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Fluorescence Transient in Ozonated Mediterranean Shrubs

By

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With 1 Figure

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Summary

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Three Mediterranean evergreen broadleaves, *Laurus nobilis* (laurel), *Arbutus unedo* (strawberry tree) and *Phillyrea latifolia* (phillyrea tree) were exposed to 0, 55 or 110 nmol mol^{-1} O_3. After 90 days, Chl a fluorescence was recorded and analyzed with the 0JIP technique. Results confirmed that these species may be considered O_3-tolerant. Even with slight responses to O_3, the analysis of fluorescence transient gave useful information and highlighted a reduction in the density of active reaction centers in a PSII cross-section, and an increase of their activity in ozonated *L. nobilis* and mainly *P. latifolia* leaves. The realistic ambient spring concentration of 55 nmol mol^{-1} O_3 slightly depressed the energy dissipation in *A. unedo*, and increased the performance index and the maximum quantum yield of primary photochemistry in *L. nobilis* and *A. unedo*. These responses are interpreted as over-compensation due to

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counter-O_3-reactions. It is concluded that present ambient O_3 levels do not impair the photosynthetic performances of these Mediterranean species in a 90-days term, even if recovery processes during the O_3-free periods cannot be excluded.

Zusammenfassung

PAOLETTI E., BUSSOTTI F., DELLA ROCCA G., LORENZINI G., NALI C. & STRASSER R. J. 2004. Fluoreszenz in Ozon behandelten mediterranen Sträuchern. – Phyton (Horn, Austria) 44 (1): 121–131, 1 Abbildung. – Englisch mit deutscher Zusammenfassung.

Drei mediterrane immergrüne Hartlaubgewaechse, *Laurus nobilis* (Lorbeer), *Arbutus unedo* (Erdbeerbaum) und *Phillyrea latifolia* (Steinlinde) wurden 0, 55 oder 110 nmol mol^{-1} O_3 ausgesetzt. Nach 90 Tagen wurde die Chl a Fluoreszenz gemessen und mit der 0JIP Methode analysiert. Die Ergebnisse bestätigten, dass diese Arten als O_3 tolerant gelten können. Sogar bei den geringen Reaktion auf O_3 gab die Analyse der Fluoreszenzinduktion brauchbare Ergebnisse und wies auf eine Reduktion in der Dichte von aktiven PSII Reaktionszentren und einen Anstieg ihrer Aktivität in Ozon behandelten *L. nobilis* und *P. latifolia* Blättern hin. 55 nmol mol^{-1} O_3, eine Konzentration wie sie im Frühjahr realistischerweise vorkommt, setzte die Energiedissipation in *A. unedo* herab und steigerte den Leistungsindex und die maximale Quantenausbeute der primären photochemischen Prozesse in *L. nobilis* und *A. unedo*. Diese Reaktionen werden als Überkompensationsreaktion auf O_3 gedeutet. Es wird daraus geschlossen, dass die gegenwärtige O_3 Umgebungskonzentration die Photosyntheseleistungen dieser mediterranen Arten innerhalb von 90 Tagen nicht beeinträchtigt, obwohl nicht ausgeschlossen werden kann, dass Erholungsvorgänge während der O_3 freien dazu beitragen.

Introduction

Tropospheric O_3 background concentrations have been increasing since the industrial revolution (ASHMORE & BELL 1991) and are at present rising at a yearly rate of 1–2 % (HOUGH & DERWENT 1990). The phenomenon is particularly evident in regions with high photochemical activity, high temperature and seasonal drought, such as the Mediterranean area (SEUFERT & al. 1997).

