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How wind affects the photosynthetic performance of trees: quantified with chlorophyll *a* fluorescence and open-top chambers

A.J. CLARK*,**, W. LANDOLT*, J.B. BUCHER*, and R.J. STRASSER**

*Swiss Federal Institute for Forest, Snow and Landscape Research, CH-8903 Birmensdorf, Switzerland**
*University of Geneva Bioenergetics Laboratory, CH-1254 Jussy Geneva, Switzerland***

Abstract

Meteorological parameters inside and outside an open-top chamber (OTC) fumigation facility were recorded and the primary photosynthetic response of four tree species measured with chlorophyll (Chl) *a* fluorescence emission. Parameters extracted from the Chl *a* fluorescence transient were used to calculate photosynthetic activity of the leaves using a performance index. Measurements were made during the night throughout a single growing season. The seasonal primary photosynthetic performance in all species was significantly altered by growth in the OTCs, and the degree of response was dependent upon the species. Wind was an important effectual component of the altered environment. The average temperature was consistently 1.94±0.70 °C higher within the OTCs, whereas wind speed fluctuated substantially more between inside and outside the OTCs (0 to 8 m s^{-1}). There was a correlation between the photosynthetic performance index and wind speed in *Fagus sylvatica*, *Fraxinus excelsior*, and *Prunus serotina*. The response to wind was also particular to each species; the photosynthetic performance of *F. sylvatica* increased with wind speed (1 to 7 m s^{-1}), decreased with *F. excelsior* (0 to 6.5 m s^{-1}) and *P. serotina* (0 to 5.5 m s^{-1}). *Abies alba*, in contrast, was almost insensitive to wind. A model was proposed and tested for the conversion of the photosynthetic performance values collected in OTCs to predict the photosynthetic performance outside OTCs. The wide variety of responses to wind and temperature of the four species conformed to linear functions that describe the relationship of the wind speed and temperature responses with the difference in photosynthetic performance between the OTC and open environments. Specific coefficients for wind and temperature were proposed. The photosynthetic response to wind of each species depends on its ecophysiological specialisation.

Additional key words: *Abies alba*; *Fagus excelsior*; *Fagus sylvatica*; *Fraxinus excelsior*; model; *Picea abies*; *Prunus serotina*; temperature.

Introduction

Open-top chambers (OTC) currently represent the compromise required for the investigation of the effects of gaseous pollutants upon plants. Although OTCs permit the effective fumigation of plants, they significantly alter the plant boundary layer climate and consequently the response to the pollutant under investigation. To improve the modelling of pollutant effects on plants living in the open field environment it is necessary to include the critical meteorological parameters that modify the boundary layer when using OTCs. An understanding of the significance of these OTC-induced modifications on photosynthesis will enhance the prognosis that can be made with respect to plants in the field.

Observed effects of growing plants in OTCs often heavily outweigh the effect caused by a pollutant, with substantially increased growth rates in OTCs (Allen *et al.* 1992, Mikkelsen 1995, Mortensen 1998). This brings

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Abbreviations: ABS, absorption; Chl, chlorophyll; JD, Julian day; k_T, specific sensitivity coefficient for temperature; k_W, specific sensitivity coefficient for wind; OTC, open-top fumigation chamber; PI_{ABS}, performance index referring to an equal absorption or equal amount of chlorophyll; PS2, photosystem 2; Q_A, quinone electron acceptor; RC, PS2 reaction centre; RH, relative humidity; T, temperature; W, wind speed.

into question two issues: first, the relevance of the detrimental effect the pollutant may have had; and second, the final estimation required for a prognosis of likely effects the pollutant will have in the absence of an OTC. Assuming that the pollutant is a threat to the health of the tree, its effect may be detectable as a deviation above and beyond that due to OTCs.

OTCs substantially increase the amount of shelter provided to the plants. The most important aspect of the shelter is the substantial reduction in wind speed (Heagle *et al.* 1973, 1989, Olszyk *et al.* 1980, Allen *et al.* 1992) and the consequent turbulent mixing in the leaf boundary layer. Generally, the protection of plants from wind may substantially alter the form and increase yields by up to 300 % in certain crop species (Carlsson and Callaghan 1991, Retuerto *et al.* 1996). However, totally restricted wind is not likely to improve yields: there is an optimum wind speed for growth (Wadsworth 1959, Tranquillini 1969), too little wind causes insufficient atmospheric mixing of gases and leaf cooling in certain circumstances. A broad range of responses to wind has been found between species (Nobel 1982) which is reflected in the range of susceptibility due to gaseous pollutants. For instance, wind affects leaf water status and stomatal behaviour, so plants with relatively high stomatal conductance can be more susceptible to damage from ozone because of the larger sub-stomatal dose intercepted (Bungener *et al.* 1999).

Previous research has shown that photosynthesis can be affected by increasing wind speed. Rates of carbon gas exchange may increase or decrease, depending upon the speed of the wind, temperature, and humidity (Tranquillini 1969, Caldwell 1970, Grace and Thompson 1973, Grace 1977). Chl *a* fluorimetry is a sensitive and non-intrusive technique for the detection of photosynthetic responses to numerous pollutants and environmental variables (Strasser *et al.* 1987, 1995, Lichtenthaler and Rinderle 1988, Larcher 1995, Clark *et al.* 1998, Soja *et al.* 1998). The predisposition of Chl *a* fluorescence techniques for the detection of stress in the field (Joshi and Mohanty 1995) combined with its ease of application make it a potentially excellent method for large scale screening and modelling. To date no work, to our knowledge, has been undertaken upon the effects of wind on Chl *a* fluorescence.

Our aim was to determine a reliable and accurate diagnostic method for the assessment of the vitality of plants inside and outside OTCs. The objective of this research was to assess the sensitivity of a recently developed performance index (PI_{ABS}) in detecting leaf responses to meteorological differences induced by OTCs. The index PI_{ABS} was derived from parameters extracted from the fast polyphasic Chl *a* fluorescence rise, and is defined by the ratio of expressions that lead to photosynthetic activity to expressions that describe absorbed energy not conserved in electron transport (see Appendix). The expressions describing the use of energy in photosynthesis are the density of photosystem 2 (PS2) reaction centres, the quantum yield of primary photochemistry (F_V/F_M), and the yield of electrons transported beyond Q_A towards carbon dioxide fixation. Those expressions indicating the loss of energy in photosynthesis are the yield of energy dissipation and the probability that an electron will not be transported beyond Q_A.

