COMMUNAUTÉ FRANÇAISE DE BELGIQUE
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FACULTÉ UNIVERSITAIRE DES SCIENCES AGRONOMIQUES DE GEMBLOUX

Mesure des flux de CO_2 et bilan carboné d'une rotation de quatre cultures

Christine Moureaux

Essai présenté en vue de l'obtention du grade de docteur
en sciences agronomiques et ingénierie biologique

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Moureaux Christine. (2008) Mesure des flux de CO_2 et bilan carboné d'une rotation de quatre cultures (thèse de doctorat). Gembloux Faculté universitaire des Sciences agronomiques. 10p., 1 fig., 6 articles.

Résumé

Le bilan carboné d'une rotation culturale de quatre ans a été établi entre 2004 et 2008 sur le site expérimental de Lonzée, Belgique. La région se caractérise par un climat tempéré océanique avec une température moyenne de l'air de 10°C et des précipitations annuelles de l'ordre de 800 mm. Le sol de la parcelle est un Luvisol. Les cultures composant la rotation sont des cultures de betterave, froment d'hiver, pomme de terre et froment d'hiver. Dans le but d'établir un bilan carboné, des mesures ont été effectuées à différentes échelles spatiales et temporelles. Un système de mesure par *eddy covariance* fournit une estimation par demi-heure de l'échange net en CO_2 de l'écosystème (NEE). La qualité des procédures de sélection et de traitement des flux de NEE a été contrôlée. A partir de ces mesures, la productivité primaire brute (GPP) et la respiration totale de l'écosystème (TER) sont déduites. Plusieurs procédures basées sur les mesures diurnes ou nocturnes de NEE sont comparées. L'intérêt d'utiliser un court pas de temps dans ces procédures et la température du sol comme température de référence a été mis en avant, ainsi que la nécessité de déterminer une valeur seuil de la vitesse de friction (u*) pour chaque culture et les longues inter-cultures. Pour la culture de froment d'hiver 2005, une estimation de la GPP déduite des mesures d'*eddy covariance* est comparée à une estimation basée sur une modélisation de mesures réalisées, une fois par semaine, à l'échelle de la feuille. La conception initiale de l'appareil de mesure a permis de réaliser les mesures sur les feuilles uniquement. Les évolutions des deux estimations sont proches à l'échelle de la saison et à l'échelle journalière. La mise en œuvre de la méthode basée sur les mesures à l'échelle de la feuille a apporté d'importantes informations en termes de réponse de la GPP aux facteurs climatiques et non climatiques et a permis une validation de l'estimation basée sur les mesures d'*eddy covariance*. Toutefois, dans le cadre de l'établissement d'un bilan carboné, la méthode basée sur les mesures d'*eddy covariance* est préférée. Des mesures de la respiration de sol, réalisées à l'échelle de la mini-parcelle de sol, et des mesures du contenu en carbone des plantes sont aussi réalisées. Combinées aux mesures d'*eddy covariance*, ces mesures permettent de déduire les parts auto- et hétérotrophiques de la respiration. Sur l'ensemble de la rotation, la parcelle apparait être une source significative de carbone de 0.17 (+/- 0.14) kg C m^{-2}. Cela suggère que, durant la rotation, le contenu en carbone du sol a diminué. Ceci peut s'expliquer par l'absence d'apport de fertilisation organique durant les 10 dernières années ainsi que par la récolte systématique des pailles des céréales.

Moureaux Christine. (2008) CO_2 fluxes measurements and carbon balance of a rotational cycle of four crops (thèse de doctorat in French). Gembloux, Belgium Gembloux Agricultural University. 10p., 1 fig., 6 articles.

Summary

The carbon balance of a full rotational crop cycle of four years was established between 2004 and 2008 on the Lonzée site, Belgium. The climate is temperate maritime. The mean annual temperature is about 10°C and the annual precipitation is about 800 mm. The soil is a Luvisol. The studied crops were sugar beet, winter wheat, potato and winter wheat crops. In order to assess the carbon balance, measurements were carried out at different spatial and temporal scales. An eddy covariance system measured the CO_2 net ecosystem exchange (NEE) every half-hour. The selection and treatment procedures quality was checked. The gross primary productivity (GPP) and the total ecosystem respiration (TER) were deduced from the eddy covariance measurements. Several procedures based on night-time or daytime NEE measurements were compared. The importance of a narrow window to fit the NEE to climate relationship was brought to the fore, like the importance of the soil temperature as reference temperature and the necessity of evaluating a friction velocity (u*) threshold value for each crop and for long inter-crops. For the winter wheat crop of 2005, a GPP assessment based on eddy covariance measurements was compared to an estimation based on measurements carried out once a week at the leaf scale. Measurements were carried out only on leaves because of the initial conception of the porometer. The evolutions of both estimations were in good agreement at both the crop time scale and the daily scale. The leaf scale model development provided important information concerning the GPP response to climatic and non climatic parameters. This modelled GPP also allowed validating the eddy covariance GPP estimation. However, in the frame of the carbon balance assessment, eddy covariance GPP estimation is preferred. In addition, soil respiration measurements were carried out at the soil mini parcel scale, and plant carbon content measurements were performed once a week. Combined to eddy covariance fluxes, these measurements allowed determining the auto- and heterotrophic respiration parts. On the whole rotational cycle, the site was a significant carbon source of 0.17 (+/- 0.14) kg C m^{-2}. This suggests that the soil carbon content decreased during the studied period. This could be explained by the crop management, as neither farmyard manure nor slurry was applied on the crop since more than 10 years and as cereal straw was systematically exported.

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Introduction et discussion

La compréhension du cycle du carbone et de sa dynamique constitue un défi majeur pour la communauté scientifique. En effet, les activités humaines provoquent d'importantes émissions de gaz qui modifient la composition de l'atmosphère. En particulier, les émissions de dioxyde de carbone (CO_2), d'hémioxyde d'azote (N_2O) et de méthane (CH_4) renforcent l'effet de serre et participent donc aux changements climatiques globaux. Il importe donc de mieux comprendre et quantifier le cycle du carbone et plus particulièrement de quantifier les quantités de carbone contenu dans les écosystèmes, terrestres ou océaniques, et de comprendre les mécanismes régissant les échanges au sein des écosystèmes et entre les écosystèmes et l'atmosphère. Effectivement, ce sont là les composantes du cycle du carbone qui présentent les plus grandes incertitudes.

Dans le but de mieux comprendre le cycle du carbone et en particulier les échanges entre les écosystèmes terrestres et l'atmosphère, des réseaux régionaux se sont mis en place. En Europe, l'origine du réseau CarboEurope-IP remonte à 1996. Le projet "Mesure des flux de CO_2 et bilan carboné des grandes cultures" (Convention n°03/08-304, Communauté française de Belgique, Direction générale de l'Enseignement non obligatoire et de la Recherche scientifique, Projet "Action de Recherche Concertée"), dans le lequel le présent travail s'insère, a été initié dans le cadre de ce réseau européen. L'objectif général du projet est de quantifier et de comprendre l'évolution des échanges de CO_2 d'une succession de cultures avec leur environnement et d'en établir le bilan carboné. Dans ce but, de nombreuses mesures ont été effectuées à différentes échelles spatiales et temporelles: mesures semi-horaire à l'échelle de la parcelle (*eddy covariance*), mesures à l'échelle de la feuille, mesures à l'échelle de la mini parcelle de sol et mesures à l'échelle de la plante. Le schéma de la Figure 1 présente les mesures effectuées et précise leurs échelles spatiales et temporelles.

A l'échelle de l'écosystème, un système mesure les flux turbulents en utilisant la technique de covariance de turbulence (*eddy covariance* en anglais). Le flux mesuré chaque demi-heure est l'échange net en CO_2 de l'écosystème (NEE pour *Net Ecosystem Exchange*). Ce flux est la différence entre le CO_2 absorbé par l'écosystème via la photosynthèse (GPP pour *Gross Primary Productivity*) et le CO_2 émis suite à la respiration des plantes et du sol (TER pour *Total Ecosystem Respiration*).

A l'échelle de la plante, des mesures diffusives de l'assimilation nette des feuilles (An) sont effectuées une fois par semaine. Ce flux est la différence entre le CO_2 que la plante assimile par photosynthèse (GPP_{LS}) et celui qu'elle émet via la respiration de ses parties aériennes (Raa).

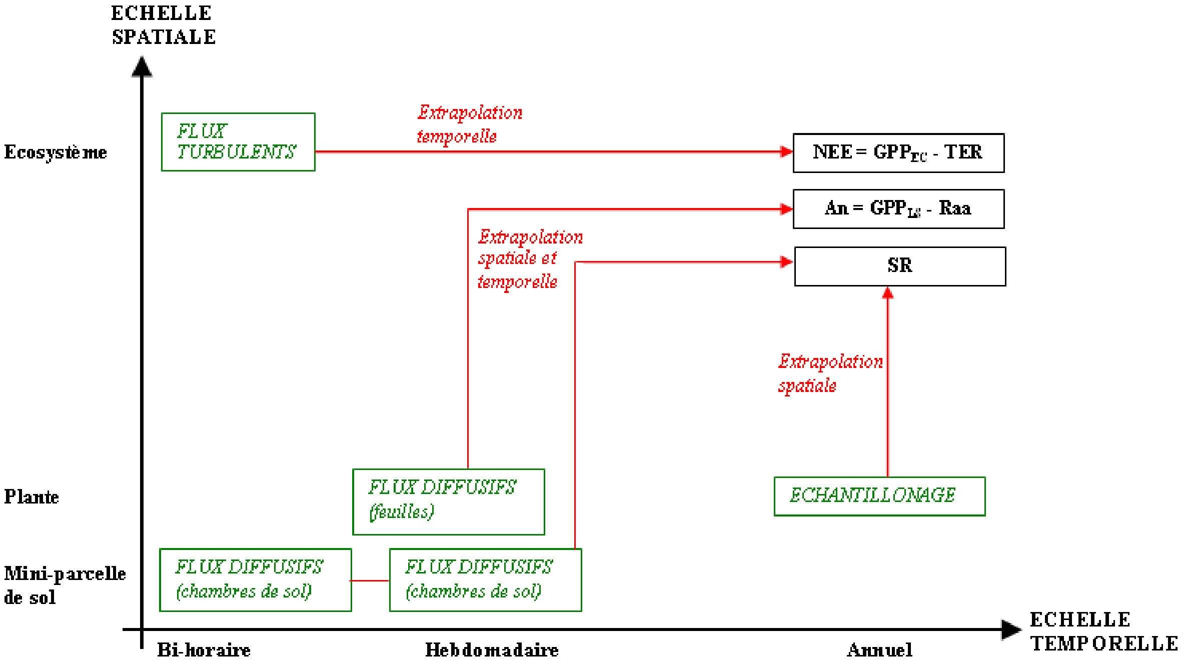

Figure 1 : Présentation des différentes mesures réalisées sur le site de Lonzée et des flux obtenus.

A l'échelle de la mini-parcelle de sol (de l'ordre du dm^2) la respiration du sol (SR) est mesurée chaque demi-heure à l'aide d'un système automatique et une fois par semaine durant les périodes de culture, en utilisant un système manuel. Les premières mesures permettent d'obtenir une bonne représentativité temporelle de la SR. Ces mesures étant réalisées sur cinq mini-parcelles distantes l'une de l'autre d'un mètre, elles ne renseignent pas de la variabilité spatiale de la respiration du sol. C'est pourquoi des mesures supplémentaires sont effectuées manuellement à travers la parcelle.

Afin de connaître les conditions dans lesquelles se produisent les différents échanges de CO_2 entre la parcelle agricole et l'atmosphère et dans le but d'étudier les réponses de ces flux aux conditions climatiques, une station météorologique fonctionne en continu dans le voisinage immédiat du système d'*eddy covariance*.

Le site expérimental (Lonzée) est une parcelle agricole de 11,8 ha sise dans la commune de Gembloux (Belgique). La région est caractérisée par un climat tempéré océanique avec une température moyenne de l'air de 10°C et des précipitations annuelles de l'ordre de 800 mm. Le sol est un Luvisol (classification FAO). La parcelle est cultivée par la même famille depuis 1933 et, durant les dix dernières années, elle a connu une rotation de 4 ans fréquemment rencontrée en région limoneuse et composée de froment d'hiver, de betterave et de pomme de terre.

Ce travail a pour objectif général d'établir le bilan carboné d'une rotation complète sur le site agricole de Lonzée. Pour atteindre cet objectif, les mesures précitées ont été réalisées sur les quatre cultures qui se sont succédé sur le site expérimental entre 2004 et 2008 : une culture de betteraves sucrières en 2004, de blé d'hiver en 2005, de pommes de terre en 2006 et à nouveau de blé d'hiver en 2007.

Le travail est composé de six articles et du présent texte. Les six articles sont classés comme suit

Article 1 : Moureaux C., B. Bodson, M. Aubinet *Mesure des flux de CO_2 et bilan carboné de grandes cultures : état de la question et méthodologie*. Accepté dans la revue BASE.
Cet article décrit le contexte général dans lequel les recherches se déroulent et il détaille le projet "Mesure des flux de CO_2 et bilan carboné des grandes cultures" et ses objectifs.

Article 2 : Moureaux C., A. Debacq, B. Bodson, B. Heinesch, M. Aubinet (2006). *Annual net ecosystem carbon exchange by a sugar beet crop*. Agricultural and Forest Meteorology, **139**, 25-39.
La première année de mesure en continu de l'échange net de l'écosystème (NEE) et sa dépendance aux variables climatiques et non climatiques est présentée. Les choix méthodologiques faits pour calculer le flux net sont évalués. La séquestration annuelle est calculée ainsi que sa sensibilité à certaines hypothèses de travail.

