Exceptional carbon uptake in European forests during the warm spring of 2007: a data–model analysis

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Abstract
Temperate and boreal forests undergo drastic functional changes in the springtime, shifting within a few weeks from net carbon (C) sources to net C sinks. Most of these changes are mediated by temperature. The autumn 2006–winter 2007 record warm period was followed by an exceptionally warm spring in Europe, making spring 2007 a good candidate for advances in the onset of the photosynthetically active period. An analysis of a decade of eddy covariance data from six European forests stands, which encompass a wide range of functional types (broadleaf evergreen, broadleaf deciduous, needleleaf evergreen) and a wide latitudinal band (from 44° to 62° N), revealed exceptional fluxes during spring 2007. Gross primary productivity (GPP) of spring 2007 was the maximum recorded in the decade examined for all sites but a Mediterranean evergreen forest (with a +40 to +130 gC m⁻² anomaly compared with the decadal mean over the January–May period). Total ecosystem respiration (TER) was also promoted during spring 2007, though less anomalous than GPP (with a +17 to +93 gC m⁻² anomaly over 5 months), leading to higher net uptake than the long-term mean at all sites (+12 to +79 gC m⁻² anomaly over 5 months). A correlative analysis relating springtime C fluxes to simple phenological indices suggested spring C uptake and temperatures to be related. The CASTANEA process-based model was used to disentangle the seasonality of climatic drivers (incoming radiation, air and soil temperatures) and biological drivers (canopy dynamics, thermal acclimation of photosynthesis to low temperatures) on spring C fluxes along the latitudinal gradient. A sensitivity analysis of model simulations evidenced the roles of (i) an exceptional early budburst combined with elevated air temperature in deciduous sites, and (ii) an early relief of winter thermal acclimation in coniferous sites for the promotion of 2007 spring assimilation.

Keywords: European forests, functional drivers, net carbon uptake, process-based model, spring

Introduction
Springtime phenological phases are recognized as one of the major determinants of the annual carbon (C) balance of temperate and boreal forest stands (Goulden et al., 1996; Berninger, 1997; Black et al., 2000; Barr et al., 2007), and further modulate the C balance at the continental scale (Keeling et al., 1996; Randerson et al., 1999). From temperate to boreal latitudes, in the springtime (hereafter defined as January–May), forest ecosystems undergo a range of functional changes that drastically affect their interactions with the atmosphere, either in terms of energy or C exchanges (Schmid et al., 2000; Wilson & Baldocchi, 2000; Blanken et al., 2001).

For deciduous species, these functional changes include bud break, leaf expansion (Davi et al., 2008) and
subsequent canopy development which, together with the assembly of the photosynthetic apparatus (Wilson et al., 2000; Grassi et al., 2005) turn deciduous trees from net C providers into net C withdrawers from the atmosphere within a few weeks. Experimental evidence and empirical modelling underline the influence of temperature on the progress of the ontogenic stages involved (see Sarvas, 1972; Chune, 2000; Schaber & Badeck, 2003 for budburst, Davi et al., 2008 for leaf mass per area).

In evergreen stands, leaf longevity dampens the seasonal variability of leaf area, so that structural changes in spring affect less drastically the canopy-atmosphere exchanges. Evergreen species adapted to live at low winter temperatures have evolved mechanisms of stress prevention: (i) frost hardening, which prevents frost damage of living tissues and (ii) downregulation of photosynthetic capacity, which prevents photo-oxidative damages at low temperatures (Öquist & Huner, 2003). These coincident mechanisms are triggered by the occurrence of low temperatures (Leinonen, 1996; Repo et al., 2006), and relaxed given above-freezing temperatures in spring (Mäkelä et al., 2004; Sevanto et al., 2006; Kolari et al., 2007), though potentially reversed during spring frost events (Leinonen, 1996; Bergh et al., 1998).

The co-occurrence of photosynthetic capacity onset in deciduous trees or upregulation in conifers with high radiation levels, favourable temperatures, low evaporative demand and nonlimiting soil water rapidly yields high values of gross primary productivity (GPP) in the spring (Falge et al., 2002). Although autotrophic and heterotrophic respiration processes are promoted during spring warming (Stockfors & Linder, 1998; Epron et al., 2001; Damesin et al., 2002), the seasonality of total ecosystem respiration (TER) is dampened compared with that of GPP in temperate and boreal forests, which leads to a strong dependency of the springtime net ecosystem productivity (NEP) on GPP (Falge et al., 2002).

The autumn 2006–winter 2007 period has been identified as likely the warmest for more than 500 years in Europe, with +1.7 and +2.4 K increases in autumn 2006 and winter 2007, respectively, compared with the 1961–1990 means at the continental scale (Luterbacher et al., 2007). These extreme temperatures were associated with delayed autumn senescence in 2006 (Piao et al., 2008; Delpierre et al., in press) and early occurrence of springtime 2007 phenophases throughout Europe (Table 1).

In accordance with our knowledge of springtime processes affecting C exchanges in forest stands and the observation of early occurrence of spring phenological events, high temperatures observed in spring 2007 were likely to have impacted C exchanges between European forest ecosystems and the atmosphere.

In the first part of this study, we took advantage of the CARBOEUROPE-IP database to conduct a data analysis aimed at illustrating the impact of the warm spring of 2007 on C fluxes across Europe (from southern France to Finland) for three forest functional types. We then used the process-based SVAT/growth model CASTANEA to disentangle for each study site the influences of climatic and biological factors on the determinism of spring GPP, TER and NEP, placing emphasis on the warm spring of 2007.

Methodology

Study sites and flux data

Six sites involved in the CARBOEUROPE-IP were selected for this study. These sites encompass three forest functional types (namely evergreen broadleaf, evergreen coniferous and broadleaf deciduous) along a broad latitudinal gradient (44–62°N). At all sites, meteorological data and net C and water exchange measurements according to the eddy covariance technique are routinely acquired on a half-hourly basis, following the standard methodology recommended by Aubinet et al. (2000). All selected sites except the FRFon forest have been continuously run for 8–11 years. The FRFon site was established more recently (three site-years), but was added to the present dataset given that it was the only one monitoring a sessile Oak forest [Quercus petraea (Matt.) Liebl], a species widely spread across Europe. A brief description of the main characteristics of the six stands and further references are provided in Table 2.