The hypothesis was that shelter provided by OTCs, which causes a reduction in wind speed and exposure, would be detectable in the performance of the photosynthetic apparatus. The effect of OTCs was expected to differ between species. The increased shelter supplied by the OTCs became apparent. Wind was found to be an important explanatory variable of the altered primary photosynthetic performance. The responses in photosynthetic performance were conformed to a linear relationship with wind speed that differs between species. A procedure to convert Chl *a* fluorescence values recorded in virtually still environments to lightly windy ones was proposed. The basis of the response of primary photosynthesis to wind remains unexplained.

Materials and methods

Plants and treatments: The experiment was performed in an open-top chamber (OTC) facility in Birmensdorf, Switzerland. Three ambient air treatments were used as a component part of an ongoing ozone fumigation experiment. The first treatment (Interior) comprised five *Perspex* OTCs, 3 m high by 2 m diameter, into which ambient air was pumped at less than 0.75 m s^{-1}. The second, a chamber-less treatment (Exterior), was also replicated five times and exposed to the ambient climate. Both treatments were partially shaded in ambient irradiances in excess of 600 μmol m^{-2} s^{-1} with the use of a translucent canopy, which automatically covered both treatments in order to stop excessive temperatures being generated in the chambers. The third treatment was situated outside the canopy and was exposed to full sunlight. It was not used in the following analysis because it was not strictly comparable, but has been referred to when necessary.

Two Swiss provenances of *Fagus sylvatica, Fraxinus excelsior, Abies alba, Picea abies,* and a single provenance of *Prunus serotina* were used. All saplings were potted in a standard soil mixture (50 % sandy soil, 25 % rown earth, 25 % peat, 2 kg m^{-3} fertiliser *Osmocote plus*), which was kept moist throughout the experiment. There was a single sapling from each provenance in each chamber. The plants were placed in the experiment from the beginning of April until the end of September during 1996 and 1997. *P. abies* trees were insensitive, though the data has been referred to when relevant.

Meteorological measurements: Meteorological values were collected throughout the experiment. Recorded were ambient wind speed with a switching anemometer (model *A100R*, *Vector Instruments*, UK), and temperature (*Skye Instruments*, Wales). An additional set of meteorological measurements was recorded in parallel from both treatments between 12 August and 30 September 1997 to provide a more detailed description of the climates. The measurements collected were temperature and wind speed, with 10-min means calculated from 30-s measurements. The instruments were certified to conform to EC Directives, the calibrations were traceable to the National Physical Laboratory, UK. Meteorological measurements were collected 1 m above the ground. The climate throughout the year was modelled by regressing the intensive meteorological collection period from 12 August to 30 September with the continually collected data.

Chl *a* fluorescence measurements: Fast Chl *a* fluorescence transients were measured at ambient temperatures with a portable fluorimeter, (PEA, *Hansatech Instruments*, UK). All fast Chl *a* fluorescence transients were recorded for a period of two seconds. The signal was digitised up to twelve bits with a time resolution of 10 µs. After 2 ms and after 1 s, the instrument automatically switched to slower digitisation rates (for details see Strasser *et al.* 1995). Fluorescence emission was induced by homogenous irradiation on a 4 mm-diameter area of the leaf samples with an array of 6 light emitting diodes and a maximal irradiance higher than 3000 µmol m^{-2} s^{-1} (red, peak wavelength 650 nm). Chl *a* fluorescence transients were recorded at night, after a period of at least 3 h of darkness to attain a fully dark-adapted state.

The Chl *a* fluorescences at 50 and 300 µs, and 2 ms, were denoted as F_0, $F_{300\mu s}$, and F_{2ms} respectively, and F_M was the maximum fluorescence intensity. These values were used to calculate the performance index, denoted as PI_{ABS}:

$$PI_{ABS} = \frac{a \cdot b}{c} \frac{a}{1-a} \frac{b}{1-b} \qquad (1)$$

where *a* is the ratio of the total variable fluorescence and the maximal fluorescence a = F_V/F_M, b is the relative variable fluorescence at 2 ms, b = $V_J = (F_{2ms} - F_0)/(F_M - F_0)$, and *c* is the relative variable fluorescence at 300 µs, c = $V_{300} = (F_{300ms} - F_0)/(F_M - F_0)$. A short explanatory derivation of PI_{ABS} is provided in the Appendix.

Statistical methods: We examined the distribution of all Chl *a* fluorescence values for non-normality and heterocedasticity to ensure that the assumptions for parametric statistics were met. The treatment effect was tested with a univariate ANOVA, designed as a mixed model three stage nested using a type III sum of squares calculation. The highest level of the hierarchy was the treatment level with five chambers nested in each treatment, and subgroups of provenances and trees, with subsubgroups of leaves within trees. The model was further developed to use the day of the year as an additional dependent variable for a repeated measures analysis, based on an orthogonal polynomial transformation, to test for time dependant effects. Tests of significance were made at the 95 % confidence level using a Tukey test.

There was a slight upward turbulent wind speed of 0.08–0.4 m s^{-1} within the OTCs, however, the lateral wind speed, as measured with switching anemometer within the OTCs, was not detectable and was considered to be zero.

The SAS system for windows (release *6.12, SAS Institute*, USA) was used for all statistical analyses.