Article 3 : Moureaux C., B. Bodson, M. Aubinet. *Evaluation of different approaches to deduce TER and GPP from eddy covariance measurements above crops*. Soumis à Agricultural and Forest Meteorology.

Différentes procédures utilisées pour séparer l'échange net de l'écosystème, mesuré par le système d'*eddy covariance*, en ses deux composantes principales : la productivité primaire brute (GPP) et la respiration totale de l'écosystème (TER) sont comparées et discutées. Les incertitudes sur la GPP et la TER résultant de ces procédures sont évaluées.

Article 4 : Hoyaux J., C. Moureaux, D. Tourneur, B. Bodson, M. Aubinet. *Extrapolating gross primary productivity from leaf to canopy scale in a winter wheat crop.* Agricultural and Forest Meteorology, **148**, 668-679.
La productivité primaire brute peut être estimée à partir de mesures faites à l'échelle de la feuille. Les mesures réalisées lors la culture de froment d'hiver de 2005 sont décrites cet article ainsi que le modèle d'extrapolation mis au point pour passer de l'échelle spatiale de la feuille à celle de la parcelle. L'estimation de la GPP ainsi obtenue est comparée à la GPP obtenue à partir des mesures d'*eddy covariance*.

Article 5 : Moureaux C., A. Debacq, J. Hoyaux, Suleau M., Tourneur D., F. Vancutsem, B. Bodson, M. Aubinet. *Carbon balance assessment of a Belgian winter wheat crop (Triticum aestivum L.).* Global Change Biology, doi: 10.1111/j.1365-2486.2008.01560.x
Sur base des différentes mesures effectuées sur le site (mesures d'*eddy covariance*, mesures à l'échelle de la feuille, mesures du contenu en carbone de la culture et mesures de respiration du sol), le bilan carboné complet de la culture de blé d'hiver 2005 est établi. L'évolution des différents flux au cours de la saison est présentée et mise en relation avec le développement de la culture.

Article 6 : Aubinet M., C. Moureaux, B. Bodson, D. Dufranne, B. Heinesch, M. Suleau, F. Vancutsem, A.Vilret. *Carbon sequestration by a crop during a four year rotational cycle.* Soumis à Agricultural and Forest.
Le bilan carboné d'une rotation de 4 ans (2004 – 2008) est établi. Cette rotation est la succession des cultures de betterave, froment d'hiver, pomme de terre et froment d'hiver. Pour établir le bilan carboné, les mesures exploitées sont les mesures d'*eddy covariance*, les mesures automatiques et manuelles de respiration du sol, les mesures d'assimilation de la feuille et les mesures de biomasse et de contenu en carbone des plantes.

Le système d'*eddy covariance* et la station météorologique ont été installés dans le cadre de ce travail. Les procédures de traitement ont été adaptées au site et la bonne qualité des procédures de sélection de données et de traitement a été montrée sur la première année de mesure (Article 2). La robustesse de l'estimation annuelle de la NEE à certains choix méthodologiques a aussi été démontrée.

Différentes méthodes de discrimination de la NEE en ses composantes, la TER et la GPP, ont été comparées à l'échelle de la saison de culture et de la journée (Article 3). En particulier deux approches ont été confrontées, l'une utilisant les mesures de jour, l'autre les mesures de nuit. De cette étude, il ressort l'importance de choisir des procédures utilisant des pas de temps courts (quelques jours) pour ajuster les relations entre la NEE et le climat de manière à reproduire des évènements particuliers comme les phases de développement intense, les périodes de sénescence ou de sécheresse. L'importance d'utiliser la température de sol et non la température de l'air comme température de référence est également mise en évidence. La comparaison entre les meilleures estimations des deux approches est satisfaisante : leur différence étant du même ordre de grandeur que les incertitudes qui leur sont associées. Pour notre site, l'approche utilisant les mesures de nuit est toutefois préférée car elle peut être utilisée lors des périodes avec peu ou pas de végétation et permet ainsi d'établir le bilan carboné sur l'ensemble d'une rotation. Enfin, la nécessité de procéder à un filtrage des données correspondant aux périodes de faible turbulence et d’évaluer ce critère de sélection des données pour chaque culture et pour les longues inter-cultures est soulignée.

Pour la culture de blé d’hiver 2005, une seconde estimation de la GPP a été comparée à celle provenant des mesures d’*eddy covariance*. Cette seconde estimation est le résultat d’un modèle basé sur des mesures effectuées à l'échelle de la feuille (Article 4). La mise au point du modèle d'extrapolation permet d’identifier plus finement les dépendances de la photosynthèse aux conditions climatiques, à la position et à l'âge des feuilles. Cependant, cette méthode est couteuse en temps de mesure. De plus, la conception initiale de l’appareil de mesure a permis de mesurer l’assimilation des feuilles uniquement. L'estimation de la photosynthèse des tiges et des feuilles demande une adaptation de la pince de mesure qui a été réalisée par la suite. L’estimation de la contribution des tiges et des épis à l’assimilation de la culture provient d’une comparaison avec les mesures d’*eddy covariance*. Même si les deux estimations ne sont plus entièrement indépendantes, leurs évolutions au cours de la saison de culture et de leurs variations journalières ont pu être comparées et sont apparues en excellent accord durant la période de mesure. Nous avons ainsi pu valider l'estimation provenant des mesures d'*eddy covariance*. Malgré les informations supplémentaires apportées par les mesures réalisées à l'échelle de la feuille, l'estimation de la GPP basées sur les mesures d'*eddy covariance* est préférée dans le cadre de l'établissement d'un bilan carboné. Les raisons en sont une plus grande fiabilité et une mise en œuvre moins couteuse en temps de mesure. Dans le but d'améliorer un modèle basé sur des mesures à l'échelle de la feuille, il est important de mesurer l'assimilation nette des différents organes de la plante, pas seulement celle des feuilles. Il est également recommandé de débuter les mesures dès l'émergence de la culture et de les continuer, de manière régulière, jusqu'à la récolte de manière à éviter de longues extrapolations et à reproduire d'éventuels effets du vieillissement de la culture, voire de sa sénescence ou d'évènements climatiques particuliers tels, par exemple, une période de sécheresse. Il est également important, particulièrement dans le cas des céréales, de suivre l'évolution de la sénescence au cours de la culture et à travers la canopée ainsi que son impact sur l'assimilation des différents organes.

L'établissement du bilan carboné complet repose donc sur les mesures d'*eddy covariance*, les mesures de respiration du sol et les mesures du contenu en carbone des plantes (Article 5). C'est en combinant ces dernières mesures avec les mesures d'*eddy covariance* que les parts autotrophes et hétérotrophes de la respiration sont déduites. La précision des mesures de NPP est donc importante dans le bilan carboné. Elles doivent être effectuées avec soin et répétées sur un nombre suffisant de plantes de manière à intégrer la variabilité existant entre plantes. L'estimation de la biomasse et du contenu en carbone des racines peut être difficile pour certaines cultures comme le froment d'hiver vu la profondeur d'enracinement. Dans cette étude, des estimations de la proportion de biomasse racinaire venant de littérature ont été utilisées pour les cultures de blé d'hiver.

Le bilan carboné complet a été établi pour la culture de froment d'hiver 2005 (Article 5). C'est la première étude publiée présentant un bilan complet d'une culture à partir de mesures. De même, l'analyse du bilan carboné d'une rotation de quatre années telle que présentée à dans l'Article 6 n'a encore été accomplie pour aucun autre site européen. Seules quelques études présentant le bilan carboné de rotations soja-maïs dans le Midwest américain sont présentes dans la littérature (Baker et Griffis, 2005 ; Verma *et al.*, 2005 ; Hollinger et al, 2005, 2006 ; Grant *et al.*, 2007). Sur l'ensemble de la rotation, la parcelle de Lonzée se comporte comme une source de carbone et émet 0,17 kg C m^{-2}. La quantité de carbone émise est significative, l'erreur associée étant de 0,14 kg C m^{-2}. Cela signifie donc, qu'au cours de la rotation, le contenu en carbone du sol de la parcelle a diminué. Cela peut être expliqué par la gestion particulière de la parcelle : pas de fertilisation organique appliquée depuis plus de 10 ans et l'exportation systématique des pailles de céréales. Notons que durant la culture de froment d'hiver de 2007, des conditions climatiques particulières ont été observées : températures particulièrement douces en hiver et sécheresse en avril. Cela a eu pour conséquence qu'une plus grande quantité de biomasse est retournée au sol. En conclusion, si l'année 2007 avait connu un climat plus proche des normales et de l'année 2005, l'intensité de la source aurait été plus grande et plus significative.

L'analyse des quatre années de mesure (Article 6) a également permis d'observer les impacts des interventions culturales. En particulier, l'impact de l'émission de CO_2 après les labours est apparu limité en intensité et en durée. Par contre, un impact significatif de la décomposition des résidus de betterave laissés sur le champ lors de la récolte a clairement été observé durant les trois semaines suivant la récolte. Cet effet s'est prolongé les mois suivants mais il n'a pas été possible de le séparer des autres contributions des flux mesurés. Une assimilation significative de CO_2 a également été observée durant les inter-cultures du fait des repousses de cultures et d'adventices.

Pour les quatre cultures, la part autotrophe de la respiration domine la respiration totale de l'écosystème et représente 65% ou plus de la TER. De même, une étroite corrélation entre cette respiration autotrophe et la GPP a été observée, démontrant que lorsque la plante est active d'un point de vue assimilation, elle l'est également en termes de respiration.

Avec les données accumulées durant les quatre premières années de mesure sur le site de Lonzée, il est également possible d'étudier plus en profondeur les mécanismes régissant les échanges de CO_2 des différentes cultures avec l'atmosphère, leurs réponses aux variables climatiques et leurs évolutions en fonction du développement de la culture. Ce dernier point a été étudié pour la culture de blé d'hiver 2007 (Article 5). L'analyse climatique des flux, réalisée dans ce travail, a permis de mettre en évidence que l'assimilation par la culture augmente lorsque la proportion de rayonnement diffus est importante, c'est-à-dire à rayonnement équivalent lorsque le ciel est couvert.

Par ailleurs, les cultures se répétant tous les 2 ou 4 ans, l'opportunité est offerte d'étudier leur variabilité interannuelle et leur comportement face à d'éventuelles conditions climatiques particulières. Par exemple, le froment d'hiver a été cultivé en 2005 et en 2007. Lors de cette deuxième année, l'hiver particulièrement doux et le mois d'avril très sec a influencé le développement de la culture et les échanges de CO_2. De plus, les modèles mis au point en 2005, pourront être validés sur les mesures de 2007. La comparaison de ces deux années de culture est actuellement en cours. Les mêmes analyses pourront rapidement être menées sur les cultures de betteraves 2004 et 2008.

Dans cette étude, une première estimation des parts autotrophes et hétérotrophes de la respiration du sol est effectuée en combinant les mesures d'*eddy covariance* et les mesures de NPP. Une deuxième méthode a été développée sur le site qui consiste à mesurer la respiration du sol sur des zones cultivées et non cultivées. Dans les secondes, l'hypothèse est faite que seule la part hétérotrophe de la respiration est mesurée. La confrontation de ces résultats est en cours d'analyse. Une troisième méthode basée sur la discrimination isotopique permettrait de valider les deux techniques précitées. A l'heure actuelle, cette technique n'est pas utilisée sur le site de Lonzée,

La parcelle étudiée dans ce travail se comporte comme une source de carbone et participe ainsi au renforcement de l'effet de serre. Ce résultat est valable sous nos conditions expérimentales et aurait peut-être été différent sous d'autres conditions expérimentales et d'autres modes de gestions culturales. En effet, les mesures d'*eddy covariance* ainsi que les autres mesures réalisées dans le cadre du bilan carboné, permettent de mesurer et de comprendre les échanges se produisant entre l'écosystème étudié et l'atmosphère. Elles ne permettent cependant pas de prédire l'évolution des flux face aux changements climatiques ou à une modification des pratiques culturales ni de prédire les flux d'une parcelle voisine ou de la région dans laquelle se font les mesures. Pour réaliser ces prédictions, il faut bâtir des modèles plus fondamentaux prenant en compte les mécanismes de base se produisant dans l'écosystème, c'est-à-dire la photosynthèse des végétaux et la respiration auto- et hétérotrophe. Les mesures d'*eddy covariance* sont idéales pour mettre au point et tester ces modèles. De tels modèles sont actuellement en cours de développement. Une étude récente (Grant et al., 2007) estime les différents termes du bilan carboné (GPP, Ra et Rh) sur une rotation maïs-soja à l'aide d'un modèle nommé *Ecosys* et la compare aux résultats de mesures d'*eddy covariance*. Quatre-vingt pourcents de la variabilité des mesures d'*eddy covariance* sont expliqués par ce modèle. Ce modèle prédit, en plus des échanges de carbone des plantes en C3 et en C4, les échanges d'énergie et la fixation symbiotique de l'azote.

Il a été établi par l'IPCC (2007) que l'agriculture participe pour 13,5 % aux émissions anthropiques en gaz à effet de serre. Elle est une des principales sources anthropiques en méthane et la plus importante source anthropique en N_2O. Dans le but d'établir le bilan en gaz à effet de serre des cultures ou des exploitations dans leur ensemble, afin de mieux comprendre les processus régissant ces échanges et d'étudier les modes de gestion permettant de les réduire, il apparait donc essentiel de tenir compte, des échanges de CO_2, de N_2O et de CH_4.

