

**Modellizzazione del ciclo del carbonio e
sue interazioni con le pratiche
gestionali in ecosistemi erbacei**

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**Modeling the carbon cycle and its
interactions with management
practices in grasslands**

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1 Overview

1.1 Sommario

Gli ecosistemi prato-pascolivi occupano il 20% della superficie terrestre e circa l'8% dell'Europa (EU-15). L'assorbimento globale di carbonio per questa tipologia ecosistemica è stimato essere di 0.5 Gt y^{-1} . Il carbonio accumulato nei suoli delle praterie nella fascia temperata è stato quantificato tra i 150 ed i 300 Gt di C, questa quantità consiste in circa il doppio rispetto al carbonio contenuto nei suoli delle foreste temperate. Tuttavia, associate a queste stime, esistono diverse incertezze alle quali contribuisce una lacuna nella conoscenza delle modalità di gestione. Talvolta questa viene marginalmente considerata ai fini del calcolo di bilanci ecosistemici, mentre è stato ripetutamente evidenziato che essa è un fattore fondamentale nel determinare il ruolo di assorbimento o di emissione di una prateria gestita. Da questo emerge l'importanza dell'approfondimento della conoscenza delle interazioni tra componenti del ciclo del carbonio e gestione in questo ecosistema.

Il modello ecosistemico Biome-BGC è stato usato in numerosi casi per simulare il ciclo del carbonio in ecosistemi forestali ma la sua applicazione ad ecosistemi erbacei è meno frequente. Questo è dovuto all'assenza di routine che simulino le pratiche gestionali. Un primo obiettivo di questo progetto è quello di colmare questa lacuna. Per questo motivo un modulo per simulare lo sfalcio ed un modulo per simulare la fertilizzazione sono stati implementati e testati.

Un'altra causa nelle incertezze nei bilanci ecosistemici è connessa al fatto che spesso i parametri di input di un modello sono definiti da valori medi di letteratura senza considerare la specificità del sito e del modello utilizzato. Con il presente progetto si è voluta colmare anche questa seconda lacuna attraverso un'analisi di sensitività ed un'ottimizzazione dei parametri di input del modello più importanti. Con l'implementazione delle suddette routine e dell'ottimizzazione dei parametri si è voluto contribuire ad una migliore comprensione delle interazioni tra pratiche gestionali e le diverse componenti del ciclo del carbonio.

Il modello

Il modello ecosistemico Biome-BGC (BioGeochemical Cycles) simula l'accumulo ed i flussi di acqua, carbonio e azoto attraverso le diverse componenti di un ecosistema terrestre. Il modello permette di simulare processi legati i) al ciclo del carbonio e dell'azoto (fotosintesi, respirazione di crescita e mantenimento della vegetazione, allocazione di C e N in radici e foglie, decomposizione della lettiera) ii) al ciclo idrologico (evaporazione, traspirazione, intercettazione delle precipitazioni e ripartizione suolo/canopy). BIOME-BGC utilizza variabili meteorologiche in modo continuo per tutto l'arco temporale della simulazione ed altre variabili che sono richieste solo per l'inizializzazione (parametri ecofisiologici relativi alla tipologia vegetazionale e caratteristiche chimico-fisiche del suolo). Il modello ha un passo temporale giornaliero. Lo sfalcio è stato implementato come una riduzione dell'indice di area fogliare in un giorno definito dall'utente. La fertilizzazione è stata implementata come un aumento dell'input di azoto durante un periodo di tempo successivo all'inizio della stagione vegetativa o agli sfalci.

Ottimizzazione delle stime dei flussi di carbonio: l'esempio di due prati estensivi

Nella prima parte di questo progetto sono state analizzate e migliorate le stime di flussi di carbonio in ecosistemi erbacei, per mezzo dell'utilizzo di una versione modificata del modello ecosistemico Biome-BGC. Le stime di produzione primaria netta (*GPP*) e di respirazione ecosistemica (*TER*) sono state comparate con le misurazioni di eddy covariance partizionate nelle due componenti in due siti di misura: Hegyhátsál (HU) e Monte Bondone (I). Si tratta di due siti diversi da un punto climatico - alpino o continentale - da un punto gestionale - uno o due tagli - e di conseguenza anche da un punto di vista vegetazionale - arrenatereto e nardeto. Per il primo sito sono stati analizzati gli anni 2003 e 2004 mentre il secondo l'anno 1999 e l'anno 2000. Questo per motivi di disponibilità dei dati sperimentali. Sono stati selezionati i parametri più importanti per ogni combinazione anno/sito, attraverso un metodo che permettesse di mantenere i valori degli altri - considerati meno influenti - costanti (metodo di Morris). I parametri selezionati sono stati utilizzati in un algoritmo di ottimizzazione. L'intervallo di variazione dei parametri è stato definito come due volte la deviazione standard dei dati ricavati da bibliografia. Sono state considerate delle distribuzioni di probabilità gaussiane. È stato utilizzato un approccio Bayesiano abbinato all'algoritmo di Metropolis-Hasting per

L'ottimizzazione dei parametri. L'analisi di sensitività ha portato alla selezione degli stessi parametri più importanti per tutti i casi considerati. Il modello è stato portato all'equilibrio per ogni simulazione - senza considerare alcuna pratica gestionale - definendo questo come stabilità negli stock di carbonio tra un anno ed il successivo. È stata valutata la capacità predittiva del modello utilizzando i valori dei parametri di input ottimizzati. In tutti i casi è stato rilevato un miglioramento nelle stime di flussi di carbonio. La distribuzione piuttosto che la frequenza di gap nelle serie temporali, ha dimostrato essere importante ai fini dell'ottimizzazione. Lo studio ha evidenziato che l'algoritmo di ottimizzazione è sensibile alla variabilità climatica in quanto l'anomalia termica dell'anno 2003 ha causato il cambiamento più significativo nei valori dei parametri ottimizzati.

Adattamento di una prateria alpina a diversi carichi di fertilizzazione

Nella seconda parte di questo progetto, sono state analizzate le strategie adattative di una prateria alpina a differenti carichi di fertilizzazione azotata. Il problema è stato affrontato applicando un metodo Monte Carlo, mediante l'inversione dei parametri di input del modello. Come elemento di inversione è stato utilizzato il contenuto di carbonio nelle biomasse raccolte durante gli sfalci in una prova sperimentale di fertilizzazione ventennale, in provincia di Belluno. Nella prova sono state considerate combinazioni fattoriali di azoto, fosforo e potassio ma il modello utilizzato non simula i cicli degli ultimi due elementi. Per questo motivo solo quelle tesi di fertilizzazione dove fosforo e potassio non erano limitanti, sono state analizzate. Gli intervalli di variazione dei parametri di input sono stati definiti dai valori minimi e massimi ricavati dalla letteratura. All'interno di questo intervallo sono state considerate distribuzioni uniformi. Inizialmente il modello è stato portato all'equilibrio, in seguito il modello è stato *costretto* in modo che simulasse la biomassa misurata in un intervallo corrispondente ad un intorno (± 7 giorni) della data di sfalcio osservata. La produttività ecosistemica è stata comparata per diversi carichi di fertilizzazione (0, 96, 192 kg ha⁻¹). Inizialmente sono stati considerati tutti i parametri di input. Attraverso un'analisi di sensitività basata sull'analisi della varianza, il numero iniziale di parametri è stato ridotto. Quei parametri definiti come non significativi sono stati fissati a valori medi da letteratura, mentre i rimanenti sono stati re-inseriti nell'algoritmo di inversione. Pochi parametri sono risultati essere migliorabili poiché molti sono coinvolti in interazioni con altri. Essi sono stati comparati tra i diversi carichi di fertilizzazione. L'approccio

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ha dimostrato che, nonostante le numerose iterazioni non lineari tra parametri, è ancora possibile migliorare le stime di alcuni di questi. Come ci si aspettava, minori livelli di fertilizzazione sembrano aumentare lo sviluppo radicale e l'investimento in organi di riserva.

1.2 Abstract

The world-wide geographical extension of grasslands consist in 20% of the land and in Europe of about 8% (EU-15). The annual sink of this kind of ecosystem is estimate to be about 0.5 Gt C y^{-1} . The carbon accumulated in the soils of temperate grasslands was estimated to be between 150 and 300 Gt C. This quantity is about double the carbon stocked in the soils of temperate forests. Anyway there are many uncertainties in these fluxes and stocks estimates. This uncertainties can in part be connected with the lack of knowledge in the applied and historical management. Frequently, these factors are only marginally accounted in ecosystem carbon budget while its importance was repeatedly stressed in literature. From this the importance of getting better insight in the interactions between carbon cycle and management practices in this type of ecosystem.

The process ecosystem model Biome-BGC is frequently used for simulating carbon cycle in forest ecosystems but its application to grasslands is uncommon. This is linked to missing routines for simulating management. A first aim of the present work is to fill this lack. For this reason a module for simulating mowing and a module for simulating nitrogen fertilisation were implemented and tested.

A reason why there are uncertainties in ecosystem carbon budgets is that frequently the model input parameters are defined by literature without taking in consideration the uncertainties associated with the model and the characteristics of the single sites. This project aimed to suggest a solution to this problem by mean of sensitivity analysis and parameter optimisation. By mean of the mentioned aims this work is a contribution for gaining a better insight in the relationships between carbon cycle and management practices.

The model

The ecosystem process model Biome-BGC (BioGeochemical Cycles) simulate stocks and fluxes of water, carbon and nitrogen through the components of a terrestrial ecosystem. The model permits to simulate processes linked to

i) carbon and nitrogen cycles (i.e., photosynthesis, respiration, allocation), ii) hydrological cycle (i.e., evaporation, transpiration and interception). Biome-BGC is driven by meteorological variables and is initialised by ecophysiological parameters and site characteristics. The model is a daily time step. Mowing was implemented as a leaf area index reduction in a user define day of the year. Fertilisation was implemented as an increase of nitrogen input during a period following the beginning of growing season and following the harvests.

Optimisation of carbon fluxes estimates: the example of two grasslands

This part of the present work aims to define and apply a method to analyse and improve carbon fluxes estimates for grasslands using the ecosystem process model Biome-BGC. The ecosystem process model Biome-BGC simulates the cycle of water, nitrogen and carbon for different plant functional types. The estimated Gross Primary Productivity (*GPP*) and Total Ecosystem Respiration (*TER*) were compared with the partitioned eddy covariance data at two measurements sites - Mt. Bondone and Hegyhátsál. First, for each site, the most sensitive input model parameters were selected using a parameter fixing method (Morris' method). Then the selected parameters were optimised using a Bayesian approach based on the Metropolis-Hastings algorithm. The sensitivity analysis of the model input parameters gave the same results for each combination of site/year/component. The most sensitive input parameters resulted to be C:N of leaves, C:N of roots, C:N of litter, specific leaf area and maximum stomata conductance. The a posteriori mean values of input parameters produced a better agreement between observed and estimated fluxes. The size of gaps influenced the potential estimates improvement. The results highlighted that the method is sensitive to climate changes because the heat wave of the year 2003 produced the most significant changes in model input parameter values.

Adaptation of an alpine grassland to different nitrogen fertilisation loads

The second part of the present work aimed to investigate how an alpine meadow adapt to different nitrogen fertilisation loads over a medium term period (18 years). Grasslands response to harvesting and to nitrogen fertilisation are well described in literature but a complete overview on the plant response is still missing. The ecosystem process model Biome-BGC was used. This was ap-

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plied to an experimental site in the Southern Alps. The model was constrained with the carbon content in yield production. For doing this a Monte Carlo approach was adopted. The model input parameters were defined having a range included in the maximum and minimum value found in literature. The input parameters were sampled randomly from an uniform distribution. The model was first taken to equilibrium, not including any management practice. Then the model was constrained to simulate the harvested biomass in the surroundings (± 7 days) of the measured harvesting date. A sensitivity analysis based on analysis of variance permitted to fix the less significant parameters to mean values. The ecosystem productivity was compared for different fertilisation loads (0,96,192 kg ha⁻¹). Transfer growth period, litterfall as fraction of growing season, new fine root C to new leaf carbon ratio, current growth proportion, C:N of leaves, C:N of roots and nitrogen input as atmospheric deposition and symbiotic fixation resulted to be constrainable. These parameters were constrained and their optimal values were compared among fertilisation regimes. The approach showed that to higher N load corresponds a decrease in C allocated to roots. A similar trend was found for reservoirs: less N induce more allocation to stocks and less to immediate growth.

