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Interactions and competition processes among tree species in young experimental mixed forests, assessed with chlorophyll fluorescence and leaf morphology

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ABSTRACT

Chlorophyll *a* fluorescence (ChlF) and leaf morphology were assessed in two sites in Europe (Kaltenborn, Germany, and Satakunta, Finland) within a forest diversity experiment. Trees at Satakunta, planted in 1999, form a stratified canopy, while in Kaltenborn the trees are 7 years old, with no apparent canopy connection among broadleaf species. The following ChlF parameters from measured OJIP transient curves were examined: F_V/F_M (a proxy for maximum quantum yield); Ψ_{Eo} (a proxy for efficiency in transferring an electron from reduced QA to the electron transport chain); *I-P* phase (a proxy for efficiency of reducing final acceptors beyond PSI); and PI_{tot} (total performance index for potential energy conservation from photons absorbed by PSII to reduction of PSI end acceptors). At Satakunta F_V/F_M and Ψ_{Eo} in *Betula pendula* were higher in monocultures and lower in mixed plots, perhaps due to increasing light availability in mixed plots, which can induce photoinhibition. The opposite trend was observed in *Picea abies*, which was shaded in mixed plots. At Kaltenborn F_V/F_M decreased in *Fagus sylvatica* and *P. abies* in mixed plots due to competition both above- and belowground. At Satakunta LMA increased in *B. pendula* leaves with increasing species richness. Leaf area of ten leaves was reduced in *F. sylvatica* in mixed plots at Kaltenborn. By up-scaling the overall fluorescence response to plot level (PI_{tot_plot}), a significant positive correlation with tree diversity was found at Kaltenborn, but not at Satakunta. This could suggest that competition/facilitation processes in mixed stands play a significant role in the early stages of forest establishment, but then tend to be compensated in more mature stands.

INTRODUCTION

Biodiversity regulates several aspects of ecosystem functioning and the delivery of ecosystem services (*e.g.* Balvanera *et al.* 2006; Cardinale *et al.* 2011). Additionally, the ecological stability of forest ecosystems has been connected to tree diversity (Bengtsson *et al.* 2000; Scherer-Lorenzen *et al.* 2005a; Thompson *et al.* 2009). Many forest ecosystem services, such as timber production and carbon sequestration, are directly related to tree growth and photosynthesis rates. A recent review (Zhang *et al.* 2012) emphasised the role of biodiversity in enhancing forest growth and the biological mechanisms and processes leading to an increased biomass production in mixed stands. This is mainly related to more efficient exploitation of ecological resources due to niche differentiation and complementary resource use among coexisting species (Tilman 1999; Loreau *et al.* 2001), *i.e.* through species interactions. Such complementarity can occur aboveground within the canopy, or in the soil. For example, different timing of leaf abscission of the various species and increased decomposition rates of litter in mixed stands allow more homogeneous release of nutrients throughout the year and enhance the biological activity of the soil (Richards *et al.* 2010). Moreover, the presence of species with symbiotic nitrogen fixation activity increases soil fertility (Forrester *et al.* 2012; Nouvellon *et al.* 2012), representing a classical example of facilitation. Overall, competition or facilitation may be established between different tree species, consequently, the performance and growth of trees may be enhanced or depressed in a species-specific manner (Reiter *et al.* 2005; Lei *et al.* 2012a,b).

Quantification of the role of tree species diversity in producing ecosystem services in naturally grown forests is problematic because of large variability in the environmental factors (Vilà *et al.* 2005). Hence, a set of experimental forests with different levels of tree diversity has been established around the world within the framework of several research programmes (Scherer-Lorenzen *et al.* 2005b, 2007). In this context, experimental forests were recently planted in Europe at Kaltenborn (Germany) and Satakunta (Finland).

During the growth of a forest stand, trees establish relationships with their neighbours, both at root and at canopy level, depending on different growth rates, space occupation

strategies and sun/shade tolerance (Kozovits *et al.* 2005; Kohyama & Takada 2012; Lei *et al.* 2012a,b). As far as canopy processes are concerned, different height and architecture of tree species result in the formation of microenvironments with a variety of light conditions, thus allowing the appearance of shade-tolerant species (Ishii & Asano 2010). A mixed forest creates varying illumination conditions which induce different photosynthetic responses in plants at both stand level and within the crown of individual trees (Ellsworth & Reich 1993; Niinemets *et al.* 2004; Niinemets 2007; Pearcy 2007; Valladares & Niinemets 2007; Way & Pearcy 2012; Mänd *et al.* 2013).

Plant responses to light can be efficiently measured using chlorophyll *a* fluorescence (ChlF) techniques (Adams & Demmig-Adams 2004; Bruce & Vasil'ev 2004). The informative potential of ChlF analysis (Papageorgiou & Govindjee 2004) has been used for forest monitoring surveys, by applying remote sensing techniques (Rossini *et al.* 2006; Meroni *et al.* 2009), in applied forestry research (see Ball *et al.* 1994; de Carvalho Gonçalves & dos Santos 2005; Bussotti *et al.* 2010 and citations therein) and, more generally, in forest ecology studies (see Stylinski *et al.* 2002; Einhorn *et al.* 2004). Nevertheless, the application of ChlF in extensive terrestrial field surveys on tall trees remains problematic (Mohammed *et al.* 1995, 2003; Sampson *et al.* 2000).