Dans le cadre du protocole de Kyoto, les accords de Marrakech (adoptés à Montréal lors de COP/MOP 1) ont autorisé que les puits et les sources biosphériques soient comptabilisées durant la première période 2008 – 2012. La possibilité de stocker du carbone dans les sols agricoles est donc proposée comme un moyen de mitigation du CO_2. A l'heure actuelle, de grandes incertitudes concernant la capacité des agro systèmes à stocker du carbone suite à la mise en place de systèmes de gestion alternatifs ressortent de la littérature scientifique (*e.g.* Smith *et al.* 2000; Vleeshouwers et Verhagen, 2002; Freibauer *et al.*, 2004; Smith, 2004). Toutefois, il apparaît que cette stratégie ne peut être efficace que durant les premières de son application (Battelle, 2000; Freibauer *et al.*, 2004). A long terme, elle n'est pas une solution pour réduire le taux d'enrichissement de l'atmosphère en gaz à effet de serre. Elle ne dispense donc pas de chercher à la fois des alternatives durables à l'utilisation d'énergie fossile et des approches permettant de diminuer la consommation d'énergie. Aujourd'hui, 80% de la production globale d'énergie viennent des combustibles fossiles et de l'énergie nucléaire. Par ailleurs, il est également impératif de s'assurer que les pratiques culturales alternatives ne présentent pas d'impacts négatifs, à court et à long terme, sur les émissions de N_2O, sur la productivité des cultures ou sur la qualité des sols.

Rappelons toutefois que le rôle premier de l'agriculture est de fournir, à une population croissante, nourriture, fourrage et fibres. En 1950, la population mondiale comptait 2,5 milliards d'être humain, elle en compte aujourd'hui plus de 6,6 milliards et elle devrait dépasser les 9,2 milliards en 2050 (United Nations, 2007). Alors que la plupart des territoires de bonne qualité sont déjà dédiés à l'agriculture et qu'il n'est pas attendu que les surfaces agricoles augmentent, le secteur de l'agriculture se trouve sous une pression croissante.

Depuis la fin des années 1950, le rythme d'accroissement de la production agricole mondiale a fortement augmenté. Les raisons principales sont l'utilisation de variétés de culture à haut rendement, l'utilisation intensive d'engrais inorganiques et de pesticide et l'utilisation plus fréquente de l'irrigation. Dans les années 1970, suite à la crise de l'énergie et à la prise de conscience des conséquences environnementales à long terme, de nouvelles préoccupations sont apparues concernant l'érosion, la compaction et la baisse de fertilité du sol, la contamination des nappes souterraines et la destruction des systèmes sociaux traditionnels. A la suite de cela, des pratiques de gestion agricole durables et efficace en ressources ont été recherchées. Ensuite, durant les années 1980, une prise de conscience des changements climatiques s'initialise. Ces changements incluent l'accroissement de la température, l'élévation des teneurs en CO_2, le bouleversement des régimes hydrologiques, l'allongement des périodes de végétation, l'occurrence d'évènements extrêmes plus grande et l'acidification des océans et représentent dés lors une pression supplémentaire pour l'agriculture et la sécurité alimentaire (FAO, 2007).

Les impacts des changements climatiques sont à la fois des impacts biologiques et des impacts socio-économiques. Parmi les impacts biologiques, on observe des effets physiologiques sur les écosystèmes ; des modifications des ressources en territoires, sols et eau ; le développement accru d'adventices et de nuisibles ; l'augmentation du niveau des mers et de la salinité des océans. La diminution des rendements et de la production, la diminution du PIB provenant de l'agriculture, la fluctuation des prix des marchés mondiaux, l'augmentation du risque d'insécurité alimentaire ; les migrations et les troubles civils font parties des impacts socio-économiques (FAO, 2007).

Différentes adaptations de l'agriculture sont envisagées pour faire face aux changements climatiques. Parmi celles-ci citons les modifications des dates de semis ; l'utilisation de différentes variétés ou espèces ; modification du travail du sol ; promotion de l'agroforesterie. Alors que les adaptions de l'agriculture face aux changements climatiques seront rapidement réalisées dans les pays développés, il n'en sera pas de même pour les pays émergents disposant de faibles ressources économiques, d'un accès réduit aux technologies, à l'information et à la connaissance ou des institutions peu efficaces.

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Article 1

Mesure des flux de CO_2 et bilan carboné de grandes cultures : état de la question et méthodologie

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Résumé

L'augmentation des concentrations atmosphériques en dioxyde de carbone (CO_2), gaz qui participe au renforcement de l'effet de serre, a mis en évidence la nécessité de mieux comprendre le cycle du carbone et sa dynamique. En particulier, de larges incertitudes sont actuellement associées aux échanges entre les écosystèmes et l'atmosphère. Des réseaux régionaux se sont constitués afin d'étudier ces flux de CO_2. En Europe, le réseau CarboEurope-IP étudie les échanges entre écosystèmes terrestres et atmosphère. Il regroupe plus de 100 sites forestiers, agricoles ou de prairie. Cet article décrit le projet "Mesures des flux de CO_2 et bilan carboné des grandes cultures" qui s'intègre dans ce réseau et dont l'objectif général est de quantifier et de comprendre l'évolution des flux de CO_2 d'une succession de cultures sur une parcelle agricole belge avec son environnement. Pour atteindre cet objectif, des mesures sont effectuées selon différentes techniques et à différents échelles spatiales et temporelles. Des mesures de l'échange net de CO_2 sont effectuées à l'échelle spatiale de la parcelle et avec une fréquence semi-horaire. A la même fréquence, la respiration du sol est mesurée à l'échelle de la mini parcelle de sol. A l'échelle de la feuille, des mesures de son assimilation nette sont effectuées chaque semaine. Enfin, des échantillonnages de plantes sont effectués dans le but de déterminer le contenu en carbone dans la culture. Après avoir décrit les objectifs du projet, cet article présente chacune des techniques de mesure effectuées et les informations qu'elles fournissent. Il expose également comment les résultats des différentes mesures peuvent être combinés afin de déduire un bilan carboné complet de la parcelle agricole.

Descripteurs

Bilan carboné - Covariance de turbulence – Cultures - CarboEurope-IP – Photosynthèse – Respiration autotrophe – Respiration hétérotrophe.

Abstract

The increase of carbon dioxide (CO_2) atmospheric concentration, which is a greenhouse gas, put in stress the need of a better understanding of the carbon cycle and its dynamic. In particular, the exchanges between ecosystems and atmosphere are characterized by large uncertainties. Regional networks were set up to study these CO_2 fluxes. In Europe, the CarboEurope-IP network studies the exchanges between terrestrial ecosystems and the atmosphere. It includes more than 100 sites of forests, croplands or grasslands. This article, presents the project "CO_2 flux measurement and carbon balance of agricultural crops" which was developed in this frame. The main aim of this project is to quantify the CO_2 flux evolution of Belgian crops and understand its response to biotic and abiotic factors. In order to meet this goal, measurements are carried out at different spatial and temporal scales. Net ecosystem exchange measurements are carried out every half-hour at the parcel scale Soil respiration is measured at the soil plot scale with the same frequency. At the leaf scale, net assimilation measurements are performed once a week. Moreover, plant samplings are carried out to determine the crop carbon content. After presenting the objectives of the project, this paper presents the measurement techniques and the fluxes they allow obtaining. The procedures used to combine the measurements in order to assess a complete crop carbon balance are also detailed.

Keywords

Carbon balance – eddy covariance – crops - CarboEurope-IP – Photosynthesis –Autotrophic respiration – Heterotrophic respiration.

1. Introduction

Les concentrations atmosphériques en dioxyde de carbone (CO_2), en hémioxyde d'azote (N_2O) et en méthane (CH_4), tous trois gaz à effet de serre, n'ont cessé d'augmenter depuis la révolution industrielle du fait des activités humaines. Le dioxyde de carbone est le gaz qui a l'impact le plus important sur l'effet de serre. Sa concentration atmosphérique ($[CO_2]$) a augmenté de 280 μmol mol^{-1} en 1950 à 379 μmol mol^{-1} en 2005 (IPCC, 2007). Les mesures effectuées à partir de carottes glacières montrent que cette valeur est supérieure aux concentrations observées durant les 650 000 dernières années, lesquelles auraient oscillé entre 180 et 300 μmol mol^{-1}. Durant les 10 dernières années, l'augmentation annuelle des $[CO_2]$ a été plus importante que l'augmentation moyenne des 45 dernières années, c'est-à-dire la période couverte par des mesures directes de concentration atmosphérique.

La composition isotopique du CO_2 atmosphérique et la diminution observée de la concentration d'oxygène démontrent que la principale cause d’émission de CO_2 est liée à la consommation de carburant fossile. Celle-ci est estimée à 23,5 ± 1,5 Gt CO_2 par an pour les années '90 (valeur ± intervalle de confiance à 90%). La deuxième source anthropique par ordre d’importance résulte des changements d'utilisation des sols et en particulier de la déforestation. Elle représente le quart de la précédente, i.e. 5,9 ± 4,1 Gt CO_2 par an pour les années '90 (IPCC, 2007). Par ailleurs, le Groupe International d'Experts pour le Climat (IPCC) affirme, avec une certitude de 90%, que ces émissions sont responsables du réchauffement climatique global.

Les émissions anthropiques de CO_2 constituent une des composantes du cycle global du carbone. Ce cycle comporte quatre grands compartiments : l'océan, l'atmosphère, les écosystèmes terrestres et les composés fossiles. Le carbone circule entre eux dans différentes proportions. Entre l’atmosphère et la biomasse terrestre se réalise un double flux : le carbone pénètre dans la biomasse par le processus de photosynthèse et retourne dans l'atmosphère par la respiration végétale et animale, par la décomposition et la respiration des microorganismes ainsi que par les activités humaines.

Durant les années '90, les échanges nets entre l'atmosphère et les écosystèmes terrestres et les océans ont été estimés à, respectivement, 5,1 ± 2,6 Gt CO_2 par an et 6,2 ± 1,8 Gt CO_2 par an (Houghton *et al.*, 2001), ces écosystèmes absorbant ainsi du CO_2 et ralentissant l'augmentation des concentrations atmosphériques. En effet, sur la même période, les émissions anthropiques résultant de la combustion de fuel fossile ont été estimées à 23,1 ± 1,5 Gt CO_2 et l'augmentation de la [CO_2] atmosphérique à seulement 11,7 ± 0,4 Gt CO_2. Depuis la seconde partie des années '90, d'énormes efforts ont été fournis pour quantifier l'ampleur de l'absorption de carbone par les écosystèmes terrestres et les localiser. Il est maintenant admis que les écosystèmes terrestres extratropicaux de l'hémisphère Nord sont les plus actifs (Schimel *et al.*, 2001; Brown, 1996; Pacala *et al.*, 2001; Tans *et al.*, 1990; Bousquet *et al.*, 2000; Baker, 2000; Peylin *et al.*, 2002; Heimann, 2001; Rayner *et al.*, 1999; Ciais *et al.*, 1995; Houghton *et al.*, 1999; Houghton *et al.*, 2001; Schimel *et al.*, 2000; McGuire *et al.*, 2001). Cependant, les contributions respectives de l'Europe, de l'Amérique du Nord et l'Asie sont très largement incertaines (Schimel *et al.*, 2001). De la même façon, la compréhension des mécanismes mis en jeu et leur vulnérabilité aux changements climatiques et aux modes de gestion sont également incertains.

L'amplitude actuelle des puits de CO_2 pourrait ne pas être maintenue dans le futur (Schimel *et al.*, 2001) car les processus principaux mis en jeu vont vraisemblablement diminuer. Par exemple, les effets de l'implantation d'une forêt sur une terre agricole peuvent décroître lorsque la forêt atteindra sa maturité (Gower *et al.*, 1996). De la même façon, la séquestration accrue de carbone par les écosystèmes résultant des concentrations croissantes en CO_2 et en azote vont saturer lorsque de hautes concentrations seront atteintes ou qu'une autre ressource deviendra limitante (Falkowski et al., 2000; Houghton et al., 2001; Canadell et al., 2004).

Les effets du changement climatiques sur les écosystèmes sont également très variables d'un écosystème à l'autre. Il semble que l'amplitude de la séquestration terrestre ait une grande variabilité annuelle en réponse aux variations climatiques (Bousquet *et al.*, 2000; Rödenbeck *et al.*, 2003) et par conséquent une grande sensibilité aux changements climatiques globaux. En 2003, une sécheresse exceptionnelle a été observée en Europe. Plusieurs études récentes en ont analysé les conséquences sur le bilan carboné d'écosystèmes terrestres européens (Ciais *et al.*, 2005; Granier *et al.*, 2007; Reichstein *et al.*, 2007). Ce type d'étude permet en effet d'analyser la réponse des écosystèmes terrestres à des conditions climatiques extrêmes qui pourraient être représentatives de notre climat à venir (Lawlor, 1998; Saxe *et al.*, 2001; Meehl et Tebaldi, 2004; Schär *et al.*, 2004; Houghton *et al.*, 2001). Il en ressort que de tels évènements climatiques peuvent significativement altérer le bilan carboné des écosystèmes européens. Ils peuvent contrebalancer les effets positifs d'une saison de croissance plus longue et plus chaude, altérer la bonne santé et la productivité des écosystèmes, voire inverser des puits en sources de CO_2 (Ciais *et al.*, 2005; Granier *et al.*, 2007; Reichstein *et al.*, 2007). Dés lors les échanges par les écosystèmes terrestres accélèreraient plutôt que ralentiraient l'augmentation des $[CO_2]$ atmosphériques.