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2.1 The global carbon cycle

The continuous rise of the atmospheric carbon dioxide concentration, and the perspective of a substantial warming of the global climate have conducted many research resources into seeking a better understanding in the components of the global carbon cycle. The rate of increase of atmospheric CO₂ content was $3.3 \pm 0.1 \text{ Gt C yr}^{-1}$ during the period 1980 to 1989 and $3.2 \pm 1 \text{ Gt C yr}^{-1}$ during the period 1990 to 1999 [4]. These rates are less than the estimates for the emissions. According to the long-term measurements on Hawaii by the National Oceanic and Atmospheric Administration (NOAA) [5], the yearly average of CO₂ emissions during the 1980's was 5.5 Gt C. The difference can largely be attributed to the oceans: their uptake rate is estimated to be around 2.0 Gt C, with an uncertainty of $\pm 1 \text{ Gt C}$ [6]. According to this budget estimate, the land biosphere appears to be nearly to equilibrium. Anyway, statistics of deforestation indicate an additional human-created source of $1.6 \pm 1.0 \text{ Gt C}$, primarily in the tropics [7]. This source is partly compensated by regrowth of forests on former agricultural land in the temperate zone, and by a largely unknown sink [8]. In contrast to the longer-term fluxes mentioned above, the short term fluctuations are largely an expression of the photosynthesis of land vegetation. In this process, plants take up an annual amount of approximately 100 Gt C, with around half of that being returned by plant respiration. This rate is much larger than the ones cited before, even though its size is still uncertain. One of the well known facts is that the largest amount of carbon (ca. 38000 Gt C) resides within the deep ocean. The exchange between atmosphere and the surface ocean is mostly influenced by the large-scale ocean circulation that runs on time scales of centuries. The surface ocean, i.e., the 50 m thick seasonally mixed surface layer (ca. 100 Gt C), is in diffusive contact with the atmosphere (ca. 750 Gt C). This means that several millennia after all fossil fuel has been used up (a few thousand Gt C) there will be a new equilibrium between the mentioned pools, with most of the carbon stocked in the ocean. For even longer time spans, the formation of sediments plays a determining

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role, while the oceanic biosphere, which is only a very small pool (ca. 3 Gt C), is of major significance for the seasonal CO₂ exchange between the ocean surface layer and the atmosphere [9]. It also mediate part of the transfer of carbon from the surface to the deep ocean. The land biosphere represents the second largest active carbon pool within the earth system, with a third of it consisting of vegetation, and the remaining part of soil carbon and plant litter. On short time scales, fluxes are determined by the CO₂ uptake during plant growth and by fast decomposition of plant litter, whereas longer-term changes concern, among others, the build-up and decline of peat bogs, growth cycles of forests, and succession, such as the intrusion of forests into steppes. Here, human influence plays an important role, (e.g., through deforestation or the conversion to arable land) [10]. Such influences, however, only cause fluxes relatively small compared to uptake rates from photosynthesis (gross primary production, *GPP*) or the net uptake during plant growth (net ecosystem exchange, $NEE = GPP$ minus plant respiration *TER*) but on long term periods are determinant for the soil carbon stocks.

2.2 Role of grasslands in the carbon cycle

World-wide, grasslands cover about 3500 million ha and are likely to remain constant in area in the nearest future [11] [12]. In Europe there are about 151 million ha of grasslands (Fig. 2.2). Since 1990 (the reference year in the Kyoto protocol) 3 million ha of grassland were converted to arable land, especially for maize cultivation [13]. Besides their natural aspect, grasslands have a pure agricultural destination as a primary food source for domesticated ruminants and wild herbivores. Actually, grasslands being a mixture of different grass species, legumes and herbs may act as erosion preventives, bird directive areas, habitat for small animals, nitrogen fixation [13]. Hence most grasslands tend to have a positive environmental role. Furthermore these ecosystems play an important role in the terrestrial carbon cycle [12] [14] [15] [16] [17], because they have a high potential sink capacity and account almost 10% of global carbon stocks [18] [19]. It was suggested that globally this ecosystem could be a sink of 0.5 Gt C yr⁻¹ but with significant uncertainties (± 2 Gt C yr⁻¹) [16]. However, intensively managed grasslands tend to release nitrate to the groundwater and are also together with the associated livestock for which the grassland is maintained, a major source of ammonia.

2.2 Role of grasslands in the carbon cycle

Grassland ecosystems are particularly complex to investigate because of the wide range of management and environmental conditions to which they are exposed. Currently, the net global warming potential (in terms of CO₂ equivalent) from the greenhouse gas exchanges with grasslands is not known. Management choices to reduce emissions involve important trade-offs: for example, preserving grasslands and adapting their management to improve carbon sequestration in the soil may actually increase N₂O and CH₄ emissions. Furthermore limited information is available regarding the actual and the past management of grasslands. On the other hand common agreement was reached in saying that carbon accumulation could be constrained by nutrients, in particular by nitrogen availability [20].

Carbon dioxide is lost from grassland soils by autotrophic and heterotrophic respiration. Changes in organic carbon content are a function of the balance between inputs to soil of carbon fixed by photosynthesis (*GPP*) and losses of soil carbon via respiration (*TER*). Rates of carbon input will therefore be dependent on the vegetation for both the managed grassland and native ecosystem. Soil erosion can also result in the unbalance of carbon, but the net effect of erosion on carbon losses as CO₂ for large areas is unclear. For soils, both the quantity and quality of organic matter inputs and the rate of decomposition of soil organic carbon is determined by the interaction of climate, soil, land use (including land-use history) and management. In native ecosystems, climate and soil conditions are the primary determinants of the carbon balance, because they control both production and decomposition rates. In agricultural systems, land use and management act to modify both the input of organic matter via residue production, organic fertiliser application, grazing management and the rate of decomposition (by modifying micro-climate and soil conditions through cultivar selection, soil tillage, mulching, fertiliser application, irrigation and liming) [21]. Management practices that increase soil and root respiration cause short-term efflux of CO₂ to the atmosphere, whilst practices that increase the rate of decomposition of organic matter lead to longer-term losses of soil organic carbon in the form of carbon dioxide. Herbage harvesting by cutting also results in carbon exports from grassland plots. Most of the carbon harvested and stored in hay or silage will be released as CO₂ to the atmosphere shortly after harvest.

Grassland management plays an important role in carbon cycle by influencing *GPP*, as well as soil respiration rates. Fertilisation practices generally increase above and below ground production. It was already recognised that fertil-

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isation and cutting regimes are influencing especially *NEE* increasing plant growth [22]. In particular proper fertilisation is considered increasing the proportion of the light fraction of organic matter in soil [23].

Soil organic carbon (*SOC*) storage in grasslands is impacted by climate, soil characteristics, topography, vegetation and management, but arguably management has the largest impact on *SOC* storage. According to estimates for the grassland management effect on *SOC* storage based on a literature review and meta-analysis of grassland studies [24], land use change from grassland to cropland systems causes losses of *SOC* in temperate regions ranging from 18% (± 4) in dry climates and to 29% (± 4) in moist climates. Converting cropland back to grassland uses for 20 years was found to restore 18% (± 7) of the native carbon stocks in moist climates (relative to the 29% loss due to long-term cultivation) and 7% (± 5) of native stocks in temperate dry climates. Grasslands that are degraded for 20 years typically have 5% (± 6) less carbon than native systems in tropical regions and 3% (± 5) less carbon in temperate regions. Improving grasslands with a single practice caused a relatively large gain in *SOC* over 20 years, estimated as 14% (± 6) in temperate regions and 17% (± 5) in tropical regions, while having an additional improvement led to another 11% (± 5) increase in *SOC*. Anyway these estimates are strongly influenced by the method used for their evaluation. When these estimates are used for modelling, these uncertainties propagate producing evaluations that could conduce to biased conclusions for example not permitting to define the sink or source role of an ecosystem in a regional budget (Fig. 2.1).

2.3 Modelling the role of grasslands in the carbon cycle

The scientific community produced in the last years a number of vegetation models. These can be classified in two main groups: biogeographical models and biogeochemical models. The first group is mainly meant to simulate equilibrium vegetation starting from a set of climatic variables and do not simulate any biochemical process. This kind of model can be used for analysing vegetation distribution in response to climate change. In contrast biogeochemical models frequently assume a constant distribution of vegetation. Biogeochemical processes (like photosynthesis and respiration) are then simulated according to the local environmental conditions. Many models of the second group are available for simulating carbon fluxes in grasslands and their interactions with

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the other biogeochemical elements. Many of these are developed around agricultural ecosystems focusing on high crop production and efficient management like CERES models [25]. In these models soil biogeochemistry is frequently simplified. Such models can't be applied for analysing in detail carbon dynamics. Other models are focusing more on biogeochemical cycles such as CENTURY [26]. These models are more focused on soil processes, but their plant representation is too simplified. Some other models like PaSim [27] or CESAR [28] are specific for grassland ecosystems and can't be extended to other plant functional types. Additionally these models were especially developed for productive grasslands composed of only one or two species (i.e., rye-grass and clover). For this project the ecosystem process-based model Biome-BGC was chosen. While it is well validated to simulate the carbon cycle in forest ecosystems, its application to grasslands is not common. On the other hand it is already applied to different plant functional types producing reliable estimates [29].

The aim of the present work is to provide a valuable tool and evaluate its capabilities for gaining a better insight in the interactions between management and carbon cycle in a type of ecosystem that seems to be among the most sensitive ones to climate changes [30]. For this reason routines simulating management practices were implemented in the original version of Biome-BGC. Such modified version was evaluated by mean of in situ comparisons. In the first part of this thesis eddy covariance measurements of CO₂ fluxes [31] were used for constraining the model to produce better estimates. This permitted to perform a comparison of the response of model input parameters among different sites and different years. In the second part of this work, the model was constrained with the carbon content in the yield production of a grassland with different fertilisation loads. The method permitted to evaluate how the ecosystem biogeochemistry is responding to variate anthropogenic pressure.

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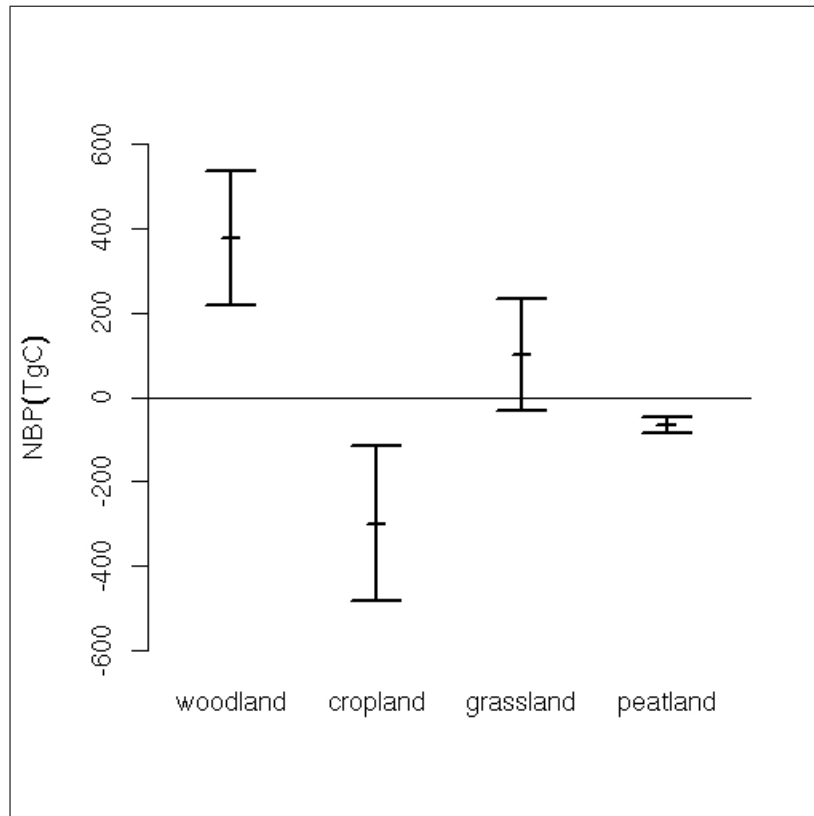


Figure 2.1: Plot of net biome productivity (NBP) of European forest, cropland, grassland and peatland (adapted from Janssens [1]). Positive fluxes indicate net uptake, negative is net loss of carbon. Uncertainties in the estimates are reported as error bars.