The survey described here represents the first experience in which ChlF techniques were used in a large-scale terrestrial ecological assessment of forests in relation to biodiversity issues. The specific aim of the present paper was to investigate the dynamics of competition and facilitation between tree species in the experimental mixed forests at Kaltenborn and Satakunta by examining their ChlF properties and leaf morphology. The specific hypothesis to be tested was that the interactions between the different tree species and their physiological requirements during forest stand development and stratification – as well as the nature of competition for space and light – are reflected in the ChlF properties. More specifically, the heterogeneity of the canopy layer in mixed forests induces species-specific strategies for the use of light, and photoinhibition conditions, according to the relative growth and crown interaction between the neighbouring tree species. In the younger plantation, where interaction between crowns is lacking, the competition for space, both at aboveground and belowground levels, may be of major importance.

MATERIAL AND METHODS

Experimental sites

The study was carried out in two experimental plantations, both included in previous projects.

Kaltenborn (Thuringia, Germany) is a part of the BIOTREE experiment (Scherer-Lorenzen *et al.* 2005b, 2007) and Satakunta (Finland) belongs to the TreeDivNet platform (Scherer-Lorenzen *et al.* 2005a,b). For details of the experimental sites see the Supporting information.

At Kaltenborn the tree species studied were European beech (*Fagus sylvatica* L., FS), sessile oak (*Quercus petraea* Liebl., QP), Norway spruce (*Picea abies* (L.) Karst., PA) and Douglas fir (*Pseudotsuga menziesii* Franco, PM). At Satakunta we analysed chlorophyll fluorescence of silver birch (*Betula pendula* L., BP), European black alder (*Alnus glutinosa* (L.) Gaert., AG), Norway spruce (*Picea abies* (L.) Karst., PA), Scots pine (*Pinus sylvestris* L., PS) and Siberian larch (*Larix sibirica* Ledeb., LS). In both of the experimental plantations, the tree species were combined in different tree species mixtures (Table 1).

Sampling

Sampling at Kaltenborn was done on 23–25 June 2011. Eight trees per species per plot were selected, taking into account the neighbouring tree species. At Satakunta, sampling was done on 11–14 July 2011. Five trees per species per plot were randomly chosen. ChlF measurements were replicated on five different leaves per tree.

In evergreen conifers (*P. menziesii*, *P. abies* and *P. sylvestris*) the ChlF measurements were conducted on the youngest mature needles, *i.e.* the previous year's needles at Kaltenborn (c+1, sprouted in 2010, because the 2011 needles were not fully developed at the time of the sampling), and current year's needles at Satakunta (c, sprouted in 2011). A preliminary survey showed that there was a significant correlation in ChlF parameters between c and c+1 needles of the species sampled at Satakunta (Table S1). In order to avoid a possible bias due to heterogeneity of light conditions and photosynthesis within the crown (see Niinemets *et al.* 2004; Niinemets 2007), measurements were done on leaves from outer, south-exposed branches, in the upper third of the crown (sun leaves).

In field conditions, the values of many fluorescence parameters vary according to the hour of day as an effect of sunlight exposure (Desotgiu *et al.* 2012). Strong light exposure can trigger processes of photoinhibition, which reduce the capacity to convert solar energy to electron transport (Takahashi & Murata 2008). The usual time (20–30 min) of dark adaptation with leaf clips, prior to ChlF measurements, removes the dynamic, but not the chronic, components of photoinhibition of leaves (Quich & Stitt 1989; Werner *et al.* 2002). To obtain more complete removal of photoinhibition, leaves can either be measured at predawn or dark-adapted for a longer time (minimum 4–5 h). Photoinhibition was removed at Kaltenborn by performing nighttime measurements directly on the crown, because plants were small enough. At Satakunta, the twig

Table 1. Experimental design of Satakunta and Kaltenborn plantations. Numbers of total and sampled plots and number of sampled trees.

	total number of plots				no.
Satakunta	mono	2-sp.	3-sp.	5-sp.	trees
Betula pendula	1	3	4	1	45
Alnus glutinosa	1	2	3	1	35
Picea abies	1	4	3	1	44
Pinus sylvestris	1	3	4	1	43
Larix sibirica	1	2	4	1	40
no. sampled plots	5	7	6	1	

Kaltenborn	mono	2-sp.	3-sp.	4-sp.	
Fagus sylvatica	1	3	3	1	63
Quercus petraea	1	3	3	1	57
Picea abies	1	3	3	1	64
Pseudotsuga menziesii	1	3	3	1	60
no. sampled plots	4	6	4	1	

sampling was performed in the morning (09:00–13:00 h) with extension loppers. Branchlets were placed in plastic bags to limit loss of water and then stored in a dark bag at ambient temperature. Measurements were done in the late afternoon, in a darkened room at the Satakunta Environmental Research Centre (Reposaari). Before the fieldwork, a preliminary survey was carried out to test the effectiveness of the methods applied.