Dans ces conditions apparaît clairement la nécessité de mieux comprendre la dynamique du cycle du carbone et d'estimer sa capacité à absorber une partie des émissions anthropiques de CO_2. Face à ce défi, la communauté scientifique a mis sur pied une structure complexe visant à comprendre les multiples composantes du système carbone – climat – écosystèmes – humains et leurs interactions.

Dans cet article, nous décrirons tout d'abord à la Section 2 le réseau européen CarboEurope-IP qui fédère la plupart des groupes de recherche européens travaillant sur les échanges écosystèmes terrestres – atmosphère et dont le site agricole de Lonzée constitue un maillon. Ce réseau trouve ces origines en 1996 et s'intéressait alors exclusivement aux écosystèmes forestiers. L'intérêt d'étudier les interactions entre les écosystèmes agricoles et le climat n'a été reconnu que plus récemment. La justification de leur étude est discutée à la Section 3. La section 4 définit les différents échanges de CO_2 pouvant se produire entre une parcelle agricole et l'atmosphère. Enfin, l'ensemble du projet de recherche "Mesure des flux de CO_2 et bilan carboné des grandes cultures" (Convention n°03/08-304, Communauté française de Belgique, Direction générale de l'Enseignement non obligatoire et de la Recherche scientifique, Projet "Action de Recherche Concertée") qui est mis en œuvre sur le site expérimental de Lonzée sera décrit à la Section 5, les conclusions et une série de perspectives de recherche étant proposées à la Section 6.

2. Le projet CarboEurope-IP

L'objectif fondamental du projet européen CarboEurope-IP (contrat n° GOCE-CT-2003-505572) est de comprendre et de quantifier, tant à l'échelle locale, régionale que continentale, le bilan carboné terrestre en Europe ainsi que les incertitudes qui y sont associées (e.g. Baldocchi *et al.*, 2001; Baldocchi, 2003, Valentini, 2003) . Cela implique de (i) déterminer le bilan carboné européen, sa structure spatiale et son évolution temporelle; (ii) comprendre les mécanismes et les processus régissant le cycle du carbone des écosystèmes européens et la manière dont ils peuvent être affectés par la variabilité et les changements climatiques et par les interventions humaines et (iii) développer un système d'observation pour identifier les changements des [CO_2] atmosphériques et des stocks de carbone dans les écosystèmes en conformité avec les engagements européens envers le protocole de Kyoto de réduction des émissions de CO_2 et d'accroissement de la séquestration dans les écosystèmes.

Le réseau CarboEurope-IP est un projet intégré du 6° Programme Cadre et a démarré en 2003. Il a émergé de la fusion de plusieurs projets européens et constitue par conséquent une communauté interdisciplinaire et cohérente de recherche dans les domaines de la mesure et de la modélisation du carbone dans les écosystèmes et dans l'atmosphère. Pour atteindre ses nombreux objectifs, le projet intégré s'est organisé en quatre composantes: (i) mesures à l'échelle de l'écosystème; (ii) mesures atmosphériques à l'échelle continentale; (iii) expérimentation régionale dans le but de réduire les incertitudes lors des extrapolations spatiales; (iv) intégration européenne regroupant les différentes données en une estimation du bilan carboné européen.

Notre projet est développé dans le cadre de la première composante qui étudie plus spécifiquement les processus d'échange entre les écosystèmes et l'atmosphère et mesure ces échanges à une échelle spatiale de l'ordre du kilomètre carré. Au total, 103 sites en Europe (Fig. 1) mesurent les échanges de CO_2 à cette échelle spatiale au moyen de la même technique de mesure appelée covariance de turbulence ou, en anglais, *eddy covariance.* Les sites étudiés sont des forêts (50%), des prairies (29%) et des cultures (21%) et couvrent toute l'Europe : du sud de l'Espagne à la Laponie et de l'Irlande à la Hongrie.

Le principe des mesures d'*eddy covariance* est basé sur le fait que la couche limite atmosphérique est caractérisée par la présence de mouvements turbulents qui sont responsables du transport vertical de traceurs comme, par exemple, le CO_2, la vapeur d'eau ou la chaleur sensible. La technique d'*eddy covariance* échantillonne ces tourbillons de manière à établir le taux d'échange de traceur entre l'écosystème et l'atmosphère. Cette mesure requiert la mesure simultanée et à haute fréquence de la concentration du traceur et de la vitesse verticale du vent. Les bases théoriques de cette mesure sont décrites par Aubinet *et al.* (2000), Massman et Lee (2002), Baldocchi (2003), Lee *et al.* (2004).

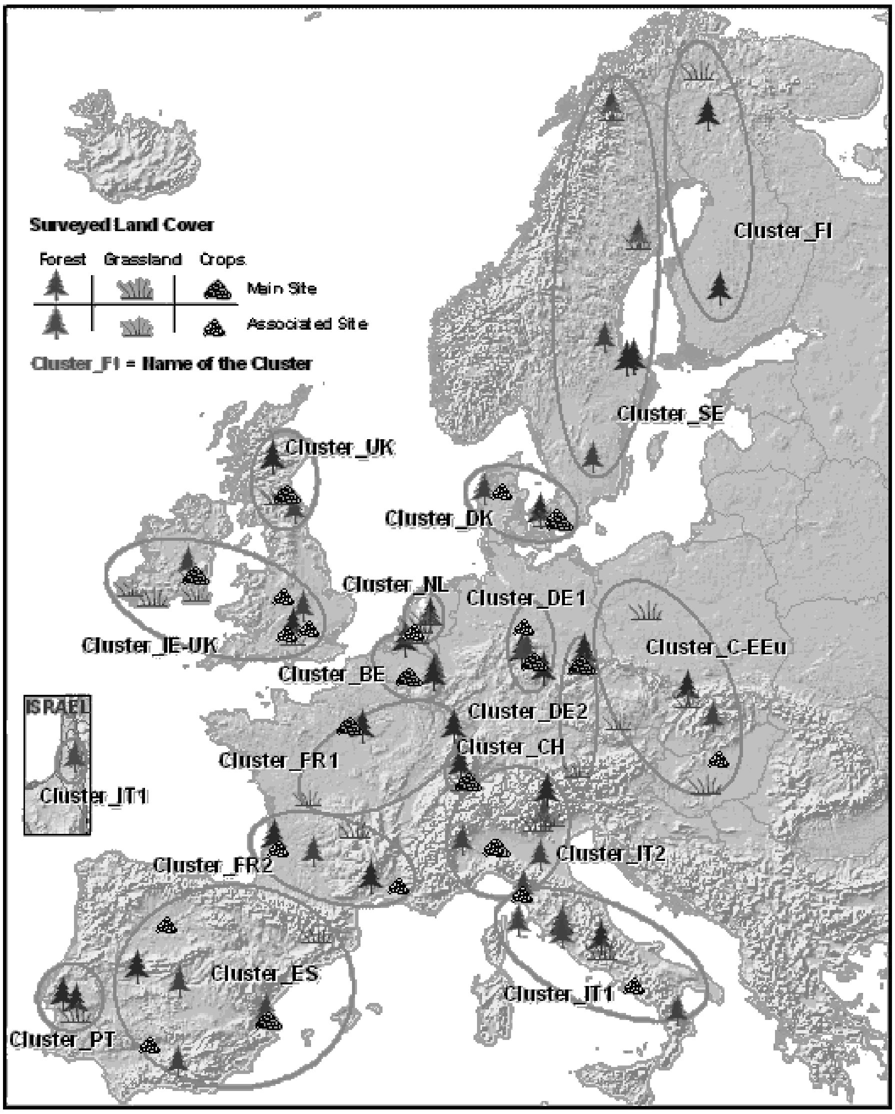

Figure 1 : Carte des sites appartenant au réseau européen CarboEurope-IP.

La théorie de la technique d'*eddy covariance* est attribuée à Sir Osborne Reynolds (Reynolds, 1895). Toutefois, l'application de la méthode à des mesures de flux de CO_2 sur de longues périodes n'a été possible qu'à la suite du développement d'anémomètres soniques (Coppin et Taylor, 1973), d'analyseurs ouverts de gaz par absorption infrarouge à réponse rapide (Bingham *et al.*, 1978; Jones *et al.*, 1978; Brach *et al.*, 1981; Ohtaki et Matsui, 1982) et de l'amélioration de la performance des systèmes d'acquisition. La première année de mesure en continu est accréditée à Wofsy *et al.* (1993). Ces mesures ayant démarré en 1990 sur une forêt décidue, se poursuivent encore aujourd'hui. Après 1993, plusieurs études mesurèrent les flux de CO_2 et de vapeur d'eau au dessus de forêts nord-américaines (Greco et Baldocchi, 1996, Goulden *et al.*, 1996a,b), japonaises (Yamamoto *et al.*, 1999), amazoniennes (Grace, 1996), européennes (Grelle and Lindroth, 1996, Valentini *et al.*, 1996) et boréales (Black *et al.*, 1996 ; Jarvis *et al.*, 1997). En 1996, le premier réseau européen de sites de mesures de flux de CO_2

s'est créé. Il comportait 16 sites, tous forestiers. Au début des années 2000, l'intérêt d'étudier les cultures et les prairies a conduit à la création de nouveaux sites. L'importance des interactions entre les cultures et le climat est présentée à la Section 3. A l'heure actuelle des réseaux similaires se sont constitués à travers le globe (Amériflux en Amérique du Nord, Asiaflux en Asie du Sud-Est, Ozflux en Australie, LBA au Brésil, Chinaflux en Chine, CarboAfrica en Afrique sub-saharienne,…). Tous ces réseaux régionaux couvrent ainsi une très large variété d'écosystèmes et ils se sont fédérés en un réseau mondial dénommé FLUXNET qui comporte, au total, plus de 400 sites (FLUXNET, 2007)

3. Interactions entre agriculture et climat

Aujourd'hui 36 % des territoires hors glaciers sont intensivement utilisés comme cultures et pâturages (Desjardins et al., 2007). En Europe, les terres arables couvrent environ un tiers du territoire. L'importance de l'agriculture en termes d'utilisation du territoire apparaît donc de manière évidente.

Les interactions entre climat et agricultures sont nombreuses. D'une part, le climat influe l'agriculture via la longueur de la saison de végétation, la température de l'air et du sol, l'humidité de l'air et du sol, le rayonnement photosynthétiquement actif disponible, l'absence ou la présence de situation de stress, … D'autre part, l'agriculture émet des gaz à effet de serre qui influent le climat. En effet, l'agriculture émet vers l'atmosphère du CO_2 mais aussi du N_2O et du CH_4. Elle est reconnue comme la plus importante source biosphérique de CO_2 et contribue aux émissions anthropiques de CH_4 et N_2O à raison de 45 – 50 % et 20 - 70 %, respectivement (Cole, 1996; Mosier *et al.*, 1998; Pattey *et al.*, 2007). Les émissions de CO_2 des cultures vers l'atmosphère sont dues à la respiration des plantes et à la décomposition de la matière organique du sol. Le N_2O provient majoritairement (plus de 90%) des sols cultivés à travers les processus de dénitrification et de nitrification de la matière organique. Les principales émissions de CH_4 sont dues aux cultures de riz irriguées ou résultent de la digestion des ruminants et des déjections animales (fumier, lisier, …) stockées de manière anaérobie. Les incertitudes associées aux émissions de N_2O et de CH_4 demeurent actuellement importantes.

La couverture du sol influence également largement le climat régional. En particulier, le type de végétation influence le climat local et régional du fait des variations de l'albédo, de l'humidité du sol, de la rugosité de la surface et de la surface de végétation à partir de laquelle des échanges de chaleur latente et sensible se produisent (Bonan, 2002). Des modifications dans la distribution et le fonctionnement des écosystèmes influencent les cycles biogéochimiques et les échanges d'énergie. La plupart des interactions surface – atmosphère se produisant par le biais de la végétation (Raddatz, 2007), ces modifications peuvent dés lors contribuer aux changements climatiques. Les techniques de gestion des cultures peuvent aussi influencer le climat local et régional. Par exemple, le surpâturage, la mise en culture et la déforestation peuvent contribuer à un affaiblissement des précipitations (Bonan, 2002). L'irrigation peut augmenter la quantité de vapeur d'eau contenue dans l'atmosphère et conduire à une augmentation de la nébulosité et des précipitations.

La possibilité de stocker du carbone dans les sols agricoles est proposée comme moyen d'atténuation dans le cadre du protocole de Kyoto. En effet, les accords de Marrakech (adoptés à Montréal lors de COP/MOP 1) autorisent que les puits et les sources biosphériques soient comptabilisées durant la première période 2008 – 2012 (Smith *et al.*, 2004). De nombreuses études sont menées dans le but de déterminer le potentiel de stockage dans les sols agricoles et les pratiques culturales capables de favoriser ce stockage (e. g. Smith *et al.* 2000; Vleeshouwers et Verhagen, 2002; Freibauer *et al.*, 2004; Smith, 2004).

