

Paired comparisons of carbon exchange between undisturbed and regenerating stands in four managed forests in Europe

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Abstract

The effects of harvest on European forest net ecosystem exchange (NEE) of carbon and its photosynthetic and respiratory components (GPP (gross primary production) and TER (total ecosystem respiration)) were examined by comparing four pairs of mature/harvested sites in Europe via a combination of eddy covariance measurements and empirical modeling. Three of the comparisons represented high coniferous forestry (spruce in Britain, and pines in Finland and France), while a coppice-with-standard oak plantation was examined in Italy.

While every comparison revealed that harvesting converted a mature forest carbon sink into a carbon source of similar magnitude, the mechanisms by which this occurred were very different according to species or management practice. In Britain, Finland, and France the annual sink (source) strength for mature (clear-cut) stands was estimated at 496 (112), 138 (239), and 222 (225) g C m^{-2} , respectively, with 381 (427) g C m^{-2} for the mature (coppiced) stand in Italy. In all three cases of high forestry in Britain, Finland, and France, clear-cutting crippled the photosynthetic capacity of the ecosystem – with mature (clear-cut) GPP of 1970 (988), 1010 (363), and 1600 (602) g C m^{-2} – and also reduced ecosystem respiration to a lesser degree – TER of 1385 (1100), 839 (603), and 1415 (878) g C m^{-2} , respectively. By contrast, harvesting of the coppice oak system provoked a burst in respiration – with mature (clear-cut) TER estimated at 1160 (2220) g C m^{-2} – which endured for the 3 years sampled postharvest. The harvest disturbance also reduced GPP in the coppice system – with mature (clear-cut) GPP of 1600 (1420) g C m^{-2} – but to a lesser extent than in the coniferous forests, and with near-complete recovery within a few years. Understanding the effects of harvest on the carbon balance of European forest systems is a necessary step towards characterizing carbon exchange for timberlands on large scales.

Keywords: eddy covariance, forest carbon cycle, gross primary production (GPP), harvest disturbance, net ecosystem exchange (NEE), total ecosystem respiration (TER)

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Introduction

Understanding the terrestrial carbon cycle requires an accurate characterization of the role of forests at diverse stages of development. Initial assessments of net

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ecosystem exchange (NEE) of CO₂ have revealed that mature and growing forests generally remove atmospheric carbon at a rate of several tons per hectare annually (Valentini *et al.*, 2000). However, large forest areas are recovering from the effects of natural and anthropogenic disturbances, and the carbon balances of such regenerating forest remain uncertain (Geider *et al.*, 2002). Recent investigations have shown that natural disturbances such as fire and wind throw can convert mature forest sinks into carbon sources, requiring decades to recover their sink status (Knohl *et al.*, 2002; Wirth *et al.*, 2002; Litvak *et al.*, 2003; Bond-Lamberty *et al.*, 2004). The primary source of variability in carbon cycling among managed forest stands is likely determined by differences in rotation stage (time since harvest). With managed forestry representing a significant fraction of land cover in many countries, the carbon accounting mandated by the Kyoto Protocol requires an assessment of the effects of harvest on forest carbon exchange.

Clear-cutting, a common harvest practice in plantation forestry, involves cutting all trees at ground level, removing commercial stemwood, and leaving foliage, twigs, branches, stumps, and root systems on site as residues. Harvest usually is followed by steps – slash management, weed control, soil preparation, and seeding or planting – intended to regenerate tree stands. Regarding the carbon cycle, clear-cutting eliminates canopy photosynthesis and affects autotrophic and heterotrophic components of ecosystem respiration, both directly due to loss of respiring biomass and indirectly by adding residues to the soil, and altering litterfall and root exudation. For some tree species, an alternative management strategy is coppicing, where stands are cut leaving roots and stumps intact to re-grow via the generation of suckers. In the coppice-with-standard approach, some trees ('standards') are spared to provide seeds for natural regeneration.

Comparisons of mature and harvested stands have been used to investigate effects of harvest on forest carbon cycling. Initial studies on the soil CO₂ efflux of subtropical pine (Ewel *et al.*, 1987) and a mixture of boreal species (Gordon *et al.*, 1987) appeared to support the intuitive hypothesis that clear-cutting enhances respiration, due to decomposition of residues. Moreover, it can be argued that respiration benefits from soil warming induced by the removal of canopy shade. This, coupled with the obliteration of photosynthesis, suggests that clear-cut stands should be quite large carbon sources. However, more recent studies indicate that this model may not always apply. For one thing, the harvest practices employed may be critical – in the pine example cited above, the slash was worked into

the soil. More important perhaps, in determining the effects of harvest on ecosystem respiration, is the type of tree harvested.

Tree species show variability in root longevity following harvest, an important factor in both the survival of decomposing mycorrhizae (Hagerman *et al.*, 1999) and the rate of mass loss from the floor (Prescott *et al.*, 2000). Among the few species studied to date, aspen roots have shown resilience to harvest impact, vs. pines. Harvest of stands including aspen, whose roots survive and begin regeneration via sucker development, can either increase or have little effect on soil (Gordon *et al.*, 1987; Mallik & Hu, 1997) and ecosystem (Amiro, 2001) respiration. By contrast, following pine harvest, below-ground respiration can be reduced by more than half (Arneeth *et al.*, 1998; Striegl & Wickland, 1998) due to root mortality, and total ecosystem respiration (TER) can also decline (Kowalski *et al.*, 2003). Other species may behave differently. After harvest of a mixed spruce/fir stand, Lytle & Cronan (1998) attributed increased soil CO₂ efflux to fine root decay; however, some trees were left on the plot, likely sustaining mycorrhizal communities (Hagerman *et al.*, 1999). Hitherto, the effect of harvest on carbon exchange components has been examined for relatively few ecosystems, and remains an open matter for continued investigation.

As part of the European Union CARBO-AGE project, this paper compares annual CO₂ exchange among recently harvested vs. mature stands in four European production forests forming a North–South transect from Finland (62°N) to Italy (44°N). The effects of clear-cutting in high coniferous forestry (British spruce, Finnish pine, and French pine) are examined and contrasted with the effects of harvest in an Italian coppice-with-standard oak plantation, where root systems clearly survive harvest and regenerate the ecosystem.

Materials and methods

Measurements

Data were collected at paired ecosystems representing mature (M) and recently cut (C) stages of managed forestry. In each of four countries, two ecosystems similar in climate, soil, and tree species were compared. Table 1 gives an overview of ecosystem characteristics. The high forests in Britain, Finland, and France are clear-cut along rotations of ca. 43, 85, and 50 years, respectively, while the Italian coppice-oak follows a rotation length of 15–20 years. In most cases, measurements at the harvested site began following harvest but prior to other major management steps. In Britain, slash

Table 1 An overview of the ecosystems examined in this study

Land	Britain	Italy	Finland	France
Landscape	Flat, in gentle hills	Flat, in gentle hills	Flat	Flat
Latitude/longitude	55°10'N, 2°3'W	42°24'N, 11°55'E	61°51'N, 24°17'E	44°35'N, 0°52'E
Soil type	Peaty gley	Volcanic luvisol	Podzol	Spodic sands
Mean T (°C)	7	14	3	12.8
Precipitation (mm)	950	755	700	930
	C	C	C	C
Mature (M)/cut (C)	M	M	M	M
Data Period	2001	2001–2002	2000	2001
Harvested	1960	1991	1962	1970
Species	<i>Picea sitchensis</i> (Bong.) Carr.	<i>Quercus cerris</i>	<i>Pinus sylvestris</i>	<i>Pinus</i> <i>pinaster</i>
LAI (m ² m ⁻²)	12	2.5 + 2	3 + 1.2	3 + 1.5
MAI (m ³ ha ⁻¹)	14	20	12	16
	N/A	N/A	N/A	N/A
		0.7 + 2	1.8	1.9
		N/A	N/A	N/A
			Grasses, dwarf shrubs	Graminae, heather, gorse

The last two lines are leaf area index (LAI, annual maxima; where two values are given, they represent canopy + understorey) and mean annual increment (MAI).
*Sitka spruce saplings (2800 ha⁻¹) were planted at the British harvested site in April 2001, but contribute relatively little to leaf area.

piling and mounding were applied to the harvested site before measurements began, and 2-year old Sitka spruce seedlings were planted in April 2001. Coppicing in Italy spared ca. 100 stems ha⁻¹ (standards unharvested to provide seeds). In Finland, soil scarification followed clear-cutting in 1996. Published papers provide additional information about measurements and flux determination at the Finnish (Rannik *et al.*, 2002) and French sites (mature, Berbigier *et al.*, 2001; harvested, Kowalski *et al.*, 2003), and Manca (2003) describes the measurements in Italy.