Reduced photosynthesis is considered as a sensitive diagnostic parameter of O_3 injury (SAXE 1991). Ozone changes the energy capture process around photosystem II (PSII) and its concurrent fluorescence emission (MIKKELSEN 1995). Chlorophyll (Chl) *a* fluorimetry provides large amounts of accurate data with a minimum of expertise and time, and without injury to plants. An 0JIP test, based on the polyphasic increase in Chl *a* fluorescence from F_0 (50 µs) to F_P (P = M under saturating excitation light), has been developed to determine certain functional and structural parameters of PSII and includes evaluation of the fluorescence intensity at the intermediate steps I (300 µs) and J (2 ms) (STRASSER & al. 1999, 2000, 2003). The 0JIP test has been proposed as an objective and simple screening for intensive monitoring assessments in *Fagus sylvatica* (CLARK & al. 2000), the forest species chosen for modelling stomatal O_3 flux across Europe

(EMBERSON & al. 2000). The OJIP technique has been successfully applied to test the response to O_3 in other herbaceous (NUSSBAUM & al. 2001) and woody species, both a conifer (MANES & al. 2001) and a deciduous broadleaf (SOJA & al. 1998).

Mediterranean evergreen broadleaves are generally assumed to be tolerant to air pollutants, thanks to their sclerophyllic adaptations (CHRISTODOULAKIS & KOUTSOGEORGOPOULOU 1991, MONK & MURRAY 1995, MANES & al. 1998). *Laurus nobilis* L., *Arbutus unedo* L. and *Phillyrea latifolia* L. have been recently demonstrated to be O_3-tolerant as regards their gas exchange ability (PAOLETTI & al. 2002a).

The aim of this work was to apply the Chl *a* fluorescence OJIP test for screening these three Mediterranean evergreen shrubs artificially exposed to O_3.

Material and Methods

Two-years-old seedlings of *L. nobilis*, *A. unedo* and *P. latifolia* were exposed to O_3 from March to May 2002 in a greenhouse fumigation apparatus, ventilated with charcoal-filtered air (two complete air changes per minute), at ambient light (40% lower than the irradiance outside the greenhouse), temperature (23 ± 2°C), and relative humidity (75 ± 5%). Ozone was generated by a Model 500 O_3-generator (Fischer, Zürich, Switzerland) supplied with pure O_2. Ozone concentration was continuously monitored with a PC-controlled photometric analyzer (Monitor Labs mod. 8810, San Diego, CA USA). The exposure regime was a square wave of 55 or 110 nmol mol^{-1} from 09:00 to 14:00. Control plants were maintained in charcoal-filtered air. All seedlings were watered until field capacity throughout the experiment.

After 90 days of exposure, Chl *a* fluorescence was recorded at midday and at ambient temperature with a Fim 1500 (ADC Ltd, Hoddesdon, England) after a 40-min dark adaptation, with 3000 μmol m^{-2} s^{-1} red-actinic-light at 50% intensity, 650-nm peak wavelength, 1-s duration of saturating light pulse, 10-μs data acquisition rate from 10 μs to 2 ms and automatic switch to slower digitization rates after 2 ms and 1 s. Measurements were carried out on seven plants per O_3 exposure and per species, three leaves in each plant, from shoots sprouted before fumigations.

The parameters were extracted from the fast fluorescence transient according to the OJIP-test (STRASSER & al. 1995). A typical fluorescence transient, exhibited upon illumination of a dark-adapted photosynthetic sample, reveals both a fast polyphasic rise and a subsequent slower decline to a steady state. Values of four direct fluorescence parameters are retained: F_0, F_{300}, F_{2000}, and F_M, i.e. the fluorescence intensities at 50 μs, 300 μs, and 2 ms, and the maximum fluorescence intensity. These values are used to calculate the performance index, PI, i.e. the ratio between two recently described Structure-Function-Indexes (SFI): SFI_R that responds to structural and functional PSII events leading to photosynthetic electron transport (TSIMILLI-MICHAEL & al. 1998), and SFI_N, that refers to the energy which is dissipated or lost from photosynthetic electron transport (STRASSER & al. 1999).

Besides F_0 and F_M, the parameters φ_{Po}, maximum quantum yield of primary photochemistry, φ_{Eo}, probability that an absorbed photon will move an electron into the electron transport chain, ψ_0, efficiency of such a movement, ABS, quantity of

photon flux that is absorbed by the antenna pigments, TR, trapping flux, i.e. the excitation energy flux that reaches RC and gets there conserved as free energy in chemical components; ET, electron transport that leaves RC by reoxidizing Q_A^- to Q_A, the primary quinone electron acceptor, DI, energy flux that is dissipated as heat or fluorescence or transferred to other systems, were calculated and expressed as spider plots by the Biolyzer© programme (by Ronald Maldonado-Rodriguez, Biogenetic, http://come.to/bionrj), version 3.0. The index 0 refers to the state at the onset of illumination. Two types of models were presented: the one that refers to the reaction center (RC) in the membrane and thus deals with the specific energy fluxes (per RC) and the other that refers to the excited cross section (CS) of a leaf and thus deals with the phenomenological energy fluxes (per CS).