All available continuous data over the January 1997–June 2007 period were quality-controlled, gap-filled and partitioned into GPP and TER, according to CARBOEUROPE database standards (Reichstein et al., 2005; Papale et al., 2006). For the FRFon site, instrumented with an open-path IRGA (LI-7500, Licor, Lincoln, NE), the density correction term was computed according to Burba et al. (2008), in order to take into account the open-path analyser self-heating. A site-specific \( u^* \) threshold value was used to filter out data acquired under stable conditions (Table 2). Parameter fitting for flux partitioning was performed according to the short-term exponential method (Reichstein et al., 2005).

Construction of phenological indices

We assessed the ability of three simple phenological indices to predict the interannual variability of springtime GPP and NEP sums. Springtime was defined as the period extending from January to May, a period that...
### Table 1  Spring 2007 phenological phases anomalies

<table>
<thead>
<tr>
<th>Species/functional type</th>
<th>Observations scale</th>
<th>Geographical range</th>
<th>Phenological stage</th>
<th>Period</th>
<th>Pre-2007 mean (SD)</th>
<th>Spring 2007 anomaly (days)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deciduous forests</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All vegetation types</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>15 forest stands</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>–5</td>
<td></td>
</tr>
<tr>
<td>Quercus petraea</td>
<td>Forest stand</td>
<td>France (49°N 3°E)</td>
<td>Budburst</td>
<td>2000–2007</td>
<td>107 (10)</td>
<td>–6</td>
<td>E. Dufrené, unpublished results</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hyacinthoides nonscripta</td>
<td>Forest stand</td>
<td>France (49°N 2°E)</td>
<td>Flowering</td>
<td>2000–2007</td>
<td>80 (8)</td>
<td>–14</td>
<td>J. Y. Pontailler, unpublished results</td>
</tr>
<tr>
<td>Corylus avellana</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>–38</td>
<td></td>
</tr>
</tbody>
</table>

Phenological series were obtained for different time periods. The pre-2007 mean occurrences of phenological phases are reported when available.

### Table 2  Study sites characteristics

<table>
<thead>
<tr>
<th>Site</th>
<th>Lat.</th>
<th>Lon.</th>
<th>Dominant Species</th>
<th>Functional type</th>
<th>Age</th>
<th>Bwood</th>
<th>LAI</th>
<th>LMA</th>
<th>Nleaf</th>
<th>Thinning</th>
<th>Study period</th>
<th>CASTANEA modelling</th>
<th>u* threshold</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>FRPue</td>
<td>43.73</td>
<td>3.58</td>
<td>Quercus ilex</td>
<td>DBF</td>
<td>60</td>
<td>53</td>
<td>2.9</td>
<td>224</td>
<td>12</td>
<td>June 2005 (15%)</td>
<td>2000–2007</td>
<td>Yes</td>
<td>0.3</td>
<td>Allard et al. (2008)</td>
</tr>
<tr>
<td>FRFon</td>
<td>48.47</td>
<td>2.77</td>
<td>Quercus petraea</td>
<td>DBF</td>
<td>150</td>
<td>115</td>
<td>5.1</td>
<td>117</td>
<td>24</td>
<td>–</td>
<td>2005–2007</td>
<td>No</td>
<td>0.25</td>
<td>this study</td>
</tr>
<tr>
<td>FRHes</td>
<td>48.67</td>
<td>7.08</td>
<td>Fagus sylvatica</td>
<td>DBF</td>
<td>30</td>
<td>35</td>
<td>5.6</td>
<td>101</td>
<td>23.4</td>
<td>1999, 2005 (25%)</td>
<td>1997–2007</td>
<td>Yes</td>
<td>0.25</td>
<td>Granier et al. (2008)</td>
</tr>
<tr>
<td>BEVie</td>
<td>50.3</td>
<td>5.98</td>
<td>Pseudotsuga + Fagus</td>
<td>ENF + DBF</td>
<td>&gt; 80</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1997–2007</td>
<td>No</td>
<td>0.4</td>
<td>Aubinet et al. (2001)</td>
</tr>
<tr>
<td>DETha</td>
<td>50.95</td>
<td>13.57</td>
<td>Picea abies</td>
<td>ENF</td>
<td>103</td>
<td>100</td>
<td>9.8</td>
<td>198</td>
<td>14</td>
<td>2002 (15%)</td>
<td>1997–2007</td>
<td>Yes</td>
<td>0.35</td>
<td>Grunwald &amp; Bernhofer 2007</td>
</tr>
</tbody>
</table>

Geographic, climatic and biological characteristics are reported. Age, estimated stand age since plantation (years); Bwood, aboveground woody biomass at the beginning of the study period (tC ha⁻¹); LAI, maximum leaf area index for the first year of simulation (hemisurface basis); Lat., latitude; LMA, leaf mass per area (gDM m⁻²); Nleaf, leaf nitrogen content (mgN gDM⁻¹); Lon., longitude; thinning, year of occurrence (January–March period unless stated) and percentage of leaf area removed; u* threshold, site-specific friction velocity (u*) threshold (ms⁻¹).

*Caterpillar (Lymantria sp.) attack
enshrined in the range of winter/spring functional changes of interest in this paper.

The first phenological index was the sum of springtime positive temperatures. The second phenological index was the onset of the net carbon uptake period (CUP), defined as the day of NEP zero-crossing during the source/sink transition period. Following Baldocchi et al. (2005), we determined the NEP zero-crossing date by regression of daily NEP on day of year, using a 30-day data subset from the source–sink transition period. The third phenological index was constructed for the sole deciduous sites and consisted of the first day of the photosynthetically active season. This date was determined through a piecewise two-segment linear model fitted to the GPP time series for clear days. The junction point of the piecewise model was considered as the start of the active season in deciduous sites (Fig. 1).

Modelling of the C balance

The process-based SVAT/growth model CASTANEA (Dufreˆne et al., 2005) was used to simulate C and water fluxes and stocks at four of the study sites (FRPue, FRHes, DETha and FIHyy, Table 2). No simulation was performed for the mixed BEVie forest, as CASTANEA is designed for monospecific stands. Simulations are not reported for the FRFOn site, as the short period of measurements and simulations (3 years) did not allow for the application of the method developed to disentangle the influences of climatic and biological drivers on C fluxes (see infra).

For this study, we relied on the original version of the CASTANEA model (Dufreˆne et al., 2005). CASTANEA SVAT and growth modules have thoroughly been validated on a range of monospecific, even-aged forest ecosystems for 1-year periods at temperate latitudes (Davi et al., 2005, 2006; Le Maire et al., 2005).

