GLOBAL BIOGEOCHEMICAL CYCLES, VOL. 23, GB4008, doi:10.1029/2008GB003381, 2009

Carbon and nitrogen balances for six shrublands across Europe

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Received 16 September 2008; revised 19 May 2009; accepted 11 June 2009; published 15 October 2009.

[1] Shrublands constitute significant and important parts of European landscapes providing a large number of important ecosystem services. Biogeochemical cycles in these ecosystems have gained little attention relative to forests and grassland systems, but data on such cycles are required for developing and testing ecosystem models. As climate change progresses, the potential feedback from terrestrial ecosystems to the atmosphere through changes in carbon stocks, carbon sequestration, and general knowledge on biogeochemical cycles becomes increasingly important. Here we present carbon and nitrogen balances of six shrublands along a climatic gradient across the European continent. The aim of the study was to provide a basis for assessing the range and variability in carbon storage in European shrublands. Across the sites the net carbon storage in the systems ranged from 1,163 g C m^{-2} to 18,546 g C m^{-2}, and the systems ranged from being net sinks (126 g C m^{-2} a^{-1}) to being net sources (-536 g C m^{-2} a^{-1}) of carbon with the largest storage and sink of carbon at wet and cold climatic conditions. The soil carbon store dominates the carbon budget at all sites and in particular at the site with a cold and wet climate where soil C constitutes 95% of the total carbon in the ecosystem. Respiration of carbon from the soil organic matter pool dominated the carbon loss at all sites while carbon loss from aboveground litter decomposition appeared less important. Total belowground carbon allocation was more than 5 times aboveground litterfall carbon which is significantly greater than the factor of 2 reported in a global analysis of forest data. Nitrogen storage was also dominated by the soil pools generally showing small losses except when atmospheric N input was high. The study shows that in the future a climate-driven land cover change between grasslands and shrublands in Europe will likely lead to increased ecosystem C where shrublands are promoted and less where grasses are promoted. However, it also emphasizes that if feedbacks on the global carbon cycle are to be predicted it is critically important to quantify and understand belowground carbon allocation and processes as well as soil carbon pools, particularly on wet organic soils, rather than plant functional change as the soil stores dominate the overall budget and fluxes of carbon.

Citation: Beier, C., et al. (2009), Carbon and nitrogen balances for six shrublands across Europe, *Global Biogeochem. Cycles*, *23*, GB4008, doi:10.1029/2008GB003381.

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0886-6236/09/2008GB003381

1. Introduction

[2] Shrublands are widespread ecosystems across Europe and are integrated parts of European landscapes varying from wet and moist moorlands in north and west Europe to dry Calluna heathlands along the Atlantic coast from northern Norway to northern Spain and continental forest-steppe shrubland in central Europe and Mediterranean maquis ecosystems in southern Europe. They are mostly cultural landscapes that have been shaped by human activities through low intensive agro/pastoral land use and have provided a variety of regulatory and provisioning ecosystem services such as grazing, hunting, and fuel provision [e.g., *Gimmingham*, 1972; *Perevolotsky and Seligman*, 1998; *Wessel et al.*, 2004; *Millennium Ecosystem Assessment*, 2005]. As natural or seminatural ecosystems with low-intensity management, they are usually considered relatively sensitive and vulnerable to environmental changes such as increased N deposition [e.g., *Bobbink et al.*, 1998], climate change [e.g., *Lavorel et al.*, 1998; *Pinol et al.*, 1998], changes in management [*Aerts*, 1993], and land abandonment [e.g., *Perevolotsky and Seligman*, 1998; *MacDonald et al.*, 2000].

[3] In the past, most research in shrublands has focused on the ecological processes at single sites while less emphasis has been attributed to their biogeochemical cycling across larger scales. However, there is a strong need for empirical studies increasing our understanding of the functioning of the shrubland ecosystems if we are to develop and test ecosystem models and predict effects of global change. In particular, the carbon storage is of interest because shrubland ecosystems constitute a significant carbon storage, e.g., in those areas where agricultural use of shrublands is noticeable [*Tate et al.*, 2003] and their potential role in driving climate change through the carbon feedback to the atmosphere is important. In this respect, significant attention has been devoted to forested ecosystems and their potential role in sequestering carbon in the wood [e.g., *Hyvönen et al.*, 2007], but recently the potential role of shrublands as carbon sources or sinks in the future has gained increasing attention [e.g., *Goodale and Davidson*, 2002].

[4] In contrast to carbon, the nitrogen status of heathlands has been the subject of many studies because of the concern that increased levels of reactive nitrogen in the atmosphere is resulting in changes in species composition and biodiversity [e.g., *Bobbink et al.*, 1998]. However, because of the strong interactions with carbon, nitrogen will potentially also have a strong influence on the magnitude of the carbon sink in shrubland ecosystems as known for other terrestrial systems [e.g., *De Vries et al.*, 2006] and thereby on shrubland responses to elevated CO_2 and climate change.

[5] In this study, we describe the carbon and nitrogen budgets from six semi-natural European shrubland ecosystems (ecosystems retaining many natural features because of low management activities) involved in the EU projects CLIMOOR and VULCAN [*Beier et al.*, 2004, 2008; *Peñuelas et al.*, 2007]. The sites represent coastal, continental, and Mediterranean shrubland ecosystem types and span gradients in precipitation, temperature, and nitrogen inputs. The aim of the study was to provide a basis for assessing the range and variability in carbon storage in European shrublands. Because of the seminatural nature of the ecosystems with low or no management we hypothesized that the carbon balance at all sites would be close to steady state and that the soil carbon pool would be dominating carbon fluxes.

2. Materials and Methods

2.1. Site Descriptions and Study Characteristics

[6] The studies were carried out at shrubland ecosystems in Wales (UK), Denmark (DK), the Netherlands (NL), Hungary (HU), Spain (SP), and Italy (IT) (Table 1) with different climatic conditions from relatively wet and cold conditions in northwest UK through continental extremes in central Europe to warm and dry Mediterranean conditions in northeast Spain and western Italy. Also, the ecosystems cover a gradient in N deposition ranging from low inputs in Spain to high inputs in the Netherlands. The sites are representative for their respective regions and differ in soil type, plant species composition, and successional stage. The latter was largely depending on time elapsed since the latest disturbance (Tables 1 and 2). They are all subject to relatively low degrees of management.

[7] At each site, three study plots (4 × 5 m) were established randomly in 1998 (DK, UK, SP, and NL) and 2001 (HU and IT) within 10–30 m from each other. Each plot was surrounded by a 0.5 m high steel frame to avoid walking and tramping in the plots, and sampling was done from movable platforms/boards in order to minimize disturbance in the plots. All measurements were replicated 2–3 times in each plot (unless otherwise stated) and averaged to provide one number per plot. An automated weather station was located centrally to the study area at each site, and air and soil temperature sensors and soil moisture probes were installed to monitor each plot [*Beier et al.*, 2004].

[8] Mean annual air and soil temperatures (3–5 years) were calculated from half-hourly measurements at each site (n = 3). Mean annual precipitation was calculated from measurements of monthly rainfall collected at each site by open funnels (n = 2/site). Wet N deposition was estimated from NO_3 and NH_4 content in the collected precipitation samples. Dry N deposition was estimated from wet N deposition assuming specific relationships between wet and dry N deposition according to standard procedures advised by the national meteorological institutes (DK, NL, and HU) or similar relationships between wet and dry N deposition as for DK (dry deposition = 51% of total N deposition) (UK, SP, and IT).