Eddy covariance flux data were combined with measurements of radiation, atmospheric state, and soil conditions for these analyses of ecosystem exchange. Eddy flux measurements were made with sonic anemometers (Solent Research, 1012R3, Gill Instruments, Lymington, UK; Italian sites: USA-1, Metek, Elmshorn, Germany) and CO₂ concentration measurements with closed-path infrared gas analyzers (6262, LI-COR, Lincoln, NE, USA). The key meteorological and soil parameters used are the friction velocity (u_* , from sonic winds), the flux of photosynthetic photons (F_p), soil temperature, volumetric soil humidity, and precipitation.

Surface exchange determinations

The techniques used to determine fluxes from half-hour covariance calculations followed the EUROFLUX methodology (Aubinet *et al.*, 2000). These include 3-D coordinate rotations, determination of system lag for gas sampling, removal of an approximated running mean from time series of turbulent fluctuations (McMillen, 1988), and corrections for the inability of the closed-path gas analysis to sample high frequencies (Moore, 1986). 'Footprint' models were used to determine the source area contributing to the fluxes (e.g. Rannik *et al.*, 2002; Kowalski *et al.*, 2003), and to filter data for acceptable flow conditions. In this paper, carbon fluxes (F_c) and NEE are defined according to the meteorological sign convention (positive upward); processes of TER and GPP are always defined positive.

When boundary-layer stratification curbs near-surface turbulence, as during clear skies at night, eddy flux measurements may not reflect surface exchange (Falge *et al.*, 2002). Techniques for coping with this limitation of eddy covariance include data rejection based on a turbulent mixing criterion (typically a threshold in u_* ; e.g. see Goulden *et al.*, 1996), and measuring other terms in the scalar conservation equation, such as advection and storage (Aubinet *et al.*, 2002). Since such measurements were not available at all sites, we followed the most frequently applied approach and determined thresholds in u_* above which, over a reference temperature range, measured nocturnal

Table 2 Threshold in u_* (m s⁻¹) for acceptance of nighttime flux data

Land	Britain	Italy	Finland	France
Mature	0.5	0.3	0.2	0.4
Harvested	0.5	0.4	0.2	0.5

Note: For the British clear-cut, a threshold in mean wind speed was applied, and the u_* value in the table is inferred.

fluxes of CO₂ from the ecosystem were independent of u_* (Table 2). Consistent with previous experience, the u_* threshold varies by site (Baldocchi, 2003). Half-hour fluxes for nighttime periods not satisfying the sufficient mixing criterion were rejected.

Gap-filling and empirical models

Long-term integration of eddy covariance ecosystem exchange data requires the filling of gaps introduced by instrument failure, system maintenance and data rejection. In this study, small gaps (maximum 2 h) in meteorological data were filled by direct interpolation, and longer gaps were replaced by mean diurnal behavior over a 2-week period. Among the eight ecosystems, valid data populations were diverse, requiring two approaches to treat missing flux data. For most of the ecosystems, good data coverage allowed the estimation of defensible annual carbon exchange by filling long-term gaps using semi-empirical methods (Falge *et al.*, 2001). However, for the clear-cut sites in Britain and Finland, which lacked permanent tower installations, the methods used to determine annual fluxes at these sites are described separately, below.

Non-linear, empirical models of ecophysiological processes were fit by a modified Levenberg-Marquardt least-squares method (PV-WAVE, Visual Numerics Inc., Houston, TX, USA). Standard errors for regression parameters were computed following Reichstein *et al.* (2002). Daytime carbon flux (F_c) measurements with no recorded precipitation were grouped into fortnightly periods, and fit to a hyperbolic dependence on the photosynthetic photon flux (F_p) according to

$$F_c = R_D - \frac{a_1 F_p}{a_2 + F_p}. \quad (1)$$

The mean of daytime respiration (estimate of F_c at zero light; i.e. the intercept) over the modeling period is estimated as R_D . At light saturation ($F_p \gg a_2$), the maximum photosynthetic uptake rate is a_1 , and the light level corresponding to half of this uptake is a_2 . Photosynthesis, defined as the difference $R_D - F_c$, is thus predicted from a_1 , a_2 , and F_p . In continuously dim conditions about the winter solstice – mainly at boreal

sites – light saturation is not reached, and these curves approach linearity with very high values of a_1 and a_2 . Direct interpretation of a_1 and a_2 is then inappropriate (such values are excluded from the model parameters trends presented in the Results section), but the models fit the data and serve to partition NEE into photosynthetic and respiratory components. For continuity in modeling ecophysiological processes and the ability to estimate annual GPP, fortnights with no valid empirical models borrowed parameters from the preceding modeling period; only for the British mature site was this necessary more than once, and then not for contiguous fortnightly periods.

Measurements of F_c near zero light have exceptional leverage in determining the hyperbolic model parameters in Eqn (1); unfortunately, these conditions correspond to a known bias in eddy covariance. Following a calm night, the morning sun re-initiates turbulence via near-surface buoyancy production, and CO_2 accumulated near the ground overnight can be flushed out of canopy airspace in a sudden burst. While this effect can be averaged out in long-term summations (Aubinet *et al.*, 2000), it is a particular hazard for model parameterization. Therefore, a parallel set of hyperbolic light-response models was defined where morning data were subjected to an additional ‘morning flush’ criterion: that both the current and previous half-hour periods satisfy the u_* criterion.

Nighttime F_c measurements satisfying both the u_* criterion and the absence of measured rain were interpreted as measurements of ecosystem respiration. These data were grouped by ecosystem – and by year, where data allowed – and fit to an exponential Q_{10} function of soil temperature (T_s in $^{\circ}\text{C}$, at 5 cm depth; 10 cm for the British clear-cut):

$$F_c = R_{15}Q_{10}^{(T_s-15)/10}, \quad (2)$$

where R_{15} is the respiratory flux predicted at 15 $^{\circ}\text{C}$ and Q_{10} is the factor increasing respiration for a 10 $^{\circ}\text{C}$ rise in temperature. Note that the Q_{10} defined here incorporates effects of numerous factors (e.g. substrate, soil moisture, root and microbial populations), and should not be taken as the temperature dependence of metabolic processes. Additional, daytime estimates of ecosystem respiration (and its temperature dependence) were determined where available data permitted. The dependence of modeled daytime, fortnightly respiration (R_D from Eqn (1)) on the corresponding mean daytime soil temperature also was fit to yield daytime estimates of R_{15} and Q_{10} . In Italy, where dry soil conditions sometimes limited respiration, Q_{10} models were developed where fractional volumetric soil water content (SWC) exceeded 0.4; water limitations were then modeled as reduced

by a linear function of soil water deficit, relative to this threshold. An attempt to derive Q_{10} values for seasonal subsets of the data revealed that, for many sites, annual temperature ranges are necessary to extract empirical relations from (relatively noisy) micrometeorological data.

Measurements of F_c passing data rejection criteria were complimented with the models described above to fill gaps and estimate daily and – where possible – annual carbon exchange (NEE) and its components (GPP and TER). For those ecosystems with two independent Q_{10} models, replacement of missing or rejected data was done in parallel. Thus, TER_1 was computed from a model fitting nighttime F_c to $T_{s,n}$ and filled gaps to integrate NEE_1 ; likewise, TER_2 and NEE_2 draw on Q_{10} models derived from daytime R_D and $T_{s,d}$.