For each species, the ozone effect was tested with a univariate analysis of variance. Significance was tested using a HSD Tukey test. The STATISTICA®6.0 package for Windows was used for all statistical analyses.

Results and Discussion

After 90 days (31.5 μmol mol^{-1}*h AOT40), exposure to 110 nmol mol^{-1} O_3 did not modify the photosynthetic performance of our evergreen Mediterranean broadleaves, as measured by the performance index PI (Fig. 1, Table 1). A previous paper (Paoletti & al. 2002a) showed gas exchange in these species as O_3-tolerant: a 45-day exposure did not modify net photosynthesis, while after 90 days ozonated leaves of *Laurus nobilis* and *Arbutus unedo* reduced assimilation with respect to control leaves, and *Phillyrea latifolia* did not. Comparatively, in *Fagus sylvatica*, a 14-days exposure to 150 nmol mol^{-1} O_3 – from 09:00 to 14:00 – depressed net photosynthesis and apparent electron transport rate through PSII, while did not modify F_M (Paoletti & al. 2002b). Again in *F. sylvatica*, PI has been shown to significantly decrease under O_3 (Clark & al. 2000).

In *L. nobilis* and *A. unedo*, PI at 55 nmol mol^{-1} O_3 even increased relative to the controls. It is known that many stress factors induce an alarm phase, during which the stress reactions are offset by counter-reactions, which may lead to over-compensation (Larcher 1995). A slight or initial O_3 stress may stimulate photosynthetic performances to activate detoxifying mechanisms.

Even φ_{Po} and φ_{Eo} in *L. nobilis* and *A. unedo* and ψ_0 in *A. unedo* tended to increase at 55 and to decrease at 110 nmol mol^{-1} O_3 so that both significantly decreased at 110 relative to 55 nmol mol^{-1} (Table 1, Fig. 1). Dissipation in *A. unedo* also showed a reduction at 55 relative to 110 nmol mol^{-1}, both when referred to the active reaction centers in the membrane (RC) and to the excited cross sections (CS_0). All these responses may be seen as an over-compensation induced by the ambient O_3 concentration.

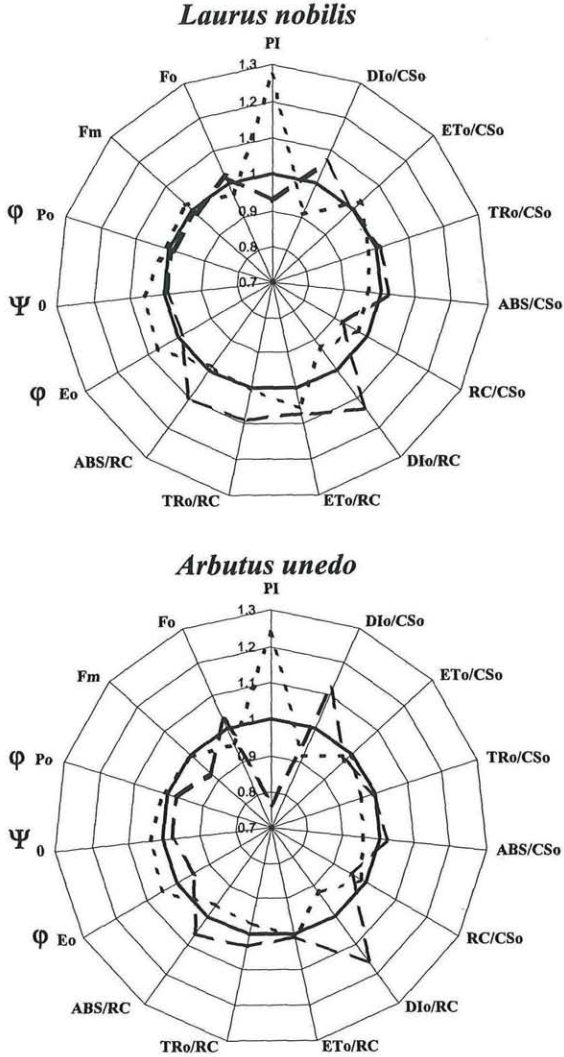
φ_{Po}, the maximum quantum yield of primary photochemistry, is the probability than an absorbed photon is trapped by the PSII RC with the resultant reduction of Q_A, but is usually expressed as ratio between vari-