We implemented to the original version of CASTANEA a photosynthesis thermal acclimation model (Bergh et al., 1998; Hänninen & Hari, 2002), in order to simulate the winter downregulation of photosynthetic capacity occurring in coniferous evergreen sites exposed to low winter temperatures. Photosynthetic acclimation takes the form of the AccP factor, varying in the [AccPmin; AccPmax] interval, and impacts potential carboxylation capacity (Vmaxc), potential electron flow (Jmax) and quantum yield as a multiplicative modifier. In autumn, first frosts cause a rapid decline of AccP from the maximal summer value (AccPmax = 1). AccP remains at its minimal value (AccPmin = 0.15) for most of the winter. In spring, AccP progressively tends towards one (AccPmax = 1) as daily mean temperature increases, though AccP potentially reverses towards AccPmin when frosts occur. The critical degree-day (d.d.) sum for AccP to equal AccPmax was 180 d.d. in Pinus (Hänninen & Hari, 2002) and was set to 150 d.d. to allow for a realistic progress of photosynthesis in Picea. For the evergreen broadleaf species Quercus ilex, winter acclimation of the photosynthetic apparatus has not been modelled, though results from field studies suggest that photoprotective mechanisms may impair assimilation during cold periods for this species (e.g. Oliveira & Peñuelas, 2000). Following several authors (e.g. Suni et al., 2003a; Mäkelä et al., 2008), no influence of soil temperature on spring photosynthesis resumption was accounted for in the model.

The simulation of budburst in deciduous stands is performed in CASTANEA through a spring warming model (Dufreˆne et al., 2005), which provides a prediction accuracy of ca. 5 days (e.g. Schaber & Badeck, 2003). As the completion of our objectives depended on the reliability of the model estimates, we could not afford this degree of error in the predicted budburst date. We instead used the inflexion point method (Fig. 1) as a benchmark for simulating budburst, forcing budburst to occur 4 days before the observed inflexion in diurnal NEP.

For the purpose of the present study, C and water balance modelling was performed from 1 January 1997 to 31 May 2007 for three sites (FIHyy, DETha and FRHes) and from 1 January 2001 to 31 May 2007 for the FRPue site. Simulations over the whole period of...
interest (i.e. not only spring) were necessary to insure continuity in the simulation of the state variables (wood biomasses, soil C pools, soil water balance, etc.). C contents of the heterotrophic pools were initiated to satisfy steady state at the end of the run. Only simulations for the springtime (January–May) period were analysed in the following work.

Model validation

A necessary step before the use of the model as a disentangling tool is the validation of simulated fluxes. Model validation was performed for two time scales. We based the model validation on the goodness of representation of (i) daily sums, which assessed the model’s ability to reproduce the seasonal pattern of the measured flux and its day-to-day variations, and (ii) semi-annual (spring) sums, which assessed the overall representation of integrated processes. In both cases, model accuracy was assessed through comparison of simulated and measured diurnal NEP (NEPd). We therefore based the model validation on the highest quality measured data and avoided consideration of potentially biased eddy covariance measurements acquired under stable nightly conditions (see Falge et al., 2003; Davi et al., 2006 for analogous model validation protocols).

Springtime patterns of C fluxes drivers

We introduce a novel method to illustrate for each study site the pattern of influence of climatic and biological drivers on GPP, TER and NEP. This method aims to express for each flux, on each day of the year, the proportion of interannual flux variance explained by potential climatic or biological drivers.

We identified as potential drivers of springtime C fluxes two climatic drivers (incoming radiation, Rg, and ecosystem temperature, Teo) and two biological drivers (canopy dynamics CDyn, and photosynthetic acclimation factor, AccP). The influences of these factors on modelled processes are summarized in Table 3. Climatic drivers exert instantaneous influences in the model equations. Conversely, the dynamics of biological drivers, which are simulated by CASTANEA through combined temperature sums (Bergh et al., 1998; Dufrêne et al., 2005), reflect the long-term integrated influences of thermal constraints. We do not consider air and soil temperatures as independent climatic drivers, as these variables are intimately correlated. It can be seen from Table 3 that in the model, TER is influenced by both soil and air temperature, and that no influence of soil temperature is accounted for to simulate GPP. Soil temperature is simulated in the model at three depths (−5, −15 and −30 cm) through a simple biophysical model (Paul et al., 2004) forced by air temperature and modulated by canopy and soil characteristics. We could not use measured soil temperature as a forcing variable because the data were only sporadically available at all sites for the period of interest. Comparison of modelled and measured soil temperatures when available where excellent at all sites (with $r^2 > 0.90$, not shown).

For the sake of completeness, we verified that soil water content (typically nonlimiting during springtime)

### Table 3  Summary of the influences of scoped climatic and biological drivers on modelled processes

<table>
<thead>
<tr>
<th>Driver</th>
<th>Symbol</th>
<th>Influence on modelled GPP</th>
<th>Influence on modelled TER</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Climatic drivers</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Incoming radiation</td>
<td>Rg</td>
<td>Modulates electron transport rate</td>
<td>–</td>
</tr>
<tr>
<td>Ecosystem temperature</td>
<td>Teo</td>
<td>Modulates electron transport and carboxylation rates</td>
<td>Modulates aboveground maintenance respiration</td>
</tr>
<tr>
<td></td>
<td>$T_{\text{air}}$</td>
<td></td>
<td>Modulates roots maintenance respiration and heterotrophic respiration</td>
</tr>
<tr>
<td></td>
<td>$T_{\text{soil}}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Biological drivers</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy dynamics</td>
<td>CDyn</td>
<td>Defines the instant amount of photosynthetically active area</td>
<td>Scales with canopy growth and dark respiration</td>
</tr>
<tr>
<td>Photosynthesis acclimation factor</td>
<td>AccP</td>
<td>Reduces potential carboxylation and electron transport rates at freezing temperatures</td>
<td></td>
</tr>
</tbody>
</table>

Only direct effects in the model are reported.

Accp, photosynthesis thermal acclimation factor; CDyn, canopy dynamics; GPP, Gross primary productivity; Rg, global radiation; $T_{\text{air}}$, air temperature; $T_{\text{soil}}$, soil temperature; TER, total ecosystem respiration.
had no impact on the variations of GPP, TER or NEP at any site during the considered January–May period (not shown). We did not consider wood biomass or soil C mass as potential drivers of C fluxes during spring. As state variables, both integrate on a given date the influence of preceding (from the past half-hour to the past 10 years in the model) climatic conditions, biological processes and possibly anthropic disturbances (thinning), so that their influences do not solely reflect the processes at stake during spring.