Chlorophyll *a* fluorescence transient analysis and parameters

Direct ChlF measurements were carried out on the plants with a HandyPEA portable fluorimeter at Satakunta, and with a PocketPEA portable fluorimeter at Kaltenborn (both instruments from Hansatech, Pentney, Norfolk, UK). The fluorescence rise from the initial minimum fluorescence F_0 to the maximum fluorescence value F_M in dark-adapted samples, induced by a saturating light pulse (intensity >3000 μmol photons·m^{-2}·s^{-1}, excitation light of 650 nm), are called 'fluorescence transients' (FT, direct or prompt fluorescence; Strasser *et al.* 2000, 2004, 2010; see also Stirbet & Govindjee 2011) and represent the fast phase of ChlF induction. Plotted on a logarithmic time scale, FT shows polyphasic behaviour. The different time steps of this polyphasic transient are labelled as: O (20–50 μs), J (2 ms), I (30 ms) and P (peak). The last indicates the highest fluorescence intensity (F_M), when saturating light is used, and is generally obtained at around 0.8 s. The parameters considered in this study are:

1 $F_V/F_M = [F_M - F_0]/F_M = \varphi_{Po} = TR_0/ABS$ = maximum quantum yield of PSII primary photochemistry measured in samples in dark-adapted state. F_V/F_M expresses the probability that an absorbed photon will be trapped by the PSII reaction centre.
2 $\Psi_{Eo} = ET_0/TR_0 = 1 - V_J = 1 - (F_{2\ ms} - F_0)/(F_M - F_0)$. Ψ_{Eo} expresses the probability that the energy of a trapped excitation is used for electron transport beyond QA. V_J represents the relative variable fluorescence at 2 ms (transients normalised between F_0 and F_M);
3 $\Delta V_{I\text{-}P} = 1 - V_I = (F_M - F_{30\ ms})/(F_M - F_0)$ (*I-P* phase; Oukarroum *et al.* 2009). $\Delta V_{I\text{-}P}$ represents the relative contribution of the *I-P* phase to the fluorescence transient OJIP; it is regarded as a measure of the efficiency of electron flux through PSI to reduce the final acceptors of the electron transport chain, *i.e.* ferredoxin and NADP. V_I indicates the relative variable fluorescence at 30 ms (transients normalised between F_0 and F_M);
4 PI_{tot} (Performance Index total). PI_{tot} is the potential for energy conservation from photons absorbed by PSII to the reduction flux (RE) of PSI end acceptors. It is a multi-parametric expression that combines four parameters related to photosynthetic activity: (i) the density of reaction centres; (ii) the quantum yield of primary photochemistry; (iii) the ability to feed electrons into the electron chain between PSII and PSI; (iv) the efficiency with which an electron can move from the reduced intersystem electron acceptors to the PSI end electron acceptors (Strasser *et al.* 2004, 2010).

$PI_{tot} = (RC/ABS)\ [\varphi_{Po}/(1 - \varphi_{Po})]\ [\Psi_{Eo}/(1 - \Psi_{Eo})]\ [\delta_{Ro}/(1 - \delta_{Ro})]$
where $RC/ABS = \varphi_{Po}\ (V_J/M_0)$

where $M_0 = [4\ (F_{300\ \mu s} - F_0)/(F_M - F_0)]$. M_0 represents the initial slope of the double normalised fluorescence induction curve, and is a proxy of the net rate of PSII closure;

$\delta_{Ro} = (1 - V_I)/(1 - V_J) = (F_M - F_I)/(F_M - F_J)$. δ_{Ro} is the probability that an electron is transported from reduced PQ to the electron acceptor side of PSI.

Leaf morphology

From each sampled broadleaf tree (*B. pendula* and *A. glutinosa* at Satakunta; *F. sylvatica* and *Q. petraea* at Kaltenborn), ten leaves from the same branch were collected and used for fluorescence measurements. Total leaf area (LA) was measured with a Li-Cor LI-3100 Area Meter (Li-Cor, Lincoln, NE, USA), and leaf dry weight (DW) was obtained after drying in an oven at 70 °C (until constant weight). Leaf mass per area (LMA) was calculated as LMA = DW·LA^{-1} (mg·cm^{-2}).

Data analysis

All data were tested for normal distribution using the Kolmogorov–Smirnov test, and the homogeneity of variance was tested with the Levene test. The effects of tree species richness on the ChlF and leaf morphology parameters were analysed using general linear models (GLM), with 'tree species richness' as a fixed factor and 'tree' as a random factor. Each species was analysed separately. The *post-hoc* Tukey test was used to test pair-wise differences between species richness levels for a given tree species. If it was not possible to use the GLM (in the case of significant Kolmogorov–Smirnov and Levene tests, also after data transformation), we used the non-parametric Kruskal–Wallis test to evaluate the difference between species richness levels. The contrasts were performed between means of the rank values. Five-species plots (Satakunta) and Four-species plots (Kaltenborn) were excluded from GLM analysis (in Tables 2–4) because these mixture levels were represented only by one plot. Pearson's correlation coefficient was calculated to analyse relationships between the photosynthetic performance of current and previous year needles in coniferous species at Satakunta. Linear regression was used to test the relationships between ChlF parameters and leaf morphology traits, with tree species richness expressed as the Shannon index, calculated on the basal area for each species per plot (Staddon *et al.* 1997; Spellerberg & Fedor 2003). The differences in fluorescence parameters between the monocultures of each species were analysed by one-way ANOVA for Kaltenborn and non-parametric statistics (Kruskal–Wallis test) for Satakunta. In order to define an indicator of PI_{tot} at plot level, we calculated (according to Bonal *et al.* 2000) PI_{tot_plot} as:

$$PI_{tot\_plot} = \frac{\sum \left(PI_{tot\_spi} \times BA_i\right)}{\sum BA_i}$$

where PI_{tot_spi} is the PI_{tot} of each species included in the plot, and BA_i is the basal area per species. All the statistical analyses were performed with the software STATISTICA 7.0 (Statsoft, Tulsa, OK, USA).