2.3 Modelling the role of grasslands in the carbon cycle

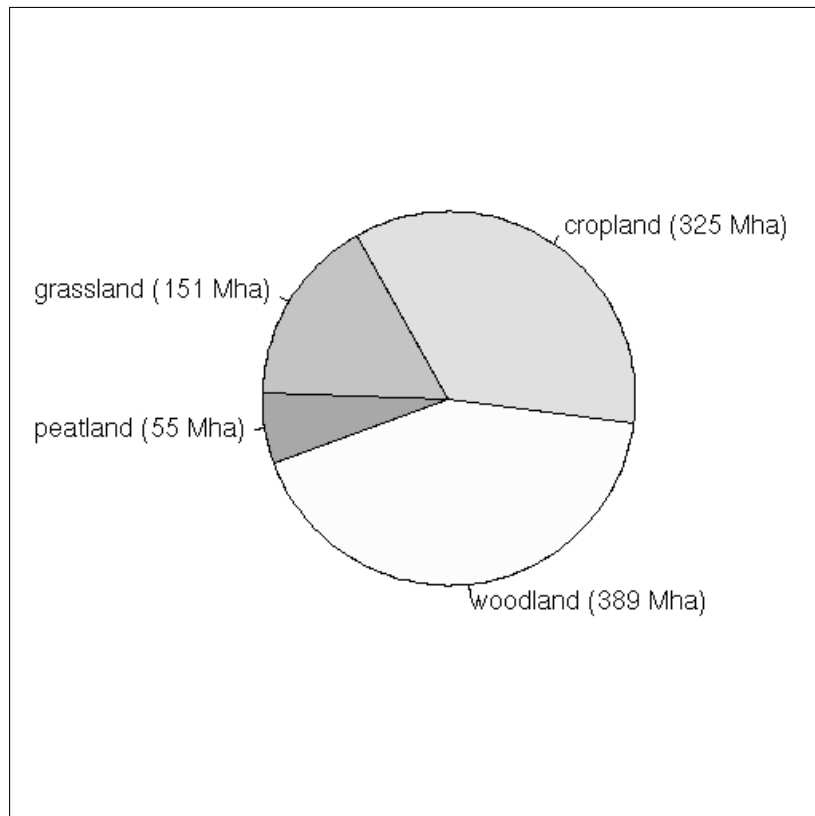


Figure 2.2: Pie chart of area occupied by woodland, cropland, grassland and peatland in Europe. Adapted from Janssens [1].

3 The Biome-BGC model

3.1 Model description

In our study the ecosystem process model Biome-BGC (version 4.1.1) was adopted. Biome-BGC has been broadly documented and validated ([32], [33], [34], [35], [36], [37], [38], [39]). Biome-BGC is a multi-parameter non-linear model that mainly simulates the storage and fluxes of water, carbon (C), and nitrogen (N) within the vegetation, litter, and soil components of a terrestrial ecosystem. Biome-BGC uses a daily time step in order to take advantage of widely available daily temperature and precipitation data from which daylight averages of short wave radiation, vapour pressure deficit, and temperature can be estimated [40], [41]. Biome-BGC simulates the development of soil and plant C and N pools; no input of soil C information or leaf area index (LAI) is required. LAI controls canopy radiation absorption, water interception, photosynthesis, and litter inputs to detrital pools and is thus central to Biome-BGC. Most algorithms have been refined for different plant functional types. Vegetation composition is described by seven different plant functional types (*PFT*) that are defined by forty-three ecophysiological parameters. Conceptually, these parameters describe biomes by rejecting excessive detail and unobtainable parameters while maintaining broadly significant vegetation descriptions. The core processes are photosynthesis and respiration. *NEE* is based on gross primary production simulated with the Farquhar photosynthesis model [42] minus maintenance respiration (calculated as a function of tissue N concentration [43]) and growth respiration (a constant fraction of gross primary production). The model is normally initialised by taking the carbon pools to steady state with a spin-up routine.

Model processes descriptions

The main physical and biological processes represented in Biome-BGC (Fig. 3.1) are here summarised.

Canopy radiation. The plant canopy leaf area is divided into sunlit and shaded fractions on the basis of a radiation extinction coefficient that varies

with canopy geometry. All plant physiological processes are simulated separately for the sunlit and shaded canopy fractions. Differences in leaf physiology between the sunlit and shaded fractions are represented as differences in SLA. The N concentration and maximum stomata conductance are considered to be constant between sunlit and shaded fractions.

Photosynthesis. Assimilation on a unit projected leaf area basis for C₃ plants is estimated independently for the sunlit and shaded canopy fractions, using a biochemical model [42]. The kinetic parameters values are obtained from Woodrow and Berry [44] and from de Pury and Farquhar [45]. The maximum rate of carboxylation (VC_{max}) is calculated as a function of the specific activity of the Rubisco enzyme (RuBpa), the weight fraction of N in the Rubisco molecule (fnr), the fraction of total leaf N in the Rubisco enzyme (flnr), the specific leaf area (SLA), and the leaf C:N ratio ($C:N_{leaf}$). One advantage of this formulation is that it makes explicit the dependence of VC_{max} on SLA and $C:N_{leaf}$. Values for fnr and RuBpa, as well as the temperature dependence of RuBpa, are assumed constant across all species.

Stomata conductance. A form of the Leuning model [46] is used, which makes actual conductance a function of a minimum value and a series of multiplicative reductions based on incident radiation, vapour pressure deficit, leaf water potential, and night minimum temperature [39]. There is no direct effect of changing atmospheric CO₂ concentration on stomata conductance, which is in agreement with recent studies [47].

Evaporation and transpiration. Both processes are estimated using the Penman-Monteith equation. Available energy is partitioned between the canopy and the soil surface. Soil evaporation depends on the number of days since wetting. Energy available in the canopy is divided between the evaporation of water intercepted on the canopy and transpiration. Both these processes depend on the leaf-scale aerodynamic conductance, with transpiration depending in addition on stomata conductance.

Autotrophic respiration. Two types of autotrophic respiration are distinguished: i) maintenance respiration, which is calculated as a function of tissue mass, tissue N concentration and tissue temperature. ii) growth respiration which is a simple proportion of total new C allocated to growth.

Phenology. For all vegetation types, some growth can be stored for display during the following growing season. For this stored growth, the model developed by White [2] is used to estimate the middle of the leaf expansion and litterfall periods for deciduous broad-leaf trees and for grasses. For all vegeta-

3 *The Biome-BGC model*

tion types the user has the option to specify the proportion of the total growing season during which stored growth is displayed. The growth that is not stored for display in the following growing season is displayed immediately, so the overall seasonal growth signal consists of one component due to stored growth and a second component due to current growth. The current growth component has a strong dependency on the stored growth, since it augments the canopy leaf area and changes the growth potential independent of the current growing season conditions. This is essential to the development of new canopy for a deciduous system in spring.

Allocation of carbon and nitrogen. The C:N stoichiometry of new plant allocation is constant, defined by ratios between allocation to new leaf and to each of the other plant tissues (fine root, live and dead stem wood, live and dead coarse root wood). The C:N stoichiometry of total plant biomass changes over time as leaves and fine roots turn over to litter pools. All plant pools for C and N are completely prognostic, so leaf area responds to changes in climate, physiological parameterisations, disturbance regimes, and dynamics in the SOM pools over time. The availability of C from assimilation and the availability of N from plant mineral N uptake must be balanced to meet this constant C:N for new growth, which is achieved by down-regulating assimilation under conditions of chronic N limitation.

Plant mineral nitrogen uptake. Plants compete with the N immobilising processes in the litter and soil decomposition dynamics for one pool of soil mineral N. This competition is based on relative demand, which is set by the plants potential assimilation rate and the potential N immobilisation rate due to decomposition, both estimated assuming current values for all the state variables. Actual assimilation and actual decomposition then proceed at either their potential rates if mineral N is not limiting, or at reduced rates if N is limiting.

Litter and SOM pools. All plant litter is divided into three pools on the basis of the weight fractions of lignin, cellulose plus hemicellulose, and remaining mass in the litter. These litter pools undergo chemical degradation at different rates, producing a connected series of SOM pools. The model structure defines a converging cascade of progressively more recalcitrant SOM [48]. C:N ratios for the litter pools depend on the inputs from plants, but C:N ratios for the SOM pools are fixed.

Heterotrophic respiration. Litter and SOM decomposition produces a heterotrophic respiration flux, which depends on the size of the litter and SOM pools and their decomposition rate constants. These rates depend on soil tem-

perature and soil moisture. Decomposition also depends on the availability of soil mineral N for those steps which are immobilising N.

Management routines description

The mowing practices were simulated as a leaf area index (*LAI*) 90% reduction in a user-defined day of the year (Fig. 3.2), here we assume that the roots are not affected by mortality as consequence of harvesting. The clippings were considered not to be totally removed, a small percentage (10%) was simulated to remain on the field and consequently re-distributed in the litter pool: this was done to simulate the harvesting efficiency. In Biome-BGC, *LAI* is a function of leaf C content (`cs.leafc`) and specific leaf area (*SLA*). Being *SLA* used as an average constant for simulating the biomass removal we acted on leaf C content. In a user defined day (`d_h1`, `d_h2`, `d_h3`), we simulated the *LAI* reduction indirectly diminishing the leaf C content (`cs.leafc`) and for consistency also the N content (`ns.leafn`). The percentage left was a priori defined (`harv_fr`). The unharvested portion (`clip_fr`) was redistributed in litter pools (`cs.litr1c`, `ns.litr1n`).

```
if (yday==d_h1 || yday==d_h2 || yday==d_h3)
{
  cs.litr1c = cs.litr1c + (cs.leafc * (1-harv_fr) * clip_fr);
  ns.litr1n = ns.litr1n + (ns.leafn * (1-harv_fr) * clip_fr);
  cs.leafc = cs.leafc * harv_fr;
  ns.leafn = ns.leafn * harv_fr;
}
```

The fertilisation practices were implemented as an increased input of N at the beginning of the growing season, after the first harvest and after each of the following harvests but not in the last when more than one. The same input way of N atmospheric deposition was followed. To simulate a slow release of N the period of increased input was set to two weeks. This quantity of N is accumulated in the mineral N pool and is influenced by volatilisation and runoff. In details: if the beginning of growing season (`epc.onday`) or an harvest day (`d_h1`, `d_h2`) was reached, the daily nitrogen input as nitrogen deposition (`daily_ndep`) flowing to the mineral nitrogen pool (`nf.ndep_to_sminn`) was increased proportionally to the total N fertilisation (`fert`) for a period of two weeks. 50% of total N was timed at first, the rest equally after the first and the second harvest. A case study with three harvests is here reported:

```
if (yday > epc.onday && yday < (epc.onday+14))
{
  nf.ndep_to_sminn = daily_ndep+((fert*0.5)/14.0);
}
```

3 The Biome-BGC model

```
if (yday > d_h1 && yday < (d_h1+14))
{
  nf.ndep_to_sminn = daily_ndep+((fert*0.25)/14.0);
}
if (yday > d_h2 && yday < (d_h1+14))
{
  nf.ndep_to_sminn = daily_ndep+((fert*0.25)/14.0);
}
```

3.2 Model parameterisation

Since many required input parameters aren't measured at the experimental sites the initial model parameter values and their ranges were set as in a literature review by White [33] or according to Schulze [3] in case of specific leaf area (*SLA*) and maximum stomata conductance (g_{max}) (Tab. 3.1). The first cited source is a dedicated review for all the input parameters of Biome-BGC organised for plant functional types. For few parameters a specific choice of a initial value would possible discriminating for the most fitting source to the here analysed ecosystems. For the reason we considered mean and extreme values from this review. An alternative literature source was used because the first cited review provided values of SLA based on effective leaf area index, while we preferred to treat this parameter as a function of projected leaf area. The initial CO₂ concentration was set to 300 ppm [4], preindustrial N deposition rate was set to $5 \cdot 10^{-4}$ kg N m² yr⁻¹ [49] and contemporary N deposition to $2.81 \cdot 10^{-3}$ kg N m² yr⁻¹ [49]. Considering that in both the semi-natural ecosystems the legume presence is low, the biologically fixed N was set at $1 \cdot 10^{-2}$ kg N m² yr⁻¹ [50]. The parameters used to describe vegetation ecophysiology in Biome-BGC are listed in table 4.1, with their units and description.