Table 1. Significance levels from the univariate ANOVA testing the effects of three ozone exposures (0, 55 or 110 nmol mol^{-1}; 5 h day^{-1}; 90 days) on selected parameters quantifying the behaviour of PSII in leaves of three Mediterranean evergreen broad-leaves: F_0, initial fluorescence intensity; F_M, maximum fluorescence intensity; φ_{Po}, maximum quantum yield of primary photochemistry; ψ_0, efficiency that a trapped exciton can move an electron into the electron transport chain; φ_{Eo}, probability that an absorbed photon will move an electron into the electron transport chain; ABS, photon flux absorbed by the antenna pigments; TR, photon flux trapped into RC; ET, electron transport that leaves RC by reoxidizing the primary electron acceptor; DI, energy flux that is dissipated; RC, number of active PSII reaction centres; CS, excited cross sections; PI, performance index. The index 0 refers to the state at the onset of illumination. Different letters indicate significant differences among O_3 exposures according to Tukey's HSD test.

Laurus nobilis	0	55	110	p-level
F_0	a	a	a	n.s.
F_m	a	a	a	n.s.
φ_{Po}	ab	a	b	0.0045
ψ_0	a	a	a	n.s.
φ_{Eo}	ab	a	b	0.0216
ABS/RC	ab	b	a	0.0264
TR_0/RC	b	ab	a	0.0306
ET_0/RC	a	a	a	n.s.
DI_0/RC	ab	b	a	0.0186
RC/CS_0	a	a	a	n.s.
ABS/CS_0	a	a	a	n.s.
TR_0/CS_0	a	a	a	n.s.
ET_0/CS_0	a	a	a	n.s.
DI_0/CS_0	a	a	a	n.s.
PI	b	a	b	0.0020

Arbutus unedo				
F_0	a	a	a	n.s.
F_m	a	a	b	0.0027
φ_{Po}	ab	a	b	0.0003
ψ_0	ab	a	b	0.0396
φ_{Eo}	ab	a	b	0.0034
ABS/RC	a	a	a	n.s.
TR_0/RC	a	a	a	n.s.
ET_0/RC	a	a	a	n.s.
DI_0/RC	ab	b	a	0.0055
RC/CS_0	a	a	a	n.s.
ABS/CS_0	a	a	a	n.s.
TR_0/CS_0	a	a	a	n.s.
ET_0/CS_0	a	a	a	n.s.
DI_0/CS_0	ab	b	a	0.0073
PI	ab	a	b	0.0043

Phillyrea latifolia	0	55	110	p-level
F_0	a	a	a	n.s.
F_m	a	a	a	n.s.
φ_{Po}	a	a	a	n.s.
ψ_0	a	a	a	n.s.
φ_{Eo}	a	a	a	n.s.
ABS/RC	b	a	a	0.0002
TR_0/RC	b	a	a	0.0001
ET_0/RC	b	a	a	0.0002
DI_0/RC	b	ab	a	0.0025
RC/CS_0	a	b	b	0.0007
ABS/CS_0	a	a	a	n.s.
TR_0/CS_0	a	a	a	n.s
ET_0/CS_0	a	a	a	n.s.
DI_0/CS_0	a	a	a	n.s
PI	a	a	a	n.s.



able ($F_M - F_0$) to maximum fluorescence, i.e. F_V/F_M. The F_V/F_M ratio usually declines in ozonated leaves, indicating a photoinhibitory damage to the PSII reaction centres (SOLDATINI & al. 1998). Despite statistical significant variations in φ_{Po}, no change in the basal and maximum fluorescence, F_0 and F_M, respectively, was recorded (Table 1), that should indicate no considerable changes in chlorophyll content (SOLDATINI & al. 1998).