The deconvolution pattern of climatic and biological drivers influences is based on the reconstruction of the originally simulated flux, obtained under full variability of the four climatic and biological factors (termed \( f_{\text{ref}} \) in Table 4), as a combination of partially forced simulations (termed \( f_1 - f_4 \) in Table 4). Under partially forced simulations \( f_1 - f_4 \), the sole factor of interest was allowed to vary freely (i.e. according to measurements for climatic factors, or following original simulations for biological factors), while all other factors were forced to their mean patterns (taking on day of year \( d \) their mean value for that day of year over all study years). For each GPP, TER and NEP flux, on each day \( d \) of the springtime period (DoY 1–151) we wrote the flux combination as a multiple linear regression (MLR) model, such as

\[
f_{\text{ref}}(d) = \sum_{i=1}^{4} \beta_i(d) \cdot f_i(d) + \epsilon,
\]

where \( f_{\text{ref}} \) represents the normalized (centred-reduced) flux simulated under full drivers variabilities; \( f_i \) the normalized flux obtained under partial forcing (i.e. the sole factor \( i \) is free to vary, Table 4); \( \beta_i \) the standard partial regression coefficient associated with the \( f_i \) flux; and \( \epsilon \) the error term of the MLR model.

The objective of Eqn (1) was to determine for each day \( d \) the influence of the \( i \)th driver on flux variability. We sampled the simulated dependent \( (f_{\text{ref}}) \) and independent \( (f_i) \) variables on day \( d \), plus 3 days before and 3 days after, therefore considering local variability around the day of interest. We extended the sampling to all occurrences of the window of interest (centred on day \( d \) over all simulation years (i.e. considering years as repetitions), therefore considering interannual variability. For each day \( d \), this resulted in a sampling size of 7 points per year multiplied by \( n \) years (\( n = 11 \) for most sites, Table 2) for each variable in the MLR model. The standard partial regression coefficient \( \beta_i(d) \) associated with each \( f_i(d) \) flux therefore indicates the signed proportion of the flux variability under the influence of the \( i \)th factor of interest.

Owing to the potential correlation between predictor variables \( f_i \) in Eqn (1), multiple regression [Eqn (1)] was processed using a selective stepwise approach. The inclusion \( P \)-value for a new predictor variable to enter the MLR was set to \( P<10^{-4} \). Such a strict criterion was used to allow only independent variables as predictors.

The proportion of flux \( \Phi \) (\( \Phi \) = GPP, TER or NEP) interannual variance on day \( d \) explained by the \( i \)th factor \( \epsilon_{\Phi,i}(d) \) was quantified as the ratio of the squared magnitudes of the \( \beta_i(d) \) standard partial regression coefficients, scaled by the squared multiple correlation coefficient \( R^2 \) of the multiple regression, such as

\[
\epsilon_{\Phi,i}(d) = \frac{\sum_{i=1}^{4} \beta_i^2(d)}{\sum_{i=1}^{4} \beta_i^2(d)} \times R^2(d),
\]

so that \( \sum_{i=1}^{4} \epsilon_{\Phi,i}(d) = R^2(d) \).

### Sensitivity of the 2007 springtime GPP and TER sums

We calculated the influence of single climatic and biological drivers on springtime annual sums for GPP and TER fluxes. For the \( \Phi \) flux (GPP or TER), the annual
relative flux anomaly caused by the $i$th driver ($RA_{\Phi,i}$) was computed as the ratio of the modelled springtime $\Phi$ flux sum (DoY 1–151) on year $y$ under full drivers variability to the modelled springtime $\Phi$ flux sum on year $y$ under partially forced simulation. Forced simulations were obtained by setting for each day of year the $i$th driver of interest to its mean value on that day of year for the 1997–2006 period (Table 4), while other factors varied freely. The spring annual relative anomaly (RA) is therefore written as

$$RA_{\Phi,i}(y) = \frac{1}{151} \sum_{d=1}^{151} f_{\Phi,i}(d,y),$$

where $f_{\Phi,i}$ represents the flux simulated under full drivers variabilities and $g_i$ is the flux simulated under forcing of the $i$th driver, while the other drivers vary freely. For instance, $RA_{\Phi,i}(y) = 1.15$ indicates a 15% increase of flux $\Phi$ spring sum on year $y$ due to the deviation of factor $i$ from its mean pattern.

### Results

The first part of this section is dedicated to flux data analysis. We characterise the anomalous 2007 spring (January–May) in terms of temperature and flux anomalies before illustrating the dependence of spring C fluxes on simple phenological indices. The second part of this section is based on the simulation analysis. After model validation, we analyse patterns of climatic and biological drivers for springtime C fluxes across sites and finally quantify the role of the drivers on spring 2007 fluxes.

**Flux data analysis**

**Springtime temperature and fluxes: the 2007 exception.** Springtime temperatures of the year 2007 were higher than the mean pre-2007 values at all sites (from +0.5 to +2.8 K, Table 5), and were highest ranked in the decade for all but the FiHyy site. Three 20-day warm spells (5 K above the decadal mean) were consistently observed across sites (DoY 1–20, 50–70 and 90–110) during spring 2007 (Fig. 2). At the boreal FiHyy site, the first spell (DoY 1–20) was later followed by a second warm period (DoY 60–90).

The 2007 springtime GPP sums were the highest recorded for all but the Mediterranean FRPue site (Table 5), as a consequence of early GPP onset (temperate deciduous FRHes, FRFon and boreal FiHyy sites) or of high GPP values compared with the decadal mean (temperate coniferous BEVie and DETha sites) (Fig. 2). The 2007 TER springtime sums were the highest recorded for three sites (FRFon, FRHes and DETha), and higher than the mean for the other sites (Table 5). Assimilation fluxes were more enhanced than respiratory fluxes, which resulted in the spring 2007 NEP sums being the highest observed over the study period for the FRFon site while above the mean for the other sites (Table 5).