3.3 Model spin-up

To quantify the dynamics of C and N in ecosystems, numerical models of biogeochemical cycles include multiple state variables corresponding to functionally and dynamically distinguishable components. Experiments with this kind of models, commonly require a steady state solution to all state variables as a control case or initial condition. We define spin-up as the process that is used for taking the system to a steady state [51]. The model was taken to steady state by mean of a spin-up simulation (in this case management wasn't ap-

3.3 Model spin-up

plied). For this purpose the native dynamics were used [52]. We can address this state as a meta-stable condition that requires a very small disturbance to be perturbed. Anyhow in the most cases ecosystems can't be said to be at the equilibrium since many natural and anthropogenic disturbances are affecting C, N and water pools. For these simulations the leaf C content was initialised at $1 \text{ g C m}^{-2} \text{ yr}^{-1}$. The N pool was consistent to specified C:N ratios. The model was then run looping through a record of a number of years of meteorological data ranging between 600 and 2000. Local meteorological data records for such periods aren't existing, the available records are replicated to fulfil the required time frame. The loop was broken only when a threshold tolerance of $5 \cdot 10^{-3} \text{ kg C yr}^{-1}$ between the total ecosystem C from one year to the next year was reached. This procedure was repeated for any model evaluation.

3 The Biome-BGC model

Table 3.1: Model input parameters and their existence range. The source is White [2] for all except for average specific leaf area and maximum stomata conductance [3]. Maximum nitrogen input was defined as 500 Kg N ha⁻¹.

ID	parameter	minimum	maximum
1	transfer growth period (yr ⁻¹)	0.0	1.0
2	litterfall (yr ⁻¹)	0.0	1.0
3	annual leaf and fine root turnover fraction (yr ⁻¹)	0.0	1.0
4	(ALLOCATION) new fine root C : new leaf C (ratio)	0.199	2.19
5	(ALLOCATION) current growth proportion (prop.)	0.0	1.0
6	C:N of leaves (Kg C Kg N ⁻¹)	14.3	58.8
7	C:N of leaf litter (Kg C Kg N ⁻¹)	32.7	69.4
8	C:N of fine roots (Kg C Kg N ⁻¹)	21.7	87.7
9	leaf litter labile proportion (%)	25.0	45.0
10	leaf litter cellulose proportion (%)	12.9	42.0
11	leaf litter lignin proportion (%)	4.1	27.4
12	fine root labile proportion (%)	22.2	35.2
13	fine root cellulose proportion (%)	38.1	59.5
14	fine root lignin proportion (%)	17.0	33.5
15	canopy light extinction coefficient (DIM)	0.314	0.778
16	canopy average SLA (m ² Kg C ⁻¹)	13.0	20.8
17	maximum stomata conductance (ms ⁻¹)	0.0046	0.0136
18	leaf water potential: start of reduction (MPa)	-1.17	-0.2
19	leaf water potential: complete reduction (MPa)	-4.0	-1.3
20	VPD: start of conductance reduction (MPa)	0.7	1.5
21	VPD: complete conductance reduction (MPa)	2.0	12.0
22	symbiotic nitrogen + deposition(Kg N m ² yr ⁻¹)	0.0	0.05

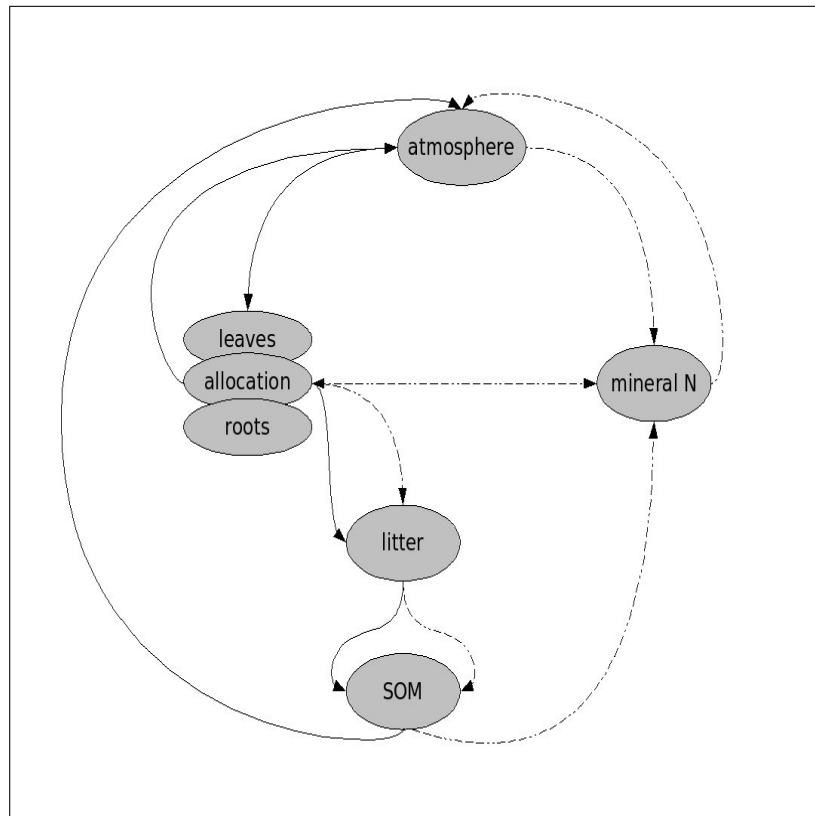


Figure 3.1: Simplified flux diagram of carbon and nitrogen pathways in Biome-BGC. The solid lines represent carbon pathway. The dashed lines represent the nitrogen pathway.

3 The Biome-BGC model

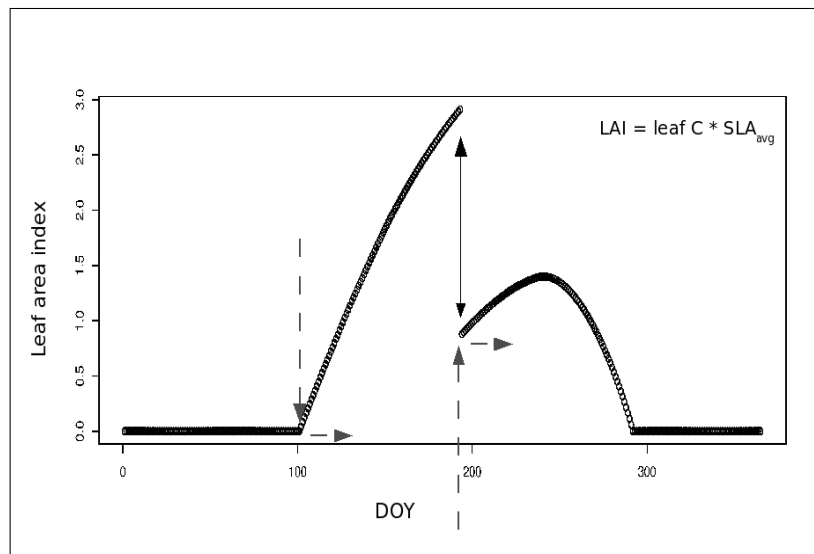


Figure 3.2: Leaf area index development during one whole year. The harvesting and fertilisation routines are represented. The first is shown by solid arrows: in a day defined by the user, the leaf carbon content (and consistently to C:N ratio also nitrogen content) are reduced. The fertilisation (dashed arrows) is applied as an increased nitrogen input lasting for a number of days. Nitrogen fertiliser is applied at the beginning of the growing season and after the harvests. If more than one harvest, after the last one, nitrogen fertilisation doesn't apply.

4 Improvement of carbon fluxes estimates: constrains on photosynthesis and respiration

The ecosystem process model Biome-BGC is designed to be applicable to a wide range of vegetation types, however when using the model in a specific context it may be required to calibrate it using observed data to obtain better estimates of the modelled processes. On the other hand, the on site calibration could limit the applicability of that model for large scale simulations. For this purpose the model and data uncertainties have to be taken in account. Uncertainties in model estimates are often - but not only [53] - related to poorly defined parameters. A first source of uncertainties is due to a lack of measured parameters in the specific context where the model is to be applied [54]. On the other hand the on-site measurement could be also affected by measurements errors. The measurement errors in the eddy covariance techniques have different sources (calibration of *IRGA* analyser, measurement of covariance, natural variability of turbulence and random sampling errors [55]). Bayesian calibration can be a solution to the calibration problem. The higher number of model evaluations required by this approach is computationally too expensive for high dimensional problems, therefore a preparatory sensitivity analysis can be necessary to identify the most important parameters to be optimised. In this contribution a general method for parameter estimation in a non-linear multi-dimensional model was developed. The aim of the approach was to provide better estimates comparing the results from different constrains (photosynthesis and respiration). The method was tested at two measurement sites showing which parameters can be efficiently constrained. This permitted the achievement of a better understanding of how the model is able to describe those ecosystem scale processes that are driving the role of grasslands in carbon cycle.

4.1 Materials and Methods

The proposed solution face one of the softer points in ecosystem modelling, parameter estimation. The procedure starts finding possible ranges of the model parameters (from the literature), estimating the most sensitive ones and finally

4 Improvement of carbon fluxes estimates: constrains on photosynthesis and respiration

calibrate these in order to gain the best fit between observations and model estimates. The first task is solved by the application of a Factor Fixing method [56] while the second task is accomplished using a Monte Carlo Markov Chain combined with the Metropolis-Hastings algorithm [57] [58]. The method was applied independently to time series of two years at two different measurement sites.

4.1.1 Measurement sites

The Net Ecosystem Exchange (NEE) was measured at both sites by mean of eddy covariance technique [55]. The first site is located in the western part of Hungary (Hegyhátsál, $46^{\circ}57'81''N$; $16^{\circ}39'81''E$) at 248 m a.s.l.. The average temperature is $8.9^{\circ}C$ and the annual precipitation is 750 mm; the climate type is continental. The vegetation typology is Arrhenatherion Kock 1926 and the soil is Alfisol [59] (clay 60%, silt 30%, sand 10%). The grassland is mowed twice per year: the first time in the beginning of June and the second time in the beginning of September. For Hegyhátsál the data for the year 1999 and 2000 were available. In the case of Hegyhátsál site, half hourly data were gap filled with an empirical method using the dependence between NEE and photon flux density for the daytime. For nighttime the relation between NEE and temperature of the air was used [60]. The partitioning in GPP and TER was made as follows: for night-time TER corresponds to the signal measured with eddy covariance while for daytime it is derived from the empirical relationship NEE , T_{10} (air temperature at 10 m above the ground). The NEE budget for 1999 is -51.3 g C m^{-2} [60] while for the year 2000 is $-220.2 \text{ g C m}^{-2}$. For convention negative signs mean sink of C, on the opposite positive signs would mean source of C. According to gap filled measurements, total ecosystem respiration was $1546.6 \text{ g C m}^{-2}$ in 1999 and $1621.6 \text{ g C m}^{-2}$ in 2000. Year-round GPP was $-1597.9 \text{ g C m}^{-2}$ in 1999 and $-1841.8 \text{ g C m}^{-2}$ in 2000 (Fig. 4.1). These results should be considered as somewhat rough estimates, since the dependency on variables like soil moisture is not taken into account [60].

The Mt. Bondone site is located in Italy, in Trento district at 1550 m a.s.l. ($46^{\circ}01'46''N$; $11^{\circ}04'58''E$). The mean annual temperature is $5.5^{\circ}C$ and the annual precipitation is 1189 mm; the climate is a typical alpine one. The vegetation type Nardetum alpigenum Br.-Bl. 1949 can be considered an example of typical alpine grassland. The soil is Typic Hapludalfs [59] (clay 30%, silt 50%, sand 20%). The grassland is managed with one mowing per year in mid July. Carbon fluxes measurements in this experimental site are available for

2003 and 2004. The gap filling was performed with a lookup table on monthly basis using soil temperature at 5 cm of depth (T_{soil}) and photosynthetically active radiation (PAR) during daytime. For nighttime, T_{soil} and soil humidity HU_{soil} were chosen [61]. The flux partitioning was performed with an exponential ecosystem respiration model on annual basis. In both the sites GPP was calculated as sum of NEE and TER [62]. The annual budget of NEE for the year 2003 is 6.2 g C m^{-2} (calculated from the flux measurements). While for 2004 the budget is -23.8 g C m^{-2} . In the first year of measure GPP was -1312.9 while in the second year it was -1219.9 . TER was 1319.1 in 2003 and 1196.1 in 2004 (Fig. 4.1). The higher values found in the year 2003 are connected with higher temperatures.

To avoid an optimisation on data series with an excessive modeled source, for both the sites the final partitioned and gap filled data series were filtered: only those daily means which were including days with less than one third of gap filled half hours were accepted.

4.1.2 The model and its parametrisation

The modified version of Biome-BGC was used for the porpoise of this work. Only mowing practices were taken in account since both the sites aren't fertilised. The values of the most sensitive parameters were sampled from a priori probability density functions (*pdf*) with mean value from literature (Tab. 4.1). Site characteristics like soil physical constants were used. Start and end of the growing season were determined from the daily gross primary productivity time series for each site-year in order to avoid the uncertainties related to the internal phenological model of Biome-BGC. Considering that in both ecosystems the legume presence is low, the biologically fixed nitrogen was set at $1 \cdot 10^{-2} \text{ kg N m}^2 \text{ yr}^{-1}$ [49].