Results

Interior daylight mean temperatures were on average of 1.4±0.5 °C warmer than the exterior, and 1.94±0.70 °C higher than the fully exposed environment (treatment III, not under the light-limiting canopy). The interior warmed at a faster rate during the morning hours and maintained a 2.0±0.9 °C higher temperature during the night compared to exterior (Fig. 1*A-D, lower panels*). The maximum temperature difference between the interior and exterior was approximately 5 °C. The exterior was 0.4±0.1 °C warmer than the fully exposed environment, it warmed up at a slower rate during the morning and never reached the same peak temperatures recorded in the fully exposed environment. Wind increased the temperature of the exterior treatment and

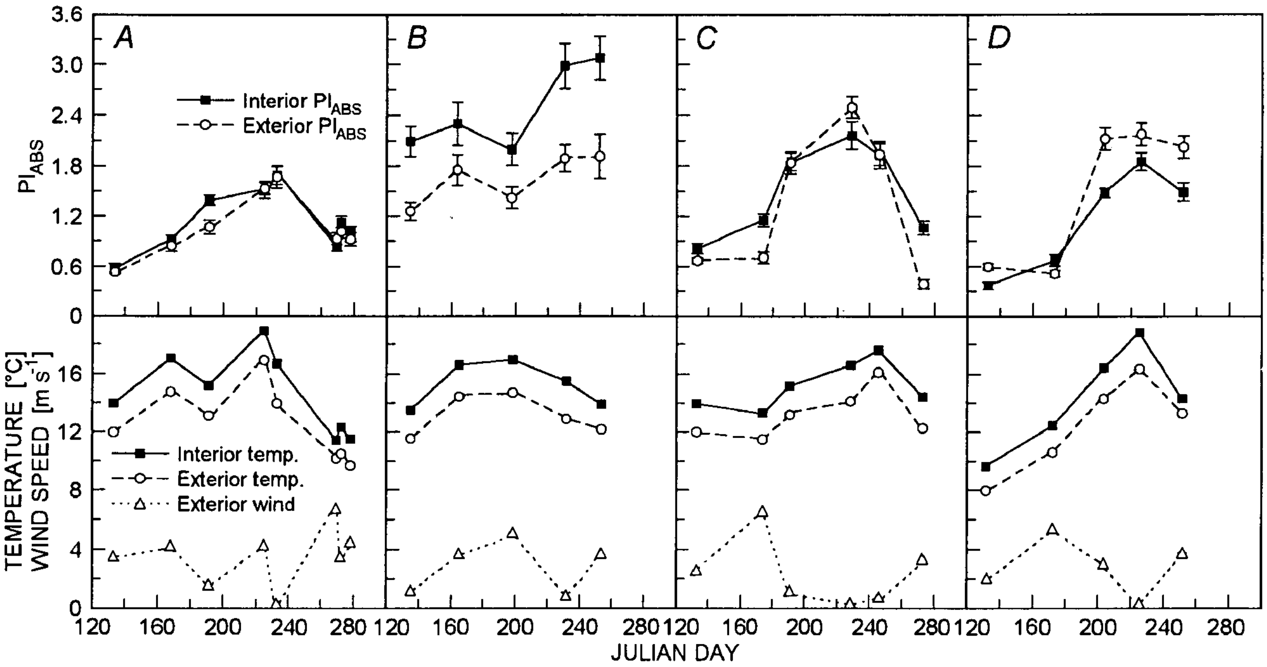

Fig. 1. *A* to *D*: *Upper plots* mean PI_{ABS} *versus* time (Julian Day), for *Fagus sylvatica* (*A*), *Abies alba* (*B*), *Fraxinus excelsior* (*C*), and *Prunus serotina* (*D*) in exterior or interior treatments. PI_{ABS} means are calculated from approx. 50 Chl *a* fluorescence measurements, error bars S.E. *Lower plots* show temperature and wind speeds measured at the same time as Chl *a* fluorescence.

Table 1. Results of a repeated measures ANOVA, testing the *between* treatment effects on the photosynthetic index, PI_{ABS}, of trees inside and outside OTCs. The model tests the significance of differences between treatment means for all samples collected during the 1997 growing season from four tree species and two provenances. Replications refer to five OTCs within each treatment. The degrees of freedom (*df*) and the mean squares (x^2) from which the results of the F-test probabilities (*Pr* > *F*) were calculated are listed. Specific errors were * for treatment (T) and ** for provenance (P), T×P, replication, and leaf.

	F. sylvatica			*F. excelsior*			*P. serotina*			*A. alba*		
	df	x^2	*Pr>F*	*df*	x^2	*Pr>F*	*df*	x^2	*Pr>F*	*df*	x^2	*Pr>F*
Treatment (T)	1	1.098	0.3048	1	3.740	0.5842	1	6.156	0.1898	1	78.516	0.1574
Provenance (P)	1	0.197	0.1541	1	0.084	0.3344	-	-	-	1	30.463	0.0003
T×P	1	5.202	0.0001	1	0	0.9993	-	-	-	1	1.055	0.4798
Replication	8	0.913	0.0001	8	11.510	0.0001	8	2.998	0.0001	8	32.271	0.0001
Leaf	77	0.095	-	80	0.089	-	39	0.303	-	68	2.089	-

Table 2. Results of a *repeated measures* ANOVA, testing the *within* treatment effects on the performance index, PI_{ABS}, of trees inside and outside OTCs. The model tests the significance of differences between PI_{ABS} means for effects between treatments on individual Julian days (JD) for four tree species from different provenances. The degrees of freedom (*df*) and the mean squares from which the results of the F-test probabilities (*Pr* > *F*) were calculated are listed. Asterisks indicate the specific error terms used.

	F. sylvatica			*F. excelsior*			*P. serotina*			*A. alba*		
	df	x^2	*Pr>F*	*df*	x^2	*Pr>F*	*df*	x^2	*Pr>F*	*df*	x^2	*Pr>F*
Julian Day (JD)	7	12.500	0.0001	5	49.111	0.0001	4	25.562	0.0001	7	15.656	0.0001
JD×Treatment (T)	7	0.399	0.0003	5	3.156	0.0001	4	1.258	0.0001	7	1.652	0.0467
JD×Provenance (P)	7	0.105	0.3955	5	2.628	0.0001	-	-	-	7	1.953	0.0227
JD×T×P	7	0.802	0.0001	5	3.870	0.0001	-	-	-	7	0.348	0.7241
JD×Replication	56	0.416	0.0001	40	2.272	0.0001	32	1.048	0.0001	56	3.184	0.0001
Leaf	539	0.100	-	400	0.111	-	156	0.162	-	539	0.675	-
Huynh-Feldt Epsilon		1.015			0.878			1.178			1.232	

slightly decreased the interior temperature by increased mixing of the air with the fully exposed environment. Wind speed fluctuated relatively much more between the interior and the exterior in comparison with temperature.