2.2. Plant Measurements

2.2.1. Aboveground Plant Biomass, Plant Growth, and Plant Tissue Chemistry

[9] Total plant biomass was estimated from pinpoint or point frequency measurements (n > 300 plot^{-1} a^{-1}) conducted each year in July (1998/2001 to 2004) by lowering a sharpened pin through the vegetation and recording each plant hit/height with the pin. In each site, similar measurements were done in plots (n = 10) outside the study plots followed by measurements of absolute biomass using destructive sampling. Regressions of biomass against pin hit

Table 1. VULCAN Site Characteristics

	Clocaenog, UK	Mols, DK	Oldebroek, NL	Kiskun Sag, HU	Garraf, SP	Capo Caccia, IT
Location	53°03′N 3°28′W	56°23′N 10°57′E	52°24′N 5°55′E	46°53′N, 19°23′E	41°18′N 1°49′E	40° 36′N 8° 9′E
Altitude (m)	490	58	25	130	210	35
Air temperature, year (°C)	8.2	9.0	10.1	10.8	15.6	15.6
Air temperature, July (°C)	12.4	18.2	17.8	22.8	24.6	24.8
Air temperature, January (°C)	4.3	1.5	2.0	−3.1	7.3	9.1
Precipitation, study period (mm a^{-1})	1741	644	940	509	580	511
Nitrogen, deposition (g N m^{-2} a^{-1})	2.1	1.6	4.1	1.2	0.5	1.0
Main growing season(s) (>5 °C more than 5 days)	April–Sept	April–Sept	April–Oct	April–Sept	Jan–May Oct–Dec	Jan–May Oct–Dec
Potential evapotranspiration (PET) (mm a^{-1})	302	590	595	1016	1034	1026
Actual evapotranspiration (AET) (mm a^{-1})	342	371	412	203	314	246
GDD (5 °C < T < 25 °C)	1312	1970	2111	2386	3079	3180
Available water content (2003) (mm)	76.4	39.1	30.1	6.3	14.4	17.4
Main plant growth limitation	T, N	N/P, H2O	P, H2O	N, H2O	H2O	H2O
Last major disturbance	Cutting (<1960)	Grazing (<1992) heather beetle + cutting (2000)	Sod cutting (1990)	Military 1970	Fire (1994)	Strip clearing after fire (1992)

numbers or height from these destructive samplings were used to estimate the biomass in the study plots [*Peñuelas et al.*, 2004, 2007]. Plant tissue C and N content was measured every year on plant tissue samples of leaves (grasses) or leaves, branches, and stems (shrubs) collected in July and August and C and N pools estimated by combining the biomass measurements and plant tissue chemistry.

2.2.2. Aboveground Plant Litter Production and Plant Litter Quality

[10] Litterfall samples from shrub vegetation of each plot were collected every 1, 2, or 6 months depending on the site, using 5–30 litterfall collectors (diameter 4.4–15 cm) randomly located under the plant canopies. The litter was oven-dried, ground, and analyzed for C and N. Litterfall

Table 2. Soil and Plant Characteristics

	Clocaenog, UK	Mols, DK	Oldebroek, NL	Kiskun Sag, HU	Garraf, SP	Capo Caccia, IT
			Soil Characteristics			
Soil type (FAO standard)	Peaty podzol	Sandy podzol	Haplic arenosol	Calcaric arenosols	Petrocalcic Calcixerepts	Luvi and Leptosoils
Top soil						
Depth (cm)	0–6	0–3	0–4	0–10	0–12	0–20
pH	3.9	3.7	3.7	7.9	8.1	7.7
C/N	37.4	18.5	22.5	14.3	12.8	34
SOM (%)	89	41	65	0.74	3.5	7.8
Bulk density (g/cm^3)	0.09	0.21	0.11	1.4	0.77	1.14
Deeper soil						
Depth (cm)	6–17	3–20	4–16	10–20	12–37	20–40
pH	4.0	4.1	3.8	8.1	8.3	7.8
C/N				6.7		52
SOM (%)	37	1.8	3.3	0.32	3.5	4.7
Bulk density (g/cm^3)	0.41	1.39	1.41	1.45	n/a	1.30
			Plant Characteristics			
Dominant plant species	*Calluna vulgaris Desch. Flexuosa Vacc. Myrtillus Empetrum nigrum*	*Calluna vulgaris Desch. flexuosa*	*Calluna vulgaris Desch. Flexuosa Mollinia caerulea*	*Populus alba Festuca vaginata Cynodon dactylon Stipa borysthenica*	*Erica multiflora Globularia alypum*	*Helichrysum italicum Cistus monspeliensis Dorycnium pentaphyllum Pistacia lentiscus*
Plant cover (%)	100	100	95	35	69	82
Number of plant species	7.4	8.7	5.5	19.3	8.1	11.6
Main rooting depth (cm)	0–10	0–10	0–10	0–10	0–10	0–10
NDVI[a]	0.77	0.66	0.71	0.30	0.58	0.60
Mean max height (cm)	50	80	50	50	100	80
Foliage N in new leaves[b] (%)	1.4	1.6	1.4	1.8	0.6	1.2

[a]NDVI, normalized difference vegetation (green biomass) index.
[b]Dominant plant species.

from grasses was estimated by assuming that the total annual biomass production is turned over every year.

2.2.3. Root Biomass and Root Litter Production

[11] Root cores (six cores in each plot, 4 cm diameter and 20 cm depth) were collected at each site and plot in 2002. All cores were divided into the upper and lower 10 cm and analyzed separately. Soil and roots in the cores were separated and analyzed for total root length [*Smit et al.*, 2000]. Because of a mistake, root biomass was not measured directly but had to be estimated indirectly from measured root lengths per soil volume based on the relationship between root length per volume and total root biomass measured by destructive sampling at the DK and UK sites (12 cores, 4.2 cm diameter) and cross checked with literature values for shoot/root ratios for the Mediterranean sites [*Silva and Rego*, 2004]. Root litterfall was estimated using the method proposed by *Gill and Jackson* [2000] who found a strong relationship between mean annual temperature and root turnover as a fraction of total roots in shrublands. On the basis of these estimates the annual root turnover fractions ranged from 28% of total root biomass at the coldest site in UK to 45% at the warm site in Italy.

2.3. Soil Measurements

2.3.1. Soil C and N Pools

[12] Soil C and N content was measured by collecting three soil cores from each study plot once. The soil cores were divided into the top organic soil layer (main rooting depth) and the top mineral soil or in the mor layer and upper mineral soil for the heathland sites. The soil was oven-dried (65°C); bulk density, carbon, and nitrogen content were measured; and the C and N pools were estimated [*Emmett et al.*, 2004].

2.3.2. Microbial Biomass

[13] The microbial biomass C was estimated from the difference in total extracted organic carbon between $CHCl_3$ fumigated and nonfumigated soil samples [*Brookes et al.*, 1985; *Vance et al.*, 1987; *Jonasson et al.*, 1996]. Duplicate samples (5 g) from each site were weighed. One sample was fumigated under a vacuum with ethanol-free chloroform overnight, and one sample kept nonfumigated. Both samples were extracted with potassium sulphate (0.5M K_2SO_4) for an hour and then filtered, and the DOC content of the filtrate was measured. Microbial biomass (g C m^{-2}) was calculated by subtracting the DOC in the nonfumigated samples from that found in the fumigated samples. A K_c-factor of 0.45 [*Vance et al.*, 1987] was used to convert the fluxes to biomass.