4.1.3 Sensitivity Analysis

Since an optimisation of forty-three parameters is computationally too expensive, we had to fix those uncertain input factors that are so non-influential on the model output that can be set to any fixed value. For this porpoise many methods are suitable [56]. Many of these have model assumptions or are computationally expensive [63]. For this reasons an extension of the method proposed by Morris [64] was chosen. The method permits to rank the parameters in order of importance as a variance-based method, but having the advantage that the number of evaluations is linearly related to the number of input parameters,

4 Improvement of carbon fluxes estimates: constrains on photosynthesis and respiration

for this reason the method is very suitable when the computational cost of a quantitative analysis is not affordable (i.e., spin-up). The experimental plan is composed by individual randomised one-factor-at-time experiments. A base vector of input parameters is sampled and evaluated in the model. This model output is used as comparison term. Starting from the base vector only one parameter values is changed and the modified vector is evaluated in the model. This for all the input parameters and for n base vectors by mean of what can be defined elementary effect:

$$d_i(x) = \frac{(f(x_1, x_2, \dots, x_{ith}, \dots, x_k) - f(X))}{\Delta} \quad (4.1)$$

where $f(x)$ is the model output with the base vector of input parameters modified for the i th parameter and $f(X)$ is the output from the original base vector. Δ is a multiple of $p/[2(p-1)]$ where p is the number of nodes used for sampling the parameters values. There isn't any general rule for fixing p . The model parameters were sampled in a discrete space defined in $\pm 25\%$ of their mean value from literature. The reiteration of n samplings of base vectors permits to produce n estimates of the elementary effect for each model parameter. The parameter importance is assessed thanks to a sensitivity index: the mean of the modulus μ^* of the n elementary effects which estimates the first order effects of one parameter on the model output. As highlighted by Saltelli [56] μ^* has similarities with the total sensitivity indexes in the sense that it tends to produce a ranking of model parameters similar to the one obtained with variance based methods.

4.1.4 Parameters optimisation

Frequentist techniques [65] [66] are superior in terms of efficiency when analysing models with parameters that can be easily identified [67]. In case of Biome-BGC, the high non-linearity of the model makes the Bayesian approach preferable. The approach provides a mechanism for obtaining a posterior distributions (σ) of model parameters that combine information from the data (L) and from an a priori parameter distribution (ρ). The solution of this approach is explained by the relation

$$\sigma(m) = \rho(m) \cdot L(m) \quad (4.2)$$

(m) means that these distributions are proper of a parameter vector. ρ is defined as

$$\rho(m) \propto \exp \left[-\frac{1}{2} (m - m_{init})^T C_p^{-1} (m - m_{init}) \right] \quad (4.3)$$

where m and m_{init} are the actual and the previous vector of parameters and C_p is the covariance matrix of input parameters. The non diagonal elements of this matrix are assumed to be zero since we don't have any a priori knowledge of the covariances. $L(m)$ is a measure of the fit between observed and predicted data and $\sigma(m)$ is the a posteriori *pdf*. The pseudo-random process whose output is assumed to be the realization of $\rho(m)$ is done by mean of a Markov Chain Monte Carlo method. It means that each sampling is independent from the previous one. For generating random numbers with a normal (Gaussian) distribution, the Box-Muller [68] method was adopted. $L(m)$ is the likelihood function that quantifies the degree of fit between model output (d_p) and observation d_o .

$$L(m) \propto \exp \left[-\frac{1}{2} E(d_p, d_o)^T C_f^{-1} E(d_p, d_o) \right] \quad (4.4)$$

where C_f is the root mean square error between the predicted fluxes in the previously accepted step and the observed data; E is the distance between d_p and d_o :

$$E(d_p, d_o) = \frac{1}{2} \sum_{i=1}^n \sqrt{(d_p^i - d_o^i)^2} \quad (4.5)$$

The algorithm adopts a global search method with an uniform walk in the model space [57] that maximises the likelihood function (L) this algorithm was first described by Metropolis [57] and modified by Hastings [58]. It is based on the following rules: i) if the "new" point has higher likelihood than the "old" point then accept the proposed transition; ii) if the "new" point has lower likelihood than the "old" point then make a decision to move or to stay with the probability given by the ratio between the present and the previous likelihood. These rules permit to explore more in details the space of parameters in the neighbourhood of already accepted solutions without leaving portions of this space unexplored.

The sensitivity analysis and the optimisation were applied separately on each combination of site/year in a way to highlight the inter-annual difference. *GPP* and *TER* were used as independent constrains in the optimisation. A multi constrains approach wasn't feasible since these two components of carbon cycle were derived from a unique measurement of *NEE*.

4.2 Results and Discussion

According to the ranking obtained with the use of μ^* , the sensitivity analysis led to the choice of the most sensitive parameters for each combination

4 Improvement of carbon fluxes estimates: constrains on photosynthesis and respiration

site/year/component. The number of parameters was fixed to five in a way to have the maximum number of common parameters among sites and years. The optimised values of the model parameters provided a general improvement of daily fluxes prediction performance in all the cases. The best agreement between measured and predicted fluxes was found for *GPP* in Mt. Bondone, year 2003 (Fig. 4.2). The worse result was achieved for *TER* in Hegyhátsál, year 2000 (Fig. 4.3).

4.2.1 Sensitivity Analysis

In the two sites, both for *GPP* and *TER*, the analysis led to the same five top ranked more sensitive parameters, showing that the sensitivity of the model is independent from site/year and from component of carbon cycle taken into consideration. Being the results similar for all the cases analysed, a general validity, of the present ranking for this model and this plant functional type, can be assumed. Three sensitive parameters regard carbon to nitrogen ratio for different pools: leaves ($C:N_{leaf}$), roots ($C:N_{root}$) and litter ($C:N_{litter}$). $C:N_{leaf}$ is connected with both the photosynthesis and respiration processes (autotrophic component): the assimilation rate is well correlated with leaf nitrogen [69] and dark respiration processes follow the same trend [70]; $C:N_{root}$ is directly connected with the autotrophic component of soil respiration; $C:N_{litter}$ has relationships mostly with the heterotrophic component of *TER*. Specific leaf area (SLA) can be considered as an indicator of the average cost of above ground productivity for an ecosystem and consequently links directly to the net carbon uptake. The last parameter, maximum stomata conductance (MSC) is a proxy of the interactions between plant and free atmosphere: low values are limiting the daily carbon fluxes, not permitting an exchange between leaf and atmosphere, while high values make the plant very sensitive to drought stress. Generally we can say that all the main processes of carbon uptake were here represented: photosynthesis, autotrophic and heterotrophic respiration.

4.2.2 Parameter estimation

In the average, the optimisations on Hegyhátsál were performing poorer, this could be connected with the gaps distribution in the eddy covariance measurements. In the average $46.3\% \pm 6.6$ of daily means are missing but while the gaps in Mt. Bondone are uniformly distributed (mean gap length 2.6 *days* ± 3.1) in Hegyhátsál the measurements started only in March 1999 and the measurement instruments were turned down for technical reasons for some periods (mean gap

length $12.9 \text{ days} \pm 26.0$). The gap filling capability to reproduce the management immediate influences on carbon fluxes should be taken in consideration for decreasing the acceptance threshold of gap filled time series. On the other hand the scattering in Hegyhátsál time series - especially in the year 1999 - is higher than for those measured in Mt. Bondone. An analysis noise/signal could help in the explanation of differences in model performance.

Generally the performance for the photosynthesis related component is better than the one related to respiration. *GPP* in Mt. Bondone 2004 is overestimated. At the same time the model lacks of performance particularly for *TER* in Hegyhátsál, it means that the selected parameters were insufficient to efficiently constrain this process. Probably autotrophic and heterotrophic components should be constrained separately being these processes connected to different ecophysiological drivers: a further investigation would be necessary. For both the components, in Mt. Bondone 2003, the bigger mean change of the expected parameters values was found (*GPP* 20.3% - *TER* 16.6%) (Tab. 4.3 and 4.4) this could be connected to the fact that the year 2003 is affected by a climate anomaly [30] and consequently the optimised parameter values resulted to be more different for that year than in the other cases (Tab. 4.3 and 4.4). The input parameters that shifted more from the a priori to the a posteriori expected values were the maximum stomata conductance (mean change *GPP* 58.2% - *TER* 45.7%) (Tab. 4.3 and 4.4) and the C:N of roots (mean change *GPP* 5.23% - *TER* 3.03%). The variation in the first parameter values can be connected with the fact that in all the four cases the mean annual temperature is above the average (Tab. 4.2), this change can be interpreted as a reaction of the ecosystem to warmer years. The same explanation can be adopted for the second parameter: during warmer periods total plant nitrogen content can decrease both in green and senescent leaves [71]. According to this sentence an increase in C:N ratio of leaves is expected: for Mt. Bondone a positive change is found, remarkably higher for the year 2003, but for Hegyhátsál there was an opposite trend. This could be connected with an erroneous initial estimate of the parameter values. Comparing the mean change of expected parameter values between components, Hegyhátsál showed a wider difference between the two components of carbon cycle (*GPP* 17.2% - *TER* 11.7%), the weaker constraining effect of the second component is related to the lack of performance that Biome-BGC was found to have for this site in these years.

4 Improvement of carbon fluxes estimates: constrains on photosynthesis and respiration

Table 4.1: Mean values of input parameters. The source is a dedicated to Biome-BGC literature review by White [2] for all the parameters except for average specific leaf area and maximum stomata conductance [3].

parameter	mean
transfer growth period (yr^{-1})	1.0
litterfall (yr^{-1})	0.7
annual leaf and fine root turnover fraction (yr^{-1})	1.0
(ALLOCATION) new fine root C : new leaf C (ratio)	1.0
(ALLOCATION) current growth proportion (prop.)	0.1
C:N of leaves (Kg C Kg N^{-1})	25.0
C:N of leaf litter (Kg C Kg N^{-1})	45.0
C:N of fine roots (Kg C Kg N^{-1})	50.0
leaf litter labile proportion (%)	68.0
leaf litter cellulose proportion (%)	23.0
leaf litter lignin proportion (%)	9.0
fine root labile proportion (%)	34.0
fine root cellulose proportion (%)	44.0
fine root lignin proportion (%)	22.0
canopy water interception coefficient ($1/\text{LAI}/\text{d}$)	0.0022
canopy light extinction coefficient (DIM)	0.48
all-sided to projected leaf area ratio (DIM)	2.0
canopy average SLA ($\text{m}^2 \text{ Kg C}^{-1}$)	16.9
ratio of shaded SLA:sunlit SLA (DIM)	2.0
fraction of leaf N in Rubisco (DIM)	0.21
maximum stomata conductance (m s^{-1})	0.0082
cuticular conductance (m s^{-1})	0.0006
boundary layer conductance (m s^{-1})	0.04
leaf water potential: start of reduction (MPa)	-0.73
leaf water potential: complete reduction (MPa)	-2.7
VPD: start of conductance reduction (MPa)	0.1
VPD: complete conductance reduction (MPa)	0.5

4.2 Results and Discussion

Table 4.2: Meteorological characteristics of the experimental sites: average temperature (temp), precipitation (prcp) growing season length (GS length), precipitation during growing season (GS prcp), growing degree days within growing season (GS GDD).

site/year	temp (°C)	prcp (mm)	GS length (dd)	GS prcp (mm)	GS GDD (°C)
Hegyhátsál, 1999	12.62	600	260	479	4495
Hegyhátsál, 2000	13.95	528	250	379	4634
Mt. Bondone, 2003	7.27	1009	190	549	2544
Mt. Bondone, 2004	6.26	1169	185	646	2254

Table 4.3: A priori and a posteriori parameters values constrained with gross primary production. In brackets there are the changes of the expected values expressed in percentage. C:N_{leaf} (ratio), C:N_{root} (ratio), C:N_{litter} (ratio), specific leaf area (SLA) (m² kg C⁻¹) and maximal stomata conductance (MSC) (m s⁻¹) are reported.