**Simple phenological indices correlate with springtime fluxes.** The relationship between the onset of the CUP and springtime NEP sum is presented in Fig. 3. Contrary to deciduous sites (FRFon and FRHes), all evergreen sites were springtime net C sinks throughout the study period. Over all sites, a decrease of the springtime net C balance with a late-starting CUP was noted. The reactivity (i.e. the slope) of springtime NEP to delayed

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*Table 5* Anomalies of air temperature and carbon fluxes for spring 2007

<table>
<thead>
<tr>
<th>Site</th>
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<th>Mean</th>
<th>SD</th>
<th>$\Delta T$</th>
<th>Rank 07</th>
<th>Mean</th>
<th>SD</th>
<th>$\Delta GPP$</th>
<th>Rank 07</th>
<th>Mean</th>
<th>SD</th>
<th>$\Delta TER$</th>
<th>Rank 07</th>
<th>Mean</th>
<th>SD</th>
<th>$\Delta NEP$</th>
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<td>2001–2007</td>
<td>9.8</td>
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<td>+1.6</td>
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<td>559</td>
<td>87</td>
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<td>73</td>
<td>+17</td>
<td>4/7</td>
<td>186</td>
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<td>+45</td>
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<tr>
<td>FRFon†</td>
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<td>+1.8</td>
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<td>378</td>
<td>35</td>
<td>+83</td>
<td>1/3</td>
<td>–36</td>
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<td>0.7</td>
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<td>1/11</td>
<td>335</td>
<td>55</td>
<td>+99</td>
<td>1/11</td>
<td>361</td>
<td>30</td>
<td>+62</td>
<td>1/11</td>
<td>–26</td>
<td>37</td>
<td>+37</td>
<td>2/11</td>
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<tr>
<td>BEVie</td>
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<td>+2.8</td>
<td>1/11</td>
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<td>+115</td>
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<td>46</td>
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<td>DETha</td>
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<td>1.1</td>
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<td>1/11</td>
<td>581</td>
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<tr>
<td>FIHyy</td>
<td>1997–2007</td>
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<td>1</td>
<td>+0.5</td>
<td>3/11</td>
<td>202</td>
<td>26</td>
<td>+40</td>
<td>1/11</td>
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<td>+29</td>
<td>3/11</td>
<td>44</td>
<td>27</td>
<td>+12</td>
<td>4/11</td>
</tr>
</tbody>
</table>

$\Delta T$, spring (January–May) 2007 anomaly of mean air temperature compared to the 1997–2006 mean (°C). $\Delta GPP$, $\Delta TER$, $\Delta NEP$, spring (January–May) 2007 anomaly of GPP, TER and NEP sums compared with the 1997–2006 mean (gC m$^{-2}$/5 months). Mean and standard deviation (SD) over the 1997–2006 period are reported for comparison. Rank 07 reports the rank of year 2007 temperature or flux anomaly over the period of interest.

*Reported means, SD and anomalies are relative to the 2001–2006 period.
†Reported means, SD and anomalies are relative to the 2005–2006 period.

GPP, Gross primary productivity; NEP, net ecosystem productivity; TER, total ecosystem respiration.
CUP onset was strikingly different between though consistent within functional types, with a mean –7.0 (range –7.5 to –6.6) gC decreased sink for each day of later starting CUP in deciduous forests, while coniferous forests showed a mean –1.3 (–1.5 to –1.1) gC day\(^{-1}\) decrease. For all sites, the 2007 onset of CUP was advanced compared with the mean pre-2007 onset, and in some cases was the earliest recorded (Fig. 3).

The springtime GPP sum was significantly correlated with the sum of positive air temperature for all evergreen sites but FRPue (Fig. 4a). For the deciduous FRHes site, the GPP starting date was a better descriptor of the springtime GPP sum variability than the temperature sum (Fig. 4). No significant relationship could be established with either index for the deciduous FRFon site (three site-years), which aligned on the FRHes site relationship (Fig. 4b). Relationships drawn for both deciduous and evergreen forests clearly illustrated the exceptional nature of the 2007 spring with the highest temperature sums (earliest GPP starting date) associated with the highest measured GPP in evergreen (deciduous) sites.

For three out of six sites, the best predictor of springtime TER was springtime GPP (Table 6). For the boreal FIHyy and temperate FRFon sites, the sum of positive air temperatures was the best predictor of springtime TER, while no significant relationship could be established with either predictor for the temperate coniferous BEVie site.

**Simulation analysis**

**Model validation.** Model simulations of the springtime dynamics of diurnal NEP (NEP\(_d\)) proved accurate across the considered latitudinal range, with squared correlation coefficients values between measured and modelled NEP\(_d\) time series in the 0.59–0.98 range (mean 0.86, Fig. 5). For sites characterized by a strong seasonality of NEP\(_d\), such as the temperate deciduous FRHes or boreal coniferous FIHyy sites, the model correctly reproduced the mean respiratory winter values, and fairly timed the subsequent sharp rise of NEP\(_d\). This feature was expected for the deciduous FRHes site where budburst was forced (‘Modelling of
the C balance’). For the temperate coniferous DETha site, the alternation between active/inhibited photosynthesis periods appearing through the rugged NEPd patterns was correctly modelled. Lower $r^2$ values were obtained for the Mediterranean FRPue forest, where day-to-day variations of NEPd (e.g. reversals from net sinks to sources caused by variations of incoming radiation) were well simulated, but the model could not capture the complete range of NEPd, particularly for years 2001 and 2003. Such underestimations of NEPd maxima appeared sporadically at other sites. The accuracy of simulations for the Mediterranean FRPue site benefited from forcing LAI reduction following the Lymantria attack on the current-year leaf cohort in June 2005 (Allard et al., 2008), though the low measurements range of 2006 caused a low $R^2$ value ($R^2 = 0.59$). The new leaf cohort emitted in 2007 allowed for a LAI increase and accurate representation of higher NEPd.

We noticed a fair simulation of the NEPd and GPP spring sums over all sites, with squared correlation coefficients values ranging from 0.55 to 0.81 for NEPd.

Table 6 Pearson’s correlation coefficients relating annual springtime variables to annual TER springtime sums

<table>
<thead>
<tr>
<th>Spring variable</th>
<th>GPP sum</th>
<th>$T_{air}&gt;0$ sum</th>
</tr>
</thead>
<tbody>
<tr>
<td>FRPue</td>
<td>0.93*</td>
<td>0.57</td>
</tr>
<tr>
<td>FRFon</td>
<td>0.94</td>
<td>0.99</td>
</tr>
<tr>
<td>FRHes</td>
<td>0.86*</td>
<td>0.49</td>
</tr>
<tr>
<td>BEVie</td>
<td>0.19</td>
<td>0.41</td>
</tr>
<tr>
<td>DETha</td>
<td>0.95*</td>
<td>0.69*</td>
</tr>
<tr>
<td>FIHyy</td>
<td>0.52</td>
<td>0.71*</td>
</tr>
</tbody>
</table>

*Significance at the 5% threshold.