In *P. latifolia*, neither the probability that an absorbed photon will move an electron into the electron transport chain, φ_{Eo}, nor the efficiency

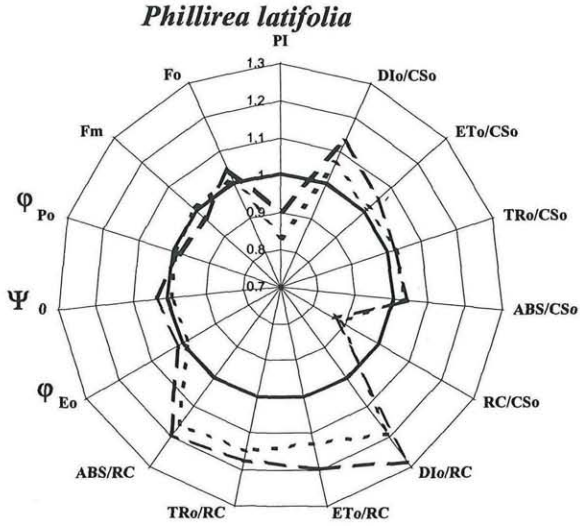


Fig. 1. Spider-plot presentation of a constellation of selected parameters quantifying the behaviour of PSII in leaves of three Mediterranean evergreen broadleaves exposed for 90 days to 55 (dotted line) or 110 (dashed line) nmol mol^{-1} O_3, relative to that at 0 nmol mol^{-1} O_3 (solid line). Acronyms and statistical significance are in Table 1.

of such a movement, ψ_0, – the latter also in *L. nobilis* – varied under O_3 (Table 1).

The photon flux absorbed by the antenna pigments, ABS; the photon flux that gets conserved in the reaction centers as free energy, TR_0; the electron transport that reoxidates the primary electron acceptor, ET_0; and the dissipated flux, DI_0 (except in *A. unedo*); did not change when referred to the excited cross sections (CS_0). When referred to the active reaction centers in the membrane (RC), they all increased in the ozonated leaves of *P. latifolia* and *L. nobilis*, even if less considerably in the latter species (Table 1). This implyes that O_3 exposure induced a reduction of the density of active reaction centers per PSII cross-section, RC/CS_0, even if such a reduction was significant only in *P. latifolia*. The less abundant the reaction centers, the more active they are in absorbing, trapping, circulating, and also dissipating the energy flux. This means that O_3 affected the functionality of PSII by modifying PSII structure. This compensatory response buffered the O_3 effect on the performance index in *P. latifolia* and induced an increase in the performance index of *L. nobilis* at 55 nmol mol^{-1} O_3. Lorenzini & al. 1999 concluded that photoinhibition in ozonated poplar leaves was caused by transformation of active reaction centers to photochemically inactive centers that dissipate excitation energy into heat. The reaction centers reside in the tylakoids and O_3 is known to impair

plant membranes (HEATH 1994). The significance of such a response to longer-term O_3 should be still evaluated.

PSII funtion is known to be highly sensitive to environmental conditions, including pollution (STRASSER & STIRBET 2000). The slight responses recorded in our 90-day-ozonated evergreen broadleaves confirms their O_3-tolerance. Mediterranean species are adapted to high radiation and water stress (NAHAL 1981). Evergreen sclerophylls are less susceptible to photoinhibition, and the diurnal decline in F_V/F_M remains fully reversible (WERNER & al. 1999).

Anyway, the species-specific responses in Chl *a* fast kinetic does not allow us to arrange the species in an O_3 tolerance order, despite they were chosen according to a gradient of xerotolerance, *P. latifolia* > *A. unedo* > *L. nobilis*.