	C:N _{leaf}	C:N _{litter}	C:N _{root}	SLA	MSC
a priori	25.00	45.00	50.00	16.90	0.0082
a posteriori					
Hegyhátsál, 1999	23.63 (5.5)	42.56 (5.43)	47.16 (5.7)	16.10 (4.7)	0.0030 (63.4)
Hegyhátsál, 2000	24.29 (2.8)	44.30 (1.56)	48.85 (2.3)	16.35 (3.2)	0.0025 (69.5)
Mt. Bondone, 2003	29.24 (17.0)	47.28 (5.07)	54.94 (9.9)	18.00 (6.5)	0.0041 (50.0)
Mt. Bondone, 2004	26.56 (6.2)	45.86 (1.92)	51.49 (3.0)	16.95 (0.3)	0.0041 (50.0)

Table 4.4: A priori and a posteriori parameters values constrained with total ecosystem respiration. In brackets there are the changes of the expected values expressed in percentage. C:N_{leaf} (ratio), C:N_{root} (ratio), C:N_{litter} (ratio), specific leaf area (SLA) (m² kg C⁻¹) and maximal stomata conductance (MSC) (m s⁻¹) are reported.

	C:N _{leaf}	C:N _{litter}	C:N _{root}	SLA	MSC
apriori	25.00	45.00	50.00	16.90	0.0082
a posteriori					
Hegyhátsál, 1999	24.54 (1.8)	44.25 (1.67)	48.75 (2.5)	16.62 (1.7)	0.0048 (41.5)
Hegyhátsál, 2000	24.65 (1.4)	44.36 (1.43)	49.00 (2.0)	16.54 (2.1)	0.0047 (42.7)
Mt. Bondone, 2003	27.74 (11.0)	46.46 (2.67)	52.92 (5.8)	17.10 (1.2)	0.0042 (48.8)
Mt. Bondone, 2004	25.91 (3.6)	45.58 (1.29)	50.91 (1.8)	16.68 (1.3)	0.0041 (50.0)

4 Improvement of carbon fluxes estimates: constrains on photosynthesis and respiration

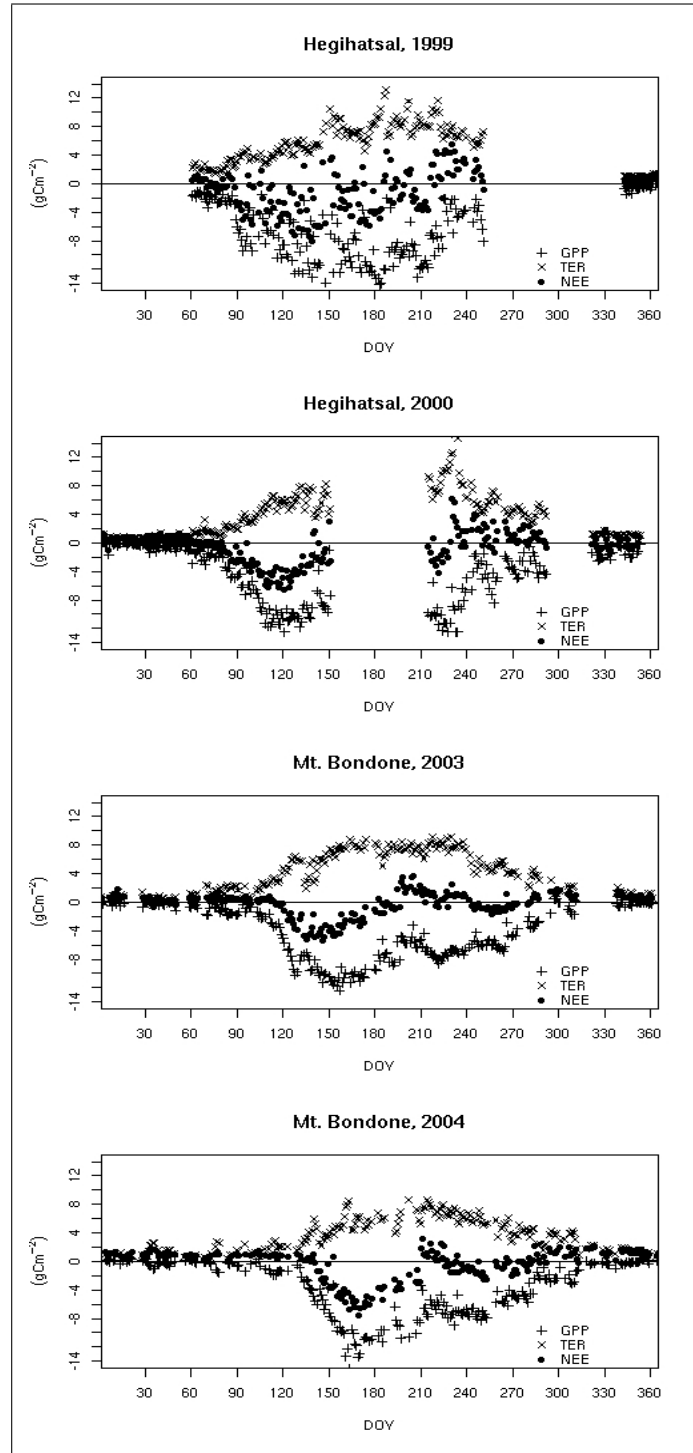


Figure 4.1: Eddy covariance measurements at Hegyhátsál and Mt. Bondone sites: partitioned fluxes in gross primary production (*GPP*) and total ecosystem respiration (*TER*) are reported. While in the first site there are few but long gaps (12.9 days \pm 26.0) in the second site there are many but short gaps (2.6 days \pm 3.1). In Hegyhátsál, total ecosystem respiration was 1546.6 g C m⁻² in 1999 and 1621.6 g C m⁻² in 2000. In the same site year-round *GPP* was -1597.9 g C m⁻² in 1999 and -1841.8 g C m⁻² in 2000. In Mt. Bondone, *GPP* was -1312.9 g C m⁻² in the first year of measure while in the second year it was -1219.9 g C m⁻². *TER* was 1319.1 g C m⁻² in 2003 and 1196.1 ³²C m⁻² in 2004.

4.2 Results and Discussion

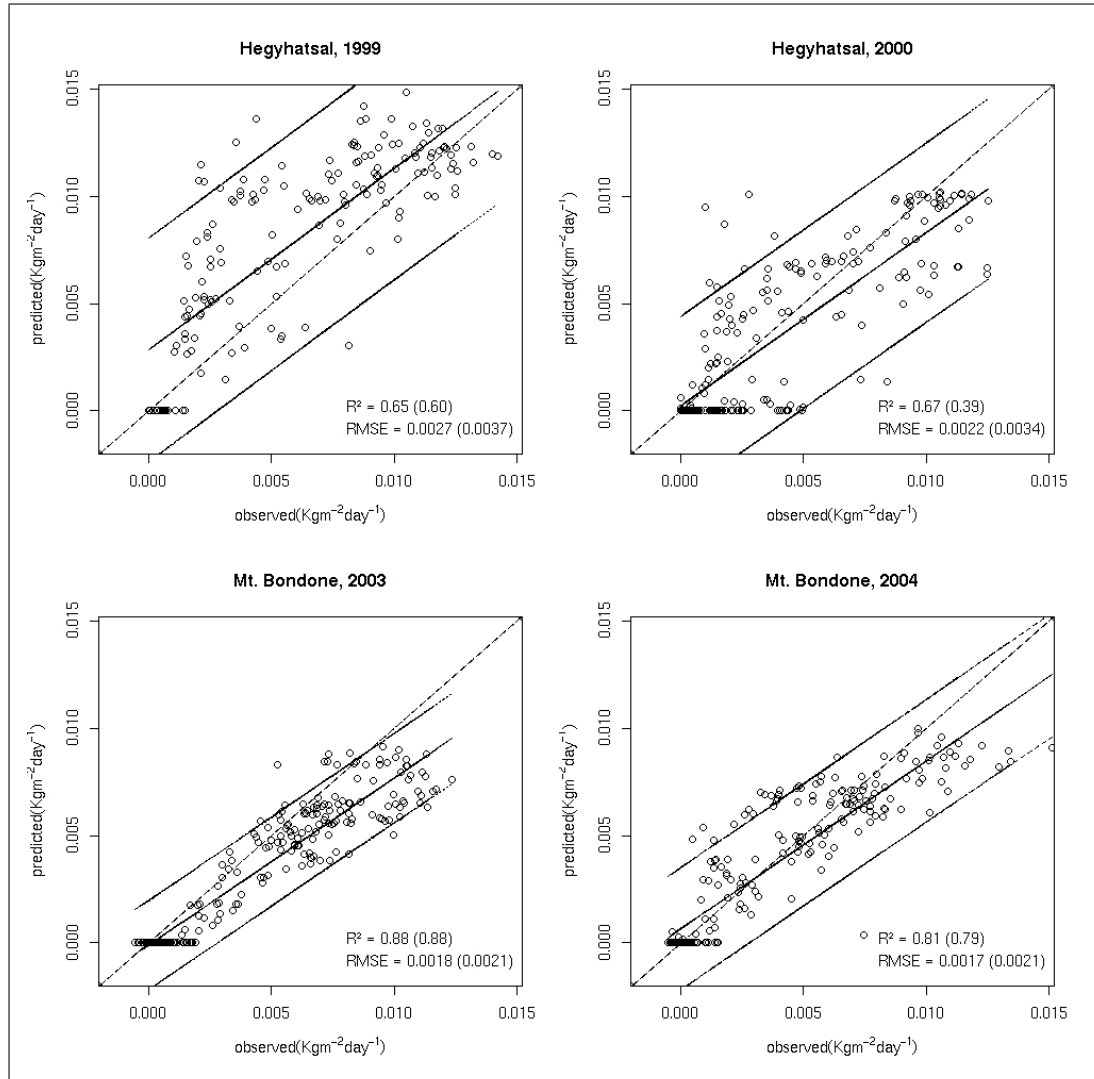


Figure 4.2: Scatterplot of observed and predicted daily gross primary production (*GPP*) obtained with a posteriori parameterisation. The regression line and the tolerance band are plotted. The coefficient of determination and the root mean square error are reported both for a priori (in brackets) and a posteriori parameterisation.

4 Improvement of carbon fluxes estimates: constrains on photosynthesis and respiration

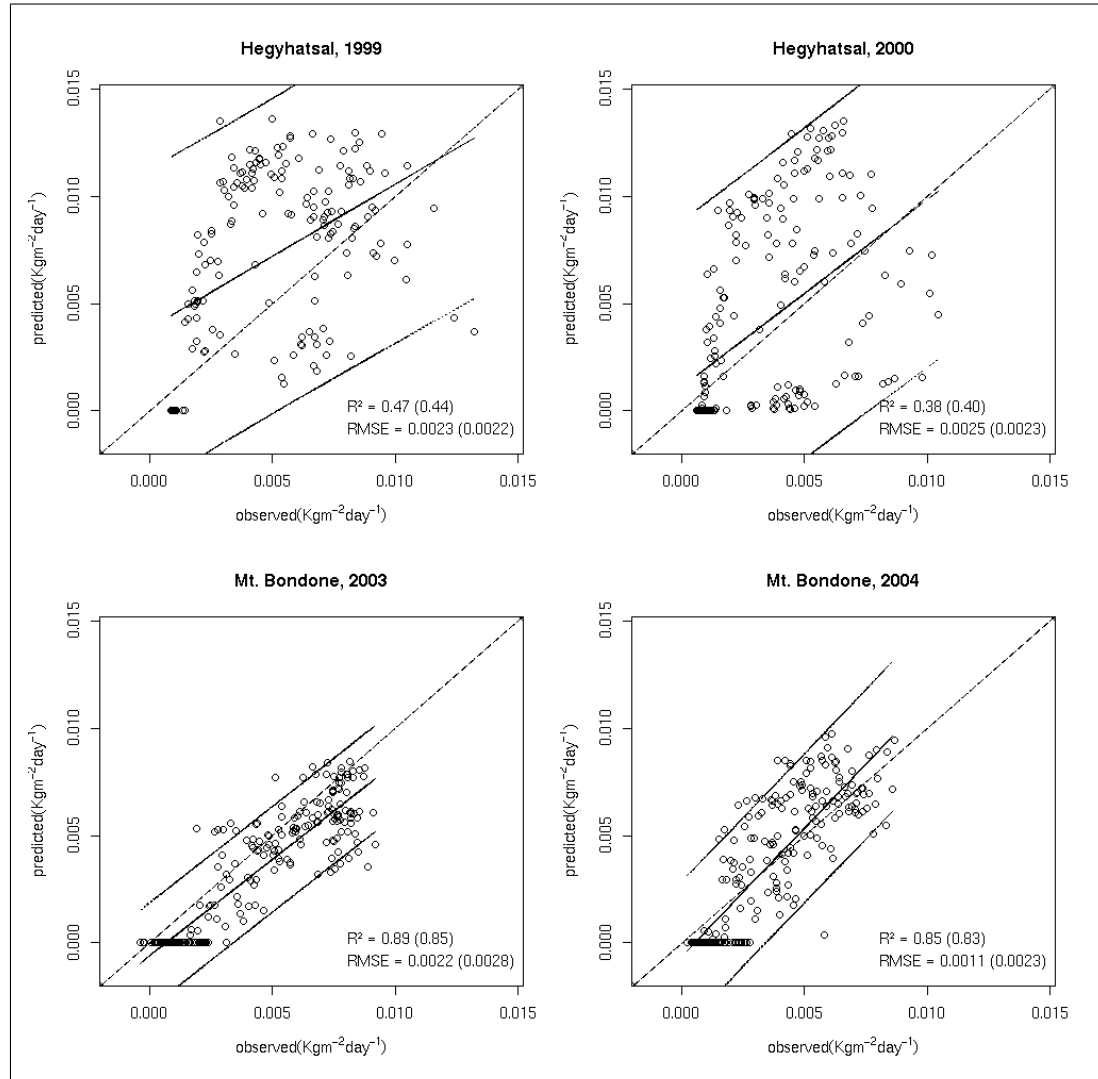


Figure 4.3: Scatterplot of observed and predicted daily total ecosystem respiration (TER) obtained with a posteriori parameterisation. The regression line and the tolerance band are plotted. The coefficient of determination and the root mean square error are reported both for a priori (in brackets) and a posteriori parameterisation.