For the British and Finnish harvested sites, continuous long-term measurements were not attempted, and annual ecosystem exchanges are inferred from available periods with reference to corresponding mature sites. Both the photosynthetic and respiratory components of F_c showed linear relationships between corresponding harvested and mature sites, and these were used to estimate annual GPP and TER from the mature site estimates. Annual NEE was then determined from respiratory release (TER), less photosynthetic uptake (GPP). Meteorological, radiation and soil data were not collected at the Finnish harvested site; therefore, data from the nearby mature site were used in conjunction with fluxes from the harvested site to develop the empirical models.

Results

Available data all come from the years 2000–2002, but vary by site. The US National Climatic Data Center (<http://www.ncdc.noaa.gov>) reports that temperatures in the study areas during these years consistently exceeded long-term climatic means by 1 $^{\circ}\text{C}$ or more. Particularly warm periods were noted during 2000 in Scandinavia and during 2002 in Britain and Italy. The same source reports neither extreme precipitation nor drought in Western Europe for these years. Table 3 indicates the periods of data that were available for these analyses. At the six sites with permanent tower installations, data coverage always exceeded 65% during day, and 35% overall (excluding low u_* at night), similar to or better than what was achieved in the EUROFLUX project (Falge *et al.*, 2001).

The degree of energy balance closure, often used to evaluate the accuracy of eddy covariance measurements, was similar to those typically reported in the literature (e.g. see Wilson *et al.*, 2002). The fraction of available energy – from net radiation and soil heat

Table 3 Summary of available data for the analyses presented in this paper

Land	Britain	Italy	Finland	France
<i>Mature site</i>				
Start date	Jan 1, 2001	Jan 1, 2002	Jan 1, 2000	Jan 1, 2001
End date	Dec 31, 2001	Dec 31, 2002	Dec 31, 2000	Dec 31, 2001
% good data	52.9	41.8	59.5	70.5
<i>Harvested site</i>				
Start date	Mar 28, 2001	Apr 3, 2000	Jul 16, 2000	May 8, 2000
End date	Jan 8, 2002	Dec 31, 2002	Oct 22, 2000	Dec 31, 2001
% good data	15.8	37.9	9.3	48.2
<i>Comparison</i>				
Start date	Mar 28, 2001	Jan 1, 2002	Jul 16, 2000	Jan 1, 2001
End date	Dec 31, 2001	Dec 31, 2002	Oct 22, 2000	Dec 31, 2001

The '% good data' entries represent available annual carbon flux data that satisfied acceptable data criteria (including nighttime u_* constraints), used in estimating annual net ecosystem exchange (NEE) in Fig. 7.

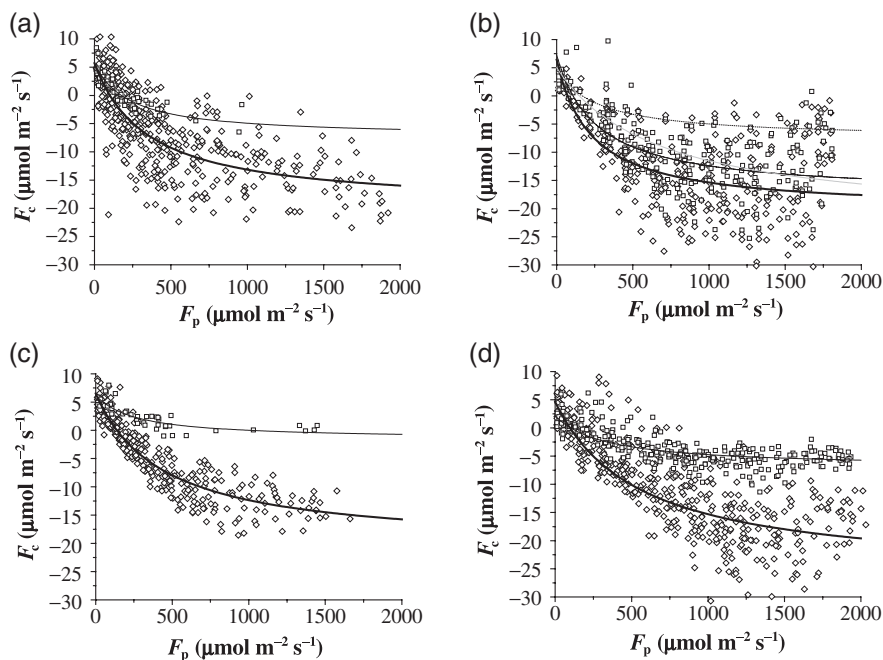


Fig. 1 Comparison of light-response curves during peak growth conditions. Carbon fluxes (F_c) are plotted vs. the photon flux (F_p) during daytime. Open symbols represent flux measurements, with diamonds for the mature site (M), and squares for the harvested site (C). Lines represent the empirical models (Eqn (1)), with thick trace for the mature site (M), and thin trace for the harvested site (C): (a) British sites during the fortnight centered on 10 June 2001; (b) Italian sites during the fortnight centered on 10 June 2002 and empirical models from the same week in 2000 (dotted line) and 2001 (gray line) are also presented; (c) Finnish sites during the fortnight centered on 21 July 2000; (d) French sites during the fortnight centered on 10 June 2001.

fluxes – explained by turbulent fluxes of latent and sensible heat averaged 78% (ranging from 61% to 88%), usually somewhat higher at harvested sites.

Response of carbon fluxes to available light

Daytime CO_2 fluxes (F_c) exhibited hyperbolic relationships with available light (F_p) at all sites. Figure 1

shows a comparison of harvested (C) vs. mature (M) stands in each country for conditions near the peak of the growing season. This comparison is summarized in Table 4, which presents parameters from Eqn (1) for the data in Fig. 1. In every comparison (country), there is little difference between the magnitudes of carbon exchange for mature and harvested sites for NEE at low light levels. With increasing light, however, the

Table 4 Light-response parameters (Eqn (1)) representative of the peak in the growing season for harvested (C) and mature (M) sites (\pm standard error estimates)

Land	Site	Date	R_D	a_1	a_2	a_1/a_2
Britain	M	10 June 2001	5.69 ± 0.94	25.4 ± 1.1	349 ± 66	0.073
	C	10 June 2001	5.66 ± 0.62	13.0 ± 1.1	228 ± 76	0.057
Italy	M	10 June 2002	6.43 ± 1.91	26.7 ± 1.9	227 ± 48	0.118
	C	10 June 2002	7.25 ± 0.70	24.8 ± 1.1	261 ± 50	0.095
	C	10 June 2001	5.00 ± 0.59	27.5 ± 1.0	669 ± 95	0.041
	C	9 June 2000	4.70 ± 0.64	12.3 ± 0.6	272 ± 57	0.045
Finland	M	21 July 2000	6.52 ± 0.31	27.2 ± 0.9	439 ± 39	0.062
	C	21 July 2000	6.22 ± 0.88	7.84 ± 1.1	260 ± 72	0.030
France	M	10 June 2001	4.64 ± 0.57	30.9 ± 1.6	546 ± 81	0.057
	C	10 June 2001	2.15 ± 0.33	9.16 ± 0.4	331 ± 38	0.028

Dates represent mid-points of fortnightly periods. Units for all parameters are $\mu\text{mol m}^{-2} \text{s}^{-1}$.

R_D , daytime respiration; a_1 , photosynthetic capacity; a_2 , the light level where photosynthesis is half of capacity.

harvested sites show greatly reduced photosynthetic uptake, with the exception of the coppice site beyond the first year after harvest. If a surrogate for apparent ecosystem light-use efficiency is defined as the ratio of a_1/a_2 (initial slope of the light-response curve, Suyker & Verma, 2001, Table 4; note that this should be defined using absorbed, rather than incident, light), it is found that the mature forests consistently make better use of light. Daytime respiration (R_D) is similar, except in France where it is distinctly higher at the mature site. Peak photosynthetic levels are consistently greater in the undisturbed stands. The ratio of undisturbed/harvested ecosystem photosynthetic capacity (a_1) is of order three in Finland and France, or two in Britain. For the Italian coppice comparison, it appears that the harvested site has reduced photosynthetic capacity in the first year (6 months following harvest), but recovers to rival the mature site by the following year. The light-level representing half of photosynthetic capacity (a_2) is higher at the mature sites, indicating that light saturation occurs at lower light levels at the harvested sites.