Le contenu en carbone organique d'un sol dépend de la différence entre les apports de carbone fixé par photosynthèse et les pertes via les processus de décomposition. A l'échelle locale, l'érosion peut provoquer une perte ou un gain de carbone estimable alors que pour de grandes superficies, l'effet net de l'érosion sur les émissions de CO_2 n'est pas facilement définissable (Smith *et al.*, 2004). La qualité et la quantité des apports de matière organique dans les sols ainsi que le taux de décomposition de carbone organique du sol sont déterminés par les interactions entre le climat et le sol ainsi que par l'utilisation du sol et le régime de restitution des matières organiques. Dans les écosystèmes naturels, le climat et les conditions de sol sont les premiers facteurs déterminant le bilan carboné du sol car ils influencent à la fois la production de l'écosystème et le taux de décomposition. Par contre, dans les écosystèmes agricoles, l'utilisation du sol et la gestion culturale modifient d'une part les apports de matière organique via le choix des cultures, l'application de fertilisants, les modalités de récolte, la gestion des résidus et d'autre part, le taux de décomposition, les conditions du sol et son microclimat par la sélection de la culture, du travail du sol, d'une éventuelle pratique de mulching, de l'application de fertilisants, de l'irrigation, du chaulage

(IPCC, 1997). Les exportations de la production agricole constituent également des pertes de carbone pour l'écosystème. Dans nos analyse, nous considèrons que ce carbone est réémis très rapidement vers l'atmosphère sous forme de CO_2.

L'évaluation des pratiques agricoles en termes de stockage de carbone est réalisée en comparant les apports et les pertes de carbone organique dans le sol. Il ne faut cependant pas négliger le fait que ces pratiques peuvent modifier les émissions de CH_4 ou de N_2O qui ont aussi un rôle déterminant dans le bilan total des gaz à effet de serre. Par exemple, un travail simplifié du sol peut accroitre la quantité de carbone séquestrée dans le sol mais il peut également augmenter les phénomènes de dénitrification et donc provoquer des émissions supplémentaires de N_2O (Six *et al.*, 2004). Le travail du sol sans labour peut également générer ou aggraver des problèmes de compaction du sol, de prolifération d'adventices ou de nuisibles (Seguin *et al.*, 2007). L'apport de matière organique peut augmenter l'émission d'N_2O. De la même manière, l'introduction de cultures intercalaires peut accroitre la séquestration de carbone mais implique une utilisation accrue des réserves en eau du sol et nécessite pour leur installation une consommation supplémentaire de carburant (Seguin *et al.*, 2007). Les impacts de ces différentes techniques sont nombreux et leurs effets à long terme doivent être analysés au cas par cas.

La séquestration de carbone est habituellement mesurée en terme de quantité totale de carbone stockée dans le sol. Toutefois, la manière dont ce carbone est stocké et la durée du stockage dépendent d'un grand nombre de paramètres (Six *et al.*, 2001; Gleixner *et al.*, 2002; Kaiser *et al.*, 2002; Balesdent *et al.*, 2000). Il faut savoir que la séquestration de carbone dans les sols n'évolue pas de manière linéaire au cours du temps: des expériences menées à long terme montrent que la teneur en carbone des sols augmente rapidement après la mise en place d'un changement d'utilisation du sol ou d'une pratique culturale (e.g. Smith *et al.* 1997a,b) mais que le taux d'accumulation diminue avec le temps. Après 20 à 100 ans, un nouvel équilibre est atteint ne permettant plus de nouvelles potentialités de séquestration (Freibauer *et al.*, 2004). Ce phénomène est parfois décrit comme un saturation du puits de carbone (Watson *et al.*, 2000). De plus, l'arrêt d'une pratique agricole permettant le stockage de carbone provoque une réémission de CO_2 plus rapide que son accumulation (Arrouays *et al.*, 20002; Smith *et al.* 1996).

La stratégie consistant à séquestrer du carbone dans les sols dans le but d'atténuer l'augmentation des concentrations atmosphériques en CO_2 peut être efficace durant les premières décennies du 21e siècle (Battelle, 2000; Freibauer *et al.*, 2004). A long terme, elle n'est pas une solution pour réduire le taux d'enrichissement de l'atmosphère en gaz à effet de serre et donc, elle ne dispense pas de chercher des alternatives durables à l'utilisation d'énergie fossile et des approches permettant de diminuer la consommation d'énergie. En effet, 80% de la production globale d'énergie viennent aujourd'hui des combustibles fossiles et de l'énergie nucléaire.

4. Les échanges de CO_2 à l'échelle d'une culture

Afin de mieux décrire le projet "Mesures des flux de CO_2 et bilan carboné des grandes cultures", il est nécessaire de rappeler quelques définitions concernant les échanges de CO_2 entre les écosystèmes terrestres et, en particulier, les cultures et l'atmosphère. Une culture absorbe le CO_2 via le processus de photosynthèse. La quantité de carbone qu'elle peut ainsi assimiler est dénommée la production primaire brute (GPP : *gross primary productivity).* Par ailleurs, cette culture réémet du CO_2 par la respiration des plantes et du sol. Ce flux est appelé la respiration totale de l'écosystème (TER : *total ecosystem respiration).* La différence entre ces deux flux importants et opposés est nommée échange net de l'écosystème (NEE : *net ecosystem exchange*). Ces flux sont schématisés à la Figure 2.

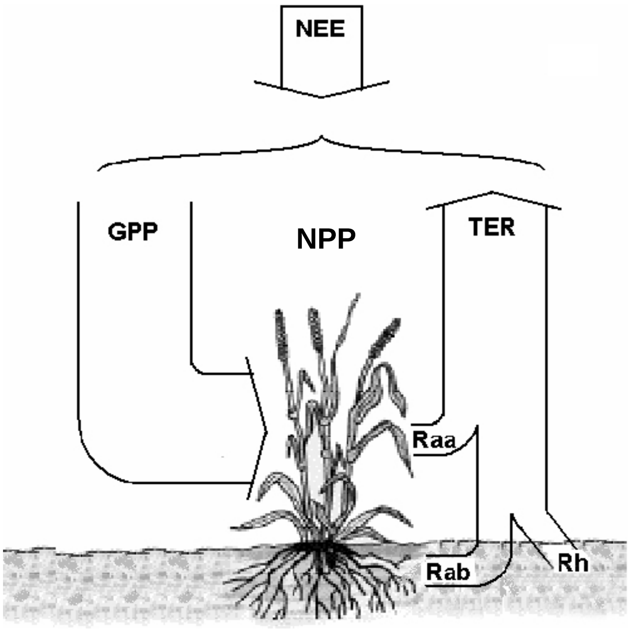

Figure 2 : Représentation des flux de CO_2 échangés entre une culture et l'atmosphère.

La TER résulte d'une part de l'activité de la plante et des mycorhizes qui sont associées à ses racines (respiration couramment qualifiée dans la littérature de respiration autotrophe, R_a), d'autre part de la décomposition de la matière organique du sol par les microorganismes (respiration hétérotrophe, R_h). La TER peut aussi être décomposée en une partie résultant des parties aériennes de la plante (R_{aa}) et une partie résultant de la respiration du sol (SR) qui est la somme de la respiration autotrophe souterraine (R_{ab}) et de la respiration hétérotrophe (R_h) (Figure 2).

Seule une partie du carbone assimilé par la culture est réémis vers l'atmosphère via les processus de respiration autotrophe. Du carbone est en effet stocké dans les tissus de la plante, c'est la production primaire nette (NPP : *net primary productivity*).

En comparant l'échange net de la culture (NEE) à la quantité de carbone qui est exportée lors de la récolte, on peut déterminer si une culture, sur un intervalle de temps donné, se comporte comme une source ou un puits de carbone. Cette différence est la NBP (*net biome productivity*).

5. Projet "Mesures des flux de CO_2 et bilan carboné des grandes cultures"

Description générale du projet

L'objectif général de ce projet est de quantifier et de comprendre l’évolution des échanges de CO_2 d'une succession de cultures avec son environnement. Plus particulièrement, les objectifs sont

- de mesurer les flux nets de CO_2 échangés par une culture avec l'atmosphère et d'estimer la séquestration ou l'émission nette de carbone par la culture.
- d'analyser les effets des variations climatiques inter et intra annuelles sur les flux de CO_2 échangés par la culture et en déduire les mécanismes qui les régissent.
- d'identifier les rôles respectifs du sol et de la plante dans ces flux et mettre en évidence les variables et les processus physiologiques qui contrôlent les mécanismes de réponse des flux au climat.
- d'étudier l'impact des interventions culturales sur les flux de CO_2 en liaison avec les mécanismes biologiques du sol.

- d'établir un bilan carboné complet de la culture et de déterminer la répartition du carbone séquestré/émis entre le sol et les parties récoltées et non récoltées de la végétation.

Dans ce but, de nombreuses mesures sont effectuées à différentes échelles spatiales et temporelles. Lorsque c'est possible, les résultats obtenus à partir de différentes techniques opérées à différentes échelles sont confrontées afin de valider les mesures. Trois équipes de la Faculté universitaire des Sciences agronomiques de Gembloux travaillent conjointement à ce projet: l'Unité de Physique des Biosystèmes, l'Unité de Phytotechnie des Régions tempérées et le Laboratoire d'Ecologie microbienne et d'Epuration des Eaux usées. Le projet est financé par le Communauté française de Belgique (Projet ARC) et par la Communauté européenne (Projet CarboEurope).

Description du site et des mesures

Les mesures sont réalisées sur une parcelle agricole de 11,8 ha, sise à Lonzée, commune de Gembloux (Belgique). Ce site est maintenu sous culture depuis plus de 70 ans et depuis près de 10 ans, il est cultivé selon une rotation de quatre ans, largement pratiquée dans la région limoneuse. Depuis le début des mesures, les cultures qui se sont succédées sont la betterave sucrière (*Beta vulgaris*, L.) (2004), le blé d’hiver (*Triticum aestivum*, L.) (2005), les pommes de terre pour plants (*Solanum tuberosum*, L.) (2006) et, à nouveau le blé d’hiver (2007). En 2008, des betteraves sucrières seront à nouveau cultivées. Le site est caractérisé par un climat tempéré maritime avec une température moyenne de 10°C et une pluviométrie annuelle de l'ordre de 800 mm. Le sol est un Luvisol (classification FAO). Le site a été décrit en détail dans Moureaux *et al.* (2006).

A l'échelle de la plante, des échantillons sont prélevés une fois par quinzaine ou une fois par semaine, selon le rythme de développement de la culture. Quatre zones de prélèvement sont définies à proximité de la station météorologique et du système d'*eddy covariance* de manière telle à ne pas perturber les mesures de ce dernier. Les échantillons sont répétés dans ces quatre zones. La matière sèche et le contenu en carbone de ces échantillons sont mesurés et extrapolés à l'ensemble de la culture. Ces mesures permettent d’obtenir une estimation de la productivité primaire nette (NPP).

A l’échelle de la plante, toujours, les surfaces des feuilles et des différents organes sont mesurées au cours du développement des cultures. Un suivi visuel régulier est également mis en place dans le but de définir les stades de développement, de suivre l'ordre d'apparition et de disparition des différents organes, d'observer l'évolution de la sénescence et de détecter d'éventuelles maladies. Les dépositions d'azote sont également mesurées.

A l'échelle de la mini parcelle de sol, les flux de respiration de sol (SR) sont mesurés, chaque demi-heure, à l'aide d'un système automatique utilisant le principe de la chambre fermée dynamique (Norman *et al.*, 1992; Longdoz *et al.*, 2000) mis au point à l'Unité de Physique des Biosystèmes (Suleau *et al.*, soumis, a). Dans ce système, un collier est inséré dans le sol. Pendant la mesure, il est fermé par un couvercle et relié par un circuit aérodynamique à un analyseur de concentration de CO_2 par spectrométrie infrarouge. Le circuit aérodynamique étant fermé, la respiration contribue à augmenter la concentration de CO_2 dans le système. La mesure est déduite de la pente de l’évolution de la concentration de CO_2 en fonction du temps. Ces mesures permettent d'étudier l'évolution temporelle et climatique de la respiration du sol. Toutefois, comme les chambres sont en nombre limité et placées en des positions fixes, elles ne renseignent pas de la variabilité spatiale des flux. C'est la raison pour laquelle, pendant les périodes cultivées et à raison d'une fois par semaine, des mesures additionnelles sont effectuées de manière extensive au travers de la parcelle agricole avec un système portatif, basé sur le même principe.

Toujours à l’échelle de la mini parcelle de sol, des mesures microbiologiques sont menées avec l’objectif de déterminer les quantités d'azote et de carbone microbiens et les respirations basales et induites. Les premières permettent d'estimer l'importance des populations microbiennes et les secondes renseignent sur leur acticité. Ces mesures sont effectuées afin d’expliquer la variabilité spatiale de la SR.

A l'échelle de la feuille, l'assimilation nette est mesurée à l'aide d'un poromètre (Licor 6400, Licor Inc, Lincoln, NE, USA). Cet appareil permet de mesurer les échanges de CO_2 d'une feuille sous conditions contrôlées (température, déficit de pression de vapeur, rayonnement incident, $[CO_2]$ ambiante). Lors des mesures, une partie de feuille est insérée dans la pince de mesure. Les conditions de température et de déficit de pression de vapeur de la feuille et de $[CO_2]$ de l'air sont maintenues constantes aux valeurs que connaissait la feuille avant la mesure. Le rayonnement varie par palier des conditions saturantes à l'obscurité. A chaque palier, l'assimilation nette de la feuille est mesurée. On obtient ainsi la réponse de l'assimilation nette d'une feuille au rayonnement (réponse A – Q).

Enfin, à l'échelle de la parcelle, un système de mesure des flux turbulents (*eddy covariance*) fournit une mesure par demi-heure de l'échange net de CO_2 par la parcelle (NEE) (cf. Section 2). Un des principaux objectifs des mesures d'*eddy covariance* étant le suivi à long terme des échanges, les flux vont être sommés à l'échelle journalière, mensuelle, saisonnière et annuelle. L'ensemble de la procédure d'acquisition et de traitement des données est décrite dans un article méthodologique (Aubinet *et al.*, 2000). Cette procédure standardisée est utilisée par l'ensemble de la communauté FLUXNET.