5 Adaptation of an alpine grassland to different nitrogen fertilisation loads

Temperate grasslands consist in almost 32% of the total earth's natural vegetation [72] and cover about 151 million of ha in Europe [1]. On perennial grasslands, where tillage isn't practised, nitrogen fertilisation increase significantly forage production. As the most limiting nutrient for plant growth, nitrogen (N) dynamics in ecosystems and their responses to global change will impact significantly on the long term carbon (C) sequestration in soils of terrestrial ecosystems [20] [73] [74]. While changes in soil N pools and dynamics under global warming have been observed in various ecosystems [75] [76], our knowledge on responses of plant to N availability and its potential impact on ecosystem C processes (e.g., plant growth, allocation, productivity and decomposition) is limited [77] [78]. Frequently single processes (i.e., quality of organic matter [74], soil C content [22], legume abundance [79], roots development [80]) are analysed in the frame of ecosystem response to management. Very few studies can be said to have a complete overview on the vegetation reaction to increased N availability. With the present work we aim to give a contribution to a better understanding of these responses, considering different ecosystem processes and their interactions. For doing this the input parameters of a ecosystem process model were constrained. The combined application of a sensitivity analysis and a parameters inversion permitted to disentangle the complex responses of plants to nitrogen fertilisation. The ecosystem process model Biome-BGC was adopted mainly for its general character, on the contrary of many other process ecosystem models it isn't focused on any specific component of the ecosystem nor on a single plant functional type. For models with a certain number of parameters (Biome-BGC has forty-three parameters), we can question whether it is necessary to take all parameters into account in inversion problems [81]. This is connected with redundancy or over parameterisation. To determine the most contributing parameters to the output uncertainty, a sensitivity analysis based on the combination of analysis of variance and Monte Carlo sampling, was conducted. The method here suggested has the advantage of simultaneously being able to: i) select parameters according to their significant influence on

the output; ii) partition the error contribution of the model input parameters in terms of explained variance; iii) moreover sensitivity estimators such as the suggested one are easy to implement, relatively computationally inexpensive and intuitive. The parameters considered sensitive were used for the optimisation. A systematic global search was adopted. The most sensitive parameters were inverted against the carbon content of the yield production combined with the harvesting date. This permitted to obtain an optimal value for maximising the number of predicted dates within a range around the observed dates. Finally, a comparison of the optimal values of each parameter was carried on among fertilisation loads. The changes in the parameter values were interpreted as adaptation.

5.1 Materials and Methods

5.1.1 Dataset

The experimental trial had been conducted between 1977 and 1994 [82]. It is located in the Southern Alps (Sedico, BL) at 420 m a.s.l.. The average temperature is 10.6°C, the average annual precipitation is 1366 mm. The meteorological variables had been recorded in an on-site weather station. The initial vegetation had been a typical *Arrhenatherion* with a low intensity fertilisation. The fertilisation trial had aimed to evaluate the effects of different level of chemical fertilisation for nitrogen (N), phosphorus (P) and potassium (K). The treatments had been obtained from a factorial combination of three fertilisation levels for each element. For each treatment, four repetitions of 24 m² were set. The grassland was managed with three cuts per year. The N fertiliser was applied once at the beginning of the growing season, once after the first cut and once after the second cut while P and K were distributed only once at the end of winter. Aboveground biomass production had been dried (DM) and weighted. We assumed a constant C content (45%) in DM. The soil is a medium sandy one (clay 12%, silt 23%, sand 65%) originated from limestone-dolomitic alluvium. In 18 years, the average C content in DM yield was 27.22 g C m⁻² for the lower level of fertilisation, 35.23 g C m⁻² for the mid level and 36.72 g C m⁻² for the higher (Fig. 5.1). The first harvest occurred in the average at the beginning of June, the second and the third after 50-60 days from the previous. For more details refer to Scotton [82]. As mentioned above, the experimental trial was planned for combinations of N, P and K. Since the adopted model simulates only the cycles of water, C and N, we had to take into account only

those combinations where P and K could be considered not limiting. For these reasons only those combinations with maximum P and K fertilisation load were selected.

5.1.2 The model and its parametrisation

A modified version of Biome-BGC including harvesting and N fertilisation was used. Biome-BGC has an internal phenological model according to White [2]. This model is based on thermal summations, it has been trained and validated for the American continent but not for Europe. For this reason we decided to use a more general phenological model according to Jolly [83]. This model is a growing season index based on variables considered good proxies for the mechanisms underlying phenology: low temperatures, evaporative demand and photoperiod. For each evaluation the model was first taken to the steady state considering absence of management. Biome-BGC has forty-three input parameters, some of these were a priori excluded from the analysis: those strictly regarding the woody compartment weren't considered. Other parameters like the water interception coefficient, ratio of shaded specific leaf area (SLA) to sunlit SLA, fraction of leaf N in Rubisco, cuticular conductance and boundary layer conductance weren't included because these can be assumed almost constant within a plant functional type [33]. Annual whole-plant mortality fraction due to herbivory was excluded because in the study site it isn't influent. Annual fire mortality fraction was also excluded because in the analysed sites fire doesn't occur. The sampling range was defined by the maximum and minimum value reported in a dedicated literature review by White [2] (Tab. 3.1). Only for maximum stomata conductance and for specific leaf area we used other data source [3]. The first parameter wasn't adequately discussed in the first review while the second parameter was erroneously calculated using effective leaf area index (e-LAI) while in the source code it was used as being a projected LAI. Uniform distributions of probability were assumed.

5.1.3 Experimental design

The most sensitive parameters were selected in order to reduce the variables in the inversion problem. For this purpose a sensitivity analysis was applied independently on the four different replicates of each N fertilisation load. Then these parameters were optimised in order to have better estimates. Since the selected parameters were in common among the fertilisation loads a final comparison among their final values was carried on. For the first two steps the same

5 *Adaptation of an alpine grassland to different nitrogen fertilisation loads*

constraining algorithm was used. The model was first taken at the steady state. Then it was run until the biomass recorded in the first cut in the first year of the experimental trial was reached. The day of the year was saved. Then the management was applied and the model was run until the next harvested biomass was reached. This was done for three cuts per 18 years. The predicted harvesting dates were compared with the observed ones. If the predicted date was in a range around the measured one (i.e., ± 7 days for the first and the second cut, ± 14 days for the third cut because clear harvesting criteria can't be identified), it was considered valid. If the total number of valid dates was higher than one third of the maximum (54 dates) then the parameters values were accepted, otherwise rejected. The algorithm was reiterated for an adequate number of accepted vectors of parameters (> 5000).

5.1.4 Sensitivity analysis

All the input parameters were varied at the same time. In order to assign a sensitivity to each parameter an analysis of variance was performed. The combination of such a method with a Monte Carlo sampling, was adopted. One drawback of the Monte Carlo technique is that a combined output uncertainty is calculated. This means that it is impossible to determine the contribution of each parameter to the overall output uncertainty. An analysis of variance can split the uncertainty associated to the model output, into its sources and can be conducted on the results of a Monte Carlo analysis. Variance based methods are generally appreciated for their accurate description of sensitivity patterns [63]. The above mentioned analysis was applied independently for each of the four replicates for all the three N loads. Those parameters that had a significant p value (≤ 0.05) in at least two replicates within a N load, were considered as sensitive. Any parameter considered sensitive in one or more N fertilisation load, was optimised in the further step of this work.

5.1.5 Parameters inversion

The most sensitive parameters were inverted against the carbon content of the yield production as described in the experimental design section. This permitted to obtain an optimal value for maximising the performance of the model. As performance we meant the number of predicted dates of harvest within a range around the observed dates (i.e., ± 7 days for the first and the second cut, ± 14 days for the third cut). This procedure was repeated for each replicate in the experimental trial. Differently than for the sensitivity

analysis, here we fixed the parameters defined as non-sensitive to a mean value from literature. After an adequate number of runs (> 5000), the optimal value of each parameter was obtained weighting the mean on a model performance index (predicted and accepted dates to observed dates ratio). The final values of parameters were compared among fertilisation loads.

5.2 Results and discussion

5.2.1 Sensitivity analysis

Of the twenty two parameters that were initially included (Tab. 3.1), six resulted to have significant effects on the model performance for all the three fertilisation loads (Tab. 5.1) these were litterfall as fraction of growing season, new fine root C to new leaf carbon ratio, current growth proportion, C:N of leaves ($C:N_{leaf}$), C:N of roots ($C:N_{root}$), nitrogen input as atmospheric deposition and symbiotic fixation (N_{in}). One more was sensitive in only one of the thesis: transfer growth period as fraction of growing season (TGr_{gs}). This resulted to be significant only for the N fertilisation treatment were no N was timed because the initial part of the growing period isn't boosted by fertilisation hence this parameter can be crucial especially for reaching the required biomass for the first harvest. The remaining input parameters were found not to have any significant effect. It could mean that they are really not significant or that they are involved in interactions with other parameters and it's not possible to extract information using the constrains here applied. The parameter annual leaf and fine roots turnover fraction was considered negligible mainly for its interaction with other parameters connected with the speed in replacing the death parts. C:N of litter was considered negligible mainly because of his correlation with the C:N of leaves in the previous year. Leaf and fine root labile, cellulose and lignin proportions are mainly involved with soil respiration. The processes in this component of the ecosystem are constrainable only indirectly by the aboveground productivity. Canopy light extinction coefficient and average specific leaf area are proxies of productivity hence we would have expected them to be strongly constrainable. Our hypothesis is that these values aren't easily constrainable because they represent average values of dynamic processes. In particular our constrain were restricted to a short period of time (less than one week) further weakening the possible interactions between constrain and parameter. This means that the applied constrains weren't sufficient for these two parameters. Leaf water potential, start and end of reduction were consid-

5 *Adaptation of an alpine grassland to different nitrogen fertilisation loads*

ered negligible. These parameters could be connected with others like C:N ratio of leaves, because lower N contents make the plant more resistant to drought stress. Finally the VPD parameters were excluded from the list of top ranked as sensitive ones, mainly for their interactions with stomata conductance.