2.3.3. Litter Decomposition and Soil Organic Matter Decay

[14] The rate of litter decomposition (g C m^{-2} a^{-1}) was studied at each site by incubation of litter from the dominant species in litterbags (mesh size 1 mm) for 6–24 months [*Emmett et al.*, 2004]. The root litter decomposition rate was not measured at the sites but for each site assumed equal to aboveground litter decomposition as recently indicated in a global review showing comparable k values for root and conifer needle litter [*Zhang et al.*, 2008]. It should be noted that decomposition of root litter is studied relatively little relative to aboveground litter fractions, and there is considerable controversy in the literature regarding root litter decomposition rates depending significantly on traditional control factors (e.g., climate and litter quality) as well as methodological considerations (e.g., aboveground versus belowground incubation, litter bag types, and root litter fractions). For reasons of consistency and comparison we used the same reasoning across all sites in this study. The decay of soil organic matter (SOM) was estimated as the difference between estimated soil respiration and the sum of plant and root litter decay ($SOM_{C-decay} = Resp_{Soil} - Litter_{C-Above\ decay} - Litter_{C-Root\ decay}$).

2.3.4. Soil Respiration

[15] Soil respiration (g C m^{-2} a^{-1}) was measured by closed chambers consisting of a permanent base installed 5 cm into the soil (n = 3 (two bases per plot) (UK, DK, IT, HU, and NL) and n = 5 (SP)) and sampled on site by infrared gas analyzers or by gas chromatography in the laboratory [*Emmett et al.*, 2004; *Lellei-Kovács et al.*, 2008]. Measurements were taken at least monthly during 2002–2005 in daylight hours together with simultaneous measurements of temperature and soil moisture. Site specific Q10 functions were estimated by the relationship between temperature and soil respiration (separated into water-limited and non-water-limited periods [*Sowerby et al.*, 2008]) (r^2: UK, 0.71; DK, 0.58; NL, 0.82; HU, 0.51; SP, 0.68; IT, 0.39). The Q10 functions were used to calculate annual soil respiration fluxes for each site by summing monthly estimates on the basis of monthly mean temperatures. Campaigns of diurnal soil respiration measurements at each site showed agreement with the general Q10 functions across the diurnal cycle. For annual C balance calculations the measured total soil respiration was fractionated into autotrophic (i.e., root respiration) and heterotrophic respiration assuming that 67% of total soil respiration was heterotrophic [*Bond-Lamberty et al.*, 2004]. To some extent this assumption was supported by a short-term investigation at the NL site where soil respiration measured close to and apart from individual shrubs showed approximately 30% lower soil respiration apart from plants. These assumptions were further tested by comparing estimates for total belowground allocation (TBCA) calculated in this study with estimates proposed by *Raich and Nadelhoffer* [1989].

2.3.5. Nitrogen Mineralization Rate

[16] Seasonal mineralization rates for the four main seasons were estimated from the difference in NO_3 and NH_4 concentrations in 1 M KCl extracted soils from preincubated and postincubated paired soil cores (n = 3.5 cm diameter) incubated for 1–2 months at actual water content using the buried bag technique [*Emmett et al.*, 2004]. Annual mineralization rates were calculated from the seasonal daily rate obtained from the four incubations.

2.3.6. Hydrology

[17] A simplified daily soil water balance model (SWBM) for natural vegetation was developed and applied to each site to estimate daily soil water fluxes [*Allen et al.*, 1998, 2000] on the basis of site-specific soil characteristics (field capacity, wilting point, depth of the topsoil layer, and rooting depth). SWBM is driven by time series of rainfall and actual evapotranspiration. Daily values of actual evapotranspiration (ET_a) were estimated from the calculation of potential evapotranspiration (ET_o) in combination with

empirically determined site-specific vegetation coefficients (K_c), which were obtained by identification of specific growth stage lengths and splitting the computation into two components (so-called dual coefficient methodology) representing transpiration and evaporation corresponding to these growth stages [*Allen et al.*, 1998]. The potential impact of lack of soil moisture on transpiration reduction was also included. ET_o values were calculated using the FAO Penman-Monteith combination equation [*Monteith*, 1981; *Allen et al.*, 1998] or the Hargreaves-Samani method [*Hargreaves and Samani*, 1982, 1985] depending on the meteorological variables measured at each site. The determination of the K_c values and the calibration of the soil water balance model were made by trial and error comparing model output to soil water content measurements in order to achieve the best model performance.

2.3.7. Soil Water Chemistry and Element Leaching

[18] Soil water beneath the rooting depth was collected once or twice a month by means of porous cup soil water samplers and analyzed for NO_3^- and dissolved organic carbon (DOC) concentration. Leaching losses of NO_3^- and DOC were estimated by multiplying soil solution concentrations with the estimated water fluxes during the collection period [*Schmidt et al.*, 2004].

2.4. Carbon and Nitrogen Budget Calculations

[19] The budgets for the aboveground and belowground ecosystem compartments as well as the whole ecosystem were calculated for each of the sites according to the general concept that the change in a compartment equals the difference between input and output to the compartment plus the change in the pools within the compartment. In all equations the following abbreviations are used: Δ, change in pool size; Uptake, uptake or fixation in the pool; Litter, litter production; In, input; Out, output; Dep, deposition; Leach, leaching with soil water percolation; Min, mineralization; and Soilresp, soil respiration with indices for heterotrophic (Het-C) and autotrophic (Aut-C), respectively. Subtexts indicate elements and pools involved.

2.4.1. Aboveground C Balance

[20] The change in aboveground carbon pool ($\Delta_{C-Above}$) is equal to carbon uptake in plants ($Uptake_{C-Above}$) minus carbon in litterfall ($Litter_{C-Above}$):

$$\Delta_{C-Above} = Uptake_{C-Above} - Litter_{C-Above} \quad (1)$$

2.4.2. Belowground C Balance

[21] The change in belowground carbon ($\Delta_{C-Below}$) is calculated as the net difference between C input in form of DOC deposition (Dep_{DOC}), the change in C pools in roots ($\Delta_{C-Root} = Uptake_{C-Root} - Litter_{C-Root}$), and SOM ($\Delta_{C-SOM}$) which again equals litter input to SOM from aboveground plant pools ($Litter_{C-Above} - Litter_{C-Above\ decay}$) and belowground roots ($Litter_{C-root} - Litter_{C-Root\ decay}$) and C output in form of SOM mineralization ($Min_{SOM\ C}$) and DOC leaching ($Leach_{DOC}$) (equation (3)). Carbon pool changes can be further rearranged and are detailed in equation (4).

$$\Delta_{C-Below} = In_C + \Delta_{C-Root} + \Delta_{C-SOM} - Out_C \quad (2)$$

$$= Dep_{DOC} + (Uptake_{C-Root} - Litter_{C-Root}) + ((Litter_{C-Root} - Litter_{C-Root\ decay}) + (Litter_{C-above} - Litter_{C-Above\ decay}) - Min_{SOM\ C}) - Leach_{DOC} \quad (3)$$

$$= Dep_{DOC} + Uptake_{C-Root} - Litter_{C-Root\ decay} + Litter_{C-above} - Litter_{C-Above\ decay} - Min_{SOM\ C} - Leach_{DOC} \quad (4)$$