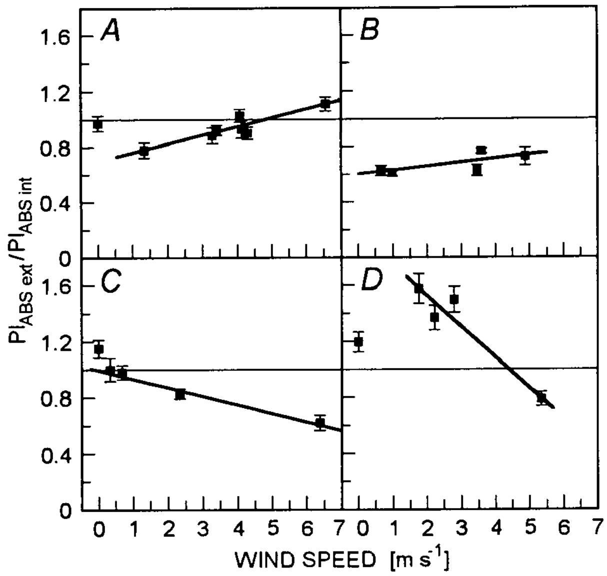

Fig. 2. Mean $\mathrm{PI}_{\mathrm{ABS}}$ outside the OTCs (exterior) relative to mean $\mathrm{PI}_{\mathrm{ABS}}$ inside the OTCs (interior) *versus* wind speed for *Fagus sylvatica* (*A*), *Abies alba* (*B*), *Fraxinus excelsior* (*C*), and *Prunus serotina* (*D*). Each graph is fitted with a linear regression model that excludes wind speeds of zero; for explanation see text. $\mathrm{PI}_{\mathrm{ABS}}$ values were collected over a 6-month measuring season and are means of approx. 50 samples from inside and outside the OTCs. Error bars S.E.

The largest proportion of the photosynthetic performance variation was seasonally dependent (Fig. 1*A*-*D*), with the difference between the $\mathrm{PI}_{\mathrm{ABS}}$ means being highly significant on individual Julian days (Table 2). $\mathrm{PI}_{\mathrm{ABS}}$ increased from spring to mid summer and then decreased with leaf senescence in the autumn in all the deciduous species. In the coniferous *A. alba*, $\mathrm{PI}_{\mathrm{ABS}}$ increased from spring until the end of August (approx. JD 240). The relative change in $\mathrm{PI}_{\mathrm{ABS}}$ during the period of the experiment varied from a minimum of 40 % in *A. alba* and *P. abies* (values not shown), to a maximum of 350 % in *P. serotina*.

The interior treatment produced a relatively narrower range of $\mathrm{PI}_{\mathrm{ABS}}$ values compared to the exterior, damping the photosynthetic performance in the deciduous species, most notably in *F. excelsior*, varying from 0.8-2.1 $\mathrm{PI}_{\mathrm{ABS}}$ in the interior treatment compared to 0.35-2.50 $\mathrm{PI}_{\mathrm{ABS}}$ in the exterior treatment (Fig. 1*C*). *A. alba* $\mathrm{PI}_{\mathrm{ABS}}$ increased relatively more inside the OTC in late summer (Fig. 1*B*). In contrast to the other species, the majority of the exterior $\mathrm{PI}_{\mathrm{ABS}}$ values of *P. serotina* were higher than the interior values (Fig. 1*D*). However, both *F. excelsior* and *P. serotina* had peak $\mathrm{PI}_{\mathrm{ABS}}$ values in the exterior treatment.

No significant difference was found between the interior and exterior treatments over the whole season in any of the species (Table 1). Therefore, OTCs produced no cumulative effect on $\mathrm{PI}_{\mathrm{ABS}}$. The difference between the $\mathrm{PI}_{\mathrm{ABS}}$ means of the interior and exterior treatments became highly significant when analysed *within* the measuring days (Table 2): *Pr* >0.0001 for *F. excelsior* and *P. serotina*, and *Pr* >0.0003 and >0.04 for *F. sylvatica* and *A. alba*, respectively, though only marginally in *A. alba*.

The *A. alba* higher altitude provenance (1025 m a.s.l.) was significantly different to the provenance collected from a similar altitude as that of the experiment (425 m a.s.l.) (Table 1). Early season mean $\mathrm{PI}_{\mathrm{ABS}}$ were 10.3 % lower in the higher altitude plants, this difference gradually increased during the summer to a peak 30.3 % difference in August when daily temperatures were highest. Only the *A. alba* provenance interaction with the treatments was significantly different on individual days (Table 2). In contrast, both *F. sylvatica* provenances were from the same altitude, and had a strong interaction with the treatment, but had no overriding provenance effect. The mean $\mathrm{PI}_{\mathrm{ABS}}$ of one of the provenances was consistently higher than that of the other at the beginning of the season that slowly decreased during the experiment from 10 to 5 %. The interaction between the measurement date and provenance was highly significant in *F. excelsior* and marginal in *A. alba*. The overall significant provenance treatment interaction of *F. sylvatica* (Table 1) became more significant when analysed *within* dates as was the interaction of provenance with Julian day of *F. excelsior*.

An explanation of the variance in the $\mathrm{PI}_{\mathrm{ABS}}$ values between interior and exterior was sought with regression models and the meteorological values. Wind had a significant effect upon the photosynthetic performance of the deciduous species. Fig. 2 shows the variety of responses to wind of each species. $\mathrm{PI}_{\mathrm{ABS}}$ of the exterior treatment was increased relative to the interior in *A*, decreased in *C* and *D*, and had nearly no effect in *B*. In Fig. 2, each point corresponds to the means from approximately fifty samples collected on each of the individual days, as shown in Fig. 1*A*-*D*. The regression models are calculated with the mean $\mathrm{PI}_{\mathrm{ABS}}$, not with individual samples, to give a more stringent test due to the most reduced degrees of freedom.