RESULTS

The forest stands at the two experimental sites had very different structures in relation to their age, competition among tree species, and dynamic processes of growth and crown

Table 2. Satakunta. Fluorescence parameters per each species in the different tree species richness level [mean ± SE; CV = (SD/mean)*100]. Number of trees per each species and site is indicated in Table 1. Five-species plot was excluded from this analysis. Uppercase letters indicate significant differences between different species at $P < 0.05$ (only in monocultures, in the column). Lowercase letters indicate significant differences at $P < 0.05$ (within the same species) between different levels of tree species richness (in the column). Tukey test was applied. The parameters F_v/F_M, Ψ_{Eo}, $\Delta V_{I\text{-}P}$ are expressed in a-dimensional ratios. PI_{tot} is in arbitary units.

		Fv/FM			Ψ_{Eo}			$\Delta V_{I\text{-}P}$			PI_{tot}		
species	mixture	mean	SE	CV	mean	SE	CV	mean	SE	CV	mean	SE	CV
Betula pendula	monoculture	0.836	±0.001 ^{a,A}	0.008	0.627	±0.005 ^{a,AB}	0.029	0.165	±0.015 ^{b,B}	0.177	17.808	±2.66 $^{a,\ AB}$	0.321
	2 sp.	0.815	±0.004 ^{b}	0.013	0.615	±0.011 ^{a}	0.041	0.255	±0.017 ^{a}	0.137	29.346	±3.092 ^{a}	0.261
	3 sp.	0.809	±0.003 ^{b}	0.016	0.558	±0.010 ^{b}	0.063	0.232	±0.007 ^{a}	0.142	22.365	±1.786 ^{a}	0.320
Alnus glutinosa	monoculture	0.792	±0.006 ^{a,B}	0.017	0.554	±0.021 ^{a,AB}	0.052	0.243	±0.029 ^{a,AB}	0.113	21.795	±6.451 ^{a,AB}	0.319
	2 sp.	0.781	±0.005 ^{a}	0.015	0.558	±0.012 ^{a}	0.034	0.276	±0.009 ^{a}	0.158	24.505	±2.968 ^{a}	0.379
	3 sp.	0.794	±0.004 ^{a}	0.016	0.583	±0.016 ^{a}	0.056	0.262	±0.024 ^{a}	0.130	25.368	±5.125 ^{a}	0.325
Picea abies	monocullture	0.786	±0.009 ^{b,B}	0.024	0.557	±0.017 ^{b,AB}	0.055	0.233	±0.018 ^{a,AB}	0.090	18.801	±3.297 ^{a,AB}	0.308
	2 sp.	0.817	±0.003 ^{a}	0.012	0.630	±0.007 ^{a}	0.045	0.225	±0.009 ^{a}	0.125	26.874	±2.507 ^{a}	0.335
	3 sp.	0.822	±0.002 ^{a}	0.012	0.624	±0.011 ^{a}	0.047	0.213	±0.012 ^{a}	0.134	26.267	±3.272 ^{a}	0.392
Larix sibirica	monoculture	0.797	±0.003 ^{a,AB}	0.037	0.548	±0.009 ^{a,B}	0.106	0.201	±0.007 ^{a,AB}	0.155	13.302	±1.171 ^{a,B}	0.336
	2 sp.	0.798	±0.007 ^{a}	0.020	0.543	±0.027 ^{a}	0.085	0.200	±0.006 ^{a}	0.143	14.836	±1.598 ^{a}	0.348
	3 sp.	0.798	±0.005 ^{a}	0.028	0.559	±0.018 ^{a}	0.106	0.196	±0.008 ^{a}	0.170	15.657	±1.529 ^{a}	0.495
Pinus sylvestris	monoculture	0.830	±0.004 ^{a,AB}	0.012	0.632	±0.008 ^{c,A}	0.046	0.255	±0.005 ^{a,A}	0.102	33.668	±3.003 ^{a,A}	0.428
	2 sp.	0.835	±0.001 ^{a}	0.008	0.687	±0.005 ^{a}	0.031	0.288	±0.007 ^{a}	0.102	44.481	±3.307 ^{a}	0.287
	3 sp.	0.834	±0.001 ^{a}	0.009	0.665	±0.005 ^{b}	0.040	0.266	±0.006 ^{a}	0.078	38.918	±2.717 ^{a}	0.273

F_v/F_M = maximum quantum yield of PSII primary photochemistry, with $Fv = F_M - F_0$, where F_0 is initial minimum fluorescence and F_M maximum fluorescence; Ψ_{Eo} = efficiency of an electron in moving from reduced QA, the secondary PSII electron acceptor, into the electron transport chain; $\Delta V_{I\text{-}P}$ = the efficiency of reducing the final acceptors beyond the PSI; PI_{tot} = total performance index for (potential) energy conservation from photons absorbed by PSII to the reduction flux of PSI end acceptors.

Table 3. Kaltenborn. Fluorescence parameters per each species in the different tree species richness level [mean ± SE; CV = (SD/mean) *100]. Number of trees per each species and site is indicated in Table 1. Four-species plot was excluded from this analysis. Uppercase letters indicate significant differences between different species at $P < 0.05$ (only in monocultures, in the column). Lowercase letters indicate significant differences at $P < 0.05$ (within the same species) between different levels of tree species richness (in the column). Tukey test was applied. Explanation of parameters is given in Table 2.