GPP, Gross primary productivity; $T_{air}$, air temperature; TER, total ecosystem respiration.

Fig. 3 Springtime net ecosystem productivity (NEP) sum as a function of the date of carbon uptake period (CUP) onset. Letters denote particular sites: P, FRPue; F, FRFon; H, FRHes; V, BEVie; T, DETha; Y, FIHyy. Year 2007 fluxes are circled. Insets report the site slopes of the relationship (significance at the 5% threshold denoted by bold characters, NA, not assessed). No relationship could be established for FRPue, as this site was a consistent C sink throughout the January-May period (no CUP onset could be detected). Overall relationships (grey lines): Evergreens: NEP = $-2.38 \times CUP\text{onset} + 290$ ($R^2 = 0.66$, $P < 10^{-4}$); Deciduous: NEP = $-7.07 \times CUP\text{onset} + 838$ ($R^2 = 0.58$, $P < 0.001$).

Fig. 4 Relating phenological indices to gross primary productivity (GPP) sums in deciduous and evergreen sites. Year 2007 fluxes are circled. Each site is represented by its initial letter, as in Fig. 3. (a) Evergreen sites, with deciduous sites reported in grey; (b) Deciduous sites. Insets report the site slopes of the relationship (significance at the 5% threshold denoted by bold characters). Overall relationships (grey lines): Evergreens: GPP = $635 \times (1 - \exp(-0.00272 \times (\Delta T-259)))$ ($R^2 = 0.85$, $P < 10^{-4}$); Deciduous: GPP = $-6.55 \times GPP_{\text{start}} + 1076$ ($R^2 = 0.60$, $P < 0.01$).
and from 0.64 to 0.90 for GPP. RMSE values ranged from 15 to 34 gC m$^{-2}$ for NEPd and from 12 to 58 gC m$^{-2}$ for GPP (Fig. 6). CASTANEA and eddy covariance estimates of spring GPP were overall within 8% of each other.

**Influence of climatic and biological drivers on C fluxes.**

We report in Fig. 7 the calculated springtime patterns of climatic and biological driver influences on GPP, TER and NEP fluxes. Squared multiple correlation coefficients ($R^2$) in the 0.6–1.0 range (most frequently between 0.8 and 1.0) for all sites and fluxes validate our reconstruction of the flux simulated under full drivers variability from partially forced simulations by the MLR method [Eqn (1)]. The weak departure of $R^2$ from 1.0 further proved that interactions terms and unconsidered potential drivers played a minor role in the modulation of simulated fluxes.

Owing to the differences in functional types (deciduous vs. evergreen) and climatic conditions range (Mediterranean to boreal), the spring drivers’ patterns of influence on a given flux appeared strikingly different between sites.

**Influence of climatic and biological drivers on GPP.** For both temperate and boreal coniferous sites (DETha and FI-Hyy), throughout the January–May period, temperature exerts a strong influence on GPP modulations, either through direct effects of air temperature ($T_{eco}$) on photosynthesis enzyme kinetics or through the photosynthesis acclimation factor (biological integrator of the thermal influence, AccP; Fig. 7a and d). The biological AccP driver dominated GPP control during most of the spring. The climatic $T_{eco}$ driver had its heaviest influence on GPP control towards the end of the springtime period when above-freezing temperatures induced a relief of the thermal acclimation constraint (AccP), but air temperatures were still low enough to limit photosynthetic enzyme kinetics. Another period during which the climatic $T_{eco}$ driver exerted its influence on GPP at the boreal FIHyy forest occurred when deep-freezing periods caused the AccP factor to maintain its minimal value from year to year (DoY 35–65; Fig. 7d).

For both temperate deciduous (FRHes) and Mediterranean evergreen (FRPue) sites, the influence of temperature drivers on GPP modulations was less important than for coniferous sites. For the evergreen FRPue site, $T_{eco}$ influence on GPP diminished across the January–May period (Fig. 7g) as rising temperatures became less limiting for photosynthesis. For the deciduous FRHes forest, the main influence of $T_{eco}$ on GPP modulations...
occurred during the transition (DoY 120–140) from foliar biomass (CDyn)-driven GPP to incoming radiation (Rg)-driven GPP (Fig. 7j). During this period, $T_{eco}$ affected GPP by both modulation of photosynthesis kinetics and leaf mass per area development.

The incoming radiation (Rg) climatic driver mainly modulated GPP after the relief of other constraints: either thermal in northern coniferous forests, or structural in deciduous forests (after canopy development). As these constraints were of less importance for the Mediterranean site, Rg appeared there as the main GPP driver throughout spring (Fig. 7g).

Structural variations of the canopy, as assessed from the CDyn factor, strongly influenced GPP in the deciduous FRHes site where GPP modulation was mainly dependent on leaf mass build-up in a 1-month period spanning DoY 100–130 (Fig. 7j). A more diffuse influence of CDyn on GPP modulation was observed for the evergreen broadleaf site (FRPue, Fig. 7g), where the 2005 caterpillar attack caused a 15% LAI decrease from the original 2.9 m$^2$ m$^{-2}$ maximum seasonal value (Table 1), generating a strong interannual variability of LAI. In coniferous sites, the impact of LAI variations, either due to interannual variations of needle flush or thinning, was discernable (Fig. 7a and d) but to a lesser extent than noticed for the FRPue site.

Influence of climatic and biological drivers on TER. Overall sites, TER modulations were first driven by $T_{eco}$ (Fig. 7). CDyn could also modulate TER following a sharp structural change in canopy structure (leaf mass develop-

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Fig. 6 Comparison of modelled and measured spring flux sums. Black bars, simulated diurnal net ecosystem productivity (NEPd); squares, measured NEPd; grey bars, simulated gross primary productivity (GPP); circles, eddy-covariance separated GPP. Dashed lines mark the 2007 spring GPP values. For each site, both the 1997–2007 springtime series and mean values before 2007 are reported. Note that for the FRHes site, eddy-covariance separated GPP before budburst were set to zero. All squared correlation coefficients between measured and modelled values were significant at the 5% threshold. X-axis represents years from 1997.
Development in FRHes, Fig. 7k, thinning on DoY 90 in DETha, Fig. 7b). Worthy of note were the influences of the Rg and AccP factors on the TER modulation, at all sites, as these drivers were not directly implicated in the model TER calculations. Their influences reflected the functional link of TER with GPP. For instance, Rg influenced TER by the end of May in FRHes (Fig. 7k), and throughout springtime in FRPue (Fig. 7h). Similarly, Rg and AccP both affected TER modulation throughout the season in DETha (Fig. 7b), and from the rise of GPP fluxes in FIHyy (Fig. 7e).