Seasonal trends in light response parameters R_D and a_1 , presented in Fig. 2, demonstrate that the above description of daytime respiration and photosynthetic capacity at harvested and undisturbed sites is generally applicable throughout the year. As expected, mature forests consistently exhibit greater photosynthetic capacity than harvested sites. However, in Italy, photosynthetic capacity appears to have recovered almost fully from the effects of coppicing by the third growing season (2002). An examination of the years immediately following harvest, for which mature site data were not available, suggests that photosynthetic capacity was dramatically reduced for at least 10 months following coppicing. The coppice plantation was also distinct in terms of respiration; only in Italy was respiration from the harvested site consistently larger than for the

mature forest. For the 3 years with measurements following harvest, there is no clear trend in daytime respiration with time since disturbance. In Britain, daytime respiration showed little difference between mature and harvested stands. In Finland and especially in France, R_D is greater at the mature (vs. harvested) sites. The Italian mature forest was the only site for which the morning flush criterion had a large impact on derived light-response parameters, reducing both a_1 and R_D .

Response of TER to temperature

Ecosystem respiration showed an exponential (Q_{10}) dependence on soil temperature when soil humidity was not limited. Differences between countries are larger than those between mature and harvested sites within countries. In general, northerly sites have greater seasonal variability in respiration, shutting down at cold temperatures and achieving very high summer respiration rates. In each case, we compare respiration and temperature dependence between mature and harvested sites for nighttime and, where possible, daytime estimates.

Figure 3 shows this for the British sites, and the respiration estimates from nighttime NEE measurements agree well with those derived from daytime light-response curves, despite certain differences in the exact parameters derived (Table 5 gives respiration model parameters for all sites). The British comparison is obfuscated both by unequal depths of soil temperature measurements, and by sporadic data coverage at the harvested site. Given that ecosystem Q_{10} increases with the depth of the soil temperature measurement – since temperature fluctuations are damped with depth – it appears that both ecosystem respiration and its temperature dependence are similar for the British mature

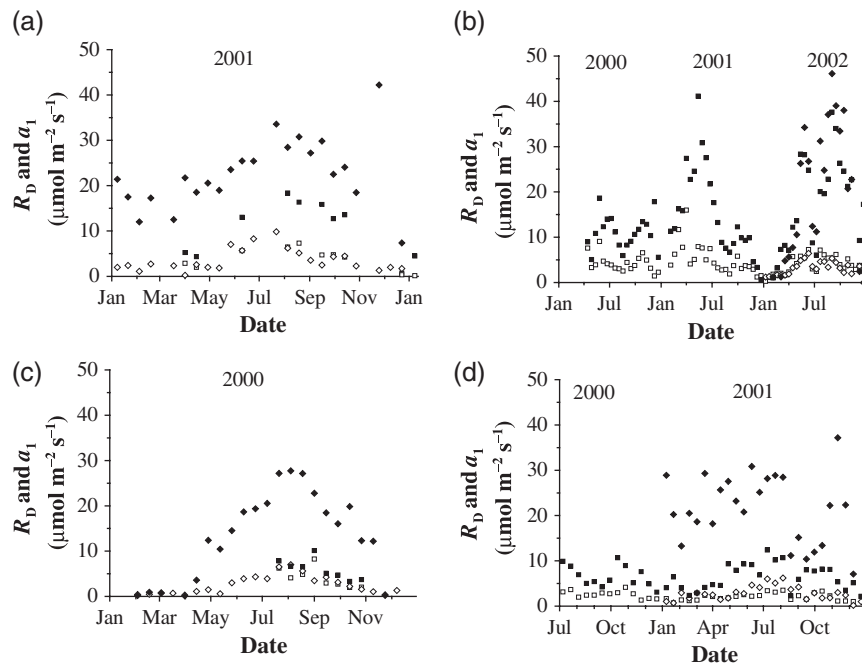


Fig. 2 Seasonal variation of light response parameters representing daytime respiration (R_D , open symbols) and ecosystem photosynthetic capacity (a_1 , closed symbols) with diamonds for the mature site (M), and squares for the harvested site (C): (a) British sites; (b) Italian sites; (c) Finnish sites; (d) French sites.

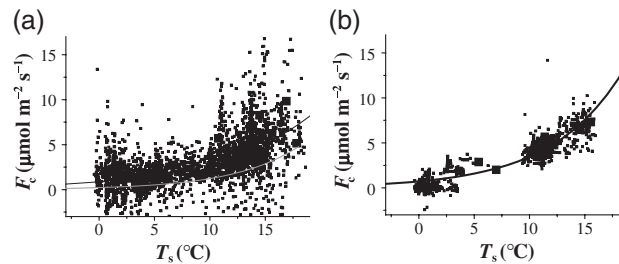


Fig. 3 Ecosystem respiration as a function of soil temperature for the British sites. For nighttime measurements, the carbon flux is plotted vs. soil temperature (F_c vs. T_s , small symbols), and the empirical model is overlaid (dark line); daytime respiration estimates are plotted vs. fortnightly, daytime mean temperature (R_D vs. T_s , large symbols), and the empirical model is overlaid for the mature site (light line): (a) mature site; (b) harvested site.

and harvested sites. In Britain, respiration varies from less than $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ in winter to approaching $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ at summer soil temperatures.

For the Italian sites, the range and seasonal variation in respiration are somewhat smaller, due in part to dry soil in summer. When soils became very warm, respiration declined due to soil dryness. Models for daytime data were not derived because of a dearth of daytime respiration estimates when applying the soil moisture criterion. The response of respiration estimates to soil temperature is presented in Fig. 4 for the two sites; all daytime estimates (R_D) are presented, whereas nighttime F_c is only plotted when soil moisture was not limiting.

For a given temperature in Italy, respiration was consistently greater at the harvested site, and this is reflected in the derived values of R_D and Q_{10} (Table 5). Although soil moisture constrains daytime respiration at high temperatures, both sites otherwise show good agreement between daytime- and nighttime-derived respiration estimates (at the mature site, this hinges on the morning flush criterion). During the coldest winter spells, respiration was typically near $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ for both sites (note that the soil was quite dry in winter 2002, so cold temperatures are not represented in Fig. 4b). At the harvested site, F_c reached ca. $9 \mu\text{mol m}^{-2} \text{s}^{-1}$ as soil temperatures warmed to approach 20°C , while the mature site had considerably less respiration.

Table 5 Q_{10} model parameters (Eqn (2)) for ecosystem respiration by the harvested (C) and mature (M) sites (\pm standard error estimates)

Country	Site	Night		Day	
		R_{15}	Q_{10}	R_{15}	Q_{10}
Britain	M	5.10 ± 0.11	3.23 ± 0.14	5.48 ± 0.67	2.87 ± 1.43
	C	7.56 ± 0.12	4.78 ± 0.16	N/A	N/A
Italy	M	3.28 ± 0.05	2.15 ± 0.09	N/A	N/A
	C	4.83 ± 0.10	2.74 ± 0.11	N/A	N/A
Finland	M	7.67 ± 0.18	5.69 ± 0.15	10.00 ± 1.64	6.24 ± 1.48
	C	4.16 ± 0.12	3.47 ± 0.24	N/A	N/A
France	M	5.39 ± 0.12	2.46 ± 0.13	2.91 ± 0.20	2.48 ± 0.64
	C	2.79 ± 0.09	2.05 ± 0.16	2.13 ± 0.11	1.64 ± 0.19

Units for R_{15} are $\mu\text{mol m}^{-2} \text{s}^{-1}$, while Q_{10} is dimensionless. Nighttime respiration estimates are from direct net ecosystem exchange (NEE) measurements, filtered by u_* . Daytime estimates from the hyperbolic empirical model, as R_D (Eqn (1)). Note that the Q_{10} defined here incorporates effects of numerous factors (e.g. substrate, soil moisture, root and microbial populations), and should not be taken as the temperature dependence of metabolic processes.