En plus de ces différentes mesures, une station météorologique automatique est installée sur la parcelle afin de mesurer en continu les conditions dans lesquelles se font les échanges et ainsi de déterminer leur réponse au climat. Cette station fournit chaque demi-heure une mesure de la température et de l'humidité de l'air (RHT2, Delta-T Devices Ltd, Cambridge, UK) à 1.3 m du sol, de la pression atmosphérique (MPX4115A, Motorola Phoenix, AR, USA), des précipitations, du rayonnement global incident et réfléchi, du rayonnement infrarouge incident et réfléchi (CNR1, Kipp en Zonen, Delft, NL), du rayonnement photosynthétiquement actif diffus et total (Sunshine Sensor type BF3, Delta-T Devices Ltd, Cambridge, UK), de la température (pt100, Jumo) et de l'humidité du sol (ThetaProbe, Delta-T Devices Ltd, Cambridge, UK) à différentes profondeurs.

Exploitation des mesures

Le schéma de la Figure 3 synthétise la procédure utilisée pour exploiter les mesures effectuées et représente les flux obtenus directement par mesure, les flux calculés à partir d’un seul type de mesures et enfin les flux obtenus par combinaison de plusieurs types de mesures.

La mesure de NEE par *eddy covariance* permet d’évaluer l’importance du puits ou de la source de CO_2 que représente une culture. La séquestration annuelle de la culture de betterave, sa sensibilité à certains choix méthodologiques lors de son estimation et la réponse des flux au climat et au développement de la culture est analysée dans Moureaux *et al.* (2006). Toutefois, la mesure de NEE ne permet pas de prédire son évolution suite à un changement du climat ou du mode de gestion de l'écosystème. En effet, l'échange net résulte de la différence entre la photosynthèse des feuilles (GPP) et la respiration de l'écosystème (TER), lesquelles répondent différemment au climat (e.g. Falge et al., 2002; Law et al., 2002). Une meilleure compréhension de l'évolution du flux net exige donc de pouvoir séparer ces deux processus et de les décrire indépendamment. La procédure que nous avons choisie est celle proposée par Reichstein *et al.* (2005). Cette méthode part du principe que les mesures effectuées la nuit par le système d'*eddy covariance* représentent la TER. La réponse de ce terme à la température peut donc en être déduite. Si l'on postule que la TER présente la même réponse à la température de jour que de nuit, elle peut dés lors être calculée pour l'ensemble de la journée en extrapolant aux conditions de jour la réponse établie la nuit. La GPP est alors calculée comme la somme de la NEE et de la TER pendant la journée et est considérée comme nulle pendant la nuit. L'algorithme utilisé pour établir une réponse de la TER à la température utilise un court pas de temps (quelques jours) de manière à pouvoir reproduire des évènements particuliers et limités dans le temps comme les périodes d'intense développement de la culture, les périodes de sénescence ou de sècheresse (Reichstein *et al.*, 2005; Moureaux *et al.*, soumis).

Les mesures de respiration du sol sont extrapolées à l'échelle de la culture en combinant les mesures automatiques et manuelles. L'extrapolation est basée sur un principe de séparation des dépendances climatique et spatiale : la réponse climatique de la respiration est caractérisée par une fonction identique en tous points de la culture laquelle est multipliée par un coefficient intégrant la variabilité spatiale. La réponse climatique est obtenue en combinant les résultats des mesures automatiques aux mesures météorologiques, le coefficient spatial étant déduit des mesures manuelles. De cette manière, la respiration mesurée à l'échelle des mini parcelles de sol peut être extrapolée aux échelles de la culture et de la saison entière. Un article présentant la mise au point d'un tel modèle, sa calibration et sa validation sur les mesures de la SR des cultures de froment d'hiver 2005 et 2007 est soumis (Suleau *et al.*, soumis, b). Il analyse également la dépendance de la respiration du sol aux précipitations et met en évidence un comportement différencié de la respiration du sol selon les stades de développement de la culture. Préalablement à telles analyses, les chambres de respiration de sol ont été adaptées pour fournir des mesures fiables sur un site agricole. Ces chambres ayant initialement été conçues pour fonctionner dans des écosystèmes forestiers et donc dans des conditions peu venteuses car à l'abri dans la forêt, un important problème de sensibilité des mesures au vent a dû être résolu. Les adaptations apportées au système sont décrites dans Suleau *et al.* (soumis, a).

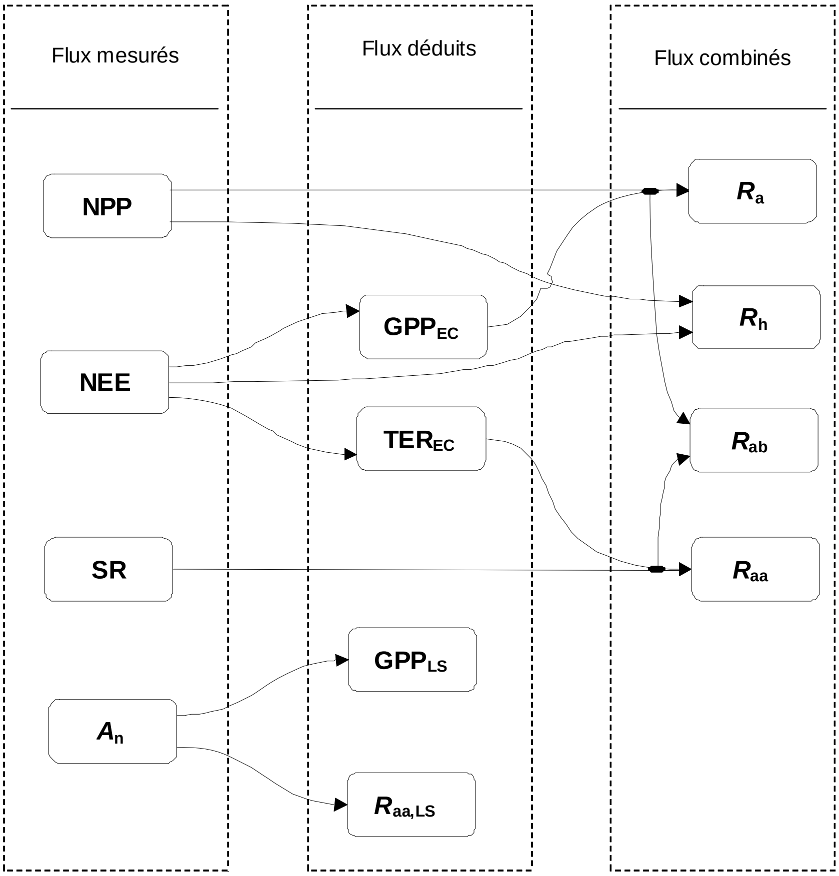

Figure 3 : Présentation de la méthodologie de calcul permettant d'obtenir les termes du bilan de carbone à partir de mesures faites à différentes échelles spatiales et temporelles.

Les mesures d'assimilation nette à l'échelle de la feuille sont répétées une fois par semaine sur différentes feuilles dans le but d'étudier la variabilité de la réponse A – Q en fonction de la position de la feuille, des conditions climatiques et de la saison. A partir de cette description, un modèle peut être développé pour extrapoler l'assimilation nette (différence entre la quantité de carbone assimilée par photosynthèse, GPP_{LS}, et la respiration des parties aériennes de la plante, $R_{aa,LS}$; Figure 3) à l'entièreté de la culture et à toute la saison de végétation. Pour ce faire, outre la description des réponses A – Q, il est nécessaire de connaître l'évolution et la répartition des organes verts dans la culture. Cette approche a été décrite et développée par Hoyaux *et al.* (accepté) pour la culture de froment d'hiver de 2005.

En combinant ces mesures, les différents termes du bilan carboné de la culture sont déduits (Figure 3), en particulier la discrimination entre les parts autotrophes et hétérotrophes de la respiration. Une autre technique pour décomposer la respiration du sol en ses parts auto- et hétérotrophes a été mise en place sur les cultures de pommes de terre (2006) et de froment d'hiver (2007). Elle consiste à mesurer la respiration du sol sur des parties plantées et non plantées. L'hypothèse est posée que les parts auto- et hétérotrophes sont présentes dans les premières alors que seule la part hétérotrophe est présente dans les secondes. Il faut toutefois tenir compte du fait que, dans les secondes, l'absence de végétation modifie les conditions climatiques locales et doit influer sur la part hétérotrophe. L'analyse de ces résultats est actuellement en cours. Ils pourront être confrontés aux estimations provenant de la combinaison de la NEE (ou de la GPP) et de la NPP (Figure 3).

Le bilan carboné de la culture de blé d'hiver est présenté dans Moureaux *et al.* (accepté). Les évolutions des différents flux et de leurs valeurs relatives sont analysées en fonction du développement de la culture. Dans leur article, Hoyaux *et al.* (accepté) comparent les estimation de la GPP obtenues à partir des mesures à l'échelle de la feuille et à partir des mesures d'*eddy covariance*. Les deux estimations de la R_{aa} sont confrontées dans Moureaux *et al.* (accepté).

Notre appartenance au réseaux européens CarboEurope-IP et NitroEurope implique la mise en commun de mesures effectuées sur notre site. En effet, l'ensemble des mesures météorologiques, des mesures faites par le système d'eddy covariance, des mesures de matières sèches et de contenus en carbone (NPP), ainsi que le suivi du développement de la culture sont à la disposition des communautés de CarboEurope, de FLUXNET et de NitroEurope sur une base de données. Celle-ci permet d'effectuer plus aisément des analyses inter sites. Un article récemment publié compare des méthodes d'estimations de la GPP pour différents sites européens (forêts, prairies, cultures) non soumis à des épisodes de sécheresse (Owen *et al.*, 2007). Plusieurs articles comparant les cultures sont en préparation. Ils sont coordonnés par différents groupes du réseau.

La base de données fournit également les mesures effectuées à l'échelle d'un site aux groupes qui établissent les bilans carbonés à l'échelle régionale, européenne ou globale (e.g. Ciais *et al.*, 2005 ; Granier *et al.*, 2007; Reichstein *et al.*, 2007,).

6. Conclusions et perspectives

Le projet pluridisciplinaire intitulé "Mesures des flux de CO_2 et bilan carboné d'une grande culture" a permis, à ce jour, de mieux caractériser les échanges de CO_2 entre une culture et l'atmosphère pendant une rotation complète de quatre ans. Une évaluation de la séquestration nette de carbone par chaque culture et de l'ensemble de la rotation a été réalisée. Une comparaison de la séquestration nette entre les cultures a aussi été effectuée. Le développement en parallèle de différentes mesures effectuées à différentes échelles spatiales et temporelles (mesure de photosynthèse à l'échelle de la feuille, mesures de matière sèche, mesures de respiration du sol) a par ailleurs permis, d'une part de réaliser une validation mutuelle des méthodes, d'autre part de mieux détailler les différentes composantes du flux net de CO_2. En particulier, les évolutions avec le climat et le développement de la culture des productivités primaires brute et nette, de la respiration totale de l'écosystème et de la respiration du sol ont pu être étudiées. La séparation entre les composantes hétérotrophe et autotrophe de la respiration a pu être réalisée et s'est avérée riche d'indications pour la compréhension de ces flux. La méthodologie permettant l'établissement du bilan carboné des cultures a été mise au point, les incertitudes liées à chaque méthode ont été évaluées et une méthode optimale a été proposée et appliquée de manière à proposer un bilan carboné des cultures.

D'autres points restent à analyser ou à approfondir. La réponse des flux au climat et aux stades de développement de la végétation reste à affiner. En effet, dans la mesure où, au cours d'une saison de culture, la succession de ces stades est corrélée aux variables climatiques qui sont souvent elles-mêmes corrélées entre elles, il n'est pas toujours possible d'identifier la cause précise de la variation du flux. Le fait de pouvoir observer des cultures identiques qui se succèdent sur le site tous les deux ou quatre ans permet d'affiner cette description et de mieux discerner l'impact de l'une ou l'autre cause. En pratique la comparaison entre deux cultures identiques développées deux années différentes fournit des séries de données indépendantes permettant de valider et calibrer des modèles décrivant le comportement des flux. Ce travail est notamment en cours pour les cultures de blé en 2005 et 2007 et est projeté pour les cultures de betteraves de 2004 et 2008. Par ailleurs cette comparaison permet d'évaluer la variabilité interannuelle des flux. Par exemple, la comparaison des flux en 2005 et 2007 va permettre d'étudier l'impact des conditions climatiques très particulières de 2007 (hiver exceptionnellement doux, printemps très sec) sur le développement de la culture et fournira de précieuses informations quant au comportement d'une culture soumise à un climat plus chaud et à une période de sècheresse.

Il est également nécessaire de vérifier la représentativité des mesures réalisées à l'échelle régionale. Les réseaux CarboEurope-IP et FLUXNET auxquels le site est rattaché offrent de nombreuses possibilités de comparaisons inter sites des différents flux. En particulier, une étude comparant les bilans carbonés de cultures ayant connu une rotation complète ou quatre ans de cultures continues serait souhaitable.