2.4.3. Total Belowground C Allocation

[22] TBCA is the sum of carbon required for root biomass change (Δ_{C-Root}), root litter production ($Litter_{C-Root}$), and root respiration (autotrophic soil respiration ($Soilresp_{Aut-C}$)):

$$TBCA = \Delta_{C-Root} + Litter_{C-Root} - Soilresp_{Aut-C} \quad (5)$$

2.4.4. Heterotrophic Soil Respiration

[23] Heterotrophic soil respiration ($Soilresp_{Het-C}$) is the sum of carbon lost by respiration in the form of aboveground plant litter decay ($Litter_{C-Above\ decay}$), root litter decay ($Litter_{C-Root\ decay}$), and mineralization of SOM ($Min_{SOM\ C}$):

$$Soilresp_{Het-C} = Litter_{C-Above\ decay} + Litter_{C-Root\ decay} + Min_{SOM\ C} \quad (6)$$

2.4.5. Total Ecosystem C Balance

[24] The ecosystem C balance ($\Delta_{C-System}$) is the sum of aboveground (equation (1)) and belowground (equation (4)) balances as given below (equation (8)) and further rearranged by use of equation (6) (equation (9)):

$$\Delta_{C-System} = \Delta_{C-Above} + \Delta_{C-Below} \quad (7)$$

$$= Dep_{DOC} + Uptake_{Net\ plant\ C} - Litter_{C-Above\ decay} + Litter_{C-Root\ decay} + Min_{SOM\ C} - Leach_{DOC} \quad (8)$$

$$= Dep_{DOC} + Uptake_{Net\ plant\ C} - Soilresp_{Het-C} - Leach_{DOC} \quad (9)$$

2.4.6. Aboveground N Balance

[25] The change in aboveground nitrogen pool ($\Delta_{N-Above}$) is equal to aboveground nitrogen uptake in plants ($Uptake_{N-Above}$) minus nitrogen in litterfall ($Litter_{N-Above}$):

$$\Delta_{N-Above} = Uptake_{N-Above} - Litter_{N-Above} \quad (10)$$

2.4.7. Belowground N Balance

[26] The change in belowground nitrogen ($\Delta_{N-Below}$) is equal to the difference between input of nitrogen by deposition (Dep_N), the change in nitrogen pools in roots (Δ_{N-Root}) and SOM ($\Delta_{N\ SOM}$), and the output of nitrogen by leaching ($Leach_N$) (equation (11)). The change in root N pools is equal to root uptake minus root litter formation ($Uptake_{N-Root} - Litter_{N-Root}$), and the change in SOM N pool equals the difference in input to SOM from aboveground plant litter ($Litter_{N-Above}$) and belowground root

Table 3. Aboveground and Belowground Carbon Pools at the VULCAN Sites

	Clocaenog UK	Mols DK	Oldebroek NL	Kiskun Sag HU	Garraf SP	Capo Caccia IT
Aboveground plant biomass C (g C m^{-2})	1825	221	389	141	278	261
Aboveground plant biomass N (g N m^{-2})	29	4	7	3	4	5
Root Biomass C (estimated) (g C m^{-2})	1616	290	495	152	318	253
SOM C (0–20 cm) (g C m^{-2})	15106	3965	5977	870	2488	8701
Microbial biomass C (0–20 cm) (g C m^{-2})	467	19	30	27	20	65

litter ($Litter_{N-Root}$) and the output in the form of SOM mineralization (Min_{SOM-N}) as detailed in equation (12) and further rearranged in equation (13):

$$\Delta_{N-Below} = In_N + \Delta_{N-Root} + \Delta_{N\ SOM} - Out_N \quad (11)$$

$$= Dep_N + (Uptake_{N-Root} - Litter_{N-Root}) + (Litter_{N-Above} + Litter_{N-Root}) - Min_{SOM-N} - Leach_N \quad (12)$$

$$= Dep_N + Uptake_{N-Root} + Litter_{N-Above} - Min_{SOM-N} - Leach_N \quad (13)$$

2.4.8. Total Ecosystem N Balance

[27] The total ecosystem N balance ($\Delta_{N-System}$) is the sum of aboveground and belowground balances (equation (10) + equation (13)) given as

$$\Delta_{N-System} = \Delta_{N-Above} + \Delta_{N-Below} \quad (14)$$

$$= Dep_N + Uptake_{Net\ plantN} - Min_N - Leach_N \quad (15)$$

[28] Plant C pools (aboveground and belowground) were assumed constant over the 3–6 year study period (uptake = litter production) for sites not recently affected by major disturbances (15 years) (UK, NL, and HU) while assumed linearly developed from the disturbance time until today for sites with disturbance within the past 15 years (SP, IT, and DK). DOC in rainwater (Dep_{DOC}) was negligible at all sites.

[29] As a second independent approach to test the assumptions, the total belowground carbon allocation (TBCA) calculated in this study (equation (5)) was compared with estimates proposed by *Raich and Nadelhoffer* [1989] as the total soil respiration minus the aboveground litterfall C (TBCA = total soil C respiration ($Soilresp_{Aut-C}$ + $Soilresp_{Het-C}$) − $Litter_{C-above}$) which was recently tested by *Davidson et al.* [2002].

3. Results

[30] The C pools ranged from 141 to 1825 g C m^{-2} aboveground and from 1022 to 16722 g C m^{-2} belowground, with the wet and cold site in UK having distinctively larger C pools than all other sites (2–16 times for both pools) (Table 3). Microbial biomass ranged from 0.5% (DK and NL) to approximately 3% (UK and HU) of the SOM. Soil fauna biomass was measured at all sites and constituted less than 0.5 ‰ at all sites (data not shown).

[31] Aboveground and belowground C pools were strongly related across all sites with 7–50 times bigger C pools in the soil compared to the aboveground biomass (Figure 1) with the Italian site having a particularly higher fraction of carbon in the soil. Across the European gradient the aboveground C pool and the plant production showed some, but in most cases not significant relationship to temperature and annual precipitation (Figures 2 and 3).