The linear regression lines of the function $\mathrm{PI}_{\mathrm{ABSext}}/\mathrm{PI}_{\mathrm{ABSint}}$ *versus* wind or temperature did not significantly explain the variation in $\mathrm{PI}_{\mathrm{ABS}}$ for *F. sylvatica* and *P. serotina* when all means were used. However, with the exclusion of readings when wind speed was zero, the regression lines became significant with the *Pr* >0.005 and an r^2 of 0.91 for *F. sylvatica*, Fig. 2*A*, and the *Pr* >0.04 for *P. serotina* with an r^2 of 0.96 (Fig. 2*D*). Exclusion of measurements when wind speed was zero can be justified. The boundary layer exchange of heat and gases when the wind speed is zero is due to diffusion, with eddy turbulence having no effect, while with a slight wind the turbulent exchange processes increase rapidly. The regression model calculated wind speed as having a significant relationship with PI_{ABS} (*Pr* >0.009, $r^2 = 0.99$) for *F. excelsior* when the values of the final measuring date of the year and wind speed being zero were excluded (Fig. 2*C*). Senescence severely affected the leaves and consequently justified the exclusion of the end of season data. Wind speed did not have any significant influence on *A. alba* (*Pr* >0.2, $r^2 = 0.68$). Temperature was significantly correlated with the responses of PI_{ABS}, and can be inferred from Fig. 1 with the consistently higher level of PI_{ABS} inside the OTCs in comparison with the exterior treatment.

From the approximate quantification of the climatic alteration caused by the OTCs and their correlation to photosynthetic performance an attempt was made to determine a method for predicting the performance index outside the OTCs (PI_{ABSext}) from the performance index measured inside the OTCs (PI_{ABSint}). By expressing PI_{ABSext} as a fraction of the experimentally measured PI_{ABSint} and attributing the difference ($PI_{ABSint} - PI_{ABSext}$) to the influence of the difference in the wind speed ($\Delta PI_{ABS(W)}$) and temperature ($\Delta PI_{ABS(T)}$) between the interior and exterior of the OTCs.

The first assumption being that for any situation, *e.g.*, inside or outside an OTC the performance index PI_{ABS} is a function of wind and temperature:

$$PI_{ABS} = PI_{ABS(W,T)} \qquad (1)$$

Therefore,

$$PI_{ABS(W,T)} = PI_{ABS(0,0)} + (\delta PI/\delta W)_{(0,0)}\Delta W + (\delta PI/\delta T)_{(0,0)}\Delta T + \text{unknown parameters} \qquad (2)$$

where (0,0) indicates that there is no difference in wind speed nor in temperature relatively to a standardised reference situation.

In the absence of data for the *unknown parameters* we have neglected this term, therefore:

$$PI_{ABS(W,T)} = PI_{ABS(0,0)} + \frac{\delta PI_{ABS}}{\delta W_0}\Delta W + \frac{\delta PI_{ABS}}{\delta T_0}\Delta T \qquad (3)$$

By making the assumption that the trees behave the same way inside and outside the OTC, and under particular climatic conditions of wind and temperature we can write:

$$PI_{ABSint(0,0)} = PI_{ABSext(0,0)} \text{ and } PI_{ABSint(W,T)} = PI_{ABSext(W,T)}$$

or considering the components for wind and temperature:

$$PI_{ABS(W,T)} = PI_{ABS(0,0)} + \Delta PI_{ABS(W)} + \Delta PI_{ABS(T)} \qquad (4)$$

where $PI_{ABS(0,0)}$ can be experimentally measured inside the OTCs and $\Delta PI_{ABS(W)} + \Delta PI_{ABS(T)}$ are calculated with experimentally recorded wind and temperature values outside the OTCs. Considering Eqs. (3) and (4) we can describe the influence of wind speed and temperature in the following way:

$$\frac{PI_{ABS(W,T)}}{PI_{ABS(0,0)}} = 1 + \frac{\Delta PI_{ABS(W)}}{PI_{ABS(0,0)}} + \frac{\Delta PI_{ABS(T)}}{PI_{ABS(0,0)}}$$

or

$$\frac{PI_{ABS(W,T)}}{PI_{ABS(0,0)}} = 1 + \frac{\delta PI_{ABS(W)}/PI_{ABS(0)}}{\delta W_0}\Delta W + \frac{\delta PI_{ABS(T)}/PI_{ABS(0)}}{\delta T_0}\Delta T$$

We define constants for the influence of wind speed and temperature as k_W and k_T, respectively:

$$k_W = \frac{\delta PI_{ABS(W)}/PI_{ABS(0)}}{\delta W_0} \text{ and}$$

$$k_T = \frac{\delta PI_{ABS(W)}/PI_{ABS(0)}}{\delta W_0}$$

It follows:

$$PI_{ABSext} = PI_{ABSint}(1 + k_W\Delta W + k_T\Delta T) \qquad (5)$$

where Δ refers to the difference between the inside and outside of the OTCs.

Experimentally, the constants k_W and k_T can be estimated if the measurements have been made at the same site (*e.g.*, outside the OTC, indicated as exterior, ext) under different climatic conditions in respect to wind speed and temperature. By using the performance index measured inside the OTC as the reference value, $PI_{ABS(ref)} = PI_{ABS(0,0)} = PI_{ABSint}$ and the PI_{ABS} measured outside the OTC is PI_{ABSext}.

The following equation, which can be measured experimentally, can be written:

$$\frac{PI_{ABS\,ext}}{PI_{ABS\,int}} = 1 + k_T\Delta T + k_W\Delta W \qquad (6)$$

Practically, the values were measured under the climatic conditions ranging from a temperature of 8-19 °C and a wind speed 0-7 m s^{-1}. The difference between the inside and outside of the OTCs for all measurements repeated had a mean of ΔT = 2.0±0.3 °C and ΔW = 2.8±2.0 m s^{-1}. Consequently, ΔT refers to only a small extent of the actual temperature range that was already accounted for in the measured value of PI_{ABSint}. However, all of the changes in wind speed are attributed to the change in the location between inside and outside the OTCs. For this reason ΔT was taken as a constant of 2 °C while the full range of ΔW from 0 to 7 m s^{-1} was included in the linear function (Fig. 3). Therefore, the approximated value of $(1 + k_T\Delta T)$ can be taken for a constant for each species. In all cases measured, the experimental plot of the normalised performance index PI_{ABSext}/PI_{ABSint} *versus* wind speed outside the OTC was a straight line with a slope, $b = k_W$, and an intercept, $a = k_T\Delta T$. Therefore, it becomes possible to predict the PI_{ABS} outside the OTCs from the measurements made inside the OTCs and the specific constants k_W and k_T for each species.