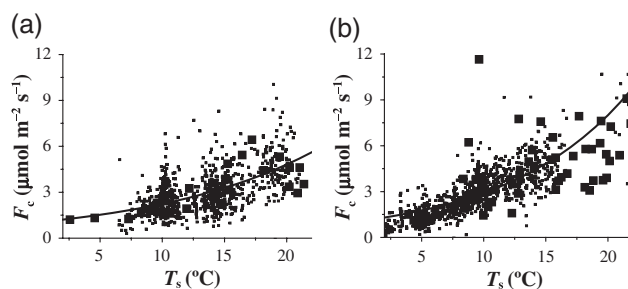


Fig. 4 Ecosystem respiration as a function of soil temperature for the Italian sites. For nighttime measurements, the carbon flux is plotted vs. soil temperature (F_c vs. T_s , small symbols), and the empirical model is overlaid (dark line); daytime respiration estimates are plotted vs. fortnightly, daytime mean temperature (R_D vs. T_s , large symbols): (a) mature site; (b) harvested site.

The Italian harvested site showed little variation in the temperature dependence of respiration between the successive years following harvest (data not shown). When discriminating between years, small differences in derived empirical models appeared to be due solely to a lack of temperature range with moist soil conditions, particularly in 2002. Therefore, a single Q_{10} model was applied for the Italian harvested site. However, despite similar air temperatures, the year 2000 had higher soil temperatures (which corresponded to higher respiration) than the following years.

Figure 5 shows the temperature dependence of respiration estimates in Finland; at any temperature, respiration was higher in the mature forest. At the clear-cut, with only a few months of measurements, there were insufficient estimates of daytime respiration (R_D) to establish a Q_{10} model. Daytime respiration estimates were larger than nighttime F_c at similar temperatures. For the mature forest, the same is true at the highest temperatures, whereas the daytime and

nighttime estimates agree well for the rest of the year. Over the range of soil temperatures sampled at the harvested site (8–16 °C), respiration is lower than at the mature site, consistent with the derived model parameters for Finland.

In France, the mature site respired significantly more than the harvested site at similar temperatures (Fig. 6). For the clear-cut, where the u_* criterion rejected the majority of the data, the daytime and nighttime respiration estimates are mostly similar, but with larger nighttime estimates at warm temperatures. If the morning flush criterion is not applied when developing light-response curves, these estimates agree better (not shown). For the mature site, nighttime TER estimates are higher than those estimated from daytime R_D across the temperature range. In addition to the Q_{10} model derived here, Fig. 6b shows the model derived by Berbigier *et al.* (2001) from nighttime NEE measurements at the same site during 1997–1998; the two models are very similar.

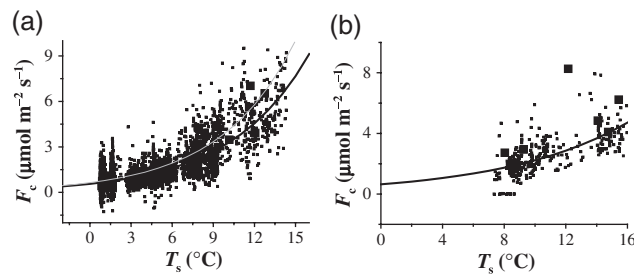


Fig. 5 Ecosystem respiration as a function of soil temperature for the Finnish sites. For nighttime measurements, the carbon flux is plotted vs. soil temperature (F_c vs. T_s , small symbols), and the empirical model is overlaid (dark line); daytime respiration estimates are plotted vs. fortnightly, daytime mean temperature (R_D vs. T_s , large symbols), and the empirical model is overlaid for the mature site (light line): (a) mature site; (b) harvested site.

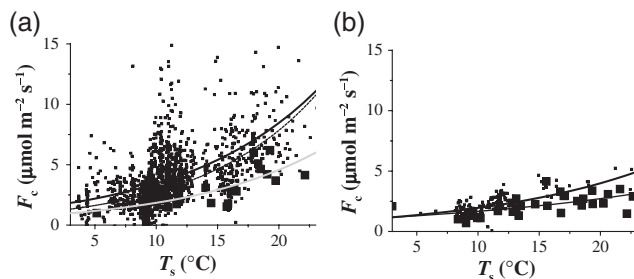


Fig. 6 Ecosystem respiration as a function of soil temperature for the French sites. For nighttime measurements, the carbon flux is plotted vs. soil temperature (F_c vs. T_s , small symbols), and the empirical model is overlaid (dark line); the nighttime respiration model for the same ecosystem derived by Berbigier *et al.* (2001) is also plotted (dashed line); daytime respiration estimates are plotted vs. fortnightly, daytime mean temperature (R_D vs. T_s , large symbols), and the empirical model is overlaid (light line): (a) mature site; (b) harvested site.

Response of TER to soil moisture

As previously noted, the response of ecosystem respiration to temperature broke down in Italy when the fractional volumetric soil water content fell below 0.4. Although the model parameters were determined from moist conditions over a somewhat limited temperature range, it was found that the deviation from this model related well to the shortfall in soil water, relative to the threshold value. Examining the soil water deficit at the mature (harvested) site, a simple linear decline in respiration explained 5.9% (19.9%) of the variance in the ratio of measured/predicted nighttime F_c – where predictions were made via the Q_{10} model developed for moist soil conditions. The ‘dry’ respiration model is simply the moist (Q_{10}) model, multiplied by the factor α :

$$\alpha = 1 - \beta(0.4 - W_s), \quad (3)$$

where W_s is the volumetric, fractional soil water content, and β is the linear decline factor of 4.02 (2.69).

Carbon exchange trends

Integrated carbon exchange estimates from these four site comparisons support the hypothesis that cutting

converts forest carbon sinks into sources. Figure 7 presents a summary of harvested/undisturbed carbon exchange comparisons across countries. Among all sites, effects of harvest disturbance explain most of the variability in NEE. Generally, mature stands were estimated as carbon sinks ranging from ca. 100 to 500 gC m⁻² annually, while harvested sites were sources of similar magnitude. However, the mechanisms by which this occurred varied between sites, as is elucidated by examining the components of NEE. Harvest reduced in GPP in every case, but the coppice site in Italy showed a capacity for rapid regeneration; the effects of harvest on respiration vary from a large increase in the coppice stand to sizeable reductions in high forestry.

In Britain, gap-filled NEE measurements indicated that the mature forest was a large carbon sink (Fig. 8a), sequestering nearly 500 gC m⁻² annually. The empirical models decomposed this net exchange into nearly offsetting photosynthetic and respiratory components of larger magnitudes. The application of Eqn (1) to measured F_p yielded an estimated 1970 gC m⁻² of annual GPP, and application of the two Q_{10} models (with daytime and nighttime respiration estimates) to soil temperatures yielded fairly consistent respiration

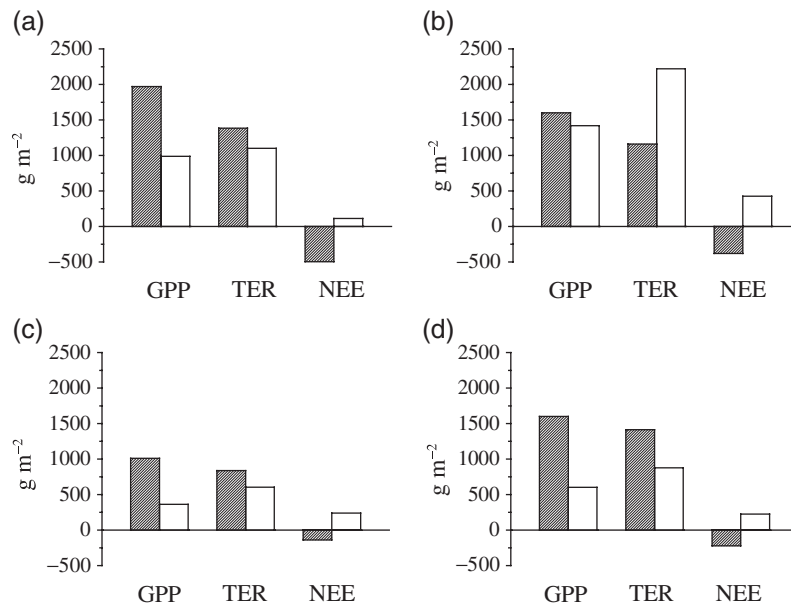


Fig. 7 Comparison of annual ecosystem carbon exchange components (GPP, TER and NEE) between mature (shaded) and harvested (clear) forest sites in (a) Britain, (b) Italy, (c) Finland, and (d) France. Where appropriate, TER and NEE represent the average of two estimates developed in parallel (e.g. TER_1 and TER_2).