Une meilleure compréhension des processus responsables des échanges de CO_2 et une meilleure prédiction de l'évolution de ceux-ci suite à un changement climatique passe par l'élaboration de modèles. Les modèles mis au point jusqu'ici sont essentiellement de type empirique. Il est maintenant nécessaire de développer des modèles plus fondamentaux prenant en compte les mécanismes de base à l'œuvre dans la culture. S'il existe des modèles fondamentaux décrivant la photosynthèse (Farquhar and von Caemmerer, 1982), les modèles décrivant les processus de respiration à l'échelle de l'écosystème et à une échelle journalière restent très insuffisants. Ils sont pourtant nécessaires pour prédire notamment l'impact de pratiques culturales sur ces flux. Ces modèles ne pouvant pas être développés *ab nihilo*, il est nécessaire de développer en parallèle des expériences spécifiques permettant leur calibration et leur validation. En particulier, les expériences mesurant les rapports isotopiques du CO_2 émis s'avèrent prometteuses dans ce contexte, permettant notamment de mieux séparer la part de la respiration provenant de l'activité des plantes et celle provenant de la décomposition de la matière organique du sol.

L'étude de l'impact des pratiques culturales sur les flux doit être approfondie. Les mesures décrites ici se rapportent à une culture de production gérée de manière traditionnelle. L'analyse des quatre années de mesure en continu de l'échange net révèle certaines « anomalies » qui sont liées à certaines interventions culturales (labour, épandage de résidus de cultures, traitement herbicide, etc.). La réponse climatique des flux ayant maintenant bien été décrite, une analyse de résidus des modèles de réponse climatique pourrait être développée afin de chiffrer l'émission de CO_2 associée à ces activités. Par ailleurs, la nécessité d'adapter l'agriculture aux changements climatiques et la volonté de mitiger l'effet de serre en tentant d'accroître le stockage de carbone dans le sol mène à l'élaboration de nouveaux itinéraires culturaux et de nouvelles pratiques de gestion des cultures. L'impact de ces pratiques sur les émissions de gaz à effet de serre, sur la productivité des cultures et sur la qualité des sols est le plus souvent hypothétique. Il est donc nécessaire de plus étudier et approfondir l’impact des pratiques agricoles sur les émissions de CO_2. En particulier l’impact d’une modification des doses ou de la distribution de la fertilisation, l’impact d’un travail du sol réduit, celui de la restitution et de l'enfouissement des résidus de cultures après récolte doivent être analysés plus en détail. Cela nécessite, outre le développement des modèles fondamentaux précités, celui d’expériences particulières.

Notre étude s’est jusqu’ici concentrée sur le CO_2 qui est le principal gaz à effet de serre. Le méthane et le protoxyde d’azote sont également des gaz jouant un rôle important; leur plus faible concentration dans l’atmosphère étant compensée par un plus grand pouvoir de réchauffement potentiel (IPCC, 2007). Les sols agricoles constituent une des sources principales de N_2O mais les modalités de cette émission, leur dépendance par rapport au climat et aux actions culturales restent mal connues et peu quantifiées. Ici également, des mesures complémentaires s’imposent afin de mieux comprendre ces phénomènes.

Enfin, les études décrites ici ont analysé les échanges à l'échelle de la parcelle agricole. L’analyse des échanges s'effectuant à l'échelle de l'exploitation voire de l’ensemble de la filière de production constitue également une piste intéressante de perspectives. Une étude récente analyse les échanges à l'échelle d'une exploitation agricole irlandaise basée sur l'élevage (Byrne et al., 2007).

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Article 2

Annual net ecosystem carbon exchange by a sugar beet crop

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Abstract

Eddy covariance measurements of CO_2 fluxes were conducted in 2004 at the agricultural site of Lonzée, Belgium, over a sugar beet crop. Additional measurements of biomass net primary production and leaf area index (LAI) were carried out. The response of the fluxes to climatic and non-climatic variables was analysed. Nighttime fluxes were dependent on turbulence, temperature and high soil water content. The u_* correction was determined using a statistically based algorithm. The lower u_* threshold was 0.1 m s^{-1}. Daytime fluxes during maximum canopy development depended mainly on incident radiation and its repartition between direct and diffuse components. A limited response to saturation deficit and soil water content was also observed. The evolution of assimilation and respiration throughout the growing season was studied. Maximum assimilation fluxes were observed in July when canopy had not fully developed and these then decreased from the end of July to the harvest, due not only to a reduction in radiation but also to a reduction in canopy assimilation capacity. Normalised respiration evolution presented two peaks during the year: the first in July, when the assimilation was at its greatest, and the second after the harvest, during the crop residues decomposition. The annual sequestration, estimated by half-hourly flux summing and measurement gap filling, was -0.61 ± 0.11 kg C m^{-2} and the impact of the u_* correction and of the residues decomposition was estimated to be 5.3 and 3.5%, respectively.

Keywords: Eddy covariance; Sugar beet crop; Annual sequestration; Net ecosystem exchange; u_* threshold

1. Introduction

Since the mid 1990s, continuous micrometeorological measurements of the net exchange of carbon dioxide, water vapour and energy among various terrestrial ecosystems and the atmosphere have been conducted worldwide (Baldocchi et al., 2001; Baldocchi, 2003; Valentini, 2003). The main objective of these measurements is to determine the contribution of various ecosystems to the global carbon cycle.

Croplands cover about one-third of the land surface of Europe (FAO Statistical Databases, 2003) and have the potential to mitigate about 16–19 Tg C per year (Freibauer et al., 2004). The cropland area represents a quarter of Belgium land surface (MRW-DGA, 2005). Most crops in the region are managed following a 4-year rotation scheme with alternation between cereals (mainly winter wheat) and crops such as sugar beet, potato, chicory and silage maize. The sugar beet crop covers more than 10% of the crop area in Belgium (INS, 2003).

The objectives of this study were: (i) to identify the environmental or biophysical factors that control the daytime assimilation and nighttime emission, (ii) to determine the seasonal distribution of these fluxes and (iii) to quantify the annual CO_2 net exchange by the crop and assess its sensitivity to management practices and methodological choices. The effects of some

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methodologies on the carbon sequestration estimation were also addressed.

2. Materials and methods

2.1. Site description

The study site is cropland in Lonzée about 45 km SE of Brussels, Belgium (50°33′08″N, 4°44′42″E, 165 m asl). The climate is temperate maritime. The mean annual temperature is about 10 °C and the annual precipitation is about 800 mm.

The cropland is a quadrilateral area of ca. 12 ha located on a fairly flat plateau with a maximum slope of 1.2% in a WSW direction. The site provides a fetch of 240 m in the SW which is the main wind direction. The farm is located 400 m WSW from the measurement point. There are no other buildings or roads for more than 1000 m. The second main wind direction is NE, with a fetch of 200 m. This side of the area is bordered by a road with very light traffic, beyond which croplands extend more than 900 m. The soil is a Luvisol (FAO classification). It is composed of 18–22% clay, 5–10% sand and 68–77% silt and contained 3.7 kg m^{-2} total organic carbon in September 2004.

The land has been cultivated for more than 70 years. For the past 6 years, the crops have been 50% cereal and 50% potato and sugar beet. In 2004, the soil was tilled to a depth of 0.30 m in late February and sugar beet (*Beta vulgaris* L.) was sown on 30 April. The crop was harvested on 29 September. The yield was 1.53 kg m^{-2} dry matter or 0.632 kg m^{-2} carbon. On 1 April 2004, 156 kg ha^{-1} mineral N were applied. In the preceding years, 180 kg ha^{-1} mineral N and 60 kg ha^{-1} organic N (sugar lime) had been applied in 2003, 156 kg ha^{-1} mineral N, 14 kg ha^{-1} phosphorus and 42 kg ha^{-1} potassium in 2002 and 180 kg ha^{-1} mineral N in 2001. No farmyard manure had been applied since 1996.

2.2. Measurement system

2.2.1. Eddy covariance and meteorological system

Fluxes of CO_2, water vapour and sensible heat were measured with an eddy covariance system placed at a height of 2.7 m and consisting of a research-grade sonic anemometer (model Solent Research R3, Gill Instruments, Lymington, UK) and an infrared gas analyser (IRGA) model Li-7000 (LiCor Inc., Lincoln, NE, USA). The eddy covariance system was the standard system used in *CarboEurope-IP* and *Fluxnet* networks (Moncrieff et al., 1997; Grelle and Lindroth, 1996; Aubinet et al., 2000). Air from the vicinity of the sonic anemometer was drawn through a 12.4 m long and 4 mm i.d. PTFE into the analyser. Data from the sonic anemometer were gathered at a sampling rate of 20 Hz using EDDY software (Kolle, Max-Planck-Institute for Biogeochemistry, Germany). This software was also used to determine online and post-process flux.

Complementary measurements were made on a half-hourly basis. They included air temperature and humidity (RHT2, Delta-T Devices Ltd., Cambridge, UK) at a height of 1.3 m, soil temperature (PT100) at a depth of 3, 5.5, 9, 26 and 56 cm and soil humidity (ThetaProbe, Delta-T Devices Ltd., Cambridge, UK) at a depth of 5, 20 and 50 cm. Global (CM21, Kipp en Zonen, Delft, NL), net (Q*7.1, REBS, Seattle, WA, USA), global photosynthetically active (PAR Quantum Sensor SKP 215, Skye Instruments Ltd., UK) and global and diffuse photosynthetically active (Sunshine sensor type BF3, Delta-T Devices Ltd., Cambridge, UK) radiation were measured at a height of 2.7 m. Rainfall and mean atmospheric pressure (MPX4115A, Motorola, Phoenix, AR, USA) were also measured at the site.

2.2.2. Data treatment

Half-hourly fluxes were calculated in the post-processing of the 20 Hz time series data. The fluxes were rotated (2D) in order to align the streamwise velocity component with the direction of the mean velocity vector. High frequency losses due to the sampling tube were corrected experimentally (Eugster and Senn, 1995; Aubinet et al., 2001). The transfer function was determined by comparing the CO_2 and H_2O flux co-spectra with the sensible heat co-spectrum. The transfer function was approximated by a first-order function equivalent to that of a low pass filter composed of a self-induction coil and a unitary resistance (Eugster and Senn, 1995). The inductances were: $L_{CO_2} = 0.1$ and $L_{H_2O} = 0.4\ \Omega$ s.

The fluxes were submitted to a stationary test (Foken and Wichura, 1996). Three levels of quality were defined: data that meet the quality test with an allowed difference of 30%, data that meet the test with an allowed difference of 50% and data that failed the test. The responses of the fluxes to environmental factors were established from data of the first category. The impact that elimination of bad quality data had on annual carbon sequestration was estimated in Section 3.5.

Half-hourly changes in CO_2 storage were calculated using a single concentration measurement at a height of 2.7 m. Although this technique is questionable when used above tall vegetation where eddy covariance systems should be placed at great heights, it works fairly well above short crops and grasslands where measurement height is lower. Notably, it was used by Anthoni et al. (2003) above a winter wheat crop. Below, we will consider the net ecosystem exchange (NEE) as the sum of storage fluxes and turbulent fluxes.

It is recognised that during stable nighttime conditions CO_2 exchange is often underestimated by the eddy covariance system (Goulden et al., 1996; Jarvis et al., 1997; Aubinet et al., 2000). A criterion based on the friction velocity (u_*) value is generally used to select valid periods. The measurements taken during stable conditions (u_* smaller than the threshold) are excluded and replaced by a parameterisation based on an empirically established respiration-to-temperature relationship derived from data measured during turbulent periods. The value of the threshold is critical because it can lead to a substantial change in the estimation of the annual carbon exchange (Goulden et al., 1996; Lindroth et al., 1998; Massman and Lee, 2002; Anthoni et al., 2003) and even to a reversal in the sign of the annual net ecosystem exchange (Goulden et al., 1997).

The u_* threshold is often found by visually examining the scatter plot of normalised nighttime fluxes versus u_*. Conceptually, it is assumed that the threshold is located where the flux starts to level off as u_* increases. This approach has been criticised because of the absence of any standard and because it depends on an individual researcher's judgement. Gu et al. (2005) proposed an algorithm called the moving point test (MPT), which is a reproducible, site-independent, statically based approach that can be automated for processing large datasets.

The MPT searches simultaneously for a lower u_* threshold (u_{*L}) below which fluxes are potentially underestimated and a higher u_* threshold (u_{*H}) above which measurements are subject to a potential pressure pumping effect. The algorithm of the MPT is an iterative procedure with two nested loops. The temperature response function of the nighttime fluxes is determined in the outer loop while, in the inner loop, the thresholds are researched. To determine a u_* threshold, two samples were compared using a statistical *t*-test: a moving sample (MS) of constant size *n*, and a reference sample. The reference sample contains the normalised fluxes assumed to be independent of u_*, and its size varies at each iteration of the inner loop. If the statistical test concludes to the equality of the average fluxes of the two samples, a new threshold can be defined as the median value of the MS. The loops stop when the u_* thresholds of two successive iterations are the same (Steps 14 and 15, p. 187 and p. 189). Gu et al. (2005) recommended a MS size smaller than one-fifteenth of the total number of data in the test and large enough to produce meaningful statistics. In practice, they suggest a size larger than 25. In this study, the smallest MS size was 31, as recommended by Dagnelie (1973) when applying a test of average equality in the case of unequal variance.

Applied directly to the Lonzée dataset, the Gu algorithm did not work as it did not detect any threshold, although a plateau was clearly apparent to the eye. We therefore modified the algorithm in order to allow such detection. In the inner loop (step 12, p. 187), we fixed the new u_{*L} (u_{*H}) threshold as the lowest (highest) u_* value of the MS rather than as its median. In addition, the convergence criterion was modified (steps 14 and 15, p. 187): it was based on the CO_2 fluxes (NEE) rather than on the u_* threshold values. Indeed, the loops stopped when the mean NEE of the MS of the current iteration was not significantly different from the mean NEE of the reference sample of the following iteration. A statistical *t*-test was performed for this purpose. Two versions of the algorithm were tested, one bypassing the higher threshold research, the other not.