Influence of climatic and biological drivers on NEP. Relative effects of climatic and biological drivers on NEP resulted from the combination of relative effects on GPP and TER. For both FRHes and FIHyy sites, which are characterized by strong NEP seasonal variations, the first part of the NEP driving pattern was dominated by $T_{eco}$ (resembling that of TER) while the second part was reminiscent of the GPP pattern (Fig. 7f and i). For DETha and FRPue, which are characterized by significant GPP fluxes throughout the January–May period, the NEP driving pattern resembled that of GPP (Fig. 7c and i).

Climatic and biological impacts on 2007 fluxes. In Figs 8 and 9 we present the GPP and TER annual RAs computed from simulated fluxes [Eqn (3)] for each site. These graphs quantify the influence of each driver on the exceptional spring 2007 flux values.

Model simulations revealed exceptional 2007 GPP...
enhancements for all sites, with a 2007 RA greater than the maximum pre-2007 value for at least one driver (Fig. 8). These results were consistent with flux measurements: for the three sites for which the model predicted exceptional enhancements in spring 2007 GPP (FRHes, DETha and FIHyy), the measured spring 2007 values were the highest recorded (Table 5, Fig. 6). For the FRPue site, the model predicted the highest spring GPP sum to occur in 2007, while the highest measured spring GPP was observed in 2001 (Fig. 6).

For both coniferous sites, the exceptional GPP of spring 2007 was, according to the model, caused mainly by the early relief of the photosynthesis acclimation constraint (AccP), resulting in a +20% GPP increase in model simulations (+100 gC m⁻² for DETha, +40 gC m⁻² for FIHyy; Fig. 8a and b), relative to simulations that compelled AccP to follow its mean pattern. The GPP anomaly during spring 2007 in the deciduous FRHes site was mainly related to the CDyn factor. The 15-day advanced canopy setup in spring 2007 caused a +42% (+125 gC m⁻²) increase in simulated GPP (Fig. 8d).

At all sites, the climatic $T_{ec}$ factor participated in the increase of spring GPP sum, as a positive anomaly from the mean of the 2007 was observed for $RA_{GPP,T_{ec}}$, (Fig. 8). However, the pure climatic $T_{ec}$ effect was of limited influence and did not fully explain the exceptional 2007 GPP.

The analysis of TER enhancement factors revealed exceptional increases for all sites, with a 2007 RA greater than the maximum pre-2007 value for at least one driver (Fig. 9). For all sites, elevated 2007 temperatures ($T_{ec}$) were the principal cause of the spring 2007 TER enhancement. This effect was associated with a promotion of 2007 TER by CDyn in the FRHes site (Fig. 9d).

**Discussion**

**SVAT models as tools to disentangle the influences of climatic and biological drivers on C fluxes**

For two decades, process-based SVAT models have been considered as fundamental tools for the study of the forest component of biogeochemical cycles (e.g.
Aber & Federer, 1992; Sala & Tenhunen, 1996; De Pury & Farquhar, 1997). SVAT models are usually used as tools for retrospectively and/or prospectively predicting the response of forest ecosystems to climate change and/or anthropogenic disturbances, in terms of C fluxes and stocks (Thornton et al., 2002; Churkina et al., 2003; Schimel et al., 2005, but see Davi et al., 2006, for a CASTANEA application). Recent modelling papers discussing the summer 2003 European heat wave/drought stress also underlined the importance of SVAT models for the study of extreme events, either in terms of spatialization (Ciais et al., 2005; Reichstein et al., 2007; Vetter et al., 2008) or for deriving ecosystem functional indexes (Granier et al., 2007). In this study, we used the CASTANEA model in a different way, as a tool for quantifying the influences of climatic and biological drivers on the interannual variability of C fluxes: (i) at a daily timescale [e; indexes; Eqn (2), Fig. 7] and (ii) at seasonal time scale [RA indexes; Eqn (3), Figs 8 and 9].

CASTANEA accurately represented net C fluxes at daily (Fig. 5) to seasonal (Fig. 6) time scales, and in previous studies proved accurate at simulating individual (organ-scale) processes (Davi et al., 2005), which gave us confidence in the model structure. CASTANEA contains more than 150 parameters, including species-specific parameters (compiled from the literature, see Dufrene et al., 2005 for a thorough review) and stand-specific parameters (collected in situ, Table 2). The use of a given set of parameters, which carry their own uncertainties, might introduce compensating errors in the model simulations (Medlyn et al., 2005), which are not detectable through validation with net C fluxes and may bias the quantification of driver influences on C fluxes. A sensitivity analysis was conducted in order to test for the robustness of e; and RA indexes to parameters uncertainties. The sensitivity analysis revealed that both e; and RA indexes departed <5% and 1%, respectively, from their original values when the five most sensitive parameters associated with each climatic and biological driver were varied by ±10% (not shown). The robustness of functional drivers indexes (e; and RA) proceeds from the very definition of the indexes, as Eqn (2) uses centred-reduced fluxes as variables, and Eqn (3) is the ratio of two fluxes, so that both indexes are marginally affected by mean-centred deviations of simulated fluxes caused by parameters uncertainties.

Resolving C fluxes determinism through simulation deconvolution

The analysis of measured spring fluxes through a correlative approach showed phenological temperature-related indexes (date of GPP onset and sum of positive temperatures, Fig. 4) to be good descriptors of the interannual variability of springtime GPP sums. Contrary to such indexes, established at an annual time scale, CASTANEA simulations could be used to disentangle the influences of climatic and biological drivers on C fluxes at both daily and integrated (annual) time scales. CASTANEA simulations of spring GPP were for three out of four sites better correlated with eddy covariance-separated GPP (GPP_e; ) sums than were phenological indexes (R2 values of simulated GPP and GPP_e; were −4% to +49% higher than R2 values of phenological indexes and GPP_e; ). This further evidenced that spring GPP sums do not rely on a sole event (GPP onset) or driver (air temperatures), but on the integration of fine time scale influences of climatic and biological drivers.