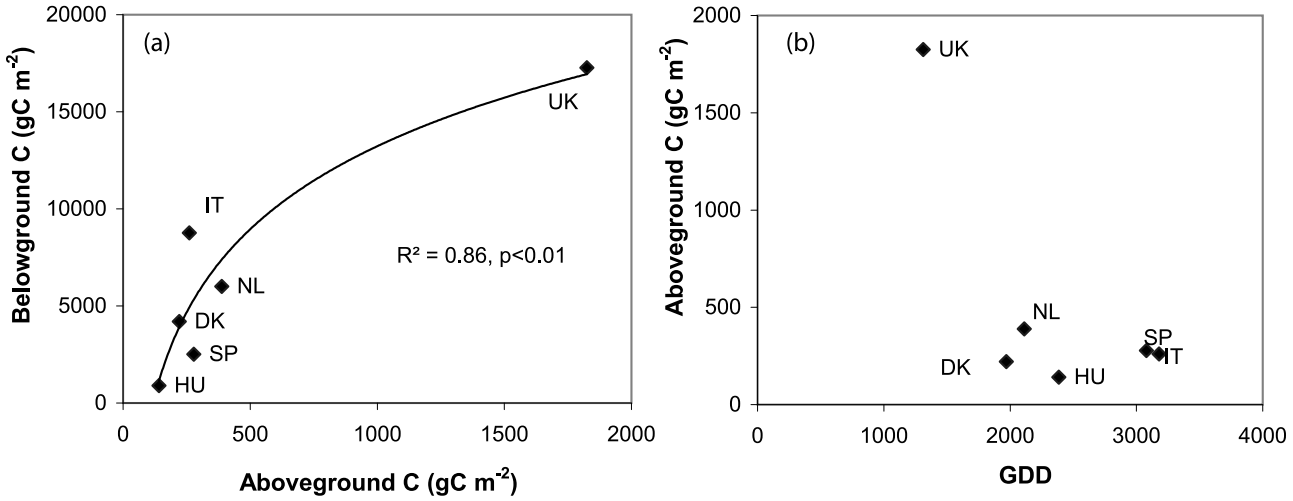

Figure 1. Relationship between (a) aboveground and belowground carbon; (b) aboveground carbon pools and growing degree days (GDD) at the six European shrubland ecosystems. GDD values were calculated using a lower temperature threshold of 5°C.

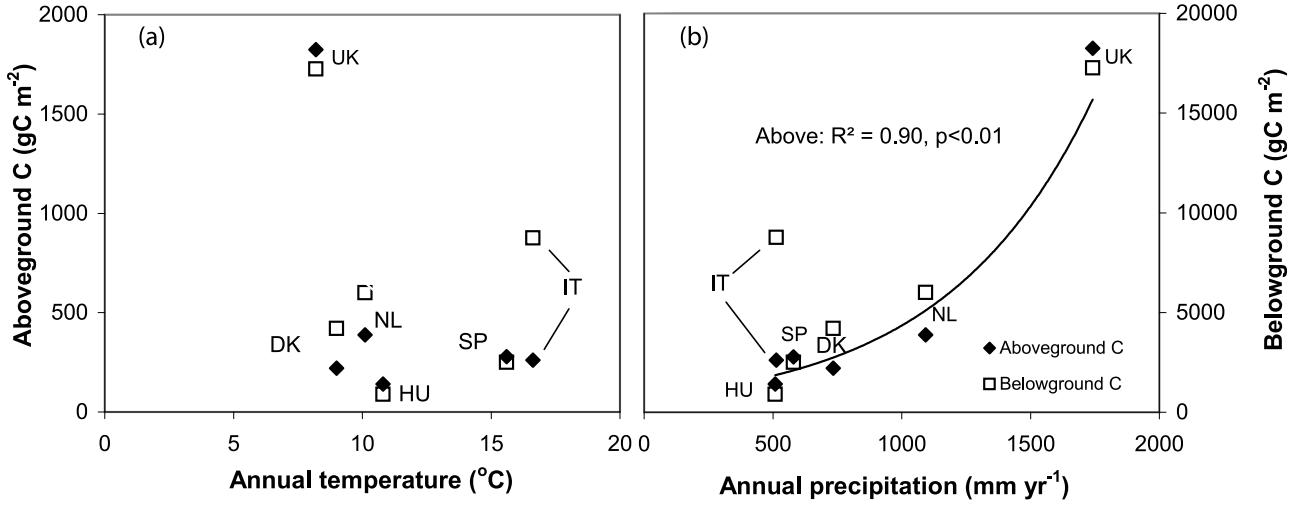

Figure 2. Aboveground (solid diamonds) and belowground (open squares) C pools related to (a) mean annual temperature and (b) mean annual precipitation at the six shrublands. Indicated response line shows significant exponential relationships between aboveground carbon and mean annual precipitation.

[32] The C balance at the six ecosystems differed clearly among the sites with the ecosystems in UK and DK being net C sinks which sequester an annual amount of C equal to ~1% of the C pool stored in the soil (Figure 4). The other sites were either at steady state (NL and HU) or sources (SP and IT) of carbon. The main carbon fluxes were the litter production and the loss of C from SOM to the atmosphere by respiration. Across the sites an amount of C equal to ~3–12% of the SOM pool was respired annually. At the NL and HU sites this loss was largely compensated by an equal input of C from litterfall, while this was not the case at the DK, SP, and IT sites, where SOM served as a C source. At the UK site, which had the biggest C pool in the soil, this pool was still accumulating because of a bigger input of C from the plant pool relative to the loss by respiration (Table 3 and Figure 4). The plant production was at steady state at the UK, NL, and HU sites while a relatively small aboveground biomass accumulation occurred at the SP and IT sites and a more significant accumulation at the DK site following the recovery from a recent heather beetle infestation. Because of the near-steady-state conditions for plant growth at five of the sites, the annual net primary productivity (NPP) of these sites was mainly determined by the total aboveground and belowground litter production. The production of litter relative to the amount of plant biomass differed significantly across the sites with high fractions (>50%) at the DK and HU sites which both had a large fraction of grass vegetation, medium fractions (~20%) at IT, SP, and NL, which were all being dominated by shrubs with large permanent biomass stores in stems, and a small

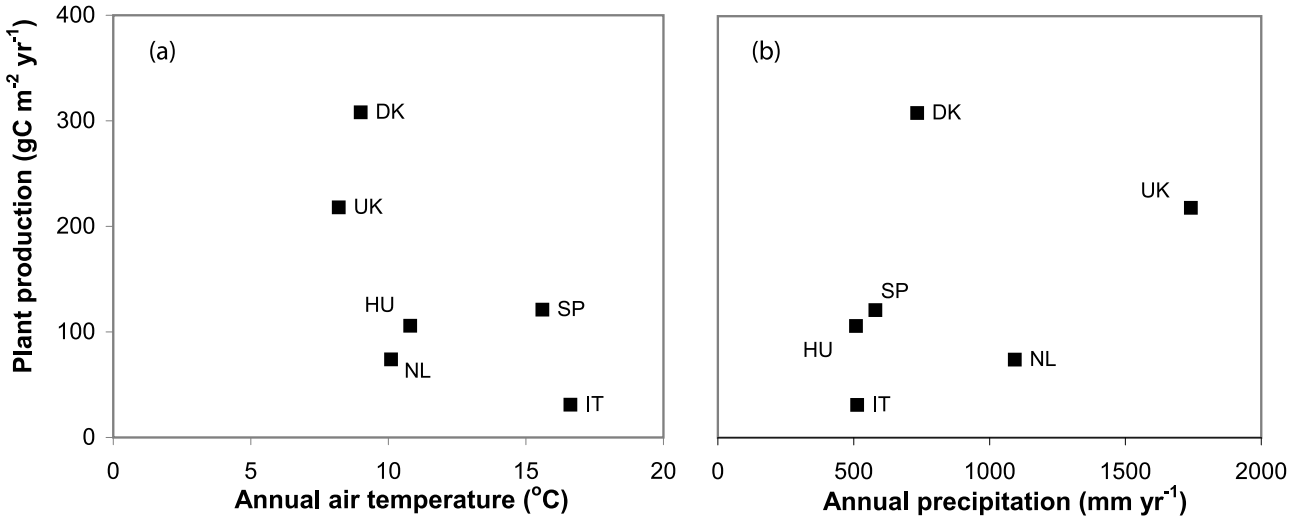

Figure 3. Average plant production (3–6 years) at the six shrubland ecosystems related to annual average climatic parameters (air temperature and precipitation).