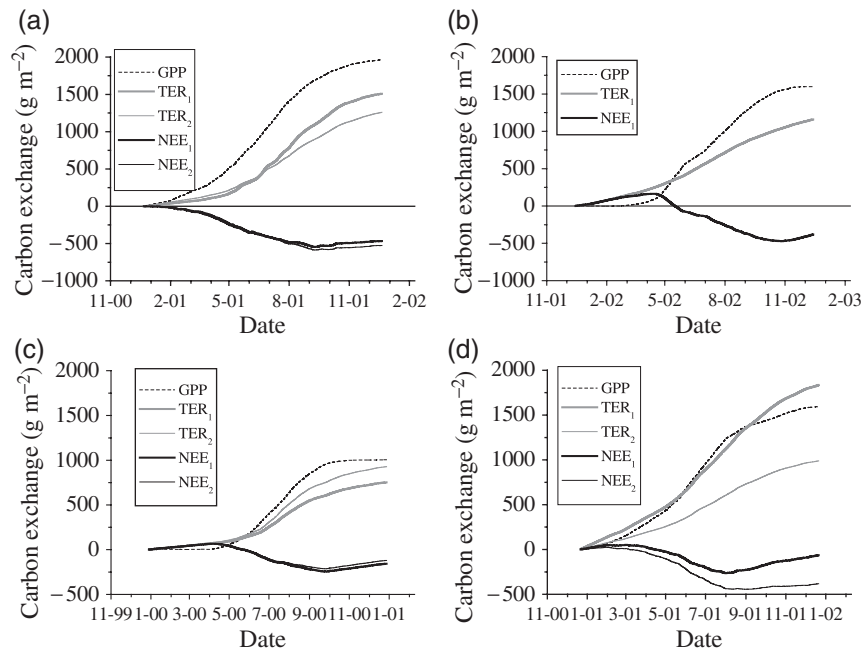


Fig. 8 Accumulated carbon exchange for the mature forest sites. GPP is from application of Eqn (1) with parameters a_1 and a_2 acting on measured light (F_p); TER is from Eqn (2) with R_{15} and Q_{10} derived from nighttime F_p measurements (TER_1) or daytime R_D (TER_2); NEE is from F_c measurements gap filled with GPP and TER_1 (NEE_1) or TER_2 (NEE_2). The mature sites are plotted: (a) Britain, (b) Italy, (c) Finland, and (d) France.

estimates ($TER_1 = 1510 \text{ g C m}^{-2}$ and $TER_2 = 1260 \text{ g C m}^{-2}$). From winter through autumn, the models estimated that GPP exceeded TER, and this agrees with negative NEE measurements; respiration made slight

gains in autumn, as NEE rose slightly towards zero. At this site, the difference between estimated GPP and TER is consistent with measured net exchange ($NEE_1 = -467 \text{ g C m}^{-2}$ and $NEE_2 = -525 \text{ g C m}^{-2}$). When

not applying the morning flush criterion, light response curves were somewhat different, with estimated GPP reduced by 8%, and TER_2 increased by 18%, such that the carbon sink estimated by gap filling with daytime respiration estimates ($-NEE_2$) is reduced by 76 g C m^{-2} .

In the spruce forest, inferential calculations suggested that harvesting (and replanting) halved photosynthesis, converting a mature stand carbon sink into a source during the years following disturbance. Direct annual integration was not attempted for the harvested site, and no daytime respiration models were developed (TER_2). Instead, tight linear relationships with negligible offsets were observed between available estimates of GPP and nighttime respiration (TER_1) when comparing with the mature site, and these were used to extrapolate to annual sums. Harvested site GPP was 50.2% that of the mature site ($R^2 = 0.92$, $N = 1546$), and TER_1 was 73.1% ($R^2 = 0.89$, $N = 3410$). As a result, annual estimates were 988 g C m^{-2} for GPP and 1100 g C m^{-2} for TER_1 at this site, suggesting an annual source of order 112 g C m^{-2} (NEE_1).

The carbon balance in Fig. 8b shows that the mature site in Italy is a carbon sink. Relative to the British mature forest, this site had somewhat less GPP (1600 g C m^{-2}), and a smaller estimate of TER_1 (1160 g C m^{-2}), and the net exchange determined from gap-filled measurements was somewhat smaller ($NEE_1 = -381 \text{ g C m}^{-2}$). The seasonal variation was also distinct, as TER dominated the leafless winter (with GPP near zero), and carbon fixation was delayed until leaf-out in spring. Also at this site, the difference between modeled GPP and TER agreed fairly well with the NEE determined from gap-filled measurements. While application of the morning flush criterion was important at this site, daytime respiration estimates were not integrated annually (TER_2), and no comparison of day/night respiration estimates was possible; when the flush criterion is not applied, annual GPP is estimated to be 8% larger.

Examination of concurrent data in Italy reveals that harvest converted the mature forest sink to a source of the same magnitude (Fig. 7), largely due to enhanced respiration. In 2002, GPP at the harvested site was 85% of that at the mature site ($GPP = 1420 \text{ g C m}^{-2}$), but TER was much larger ($TER_1 = 2220 \text{ g C m}^{-2}$). However, this period is more than two years after harvest. Unfortunately, the data from the Italian harvested site were divided by a long gap in F_p data, which prevented the calculation of GPP and thus gap-filling of NEE. Therefore, the period from 4 April to 31 December is examined for every year; comparison of this period in 2002 with the entire year reveals that virtually all of GPP is contained in this time frame ($GPP = 1350 \text{ g C m}^{-2}$), which encompassed virtually all of the

leafy season, while perhaps 10% of TER is lost ($TER_1 = 1990 \text{ g C m}^{-2}$) such that the NEE estimate for this fraction of the year ($NEE = 288 \text{ g C m}^{-2}$) underestimates the annual value considerably.

For the postharvest period from April to December of 2000 in Italy, GPP is reduced by about 40% ($GPP = 956 \text{ g C m}^{-2}$), while TER roughly doubles ($TER_1 = 2280 \text{ g C m}^{-2}$), relative to the undisturbed case. During these 9 months, the Italian harvested site was a sizeable carbon source ($NEE = 591 \text{ g C m}^{-2}$), and for the year immediately following harvest, the site must be estimated as a large carbon source, with NEE approaching 1000 g C m^{-2} . During the same nine-month period in 2001, carbon exchange values were similar to those for 2002 ($GPP = 1290 \text{ g C m}^{-2}$; $TER_1 = 1950 \text{ g C m}^{-2}$; $NEE_1 = 212 \text{ g C m}^{-2}$). For this site, it cannot be claimed that the difference between modeled GPP and TER agrees with NEE determined from gap-filled measurements during any year. This is largely because of difficulties in (empirically) modeling respiration at high temperatures. For example, when Eqn (3) was applied to fortnightly daytime means of soil temperature and moisture content (analysis not presented), modeled respiration corresponded well to the R_D estimate, but only at soil temperature less than 20°C . At warmer temperatures, the model consistently yielded larger respiration estimates than R_D . This suggests that the empirical model for respiration could be greatly improved, and TER is likely overestimated in summer. However, this is not very important to the estimate of NEE, since gap-filling at this site was minimal. When not applying the morning flush criterion, light response curves were only slightly different, such that estimated GPP was 3.7% smaller in 2000, 0.3% smaller in 2001, and 3.5% larger in 2002.