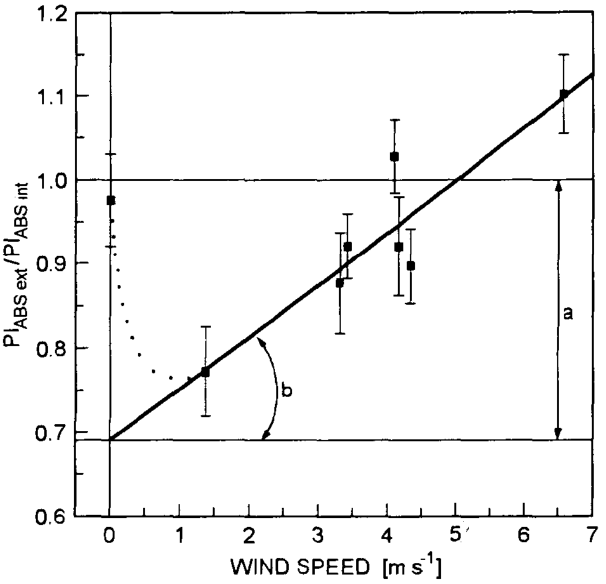

Fig. 3. Mean PI_{ABS} outside the OTCs (exterior) relative to mean PI_{ABS} inside the OTCs (interior) *versus* wind speed of *Fagus sylvatica*. The *linear regression line* assists in the estimation of the wind and temperature constants k_T and k_W. The extrapolation of the regression line to wind speed = 0 provides an estimate for the intercept $a = k_T\Delta T$ at wind speed 0. The difference in temperature between inside and outside the OTCs was measured and, therefore, k_T can be calculated. The slope b of the regression line can be taken as an estimation of k_W according to the equation given in the text.

That means the basic concept of transforming the experimentally measured PI_{ABSint} into an expected value of the PI_{ABSext} refers to all the possible dependencies of wind and temperature. However, the calculated and reported values have only been tested for the indicated temperature and wind speed differences between inside and outside the OTCs.

Table 3. The specific wind and temperature coefficients of four tree species. The coefficients are derived from values obtained within the wind speed range of 0 to 7 m s^{-1}.

Species	k_W	k_T
F. sylvatica	0.061	0.151
A. alba	0.025	0.203
F. excelsior	-0.065	-0.007
P.serotina	-0.215	-0.508

Defining the range for the linear function of the wind speed *versus* relative PI_{ABS} to be within the limits of wind speed measured (wind speed > 0 < 7 m s^{-1}), the values for $k_T\Delta T$ and k_W were calculated. An example is in Fig. 3 using the values for *F. sylvatica*. The regression has been extrapolated to the intercept *a* at wind speed zero to estimate $k_T\Delta T$. Here ΔT at wind speed zero was measured, so k_T can be calculated. However, the average ΔT was used in the calculations of k_T instead of the ΔT value at zero wind speed. The average ΔT was considered to be a good estimate. The slope $b = k_W$ and the wind speed outside relative to inside the OTC ΔW

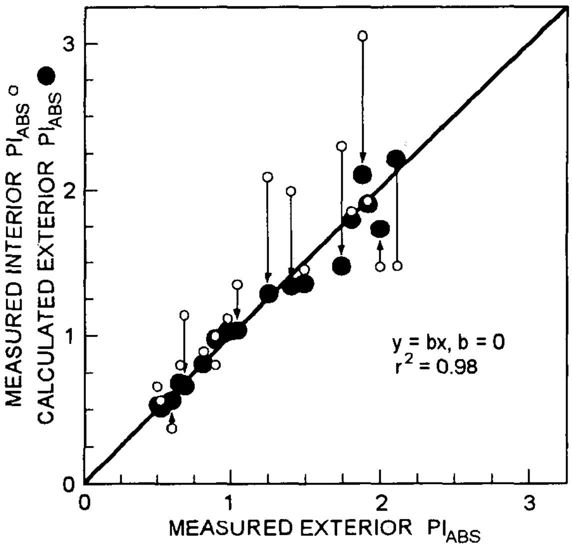

Fig. 4. Application of the equation derived (see text) to predict the PI_{ABS} of plants outside OTCs with the PI_{ABS} values measured inside the OTCs and the climatic conditions (wind and temperature) outside the OTCs. The values were transformed according to the equation $PI_{ABSext} = PI_{ABSint}(1 + k_T\Delta T + k_W\Delta W)$. The values of the measured PI_{ABSext} outside the chambers are plotted *versus* the corresponding calculated values. The ideal line, with the slope equal to unity, and the results of a linear regression of the calculated values are shown. Arrows indicate the magnitudes and directions of the transformation of measured PI_{ABSint} samples (*small open circles*) to the calculated PI_{ABSext} (*large closed circles*). The graph contains values of four species, and each plotted point summarises about 100 measured Chl *a* fluorescence transients with more than 1000 digitised data points each, collected over an experimental period of six months.

was measured so $k_W\Delta W$ can be calculated.

The derived concept so far has been experimentally tested by measuring the PI_{ABSint} and PI_{ABSext} and by calculating PI_{ABSext} according to Eq. (6). The prediction of the exterior PI_{ABS} data using Eq. (6) was calculated for all PI_{ABS} means for all species and compared to the measured external PI_{ABS} data and plotted in Fig 4. The interior PI_{ABS} data are shown and arrows indicate the distance and direction of the transformation by the equation. The regression line illustrates that the prediction of the PI_{ABS} values outside the OTC is highly significant.

k_T and k_W can be termed specific temperature and wind coefficients. The coefficients in Table 3 reflect the variety of responses illustrated in Fig. 2. *F. sylvatica* PI_{ABS} responds positively to a relative increase in wind and temperature outside the OTCs. *A. alba* is almost insensitive to a relative change in the wind speed but responds positively to a relative increase in temperature. *F. excelsior* has the opposite response to *A. alba*, being almost insensitive to a relative change in temperature but PI_{ABS} being reduced as the relative wind speed increases. *P. serotina* PI_{ABS} responds negatively to relative increases of both temperature and wind speed.

