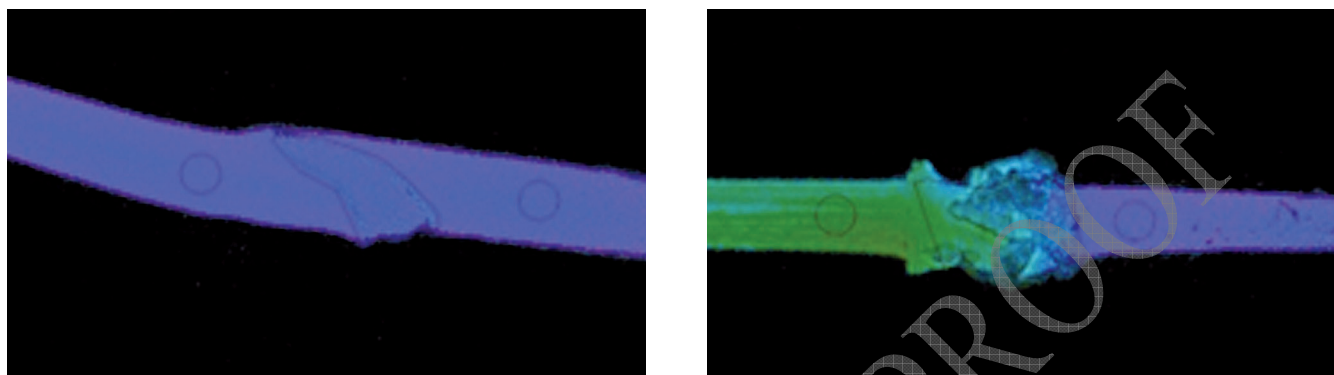


Figure 3. Chl fluorescence images of F_v/F_m recorded in stems of pepper (cultivar Adige) grafted onto pepper rootstock *Capsicum annuum* (left) or onto tomato rootstock Beaufort (right).

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