Figure 8c presents the carbon exchange estimates for the Finnish mature site, which was a carbon sink in 2000. This site has modest photosynthesis for a mature forest, with GPP more similar to harvested sites in other countries ($GPP = 1010 \text{ g C m}^{-2}$). However, TER is also quite low ($TER_1 = 750 \text{ g C m}^{-2}$; $TER_2 = 927 \text{ g C m}^{-2}$), and the forest is a net carbon sink over the year ($NEE_1 = -157 \text{ g C m}^{-2}$; $NEE_2 = -119 \text{ g C m}^{-2}$). There was a significant difference at this site when Q_{10} models were derived from nighttime F_c vs. from daytime R_D , and the annual TER estimates diverge significantly. However, the effect on annual NEE (via gap filling of nighttime data) was not very large in absolute terms. At this site, application of the morning flush criterion did not change the hyperbolic light-response models.

As was the case in Britain, inferential calculations suggest that harvest disturbance in Finland converted carbon sequestration by mature Scots pines into an annual source. Estimates of GPP and TER for the

Finnish harvested site, with no permanent tower, were related linearly to corresponding values for the mature site, again with negligible intercept. During periods with appropriate estimates, the harvested site had 36.0% of photosynthesis ($R^2 = 0.71$, $N = 2890$), and 80.3% of respiration ($R^2 = 0.93$, $N = 5376$), relative to the mature site. Extrapolating these relationships to annual values yields predictions of 363 g C m^{-2} for GPP and 602 g C m^{-2} for TER at this site, predicting that the harvested ecosystem released 239 g C m^{-2} to the atmosphere during 2000.

Trends in the carbon balance for the French mature site are shown in Fig. 8d, depicting a carbon sink. The site had GPP similar to, or perhaps a bit smaller than, the mature sites in Italy and Britain (1600 g C m^{-2}). However, depending on the parameters used to model respiration, TER was either very large ($\text{TER}_1 = 1840 \text{ g C m}^{-2}$), or half that ($\text{TER}_2 = 989 \text{ g C m}^{-2}$). The differences in respiration estimates were so great that they affected the estimated annual NEE, via gap-filling. When filling gaps with nighttime-derived R_D and Q_{10} , which predict large respiration, annual carbon fixation was modest ($\text{NEE}_1 = -63.1 \text{ g C m}^{-2}$); on the other hand, gap filling with daytime-derived model parameters led to an estimated carbon sink typical of those reported for forests ($\text{NEE}_2 = -381 \text{ g C m}^{-2}$). The morning flush criterion had negligible effect on the light-response curves, and therefore annual carbon flux estimates at this site.

Lastly, the harvested French site was a carbon source. This site had quite weak GPP (602 g C m^{-2}), and respiration was also low relative to other ecosystems ($\text{TER}_1 = 993 \text{ g C m}^{-2}$; $\text{TER}_2 = 763 \text{ g C m}^{-2}$) such that the ecosystem was a moderate carbon source for the 2001 calendar year ($\text{NEE}_1 = 273 \text{ g C m}^{-2}$; $\text{NEE}_2 = 177 \text{ g C m}^{-2}$). The morning flush criterion also had little influence at this site.

Discussion

Apparent effects of harvest disturbance on carbon exchange

These results support the hypothesis that harvest converts mature forest carbon sinks into ecosystem carbon sources of similar magnitude for a number of years; however, the effects of the disturbance on NEE component processes (GPP and TER) varied according to harvest practice or tree species. While harvest led to a substantial drop in GPP in every case, in Italy this was mitigated by the coppice-with-standard harvest practice and the oaks' regenerative capability such that photosynthetic recovery was rapid in comparison with the clear-cuts. The coppice stand was even more

distinct in the response of respiration to harvest, showing increased respiration whereas the clear-cuts showed reductions.

The coppiced site enjoyed two advantages over the clear-cuts in the recovery of GPP. Firstly, the sparing of the 'standards' meant that the canopy, although dramatically reduced, was not obliterated. Due to loss of leaf area, all harvested sites showed dramatic reductions in photosynthetic capacity and apparent light-use efficiency, relative to the undisturbed sites, but the immediate effect of disturbance was mitigated in Italy. Secondly, the coppice site showed rapid regeneration of GPP, whereas meager photosynthesis persisted at the clear-cut sites for many years. By the second growing season after coppicing, both photosynthetic capacity and GPP had rebounded nearly to preharvest levels. Photosynthesis fared far worse in the clear-cuts. Despite replanting in Britain, the clear-cut showed only half the GPP of the mature forest in the third year following the disturbance; in Finland (France), GPP by the naturally regenerating clear-cut was less than 40% that of the mature forest in the fifth (second) year following harvest.

As suggested in the Introduction, differences in the reaction of TER to harvest appear to correspond to the fate of the roots. Following clear-cutting of spruce and pine, root death led to declines in respiration (particularly autotrophic), notwithstanding any presumed enhancements in heterotrophic respiration due to soil warming or the input of residues to the soil. In fact, the heterotrophic communities likely suffered from lack of photosynthetic assimilates (Hagerman *et al.*, 1999; Högberg *et al.*, 2001; Janssens *et al.*, 2001); in any event, reduced TER in the clear-cuts does not support the enhanced decomposition premise. In the coppiced stand, however, the oaks (like previously studied aspens) responded strategically to harvest disturbance, mobilizing carbohydrate reserves in order to sustain roots (autotrophic respiration), to develop suckers and regenerate leaf area (growth respiration). The flow of photosynthates also continued via the 'standards' sustaining the heterotrophic community, which could exploit detritus inputs from harvest residues. Soil temperatures were enhanced during the first year after coppicing, and respiration was higher. Regardless of temperature, however, respiration was enhanced in the coppiced stand relative to the undisturbed oaks.

While species-dependent characteristics are important, ecosystem recovery from any disturbance can also depend on general conditions for growth (Law *et al.*, 2003), as has been seen in the case of fire. Using stock changes in black spruce to examine NPP and measurements of heterotrophic respiration, Bond-Lamberty *et al.* (2004) inferred that NEE increases following fire

because the total elimination of photosynthesis more than offsets ecosystem respiratory reductions. While the effect of fire on carbon exchange in these forest sites was quite similar to those of clear-cutting in the present study, recovery was found to depend on stand drainage (Wang *et al.*, 2003) and was delayed in the limited water case. Similarly, Wirth *et al.* (2002) determined that site quality was key in determining the recovery time (from post-disturbance source to carbon sink) for Scots pines following fire. Finally, as extreme examples, fire has been found to stimulate carbon fixation in both tropical savanna (Santos *et al.*, 2003) and successional temperate sedgebrush (Obrist *et al.*, 2003).