5.2.2 **Parameter inversion**

The inversion algorithm permitted to obtain optimal values for each parameter. The parameter describing the length of the transfer growth period (Fig. 5.2.A) resulted to have a lower optimal value for the highest level of fertilisation. The smallest uncertainty is associated to the absence of N fertilisation. The first fact is connected to the higher productivity of a N fertilised ecosystem: annual potential productivity can be reached also with shorter growing periods. Less fertilised systems could need a longer growing period for reaching their potential productivity. The second observation is related to the need of a not fertilised system to have a determined length of growing period: too long periods could deplete reservoirs, too short periods could be not enough to replenish the reservoirs for the next year. The optimal value for the parameter describing the length of litterfall (Fig. 5.2.B) was found to be higher for the highest level of fertilisation. Extensively managed systems could have limited productivity in the final stage of growing season if senescence processes occur too early. About the ratio of photosynthetized carbon used for growing new roots or new leaves (Fig. 5.2.C), a decreasing trend from 0 kg N yr⁻¹ to 192 kg N yr⁻¹ was found. A similar trend was found also for the parameter describing how much of photosynthates is used for immediate growth or as reserve (Fig. 5.2.D). The trend found for the first parameter is a signal that the plant is investing more in root apparatus when N isn't abundant. On the opposite the abundance of this nutrient push the plant to produce more above ground biomass. The second parameter showed that while a not fertilised ecosystem is investing more in reservoirs, a fertilised ecosystem is investing more in present growth. The values of C:N ratios for leaves and roots were similar in the three cases (Fig. 5.2.E, Fig. 5.2.F). In these cases a decreasing trend was expected. It may be that the interactions between these two parameters don't permit to obtain more information from the inversion parameters. The nitrogen input optimal absolute value (Fig. 5.2.G) was found to be higher for the medium N fertilisation while the uncertainties associated with the third N fertilisation load don't permit to distinguish. Our expectation was to find lower N input values for the highest N fertilisation since the legume reduction connected with higher N availability

5.2 Results and discussion

is well documented in literature. On the other hand the difference between the lower and the medium N fertilisation load was low (ca. 40 kg N yr⁻¹). Anyway, we should keep in mind that the values reported are too high for the examined site. For all the parameters, the uncertainties associated with the higher level of N fertilisation were broader than in the other two cases. This may be connected with the fact that 192 Kg N ha⁻¹ could be near to a saturation threshold for this ecosystem. In this case the marginal response of the vegetation to N addition is decreasing making more difficult to find a solution to the inversion problem.

5 Adaptation of an alpine grassland to different nitrogen fertilisation loads

Table 5.1: Analysis of variance: the significance codes are reported for each input parameter (refer to table 3.1 and for each of the four replicates per nitrogen fertilisation load. The sensitivity analysis was performed independently for each replicate in each fertilisation level. Only those parameters that were found to be significant in more than one replicate per fertilisation level were considered as sensitive. Significance codes: p value \leq *** 0.001 ** 0.01 * 0.05.

ID	0 Kg N ha ⁻¹				96 Kg N ha ⁻¹				192 Kg N ha ⁻¹			
	rep1	rep2	rep3	rep4	rep1	rep2	rep3	rep4	rep1	rep2	rep3	rep4
1	***	**										***
2	***	***	***	***	***	***	***	***	***	***	***	***
3												
4		***		***	***	***	**	**	***	***	**	
5	***	***				***	***	*	***	**		***
6	***			**	***	***	***	***	***			***
7		**										
8	***	***	***	*	***		**	***	***	***		***
9									*			
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13									*			
14					*	*						
15			**	*								***
16					**		*					**
17					*		*	*	***			*
18											*	*
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5.2 Results and discussion

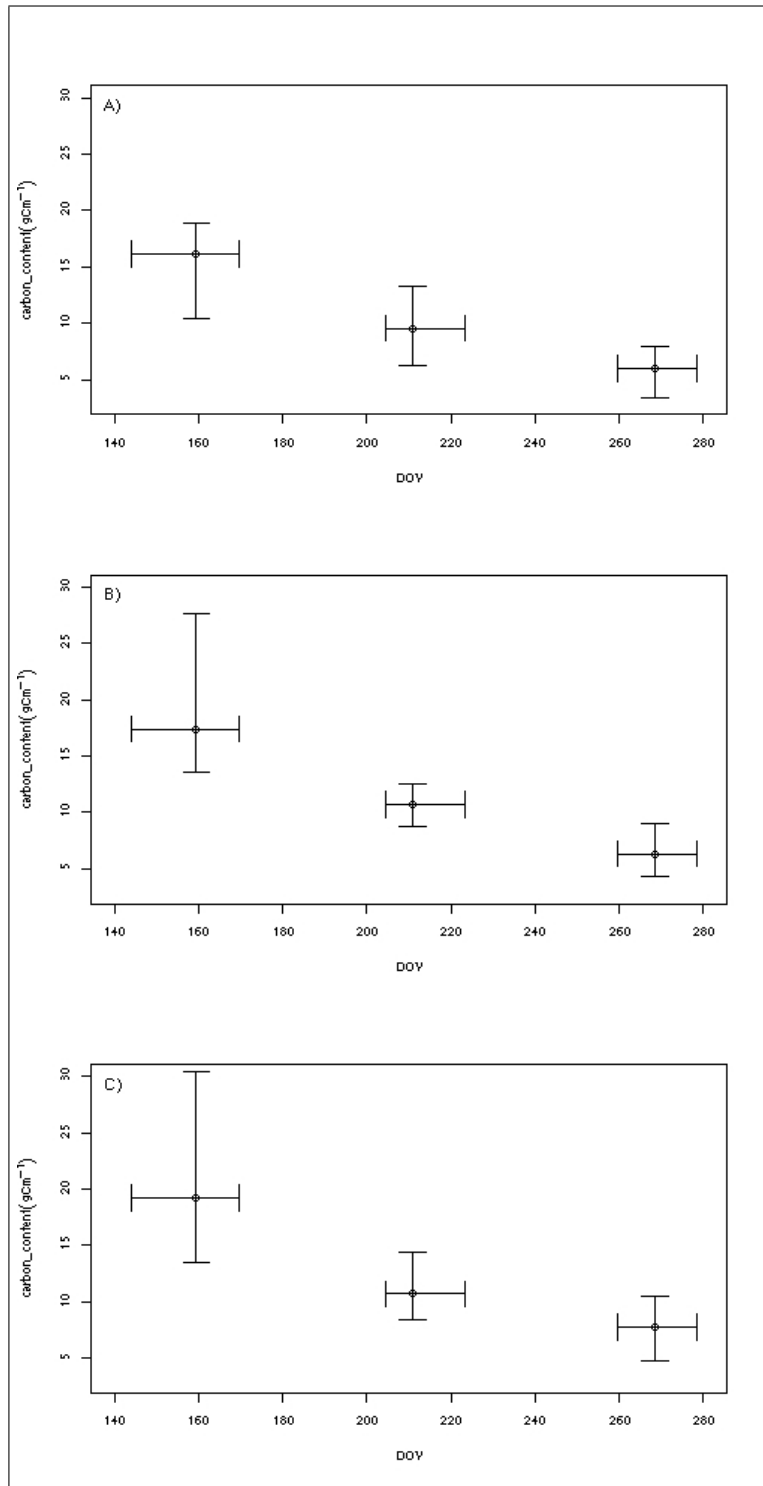


Figure 5.1: Medians of carbon content in yield production and harvesting dates for three N fertilisation loads in the experimental trial in Candaten (I): A) 0 Kg N ha⁻¹ yr⁻¹, B) 96 Kg N ha⁻¹ yr⁻¹, C) 192 Kg N ha⁻¹ yr⁻¹. The confidence intervals at 95% are plotted, both for C content and harvesting dates.

5 Adaptation of an alpine grassland to different nitrogen fertilisation loads

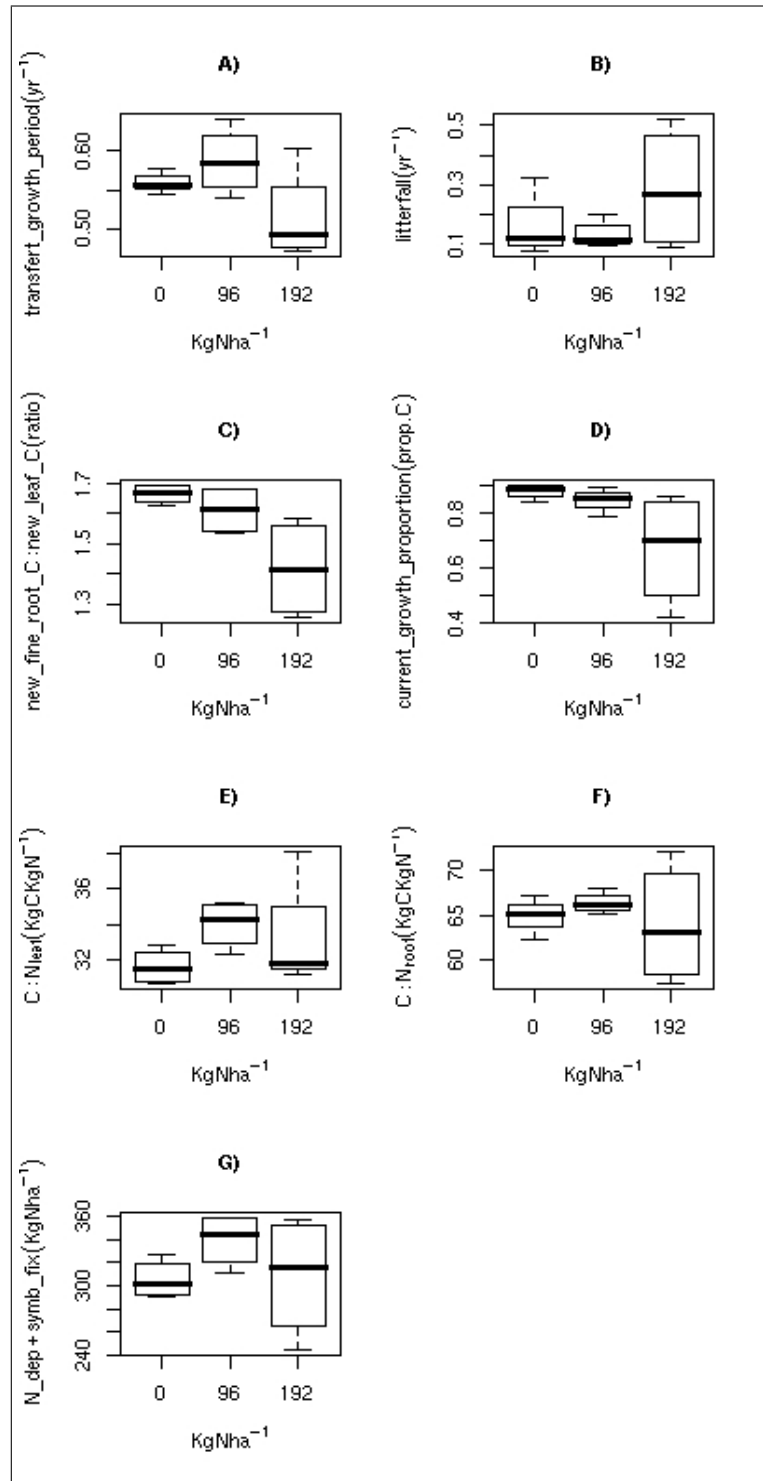


Figure 5.2: Box-and-whisker plots of the optimised values of sensitive parameters for four replications of the fertilisation trial. A) transfer growth period, B) litterfall as fraction of growing season, C) new fine root C to new leaf carbon ratio, D) current growth proportion, E) C:N of leaves, F) C:N of roots, G) nitrogen input as atmospheric deposition and symbiotic fixation. The box in the middle indicates hinges and median of the four replicates. The whiskers show the minimum/maximum value that falls within a distance of 1.5 times the box size from the nearest hinge.

6 Conclusions

At first we showed that the sensitivity of the model is independent from site, component and meteorological variable taken into consideration. The method showed to be effective in improving carbon fluxes estimates. For the application of it the gap distribution should be taken in consideration especially in the case of long missing periods. Furthermore the possibility of constraining autotrophic and heterotrophic respiration as contributors to total ecosystem respiration should be taken into account, being these two processes conducted by different drivers. Since different a posteriori parameter values estimates were reached in the four analysed cases and especially since these parameters can assume different values in the same site and in distinct years, in a climate change scenario, general parameterisations should be treated carefully, bearing in mind that uncertainties in estimates could conduct to biased conclusions.

In the following part of this work, a broader sensitivity analysis was performed, showing again that many parameters have a small or negligible effect on model output. Five out of forty-three sensitive parameters were efficiently constrained. The interpretation of these input parameters permitted to have an ecosystem perspective on the adaptation of a grassland to fertilisation loads. Being the proposed method general and hence not site specific, it could be applied to a wider range of experimental trials permitting a comparison among vegetation types. The generality of the modified version of Biome-BGC should be in some ways restricted in order to simulate the different effects obtained with different kind of fertilisers (i.e., poultry, manure, etc.).

Concluding we can say that a valuable tool for predicting carbon fluxes in managed grasslands was developed. The model showed its potential both for prediction and interpretation of the pathways of carbon from atmosphere through vegetation to soil, and its interactions with nitrogen. Anyway a lot has still to be done for simulating effects of different kinds of management on grassland ecosystems and for understanding interactions among biogeochemical cycles. This should be done for reducing more and more the uncertainties in model predictions and in future projections, especially considering that uncertainties in greenhouse gasses effects could have a key role in climate research in a contest

6 *Conclusions*

of climate anomalies.

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