		Fv/FM			Ψ_{Eo}			$\Delta V_{I\text{-}P}$			PI_{tot}		
species	mixture	mean	SE	CV	mean	SE	CV	mean	SE	CV	mean	SE	CV
Fagus sylvatica	monoculture	0.779	±0.004 ^{a,B}	0.018	0.479	±0.026 ^{a,B}	0.156	0.193	±0.012 ^{a,B}	0.177	31.840	±5.882 ^{a,B}	0.523
	2 sp.	0.758	±0.005 ^{a}	0.038	0.506	±0.015 ^{a}	0.147	0.187	±0.007 ^{a}	0.187	30.373	±4.465 ^{a}	0.705
	3 sp.	0.743	±0.009 ^{a}	0.062	0.487	±0.025 ^{a}	0.253	0.190	±0.008 ^{a}	0.231	32.663	±4.250 ^{a}	0.637
Quercus petraea	monoculture	0.782	±0.007 ^{a,B}	0.028	0.524	±0.035 ^{bc,B}	0.192	0.237	±0.015 ^{a,AB}	0.184	56.284	±11.784 ^{bc,AB}	0.592
	2 sp.	0.799	±0.004 ^{a}	0.029	0.620	±0.013 ^{a}	0.099	0.265	±0.008 ^{a}	0.265	93.801	±6.962 ^{a}	0.348
	3 sp.	0.788	±0.005 ^{a}	0.031	0.550	±0.017 ^{c}	0.138	0.246	±0.009 ^{a}	0.164	63.249	±7.209 ^{c}	0.497
Picea abies	monoculture	0.790	±0.005 ^{a,AB}	0.018	0.559	±0.007 ^{b,AB}	0.038	0.249	±0.005 ^{a,A}	0.059	46.959	±3.100 ^{a,AB}	0.187
	2 sp.	0.805	±0.006 ^{a}	0.038	0.614	±0.012 ^{a}	0.103	0.263	±0.010 ^{a}	0.263	85.574	±9.327 ^{a}	0.819
	3 sp.	0.780	±0.005 b	0.036	0.597	±0.011 ^{ab}	0.093	0.275	±0.007 ^{a}	0.131	74.169	±8.615 ^{a}	0.557
Pseudotsuga menziesii	monoculture	0.809	±0.008 ^{a,A}	0.030	0.632	±0.016 ^{a,A}	0.074	0.245	±0.012 ^{a,A}	0.148	74.787	±13.872 a,A	0.525
	2 sp.	0.796	±0.005 ^{a}	0.033	0.571	±0.014 ^{a}	0.125	0.226	±0.007 ^{a}	0.226	51.666	±6.652 ^{a}	0.631
	3 sp.	0.791	±0.006 ^{a}	0.035	0.613	±0.016 ^{a}	0.123	0.255	±0.010 ^{a}	0.178	73.946	±9.751 ^{a}	0.590

Table 4. GLM analysis for the effect of tree species richness on the fluorescence parameters. The five-species plot (Satakunta) and four-species plot (Kaltenborn) were excluded from this analysis. Levels of significance are indicated for $P < 0.05$, $P < 0.01$ and $P < 0.001$. Values are reported for each specie at the two experimental sites. Explanation of parameters is given in Table 2.

	F_V/F_M	Ψ_{Eo}	$\Delta V_{I\text{-}P}$	PI_{tot}
Satakunta				
Betula pendula	<0.01	<0.001	<0.01	<0.05
Alnus glutinosa	–	–	–	–
Picea abies	<0.01	<0.01	–	–
Pinus sylvestris	–	<0.001	<0.05	–
Larix sibirica	–	–	–	–
Kaltenborn				
Fagus sylvatica	<0.01	–	–	–
Quercus petraea	–	<0.01	–	<0.01
Picea abies	<0.001	<0.05	–	–
Pseudotsuga menziesii	–	<0.01	<0.001	<0.001

stratification. At Kaltenborn, the trees were still young and canopies were not fully closed but, as shown in Lei *et al.* (2012a), there were already competitive belowground interactions among species. At Satakunta, the forest was structured into different canopy layers, according to the growth rate of each species in the mixed plots, and *B. pendula* was – where present – the tallest tree species.

A preliminary analysis of the ChlF parameters considered in this study examined their variability within the crown of an individual tree (five measurements per tree) and between the trees of a given species in an individual plot (five trees per plot at Satakunta; eight trees per plot at Kaltenborn). The results (Table S2) show a very small coefficient of variation [CV = (SD/Mean)100] for F_V/F_M, but a large CV for PI_{tot}, both within and between trees.

The species-specific characteristics of the different tree species – obtained by comparing the monocultures – are shown in Table 2 (Satakunta) and Table 3 (Kaltenborn). At Satakunta (Table 2), *B. pendula* had the highest values of F_V/F_M but overall, *P. sylvestris* was the best performing tree species (higher PI_{tot}, Ψ_{Eo} and $\Delta V_{I\text{-}P}$). At Kaltenborn (Table 3), the best performing tree species was *P. menziesii* (all fluorescence parameters examined were higher in this species).