Discussion

The climatic differences measured between the OTCs (interior) and canopy environments (exterior) were comparable with those recorded in previous investigations (Heagle *et al.* 1973, 1989, Olszyk *et al.* 1980, Landolt *et al.* 1989, Allen *et al.* 1992, Janouš *et al.* 1996). The OTCs severely reduced wind speed and they were warmer by an average of 2 °C.

The physiological age of the leaves and needles produced the majority of the variation of the mean PI_{ABS} for the four species during the six months of the experiment. The characteristic seasonal variations of photosynthetic performance PI_{ABS} are in accordance with those recorded using CO_2 gas exchange measurements (Schulze 1970).

The variety of responses to wind found in our investigation are consistent with previous research (Tranquillini 1969, Grace 1977, Nobel 1982). However, the explanation of the influence of wind on photosynthesis remains unclear. Caldwell (1970) found that a wind speed of 15 m s^{-1} caused a reduction in photosynthesis and a relatively larger decrease in transpiration in *Rhododendron ferrugineum*. The explanation is that it was a response to an increased stomatal resistance; photosynthesis should be less reduced than transpiration because CO_2 has a longer diffusion path and therefore changes in stomatal resistance have a smaller influence on total resistance (Grace 1977). However, *Pinus cembra* under the same conditions demonstrated no change in transpiration rate, while photosynthetic rate was reduced. Caldwell concluded that the deflection of the needles reduced the interception of radiant energy. In our experiment, the reduction in photosynthesis cannot be attributed to leaf deflection due to the absence of light or to stomatal resistance to CO_2 because it was unlikely to have been limiting. An investigation by Grace and Thompson (1973) exposed *Festuca arundinacea* for a period of days at 3.5 m s^{-1} and found a delayed 25 % reduction in photosynthesis that could not be attributed to an increase in the stomatal resistance or to a leaf water deficit. Tranquillini (1969), with wind speeds increasing from 0.5 to 20 m s^{-1}, also found a net decrease in photosynthesis and transpiration in several species. The effects were attributed to mechanical rubbing causing cuticular damage and localised desiccation of the leaf surfaces leading to an increased diffusion resistance to gaseous currents. Analyses of CO_2 and H_2O pathways indicate increased mesophyll resistance due to a localised reduction in water content (Grace and Thompson 1973). This might influence our results, but it is difficult to see how it could explain an increase in photochemistry at low wind speeds measured in our investigation and previous ones (Wadsworth 1959, Tranquillini 1969).

Our hypothesis is that the photosynthetic performance index is responsive to changes in the heat balance of the leaf. Generally, nocturnal stomatal conductance is considered to be close to zero and the heat balance of the leaf is the consequence of conductance and convection through the boundary layer. When wind speed is zero, the relative PI_{ABS} ($PI_{ABSrel} = PI_{ABSint}/PI_{ABSext}$) between inside and outside the OTC tends towards one. Increased wind speeds would reduce the thickness of the boundary layer bringing the leaves closer to the ambient air temperature, which is exemplified by the needles of *A. alba* which have higher boundary layer conductances and are more closely coupled to the ambient temperature (Grace 1981). However, stomata can be open in the absence of light (Tobiessen 1982, Matyssek *et al.* 1995), that usually occurs under warm and humid conditions (Schulze and Hall 1982) as were present in our experiment. If stomatal resistance was to decrease and transpiration increase, the consequence would cause a further substantial alteration of the heat balance of the leaves, due to evaporative cooling. The influence of evaporative cooling, whether from transpiration or leaf surface wetness, on PI_{ABS} would depend upon the optimum temperature for primary photosynthesis.

The equation proposed takes into account wind speed and temperature of PI_{ABS} values collected in OTCs and enables the accurate prediction of PI_{ABS} measurements recorded outside the OTCs within the limits of wind speed of this experiment (wind speed >0 and <7 m s^{-1}). The equation is appropriate for the species tested, they all conform to the same function even though the response to wind is highly specific for each species. The conversion equation transforms interior PI_{ABS} values negatively if wind has a positive effect on the PI_{ABS} and positively if it has a negative influence. The equation includes a differential sensitivity to wind and temperature between species, demonstrated by the relative insensitivity of *A. alba* to wind and of *F. excelsior* to temperature. These results emphasise a lack of understanding of the causative relation between wind and photosynthesis. The statistical analysis distinguished the significance of both adaptation and acclimatisation in their contribution to the photosynthetic response to a particular climate and environment.

Exposure to wind may help to explain the absence of visual damage in the field compared to fumigation experiments in OTCs. Increased exposure to wind may assist leaves in reducing the damage incurred by fumigating plants with pollutants in OTCs. Wind induced reduction of stomatal conductance (Tranquillini 1969) would restrict the influx of pollutants and the development of damage. Wind exposure provides convincing evidence for the large growth reductions recorded between plants in the field and those in OTCs. From our experiment, for example, the mean mass of the *F. sylvatica* seedlings inside the OTCs was 1.57 g compared to 1.34 g outside the OTCs, a decrease of 26 % caused by the removal of the OTC. This experiment highlights one of the possible pitfalls in interpreting values from fumigation experiments, that the response to the OTC environment is highly dependent upon the species which will have repercussions in susceptibility to damage by pollutants.