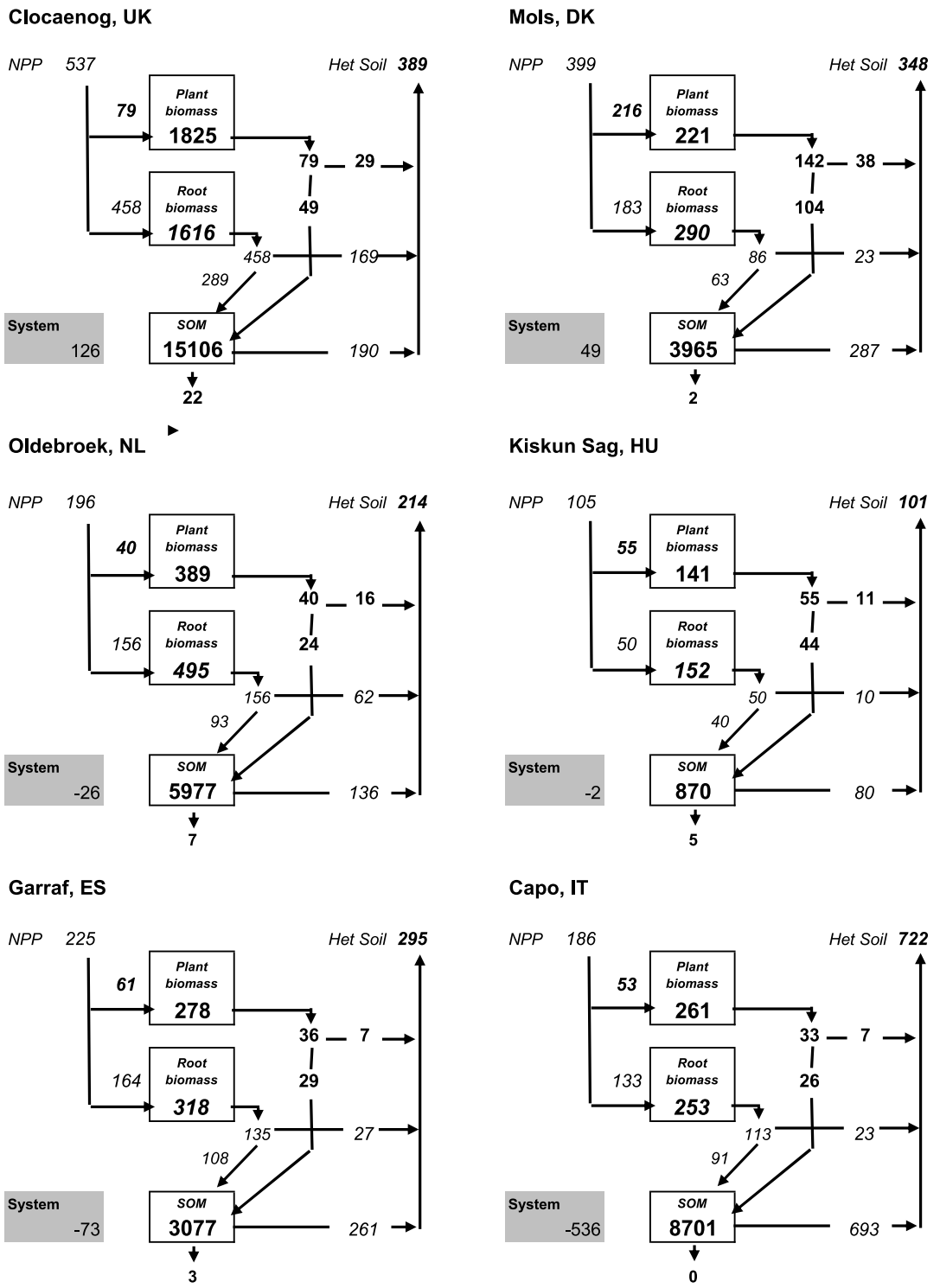

Figure 4. Carbon balances for the six shrubland sites showing pools (g C m^{-2}) and fluxes (g C m^{-2} a^{-1}) of carbon for a 5-year steady-state situation (accumulation in biomass assumed equal to 0 for sites with last disturbance >15 years ago). Numbers in italic obtained from estimation, in bold from measurements, and italic and bold by a combination. Overall carbon balance for the system is shown in gray box. Fluxes are input of C from the atmosphere to the ecosystem by aboveground and belowground net C uptake; the flux of C from the aboveground C pool by litterfall which is split into leaf litter respiration and humification; the loss of C from the root C pool by root litter production which is further split into root litter respiration and humification; inputs of C to the SOM pool from humification of the leaf and root litter; and, finally, loss of C from the system by respiration of SOM (heterotrophic respiration) and leaching of DOC.

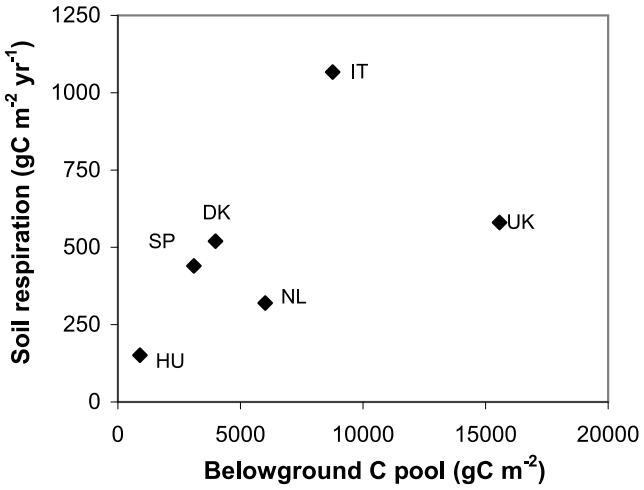

Figure 5. Total annual soil respiration (g C m^{-2} a^{-1}) in response to belowground carbon pools across the six sites.

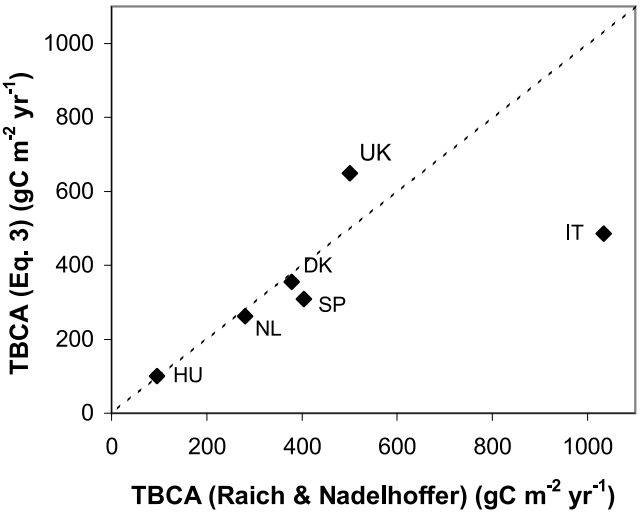

Figure 6. Relationship between total belowground carbon allocation (TBCA) calculated in this study (equation (5)) and by *Raich and Nadelhoffer* [1989].

fraction (<10%) at UK. The shrub-dominated sites in UK, NL, SP, and IT all allocated relatively large amounts of the C uptake belowground, while the more grass-dominated sites in DK and HU had a more equal allocation of C inputs aboveground and belowground.