The effect of tree species richness was tested with a GLM (Table 4) and *post-hoc* comparison (Tables 2 and 3), whereas the role of biodiversity level (expressed by the Shannon index) was evaluated with linear regressions (Table 5). The results show different patterns of each analysed ChlF parameter for each tree species. At Satakunta, the most sensitive parameters were F_V/F_M and the Ψ_{Eo} in *B. pendula* (both negative, decreasing as the Shannon index increased) and *P. abies* (both positive, increasing as the Shannon index increased). The $\Delta V_{I\text{-}P}$ increased in mixed plots of *B. pendula*. F_V/F_M increased also in *P. sylvestris* at Satakunta, but decreased at Kaltenborn in *F. sylvatica*, *P. abies* and *P. menziesii* with increasing Shannon index. Other significant patterns were an increase of PI_{tot} in *P. abies* at Satakunta, and increase of $\Delta V_{I\text{-}P}$ and PI_{tot} in *P. menziesii* at Kaltenborn.

Among the ChlF parameters, PI_{tot} was up-scaled in order to obtain an average value (see Material and Methods) representative of the overall 'plant fitness' of each plot – PI_{tot_plot}. Figure 1 ranks the plots assessed at Satakunta (A) and Kaltenborn (B),

Table 5. Results of linear regression of fluorescence parameters in relation to tree species diversity, calculated with the Shannon index. In bold are values of regression with $P \leq 0.05$. Number of trees per each species and site is indicated in Table 1. Explanation of parameters is given in Table 2.

species	parameter	slope	intercept	r^2	*P*-value
Satakunta					
Betula pendula	F_V/F_M	−0.024	0.828	0.230	**0.009**
	Ψ_{Eo}	−0.094	0.640	0.353	**0.000**
	$\Delta V_{I\text{-}P}$	0.011	0.225	0.006	0.607
	PI_{tot}	−3.510	26.266	0.020	0.357
Alnus glutinosa	F_V/F_M	0.007	0.784	0.028	0.335
	Ψ_{Eo}	0.008	0.556	0.004	0.713
	$\Delta V_{I\text{-}P}$	0.010	0.253	0.004	0.726
	PI_{tot}	5.501	20.106	0.025	0.367
Picea abies	F_V/F_M	0.025	0.798	0.331	**0.000**
	Ψ_{Eo}	0.038	0.591	0.131	**0.015**
	$\Delta V_{I\text{-}P}$	0.002	0.219	0.000	0.894
	PI_{tot}	8.883	19.201	0.107	**0.030**
Pinus sylvestris	F_V/F_M	0.007	0.830	0.103	**0.034**
	Ψ_{Eo}	0.020	0.656	0.082	0.059
	$\Delta V_{I\text{-}P}$	−0.002	0.274	0.001	0.849
	PI_{tot}	4.330	37.585	0.020	0.357
Larix sibirica	F_V/F_M	0.002	0.798	0.001	0.823
	Ψ_{Eo}	−0.033	0.571	0.029	0.294
	$\Delta V_{I\text{-}P}$	−0.002	0.197	0.001	0.849
	PI_{tot}	−0.324	15.008	0.001	0.888
Kaltenborn					
Fagus sylvatica	F_V/F_M	−0.050	0.782	0.212	**0.000**
	Ψ_{Eo}	−0.019	0.503	0.005	0.585
	$\Delta V_{I\text{-}P}$	0.000	0.189	0.000	0.990
	PI_{tot}	−2.216	31.988	0.002	0.750
Quercus petraea	F_V/F_M	−0.003	0.798	0.001	0.778
	Ψ_{Eo}	0.036	0.560	0.019	0.298
	$\Delta V_{I\text{-}P}$	0.020	0.242	0.025	0.244
	PI_{tot}	17.849	67.374	0.027	0.219
Picea abies	F_V/F_M	−0.031	0.809	0.122	**0.005**
	Ψ_{Eo}	0.027	0.583	0.030	0.174
	$\Delta V_{I\text{-}P}$	0.018	0.254	0.025	0.215
	PI_{tot}	7.493	68.098	0.005	0.602
Pseudotsuga menziesii	F_V/F_M	−0.018	0.807	0.065	**0.050**
	Ψ_{Eo}	0.026	0.588	0.018	0.308
	$\Delta V_{I\text{-}P}$	0.047	0.218	0.125	**0.006**
	PI_{tot}	38.91	−47.34	0.085	**0.024**

whereas Fig. 2 expresses the linear regression between the Shannon index and PI_{tot_plot} in the experimental forests of Satakunta (A) and Kaltenborn (B). While at Satakunta no relationship was found between the investigated variables, at Kaltenborn a positive correlation was found (Table S1, Pearson's coefficient r = 0.597; $P = 0.001$).

At Satakunta, leaf mass per area (LMA) increased with increasing tree species richness in *B. pendula* (Table 6), but not in *A. glutinosa*. No significant trend for LMA was detected on *Q. petraea* and *F. sylvatica* at Kaltenborn (Table 6), but in *F. sylvatica* the leaf area (LA) decreased with increased tree species richness.