An important result of the analysis of driver influences was the illustration of the functional link between GPP and TER fluxes. Experimental studies demonstrated that soil respiration (Tang et al., 2005; Sampson et al., 2007) as well as trunk respiration (Zha et al., 2004) were partially correlated with GPP, which provides photosynthates used for growth or maintenance of tree organs and rhizosphere (Hogberg et al., 2001). At all study sites, the principal driver of simulated TER variability was temperature (Fig. 7). However, TER variability was also influenced by GPP drivers, which do not directly impact TER in the model calculations (i.e. radiation Rg and thermal acclimation factor AccP; Fig. 7). For most of the January–May period, no wood growth was simulated in CASTANEA for either species. In the model, wood growth is triggered after budburst in Fagus (April), within days following needle flush in conifers (May), and begins in April for Q. ilex, consistently with experimental results (Rambal et al., 2004; Zweifel et al., 2006; Granier et al., 2008). However, experimental studies showed that fine root growth continues throughout the winter in Pinus sylvestris (Konopka et al., 2005) and Q. ilex (Lopez et al., 2001). Accordingly, the dependency of simulated TER on GPP drivers was due to fine root growth, which could in the model represent up to 20% of late spring TER in coniferous sites (DETha and FIHyy), 15% in the Mediterranean evergreen (FRPue) and 5% in the deciduous site (FRHes).

The mechanisms of spring photosynthesis resumption in conifers are still subject to debate, as several authors (e.g. Schwarz et al., 1997; Jarvis & Linder, 2000) hypothesise a decisive role of soil temperature, on the argument that spring transpiration recovery accompanying photosynthesis resumption requires soil water to be in liquid phase (i.e. soil thaw) in order to be absorbed by active (temperature-limited) roots. Suni et al. (2003a) demonstrated that for sites of moderate
soil freezing, photosynthetic activity was detectable up to 1.5 months before soil thaw, as trees could probably partly rely on xylem water content to satisfy the very low evaporative demand (Sparks et al., 2001). In CASTANEA, the resumption of photosynthesis in coniferous forests is not dependent on soil temperature (the AccP factor relies on air temperature, see ‘Modelling of the C balance’). On the other hand, the northernmost site scoped in this study (FIHyy) is not subject to winter soil freezing (Suni et al., 2003a, b). The CASTANEA model was not tested at higher-latitude (colder) sites than FIHyy, so we cannot conclude whether it is useful to implement in the model the influence of soil temperature on spring photosynthesis resumption for higher-latitude sites. If relevant, the integration of such a soil temperature effect might modify the indicative pattern of functional constraints presented in Fig. 7 for a boreal forest, based on the FIHyy example.

Analogous responses of temperate coniferous and deciduous forests to spring temperature anomaly

In a recent study addressing the question of differential responses of the C balance of boreal forests to spring warming, Welp et al. (2007) reported a higher anomaly of spring GPP (April–June in their study) in a boreal deciduous stand (Populus tremuloides, +106 gC m$^{-2}$) as compared with a boreal coniferous stand (Picea mariana, +28 gC m$^{-2}$), in response to a +3°C temperature increase (Table 2 in Welp et al., 2007). Concomitant increases in TER (+54 and +17 gC m$^{-2}$, respectively) led to a higher enhancement of NEP in the deciduous stand compared with the coniferous stand. The authors suggested that their results might illustrate the differential responses of deciduous and coniferous species to future climate changes. Our study complemented these results, as we showed that a +2.3 to +2.6 K temperature anomaly led to comparable anomalies in GPP (+100–130 gC m$^{-2}$), TER (+60–90 gC m$^{-2}$) and NEP (+40 gC m$^{-2}$) in two deciduous and coniferous forests located at temperate latitudes (FRHes and DETha, Table 5). Compared with the results of Welp and colleagues, our findings illustrate a modification of the relative sensitivities of coniferous and deciduous forests to spring warming from temperate to boreal latitudes. Our results further temper the conclusions about the supposedly higher contribution to the variability of CO$_2$ atmospheric concentration from deciduous forests relative to coniferous forests, which arose from work published for boreal forests (Arain et al., 2002; Welp et al., 2007).

Will warm springs enhance annual NEP?

The exceptional GPP and NEP of European forests during the spring of 2007 appear in line with a trend towards an earlier onset of C uptake, demonstrated back to the 1980s through flask sampling/atmospheric inversion (Randerson et al., 1999) and remote sensing of continental greenness (Myneni et al., 1997; Zhou et al., 2003). Climate models predict winter temperatures at the continental scale to increase up to three standard deviations from the 1961–1990 mean by the end of the 21st century (Scherrer et al., 2005), such that winter
2006–spring 2007 temperatures today considered as exceptional may become more and more commonplace. The frequency of late frosts should further decrease (Tebaldi et al., 2006), as should the risk of frost injury to canopy resulting in negative anomalies in the absorbed PAR fraction (Gu et al., 2008). One may thus expect spring GPP to increase in the forthcoming decades.

In a recent analysis of the last two decades of atmospheric CO\textsubscript{2} concentrations in the northern hemisphere, Angert et al. (2005) observed a trend towards an earlier resumption of spring CO\textsubscript{2} uptake. They further reported no trend towards higher CO\textsubscript{2} uptake for late summer data, and therefore concluded that warmer and drier summers tend to compensate for the increased uptake caused by warmer springs. Accordingly, a comparison of the spring 2007 C uptake anomaly with the summer 2003 heat wave and subsequent drought (Ciais et al., 2005; Granier et al., 2007; Reichstein et al., 2007; Vetter et al., 2008), shows that if both extreme events were to occur in a single year, the occurrence of a summer heat wave and drought would indeed cancel out the benefits from spring warming in terms of net uptake (Fig. 10). Such a coincidence of warm springs (Scherrer et al., 2005) and warm and dry summers (Schär et al., 2004) is likely to increase during the 21st century. CASTANEA simulations show that warmer springs might even hasten the occurrence of drought, with early resumption of transpiration causing earlier depletion of soil water (conditional to low soil water recharge following transpiration onset; N. Delpierre, unpublished results), which would further compromise the beneficial effect of warm springs on the annual C balance.

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