Comparatively, the interspecific distribution of constitutive total superoxide dismutase activity before O_3 fumigation, as well as the changes of such activity in ozonated leaves, were in accordance with the range of gas exchange sensitivity to O_3 (PAOLETTI & al. 2002a), going from the most sensitive laurophyllic *L. nobilis* to the most tolerant sclerophyllic *P. latifolia*, with *A. unedo* showing intermediate morphological adaptations and ecology (DE LILLIS 1991). This would lead to conclude that O_3-induced limitations in the photosynthesis of these species are primarily controlled by stomata, adversely to that reported for deciduous broadleaves (MATYSSEK & al. 1991, CLARK & al. 1996, PAOLETTI & al. 2002b).

Chl *a* fast kinetics provides an insight into the complexity of the photosynthetic apparatus, especially of PSII, and gives information useful to detect effects as slight as those here reported. It enables many attached leaves to be screened in a short time and has the potential to be used in setting and mapping critical level for O_3 (CLARK & al. 2000). More data are anyway needed for Mediterranean environments and species.

Fifty five nmol mol^{-1} is the mean hourly O_3 concentration recorded in spring (March to May) in 1999, 2000 and 2001 from 11:00 to 15:00, at a Mediterranean rural site in Tuscany (Gabbro, central Italy), with peaks up to 90 nmol mol^{-1} (M. CHINI personal communication). It is concluded that present ambient O_3 levels do not impair the photosynthetic performances of these Mediterranean species in a 90-days term, even if recovery during the O_3-free hours over the 90 days cannot be excluded (NALI & al. 1998) and the effect of co-occurring factors should be evaluated.

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Recensio

KJELLSSON Gösta & STRANDBERG Morten 2001. Monitoring and Surveillance of Genetically Modified Higher Plants. Guidelines for Procedures and Analysis of Environmental Effects. – Gr. 8°, VI + 119 Seiten; kart. – Birkhäuser Verlag Basel, Boston, Berlin. – € 45,–, ISBN 3-7643-6227-8.

Dieses Heft ist als Ergänzung zu den drei Bänden über Methods for Risk Assessment of Transgenic Plants gedacht, die im selben Verlag erschienen sind und in Phyton 35(2): 317, 38(1): 157–158, bzw. 42(2): 267–268 besprochen worden sind. Inzwischen ist ein vierter Band erschienen (dieses Phyton-Heft, p. 144). Außerdem wäre in diesem Zusammenhang noch ganz besonders auf einen Bericht an den Deutschen Bundestag zu erinnern, der in Phyton 42(1): 37–38 referiert worden ist.

Von der Form her ist das Buch dadurch ausgezeichnet, daß im linken Teil jeder Seite Raum für Marginalien ausgespart ist, sodaß es neben den meisten Absätzen Kurzhinweise von Stichwortcharakter bis Kurzzusammenfassungen gibt. Vom Konzept her wird offenbar davon ausgegangen, daß einheitliche, internationale Richtlinien für den Umgang und die Überwachung von Versuchen mit oder der praktischen Nutzung von genetisch modifizierten höheren Pflanzen (GMHP) dringend notwendig seien. Das Buch will neue umweltrelevante Fakten bringen und Maßstäbe zur Analyse möglicher Effekte, wenn GMHP großflächig kultiviert werden, setzen und damit Ideen und Wege zu solchen Richtlinien aufzeigen, mit deren Hilfe Ausbreitung und Umwelteffekte transgener Pflanzen (nach deren Ausbringung) erkannt werden sollen. Die Einleitung (p. 1–6) behandelt u.a. Verantwortlichkeit, die Kapitel-Inhalte dieses Buches, Trends der kommerziellen GM-Sortenentwicklung und EU-Direktiven. Der 2. Abschnitt „environmental concerns and concepts" (p. 7–16) enthält u.a. die bekannte, problematische Formel risk = probability × hazard, geht auf die Möglichkeit der Einwanderung GMHP in natürliche Lebensräume und andere ökologische Effekte ein und enthält ca. vier Seiten mit Definitionen zu diesem Thema [z.B. acceptable effect = an effect of the GMHP on the environment, which occur at a low level and is assessed as being ecologically insignificant and not adverse. Baseline information = the base or expected normal situation including variation from which future change in a habitat may be detected. Monitoring = data sampling and detec-