Caution is needed in the interpretation of the results. Firstly, they are valid only within the limits of linear behaviour measured, *i.e.*, wind speeds > 0 < 7 m s^{-1}. Secondly, the temperature range measured, 8 to 18 °C, varied over the experimental period of six months, giving the plants time to acclimatise to the gradual changes in mean temperature. If measurements were to be made at temperatures that varied from 8 to 18 °C, from one day to the next, it is unlikely that a reasonable result would be produced from our model. Thirdly, the relationship of the two expressions $k_T \Delta T$ and $k_W \Delta W$ is additive and independent, therefore, any conclusion concerning the ecological significance of the specific sensitivity coefficients, k_W or k_T, may or may not be related to the other. Finally, the results do not suggest that the mechanistic cause for the sensitivities of one species are identical for another. The results demonstrate that phenomenologically they conform to a single relationship with wind and temperature that need not necessarily be due to a similarity in physiology. Observation of plants growing naturally, clearly demonstrates that they are sensitive to wind and temperature to different degrees. These results lead to the quantification of these sensitivities and to the relationship plants have with their climate, in terms of a physiologically optimal state.

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Appendix

PI_{ABS} has been defined as the ratio of two recently described Structure-Function-Indices, SFI_P and SFI_N. The first, SFI_P (Tsimilli-Michael *et al.* 1998) responds to structural and functional PS2 events leading to electron transport within photosynthesis:

$$SFI_P = \left(\frac{Chl_{RC}}{Chl_{tot}}\right) \varphi_{PO} \; \Psi_0 \tag{1}$$

The second, SFI_N (Strasser *et al.* 1999), refers to the energy that is dissipated as heat or not conserved in the photosynthetic electron transport. It has been defined as:

$$SFI_N = \left(1 - \frac{Chl_{RC}}{Chl_{tot}}\right) (1 - \varphi_{PO}) \; (1 - \Psi_0) \tag{2}$$

The ratio of the two indices has been defined as the performance index (Clark *et al.* 1999, Srivastava *et al.* 1999, Tsimilli-Michael *et al.* 2000)

$$PI_{ABS} = \frac{SFI_P}{SFI_N} = \frac{Chl_{RC}/Chl_{tot}}{1 - Chl_{RC}/Chl_{tot}} \; \frac{\varphi_{PO}}{1 - \varphi_{PO}} \; \frac{\Psi_0}{1 - \Psi_0} \tag{3}$$

where Chl_{tot} is the total quantity of chlorophyll *a*, and $Chl_{tot} = Chl_{ant} + Chl_{RC}$. The ratio Chl_{RC}/Chl_{ant} can be replaced by the ratio RC/ABS, where RC is the number of active PS2 reaction centres, and ABS is the quantity of photons absorbed by the antenna:

$$PI_{ABS} = \frac{RC}{ABS} \; \frac{\varphi_{PO}}{1 - \varphi_{PO}} \; \frac{\Psi_0}{1 - \Psi_0} \tag{4}$$

Consequently, PI_{ABS} defined here refers to photochemical events relative to the photons absorbed and is specified as PI_{ABS}. The expressions RC/ABS, φ_{PO}, and ψ_0 can be calculated according to the JIP-test using the experimentally collected parameters (Strasser and Strasser 1995, Strasser *et al.* 1995). The experimental values for φ_{PO} and ψ_0 are probabilities between zero and unity, whereas the expressions RC/ABS can only be expressed here as a relative value.

The maximum quantum yield of primary photochemistry

$$\varphi_{PO} = \frac{TR_0}{ABS} = F_V / F_M \qquad \text{therefore} \qquad \frac{\varphi_{PO}}{1 - \varphi_{PO}} = \frac{F_V / F_M}{1 - F_V / F_M} = \frac{F_V}{F_0} \tag{5}$$

where TR_0 stands for the flux of exciton trapping at the onset of irradiation.

A relative value for the density of reaction centres per Chl can be calculated from the experimental values

$$\frac{RC}{ABS} = \frac{TR_0}{ABS} \; \frac{RC}{TR_0} = \varphi_{PO} \left(\frac{RC}{TR_0}\right) = \frac{F_V}{F_M} \; \frac{M_0}{V_J} \tag{6}$$

The specific trapping flux TR_0/RC can be measured as M_0/V_J, where V_J is the relative variable fluorescence at 2 ms of the fluorescence rise and F_0 is the Chl *a* fluorescence intensity at 50 μs.

$$V_J = \frac{(F_{2ms} - F_0)}{(F_M - F_0)} \tag{7}$$

and M_0 is the slope at the origin of the relative variable fluorescence

$$M_0 = \frac{(F_{300\mu s} - F_0)}{(F_M - F_0)} \tag{8}$$

The probability ψ_0 that an electron is transported (ET) beyond Q_A^- per exciton trapped can be written as:

$$\Psi_0 = \frac{ET_0}{TR_0} = 1 - V_J \qquad \text{therefore} \qquad \frac{\Psi_0}{1 - \Psi} = \frac{1 - V_J}{V_J} \tag{9}$$

The index 0 refers to the state at the onset of irradiation. Therefore the performance index is defined as:

$$PI_{ABS} = \frac{RC}{ABS}\ \frac{\varphi_{P0}}{1-\varphi_{P0}}\ \frac{\Psi_0}{1-\Psi_0} \qquad (1)$$

$$PI_{ABS} = \frac{RC}{ABS}\ \frac{TR_0}{ABS-TR_0}\ \frac{ET_0}{TR_0-ET_0} \qquad (2)$$

$$PI_{ABS} = \frac{V_J}{M_0}\ \frac{F_V}{F_M}\ \frac{F_V}{F_0}\ \frac{1-V_J}{V_J} \qquad (3)$$

$$PI_{ABS} = \frac{ab}{c}\ \frac{a}{1-a}\ \frac{b}{1-b} \qquad (4)$$

(*1*) in biophysical terms, as in Eqs. (3) and (4);
(*2*) in terms of chlorophylls and energy fluxes;
(*3*) in experimentally measured fluorescence intensities;
(*4*) in an algebraic form as indicated in the Materials and methods section, where a = F_V/F_M, b = V_J = $(F_{2ms} - F_0)/(F_M - F_0)$, and c = V_{300} = $(F_{300ms} - F_0)/(F_M - F_0)$.

The performance index, PI_{ABS}, described and used here is based on an equal absorption basis (or per excited Chl). In many cases one wishes to express the changes of the performance index on a leaf area basis. For this reason, the performance index, PI_{CS} (not used here), is based on a leaf cross section basis (or leaf area), for details see Srivastava *et al.* (1999).