Comparison with other studies

The forest carbon exchange estimates reported here agree with previous reports from the same or similar sites, to within the typically reported NEE uncertainty of ca. 100 g C m^{-2} (e.g. Anthoni *et al.*, 1999; Kowalski *et al.*, 2003). In Britain, the 500 g C m^{-2} sink represented by mature sitka spruce is not different from that determined for a UK site in similar climatic conditions (Valentini *et al.*, 2000). At the coppiced site in Italy, Rey *et al.* (2002) reported 900 g C m^{-2} of soil respiration for the year 2000 (excluding January), explaining roughly half of the TER estimated here; the remainder must therefore be explained by above-ground (largely growth) respiration as the canopy regenerates via suckers. Also in agreement with the mature/coppiced comparison here, Tedeschi *et al.* (in preparation) examined soil CO_2 efflux vs. stand age in the same forest, and found maximum efflux in the recently coppiced stand, then decreasing with time since harvest. In Finland, the 140 g C m^{-2} annual fixation by the mature site is consistent with previous reports from the very same forest (Valentini *et al.*, 2000). The same can be said about the French clear-cut as a 240 g C m^{-2} annual source (cf. Kowalski *et al.*, 2003). Finally, while the French mature site was found to be a sink, uncertainties in estimated TER, combined with gaps introduced by the u_* criterion, led to large uncertainties in the sink strength, which is either lower or much lower than the previous estimate for the same forest in 1997–1998 (Berbigier *et al.*, 2001). Nonetheless, carbon exchange estimates are consistent with the (admittedly large) range of values previously reported for this site (Valentini *et al.*, 2000; Berbigier *et al.*, 2001; Kowalski *et al.*, 2003).

The greatest differences in the magnitude and temperature dependence of respiration were observed when comparing northerly vs. southerly, rather than mature vs. harvested, sites. The combination of large carbon reserves and cold temperatures that often

suppress respiratory processes leads to enhanced seasonality and temperature dependence in more northerly sites. In the Mediterranean climate, suppression of respiration occurred in summer as well (via moisture constraints) and maximum respiration rates occur in autumn (Fig. 2b). Elsewhere, and particularly in the boreal forest, peak respiration coincides with summer heat. These variations with climate appear to hold, independent of the effects of harvest.

Methodological considerations

At all sites, the response of carbon fluxes (F_c) to light (F_p) conformed to non-linear, fortnightly empirical models that are consistent with our understanding of ecophysiology at the sites, and further provide insight regarding unexpected aspects of carbon exchange processes. At any given site, seasonal trends in respiration (R_D) and apparent photosynthetic capacity (a_1) correspond to expected, respective dependencies on soil temperature and phenology. When examining weekly empirical models, Kowalski *et al.* (2003) observed a lag in R_D relative to a_1 , and suggested that this may reflect the dependence of below-ground respiration on photosynthetic assimilates. Such a lag is not noted here, possibly due to lack of temporal resolution in the two-week model period, which was selected according to criteria facilitating annual integration.

When neither turbulent mixing nor soil moisture was limiting, nighttime F_c measurements corresponded to soil temperature following a Q_{10} relationship. The friction velocity (u_*) thresholds determined here for mature forest sites correspond to those published elsewhere (Baldocchi, 2003), while larger thresholds were needed for harvested sites. We propose that this may be due to the depressed surface (relative to nearby forest), which is nonetheless rough and further inhibits turbulent exchange under stable conditions. By contrast, exposed and smoother sites such as prairies appear to achieve sufficient mixing with less vigorous turbulence (Suyker & Verma, 2001).

The magnitude and temperature dependence of respiration estimates during nighttime (from measured F_c) vs. daytime (from modeled R_D) generally agreed well. The exceptions were in Finland where daytime R_D was larger than nighttime F_c at the harvested site and in summer at the mature site, and in France where nighttime F_c exceeded daytime R_D at the mature site and in summer at the harvested site. It should be recognized that respiration determined from nighttime eddy fluxes may suffer from large uncertainties, the u_* criteria notwithstanding. The daytime/nighttime respiration comparison depended on the morning flush

criterion at some sites, with notable improvement in the coppiced site, but slight deterioration in the French clear-cut (in summer). At any rate, the differences between harvested and mature sites in each country exceeded these differences corresponding to different estimation methods.

In fact, the conclusions drawn from comparisons of respiration in harvested vs. mature sites are independent of whether derived from nighttime flux measurements or daytime (empirical modeling) estimates. Although the derived values of R_{15} and Q_{10} were somewhat different, these may be determined more by differences in the seasonality of respective temperatures, rather than annual respiration (e.g. Xu & Qi, 2001). In the case of Italy, the empirical respiration model must be considered suspect at high temperatures. Nevertheless, from examination of daytime and nighttime respiration estimates, it is clear that the coppiced oak site had greatly enhanced respiration relative to the mature site; enhanced respiration was noted at equivalent soil temperatures, and these were elevated in the harvested site due to lack of canopy shade, particularly during the year 2000. Conversely, at all of the clear-cut sites, respiration was reduced relative to the undisturbed case.

Following the general approach of combining measurements with empirical modeling, a simple reduction in respiration related to the soil water deficit was observed and applied for the Italian sites. The approach employed here is a hybrid of previously used techniques to model soil temperature and humidity effects on respiratory processes. It includes the constant influence of temperature via a Q_{10} or exponential model (Hanson *et al.*, 1993; Epron *et al.*, 1999), and the on/off influence of drought based on a threshold in soil water content (Rey *et al.*, 2002). These latter investigators, working in the same (Italian harvested) ecosystem, determined a lower threshold for the onset of drought, the difference being that they excluded the influence of temperature on respiration during drought conditions. In the present study, the model fit the data reasonably well, and served for gap filling in a way that does not bias annual estimates. However, this simple model is in no way intended to describe processes limiting soil respiration, a subject with abundant opportunities for future investigation.

Uncertainties in carbon exchange estimates

While it is always a challenge to estimate uncertainties in such carbon exchange estimates, these paired comparisons of (otherwise similar) harvested and mature stands via like methodologies have yielded certain distinct conclusions. Estimates of NEE from

integration of direct measurements – with typical uncertainties of ca. 15% (e.g. Goulden *et al.*, 1996; Anthoni *et al.*, 1999) – must be considered more reliable than model-decomposed components GPP and TER. The mean effect of harvest on NEE (+560 gCm⁻², consistently converting sink to source) far exceeds typical annual uncertainties of order 100 gCm⁻² (see above). If larger uncertainties in TER and GPP must be accepted, nevertheless evidence from half-hour fluxes strongly supports the conclusions regarding the effect of harvest on annual exchange. Figures 3–6 clearly show that, at equivalent temperatures, harvest reduced respiration in coniferous high forestry, whereas respiration was provoked by coppicing in Italy. Finally, the effects of harvest on GPP reflected in both Fig. 1 and annual exchange estimates are consistent with the devastation of canopy photosynthesis, followed by rapid recovery in the case of the coppice ecosystem.

Annual carbon exchange estimates for the British and Finnish harvested sites must be considered less reliable than elsewhere, due to extrapolation from sparse data coverage. Here, errors in mature-site GPP and TER estimates propagate to the post-harvested estimates, and even small errors in these nearly offsetting terms imply relatively large errors in NEE. In Britain, sampling covered the range of seasons, and the correlation between mature and harvested sites was always high, lending credibility to the annual GPP and TER estimates. Estimates for the Finnish harvested site, with measurements limited to late summer and early fall, are more dubious. The simple model employed ignores differences in phenology; likewise neglected are soil snow-cover and particularly early summer soil warming, both likely enhanced in the clear-cut. Finally, a single fortnight in late summer at this site had unusually high estimates of R_D and a_1 (Fig. 2c), with unusually large standard errors; the influence of a single fortnight, whether included or rejected, is enhanced by the short sampling period at this site.

Conclusions

Paired comparisons of undisturbed forest vs. stands harvested via two methods – clear-cutting and coppicing with standard – revealed the effects of harvest on forest ecosystem carbon exchange. Clear-cutting of coniferous forests led to declines in TER, whereas respiration was found to increase following coppice harvesting of oaks. Harvest reduced GPP in every case, but in the case of coppicing both mitigation and rapid recovery were observed. Despite these different impacts on component processes GPP and TER, the two harvest types yielded similar effects on NEE: harvesting consistently converted mature forest carbon sinks into

sources. For each of the managed forest types examined, these results provide two essential points in the carbon balance timeline. However, an accurate model of the forest carbon balance as a function of time since harvest (NEE vs. age), including the critical compensation point where stands regenerating from harvest revert to fixing carbon annually, will be necessary in order to characterize net biome production, or the carbon balance of managed forestry.

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