[33] The loss of carbon to the atmosphere by soil respiration appeared to be related to the size of the soil carbon pool suggesting carbon loss was dominated by mineralization of SOM rather than root respiration (Table 4 and Figure 5). Values for both parameters were at the low end of that reported for forests by *Davidson et al.* [2002] but do not show any clear pattern with litter production. Total belowground carbon allocation values calculated using our approach (equation (5)) were similar to those calculated using the *Raich and Nadelhoffer* [1989] method with the exception of the IT site (Table 4 and Figure 6). TBCA was a factor of ~2 to 9 relative to litterfall excluding the IT site (Table 4).

[34] The nitrogen balance at all sites was characterized by almost insignificant fluxes relative to the pools and by a relatively small aboveground pool relative to the belowground N pool (2–6%) and by moderate inputs from deposition except at the NL site (Figure 7). At the NL site, where the atmospheric input was substantial, the internal cycling of nitrogen was intensified and the loss of nitrogen to the groundwater was significant (Figure 7).

4. Discussion and Conclusions

[35] A wide range of carbon storage in shrubland ecosystems has previously been reported with standing biomass ranging from 100 to 2000 g C m^{-2} [e.g., *Gimingham*, 1972; *Aerts*, 1993; *Robertson and Davies*, 1965; *Miller and Miles*, 1970; *Chapman*, 1967]. The biomass carbon pools, litterfall fluxes, and annual carbon exchange found in our study of six European shrubland ecosystems were within the wide range shown by these previous studies and of the same order of magnitude as shown for grasslands [e.g., *Jones and Donnelly*, 2004] and a factor of 3–25 lower than for many forest ecosystems [e.g., *Houghton*, 2005].

[36] There was a 16 times difference in the pools of organic matter in the soil from the smallest pools at the HU sites to the largest pools at the UK site. There was a tendency toward higher soil respiration at sites with higher soil carbon stores (Figure 5) supporting our assumptions and calculations that it is heterotrophic decomposition of

Table 4. Carbon Fluxes and Total Belowground Carbon Allocation[a]

	Clocaenog, UK	Mols, DK	Oldebroek, NL	Kiskun Sag, HU	Garraf, SP	Capo Caccia, IT	Mean (Excluding IT)
Total soil respiration	580	520	320	151	440	1067	402
Root respiration ($Soilresp_{Aut-C}$)	191	172	106	50	145	352	133
Het. respiration ($Soilresp_{Het-C}$	389	348	214	101	295	715	269
Allocated to roots minus root respiration	458	183	156	50	164	133	202
Aboveground litterfall	79	142	40	55	36	33	70
TBCA (Raich and Nadelhoffer)	501	378	280	96	404	1034	332
TBCA (equation (5))	649	355	262	100	309	485	335
TBCA/litterfall (Raich and Nadelhoffer)	6,3	2,7	7,0	1,7	11,2	31,3	5,8
TBCA/litterfall (equation (5))	8,2	2,5	6,6	1,8	8,6	14,7	5,5

[a]Carbon fluxes used to calculate total belowground carbon allocation TBCA according to *Raich and Nadelhoffer* [1989] and according to equation (5) and the ratio of TBCA over litterfall. Calculations done for each site and the mean of all (excluding the Italian site (see section 4)). Units are g C m^{-2} a^{-1}.

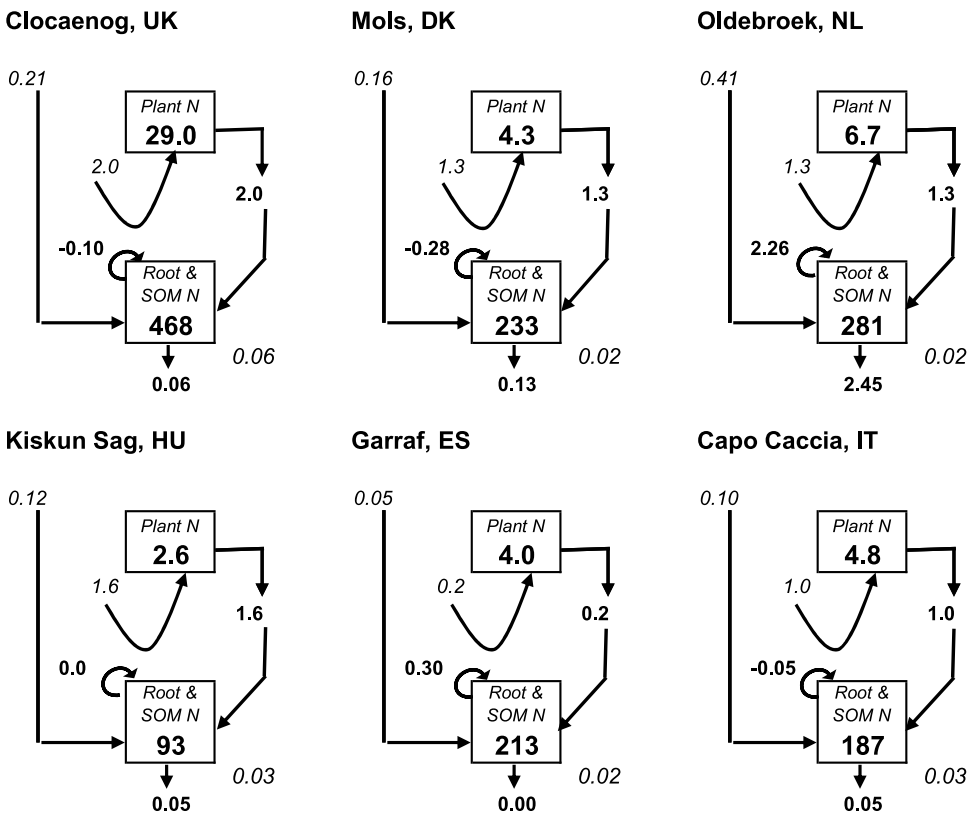

Figure 7. Nitrogen balances for the six shrubland sites showing aboveground and belowground pools (g N m^{-2}) and fluxes (g N m^{-2} a^{-1}) for a 5-year steady-state situation (accumulation in biomass assumed equal to 0). Numbers in italic obtained from estimation, numbers in bold obtained from measurements, and numbers in italic and bold obtained by a combination. Fluxes are input of nitrogen to the belowground N pool by N deposition and litterfall; input of nitrogen to the plant N pool by plant N uptake from the soil; loss of nitrogen from the plant N pool by litterfall; internal transformation of nitrogen by mineralization; and loss of nitrogen from the system by N leaching.

SOM which is the dominant component of soil respiration loss rather than autotrophic respiration from roots. It should be noted that the carbon budget calculations made here are associated with some uncertainty, in particular because the use of simple Q10 functions to estimate the annual soil respiration only takes the temperature control into account. On the other hand, the generally high r^2 in the Q10 functions show that temperature is a good predictor for soil respiration, and the calculation of soil respiration in water-limited and non-limited periods independently to some extent takes the moisture control into account while other potential controls were not accounted for. Also the general lack of knowledge on the fractionation of soil respiration into heterotrophic and autotrophic fractions provides some uncertainty in the calculations.