DISCUSSION AND CONCLUSIONS

The survey presented in this paper took into account different tree species co-occurring in experimental plots with different levels of tree species richness. A first result was to highlight specific ChlF properties of the different tree species examined. These properties are not directly connected to growth, but may reflect the strategies to cope with stress and carbon allocation (Marshall *et al.* 2001). In general, conifers performed better than broadleaf species, with higher levels of PI_{tot}. The parameters that revealed the most evident responses connected to species diversity were F_V/F_M and the Ψ_{Eo}. F_V/F_M expresses the maximum quantum yield of PSII primary photochemistry. It is well known that this parameter is barely responsive to the action of several stress factors, such as drought stress (Cornic & Fresnau 2002), but is very sensitive to the light environment, and especially to excess light (Adams & Demmig-Adams 2004). Leaves grown in high light conditions (sun leaves) are efficient in dissipating energy as heat (Ballottari *et al.* 2007). This phenomenon is partly due to photoinhibition, which involves the deactivation and turnover of the protein D1 in PSII (Ohira *et al.* 2005). The concomitant decrease in the capacity to trap solar energy and to feed the electron transport chain is considered a down-regulation mechanism (Adir *et al.* 2003; Cui *et al.* 2003; Stroch *et al.* 2008). In fact, it reduces the flow of electrons within the electron transport chain when the reduction potential, originating from high light intensity, is too high for the requirements of the photosynthesis processes and cannot be utilised for metabolism (Lu *et al.* 2001; Ogaya *et al.* 2011).

At Satakunta the pattern of F_V/F_M and Ψ_{Eo} in *B. pendula* (decreasing when the level of tree species richness increases) is consistent with a gradient of diffusion and availability of light. *B. pendula* monocultures form a continuous canopy layer; the upper leaves sampled in this survey may be shaded by lateral branches of the same tree or of neighbouring trees. With increasing tree species richness, the canopy structure is more irregular because of the different growth rates and growth forms of the different tree species. Kaitaniemi & Lintunen (2010) reported that in *B. pendula* the increase in height was accelerated by competition with *L. sibirica* and *P. sylvestris* in mixed experimental forest stands in Finland. In *L. sibirica*, on the other hand, the average height increment was reduced by competition with *B. pendula* in the same study. These differences in growth create a large heterogeneity of light availability at the canopy level. Because of an increasing admixture of smaller trees, the top leaves of *B. pendula* are exposed to increasing average light intensities. Unlike *B. pendula*, at Satakunta the F_V/F_M and Ψ_{Eo} of *P. abies* increased with increasing species richness. This species has a lower growth potential in height than *B. pendula*, *L. sibirica* and *P. sylvestris*. Consequently, in mixed stands *P. abies* was found under the canopies of the tallest tree species, with lower light availability and absence of photoinhibitory conditions. In both tree species, *B. pendula* and *P. abies*, the CV of F_V/F_M increased with decreasing values of F_V/F_M and Ψ_{Eo} (Table 2), confirming the relevance of the heterogeneity of light environments in mixed plots.

It was expected that the heterogeneity of luminous environments would also be reflected in the behaviour of the $\Delta V_{I\text{-}P}$. $\Delta V_{I\text{-}P}$ is considered to be sensitive to the light environment, although in the opposite way to F_V/F_M. Sun leaves have a lower capacity to trap electrons (low F_V/F_M) and a higher capacity to reduce the final acceptors of electrons beyond PSI (Cascio *et al.* 2010; Desotgiu *et al.* 2012). Nevertheless, no relationship was found between $\Delta V_{I\text{-}P}$ and light availability in the mixed plots at Satakunta.

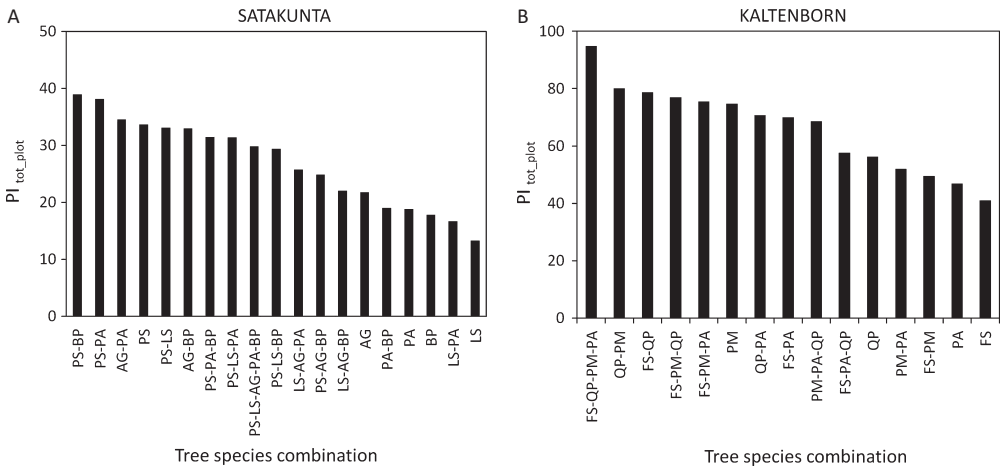

Fig. 1. Rank of the PI_{tot} at plot level (PI_{tot_plot}) in relation to tree species combination in Satakunta (A) and Kaltenborn (B). BP = Betula pendula; AG = Alnus glutinosa; LS = Larix sibirica; PA = Picea abies; PS = Pinus sylvestris; FS = Fagus sylvatica; PM = Pseudotsuga menziesii; QP = Quercus petraea.