[37] There was no relationship between litterfall and soil respiration as reported for global forest ecosystems which is often the case for individual forest site studies because of either interannual variability in measurements or non-steady-state conditions [*Davidson et al.*, 2002]. However, as the data from five of our six sites fit within the 95% percentiles of the overall global relationship for forests reported by *Davidson et al.* [2002], we estimated total belowground allocation (TBCA) using the method proposed by *Raich and Nadelhoffer* [1989] to provide an independent test of our method for allocating TBCA (Table 4). There is a good relationship between the two estimates for the five sites (Figure 6) providing some confidence in the assumptions made here and also confirming that the method proposed by *Raich and Nadelhoffer* [1989] is relatively robust also for shrublands and even to non-steady-state conditions. The one exception is the IT site which appears to be furthest from steady-state conditions. This is most likely because the site is situated where a major strip was cleared in 1992 which left major woody plant debris in the soil. When these debris are decomposed, this may cause higher rates of respiration relative to sites where the soils only contain SOM. Furthermore, since TBCA for the five sites (excluding the IT site) on average was a factor of 5 times greater than litterfall compared to a factor of 2 for most of the forested systems [*Davidson et al.*, 2002], these five shrubland sites appear to allocate large amounts of carbon belowground relative to litterfall compared to forest systems. Such high rates of carbon allocation belowground were suggested for forests with low rates of litter production based on the presence of a nonzero y intercept [*Davidson et al.*, 2002]. Our results may therefore suggest this to be a more general phenomenon.

[38] The aboveground and belowground pools of C were clearly linked. Furthermore, the fraction of shrubs clearly determined the carbon pools as the sites with the largest fraction of woody evergreen shrubs had the biggest belowground biomass (UK, SP, NL, and IT), while sites with a larger fraction of grasses and herbs had a smaller belowground biomass (DK and HU). At sites where shrubs were being replaced by grasses gradually or suddenly by ecosystem disturbances like at the DK site this may be accompanied by a loss in soil carbon. In general, the dominant carbon pools in all the studied shrubland ecosystems were belowground, amounting to 10–30 times the carbon stored in the aboveground pools. This has two consequences:

[39] First, the stability of the soil carbon upon changes is likely to determine the overall change in carbon sequestration because of changes in land cover or climate rather than more moderate changes in aboveground carbon pools following such changes.

[40] Second, the wet site in UK had by far the highest carbon pools both aboveground and belowground (2–20 times) as well as the highest belowground carbon allocation compared to the other sites (2–6 times). This emphasizes that in this wet ecosystem even moderate changes in the soil carbon storage due to increased temperature or oxidation by increased droughts [e.g., *Emmett et al.*, 2004] or changes in plant cover could be overwhelmingly more important than any changes in carbon storage in the drier sites such as the other five ecosystems in this study.

[41] The latter is supported by observations of accelerated loss of soil carbon from the wetter UK site in response to repeated drought contrasting a reduction in the more mesic NL and DK sites [*Sowerby et al.*, 2008]. This response at the UK site extended throughout the winter period between droughts because of a lack of recovery in soil moisture despite the annual amount of 1000 mm rainfall. This provides a possible mechanism for the large losses of soil carbon in organic soils reported for the UK by *Bellamy et al.* [2005] and is in agreement with *Jackson et al.* [2002] who also concluded that the organic rich and wetter soils accounted for the majority of the change in C storage due to climate change, although, as pointed out by *Smith et al.* [2007], temperature change has not been sufficient to date to reduce soil carbon storage.

[42] It has been speculated how potential land cover change between grasslands, shrublands, and forests may affect the carbon storage in these terrestrial ecosystems, and there is still significant doubt and discrepancy about the direction and effect of change due to different environmental drivers, their interactions, and variable responses by shrublands. For example, in a recent model study, *Bachelet et al.* [2001] found that under climate change scenarios and in particular with stronger temperature increases, the shrubland area in USA would be reduced by replacement to savanna and thereby a reduction in C sequestration would occur. A climate-driven increase in fire frequency was also predicted to promote grasslands [e.g., *McCarron et al.*, 2003] and thereby counteract a climate-driven shrubland expansion and increased carbon storage. However, a reduction in management and land abandonment is increasingly causing an increase in shrubland cover which has implications for carbon storage. For example, *Tate et al.* [2003] found in a model study supported by measurements that reversion of grazed grassland into indigenous shrubland in New Zealand will increase the C sink by ~40% per unit area mainly because of an increase in the biomass carbon. Belowground carbon fluxes are particularly affected by conversion of grassland into shrublands as shown for shrub encroachment in mesic and dry grasslands [*Hibbard et al.*, 2001; *McCarron et al.*, 2003]. Consequently, a future climate-driven land cover change between grasslands and shrublands in Europe will likely lead to increased ecosystem C where shrublands are promoted and less where grasses are promoted. The direction of change is, however, difficult to predict because of the potentially complex interactions between management, climate change, and fire frequency for many shrublands and their different use and status globally. On the other hand, *Jackson et al.* [2002] found that the overall effects of land cover changes on the carbon storage may be more determined by changes in soil carbon storage on wet soils rather than differences in the carbon storage in the biomass between shrublands and grasslands suggesting it is hydrological controls on soil carbon storage which are also important to understand and build into models.

[43] Not only climatic changes but also changes in nutrient availability may affect carbon sequestration in shrubland ecosystems where nutrient availability is limiting plant growth. This may be particularly important for nitrogen because of substantial and increasing inputs of nitrogen from deposition. In this study, N was limiting growth at several sites, and increasing levels of N deposition may therefore lead to increased growth of aboveground and belowground organic matter pools and thereby C sequestration. On the other hand, ecosystems already receiving large amounts of N deposition and not being N-limited, such as the NL site in this study, are unlikely to respond to further increases in N deposition. Furthermore, since N availability is also affecting plant species composition and promoting conversion of shrublands to grasslands [*Bobbink et al.*, 1998], which potentially store less carbon [*Tate et al.*, 2003], the potential increase in plant growth and carbon storage from increased N deposition in shrublands may be offset by such a land cover change.

5. Summary

[44] European shrublands provide several ecosystem services, of which carbon sequestration is of particular importance in the present climate change discussion. In the present study the majority of the carbon was stored in the soil which in itself points to the fact that the potential for climatic-driven changes in carbon storage of shrublands is most likely associated with changes in the soil pool. Total belowground carbon allocation was considerably higher (relative to aboveground litterfall) than observed in forest systems further emphasizing the importance of understanding the controls and ultimate fate of soil carbon in shrubland systems and forest and grassland systems under transition toward shrubland. The vulnerability of the soil carbon stores is particularly important at colder/wetter climates which in

the present study hold up to 16 times more carbon than the drier sites. Any major change in the soil carbon storage driven by land cover or climate change at this one site will be far more important than corresponding changes in the drier sites with much smaller carbon stores.

[45] **Acknowledgments.** The present study was carried out and funded by EU as part of two research projects CLIMOOR (contract ENV4-CT97-0694) and VULCAN (contract EVK2-CT-2000-00094), the participating research institutes, the CLIMAITE project, the Spanish (grant CGL2006-04025/BOS) and the Catalan (grant SGR2005-00312) governments, and the EU FP6 project NitroEurope (contract 017841). We want to thank the colleagues and technicians at our institutes for skillful work in the field and the laboratory. We want to thank Christy Goodale for ideas and discussions. In memory of Olevi Kull.

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