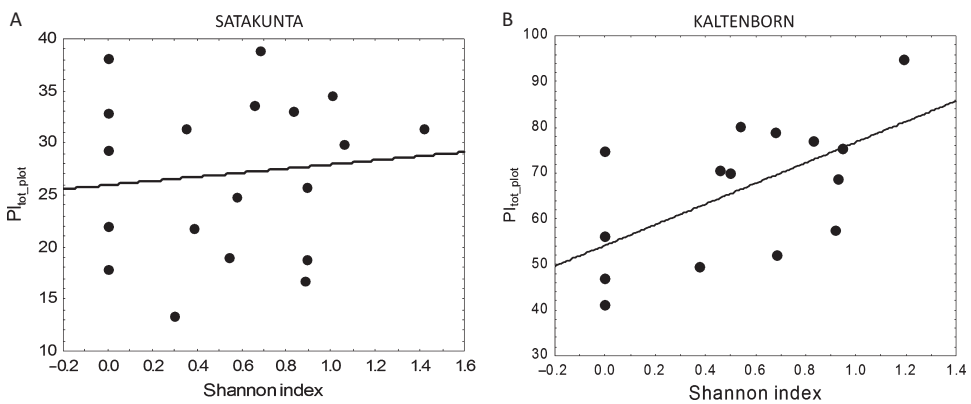

Fig. 2. Correlations between the PI_{tot_plot} and Shannon Index in the two experimental forests (A: Satakunta: r = 0.110; r^2 = 0.012; $P > 0.05$, not significant; B: Kaltenborn: r = 0.597; r^2 = 0.357; $P < 0.05$, significant).

Table 6. Results of linear regression of foliar morphology parameters in relation to tree species diversity, calculated with the Shannon index.

	leaf mass per area			leaf area		
	r	r^2	*P*	r	r^2	*P*
Satakunta						
Betula pendula	0.570	0.324	<0.001	−0.010	0.000	>0.05
Alnus glutinosa	−0.113	0.013	>0.05	0.105	0.011	>0.05
Kaltenborn						
Fagus sylvatica	−0.094	0.008	>0.05	−0.451	0.203	<0.001
Quercus petraea	0.064	0.004	>0.05	−0.176	0.031	>0.05

At Kaltenborn, F_V/F_M values decreased in *F. sylvatica* with increasing tree species richness. This pattern is apparently in contrast to the availability of light in the different mixture conditions. In fact, the monoculture of *F. sylvatica* is made up of small trees, isolated from each other and exposed to full sunlight at midday. This pattern can be compared to the competition processes in the first phases of establishment in a mixed forest stand. Many studies have shown that in its juvenile stage *P. abies* is very competitive in relation to *F. sylvatica*, both aboveground (Kozovits *et al.* 2005; Reiter *et al.* 2005; Gayler *et al.* 2006) and belowground (Bolte & Villanueva 2006). A possible explanation for decreasing F_V/F_M ratios of *F. sylvatica* with increasing species competition could be competition for soil resources, *i.e.* water and/or nutrients, provided that the other three species are more competitive. Nitrogen is known to depress F_V/F_M in *F. sylvatica* (Percival *et al.* 2008), whereas the effect of water shortage is more questionable (Tognetti *et al.* 1995). The competition processes in the mixed plots of Kaltenborn may be very variable, and the specific competitiveness of neighbouring tree species may depend on physical distance. Another point that should be considered is that – in relation to tree size and plot structure – the different species are not only competing for water and/or nutrients with each other, they are also competing with the understorey, primarily in the monocultures. It can be assumed that competition with the herb layer for the smaller trees, like *Q. petraea* and particularly *F. sylvatica*, was much stronger than for *e.g. P. menziesii*, which displaced the understorey vegetation more or less completely.

Leaf morphology supports the importance of the distribution of light at the canopy level at Satakunta. Sunlight is a very powerful factor that is able to determine foliar morphology, and results in an increase of leaf mass per area (LMA) in sun-exposed leaves (Bussotti 2008). In this study, LMA of *B. pendula* reflected a gradient of available light intensity;

indeed *B. pendula* crowns have sun leaves in the highest mixture plots. A very different dynamic was observed at Kaltenborn, where the leaf area of *F. sylvatica* was reduced in highly mixed plots without changes in LMA, suggesting a worsening of the growth conditions in these plots with the admixture of the (faster growing) coniferous species, which is not connected to light availability.

The differences and trends highlighted for F_V/F_M and Ψ_{Eo} with biodiversity were no longer significant at Satakunta with PI_{tot}, thus suggesting compensation between the different photosynthetic processes described by the various parameters. The overall results from the two sites reveal, in general, higher PI_{tot} values at Kaltenborn than at Satakunta. The authors consider that it is not possible to compare the two sites because they were assessed on different months of the year, and using two different instruments. It is possible, however, to compare the trends of fluorescence parameters and behaviour of the different species across the levels of species richness and combination within each plot.

The analysis of the Performance Index total up-scaled to plot level (PI_{tot_plot}) suggests an effect of the species composition (Fig. 1) on the overall photosynthetic efficiency, but the lack of replicates for each kind of mixture does not allow a statistical verification of this aspect. This survey was designed to evaluate the role of tree diversity *per se* rather than the neighbouring tree species effect. A positive response to tree diversity on PI_{tot_plot} was found at Kaltenborn but not at Satakunta (Fig. 1). This behaviour may suggest that the overall role of the competition/facilitation processes in mixed stands is detectable in the early stages of forest establishment, but then tends to be compensated for in more mature stands.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Data S1. Description of experimental sites.

Table S1. Pearson's coefficient of correlation (r); significance level (*P*) and coefficient of determination (r^2) between the fluorescence parameters of current year (c) and previous year (c+1) needles in *P. abies* (A) and *P. sylvestris* (B) at Satakunta.

Table S2. Coefficient of variation [CV = (SD/mean)*100] of selected fluorescence parameters for each tree species at the two experimental sites of Satakunta and Kaltenborn.

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