In order to estimate the annual NEE, missing measurements resulting from system failures, power cuts or data removal because of their bad quality or because they corresponded to stable periods had to be estimated. Daytime gaps were filled using NEE–photosynthetically active photon flux density (PPFD) relationship based on 10-day periods, and nighttime gaps were filled using an NEE–temperature function estimated from the non-affected turbulence data for the whole year except October 2004 (cf. Section 3.3.1). In the case of missing meteorological data, the mean diurnal variation was applied using an 11-day data window (Falge et al., 2001).

2.2.3. Phenological measurements

Leaf area index (LAI) measurements were conducted from 26 July to the harvest. Every 2 weeks, between four and six sugar beet plants were lifted and their leaf area estimated using a camera and a picture analyser (Windias, Delta-T Devices, Cambridge, UK). The LAI was also estimated from the radiation absorption measurements using a ceptometer (Sunscan, Delta-T Devices, Cambridge, UK). This measurement was repeated three times in September. The dry matter (DM) content was measured fortnightly. Two meters of three adjacent rows of sugar beet were harvested at four locations in the field and the total DM content was measured from 17 May to the harvest. From 16 July, DM measurements were performed separately for the leaves and the roots. In addition, the number of leaves on 24 plants was counted every week from mid May to the harvest.

2.2.4. Parameterisation

In the following analysis, we use the micrometeorological convention that downward fluxes are counted as negative and upward fluxes as positive.

2.2.4.1. Daytime fluxes. The net ecosystem exchange (N_e) was expressed as the difference between the gross primary production (G_p) and the total ecosystem respiration (R_t):

$$N_e = G_p - R_t \tag{1}$$

The gross primary production (GPP) was parameterised as a curvilinear function of the incident PPFD (Q_i) (Aubinet et al., 2001):

$$G_p = G_s\left(1 - \exp\left\{-\frac{\alpha Q_i}{G_s}\right\}\right) \tag{2}$$

where G_s is the assimilation flux at light saturation and α is the apparent quantum efficiency (i.e., the initial slope of the curve).

The total ecosystem respiration (TER) is expected to depend heavily on temperature. This relationship is parameterised using an exponential function (Lloyd and Taylor, 1994):

$$R_t = R_{10}\exp\left\{T_R\left(\frac{1}{56.02} - \frac{1}{T_{s5} - 227.13}\right)\right\} \tag{3}$$

where R_{10} is the respiration flux at 10 °C, the soil temperature measured at a depth of 5 cm (T_{s5}) is used as a reference and T_R is a parameter characterising the respiration sensitivity to the temperature.

The daytime NEE was modelled using Eqs. (1)–(3). The residuals are defined as the difference between the measured and the modelled fluxes. Positive residuals indicate thus that measured fluxes are smaller, in absolute value, than the predicted ones.

2.2.4.2. Nighttime fluxes. At night, CO_2 fluxes come only from respiration thus only the exponential respiration function (3) was used.

When it was necessary to eliminate the impact of the temperature, the nighttime fluxes were normalised (R_{10}) at 10 °C, using:

$$R_{10} = \frac{N_e}{\exp\{T_R((1/56.02) - 1/(T_{s5} - 227.13))\}} \tag{4}$$

The nighttime NEE was modelled using Eq. (3). Here again, the residuals are defined as the difference of the measured fluxes and the modelled fluxes. However, as the fluxes are positive, positive residuals indicate that measured fluxes are larger, in absolute value, than the predicted ones.

3. Results and discussion

3.1. Management, climate and development of the crop

Sugar beet was sown on 30 March 2004 and leaf emergence occurred on 21 April. The crop was harvested on 28 September 2004 and the following crop, winter wheat, was sown on 14 October 2004 using no-tillage practices. Emergence occurred about 1 week later.

The mean annual air temperature was 9.7 °C and the total precipitation was 725 mm. The total annual net radiation and PPFD were 1640 MJ m^{-2} and 7830 mol m^{-2}, respectively. Figures 1a–d shows the course of daily climate between 1 April 2004 and 31 March 2005. The mean daily air temperature (Fig. 1a) rose continuously from mid April to mid August, reaching 24 °C and then decreasing through to December. It remained negative for 25 days in the winter, with the minimum value of −5.4 °C recorded on 28 February 2005.

The mean daily PPFD (Fig. 1b) grew from about 200 μmol m^{-2} s^{-1} in April to 600 μmol m^{-2} s^{-1} in late June, and then fell to below 100 μmol m^{-2} s^{-1} in late December. Climate variability caused large day-to-day variations (up to 415 μmol m^{-2} s^{-1} in early June).

The mean daily saturation deficit (D) (Fig. 1c) remained below 5 kPa for 74% of the time. The longest period with a large saturation deficit was in late July and early August, when the average was 6.6 kPa over 16 days.

Rainfall (Fig. 1d) occurred fairly evenly during the year, with a slight maximum in July and August. The maximum number of consecutive dry days was 11 in mid May. Soil moisture (Fig. 1d) ranged from 0.21 to 0.39 m^3 m^{-3}. After rain, the soil moisture decreased rapidly.

The evolutions of the LAI and of total and leaf dry mass are given in Fig. 1e. The LAI values were between 4 and 5 m^2 m^{-2} and were characterised by large confidence intervals (0.05 level of significance) resulting from the limited number of samples (four to six plants). However, these values agreed well with estimations based on radiation absorption. Moreover, as the leaf DM was found constant (5.2 t DM ha^{-1}) from late July to the harvest we consider that the oscillations in LAI estimates were due to sampling errors and that it was essentially stable and equal to 4 m^2 m^{-2} from late July to the harvest. It is remarkable

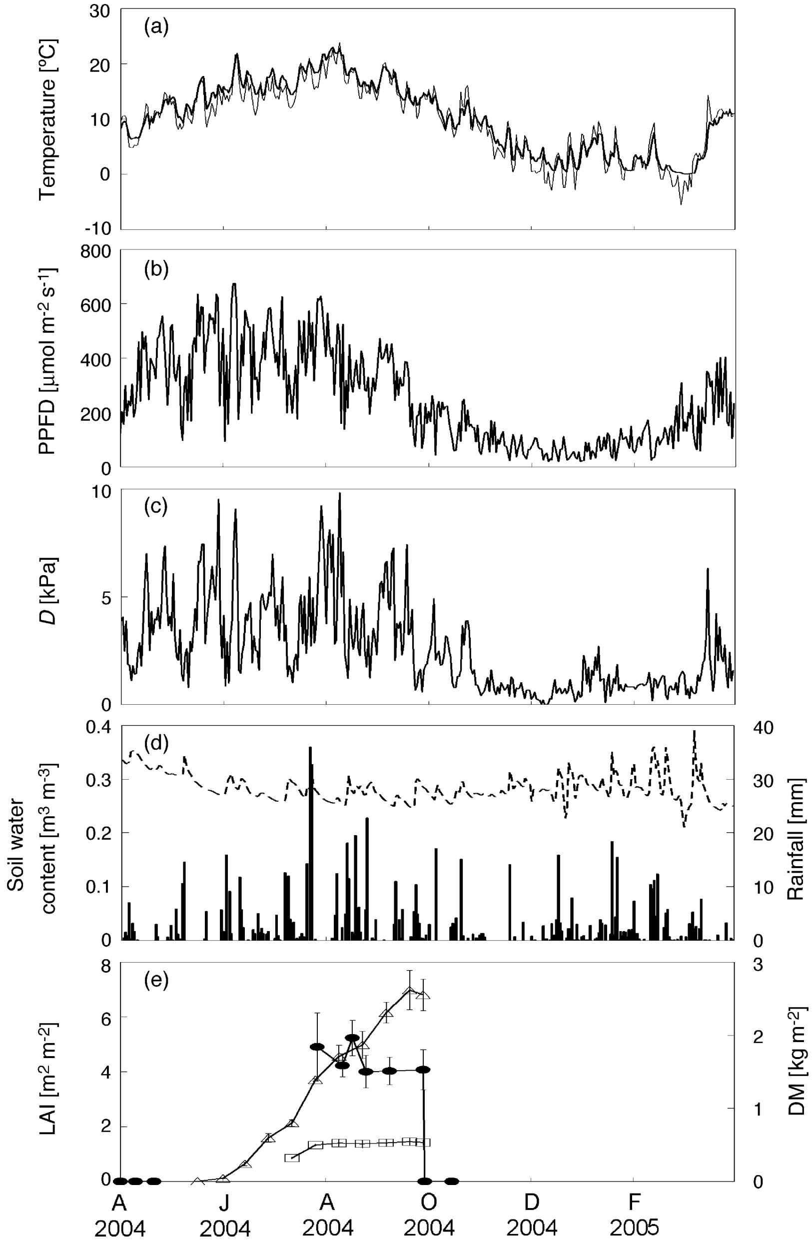

Fig. 1. Mean daily meteorological conditions and crop evolution between 1 April 2004 and 31 March 2005: (a) air (thin line) and soil (bold line) temperature, (b) photosynthetic photon flux density (PPFD), (c) air saturation deficit (*D*), (d) soil water content (dashed line) and rainfall (solid line) and (e) leaf area index (LAI; full circle), total (empty triangle) and leaf (empty rectangle) dry matter (DM) content.

that the LAI was maintained constant in spite of the continuous increase of leaf number, new leaves appearing continuously throughout the season with a rate that exceeded older leaf disappearance. This is because the area of the leaves produced after June were smaller than those of older leaves as already observed by Bouillenne et al. (1940) and Jaggard and Scott (1985). As a consequence, the area proportion of old leaves is growing. Figure 2 presents the leaf mean age evolution from May to the harvest. It increased throughout the period to reach 60 days at the harvest.

3.2. Determination of the u_* thresholds

The u_* thresholds were estimated separately during two periods: Period 1 extended from April to May 2004 and from November 2004 to January 2005 and corresponded to the times with bare soil or no carbon

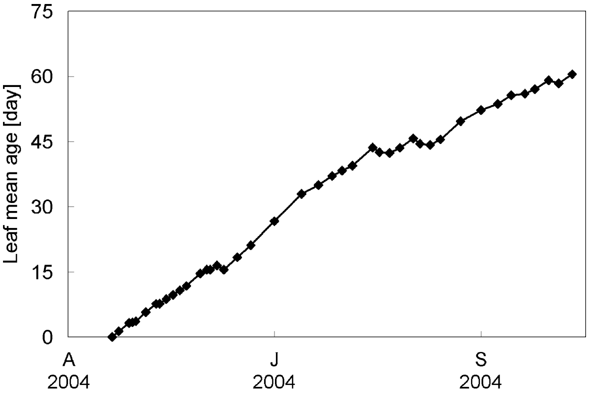

Fig. 2. Evolution of the mean age of the sugar beet leaves between May and September 2004.

sequestration (i.e., positive mean daily CO_2 fluxes). Period 2 extended from June to September 2004 and corresponded to the times when there was vegetation (i.e., negative mean daily CO_2 fluxes). October 2004 was not included in either period because it was characterised by a larger respiration due to harvest residues decomposition. Indeed, at the harvest time, leaves and beet crowns were cut by the defoliator and left on the ground. Their decomposition produced an additional CO_2 emission. As the number of data for this period was insufficient to determine specific u_* thresholds with enough confidence, we used the threshold of Period 2 for this time. Figure 3 presents the response of the normalised nighttime fluxes to u_* for each period. Each point on the graphs represents an average of at least 100 measurements.

The Gu et al. (2005) algorithm modified as described above was applied several times to these two datasets, varying the MS size (n) from 31 to one-fifteenth of the total sample size. The evolution of the threshold with n is given in Figs. 4a and b. It appears that, contrary to what Gu et al. (2005) suggested, the threshold values are not completely independent of the MS size: during Period 1, they are stable ($u_{*L} \approx 0.05$ m s^{-1} and $u_{*H} \approx 0.31$ m s^{-1}) for n between 41 and 111, but below $n = 41$, u_{*H} rose to 0.4 m s^{-1} and above $n = 111$, u_{*L} rose to 0.1 m s^{-1}. For Period 2, u_{*L} increased slightly with n (from 0.05 m s^{-1}, at $n = 30$ to 0.06 m s^{-1}, at $n = 101$), but u_{*H} was more sensitive (decreased from 0.43 m s^{-1}, at $n = 31$ to 0.31 m s^{-1}, at $n = 101$).

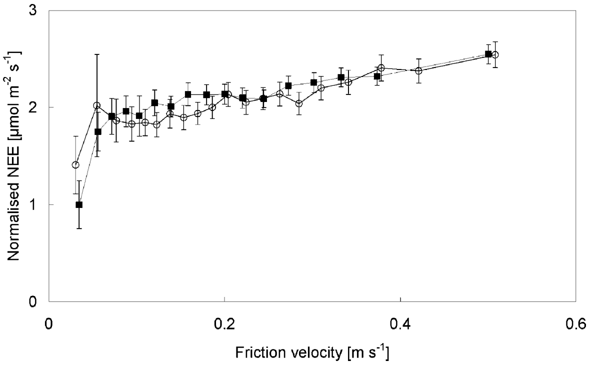

Fig. 3. Evolution of the normalised nighttime net ecosystem exchange (NEE) in relation to the friction velocity for Period 1 (empty circles) and Period 2 (full squares). Each point on the graph is the mean of 100 data except for the last point of each series which corresponds to 124 points.

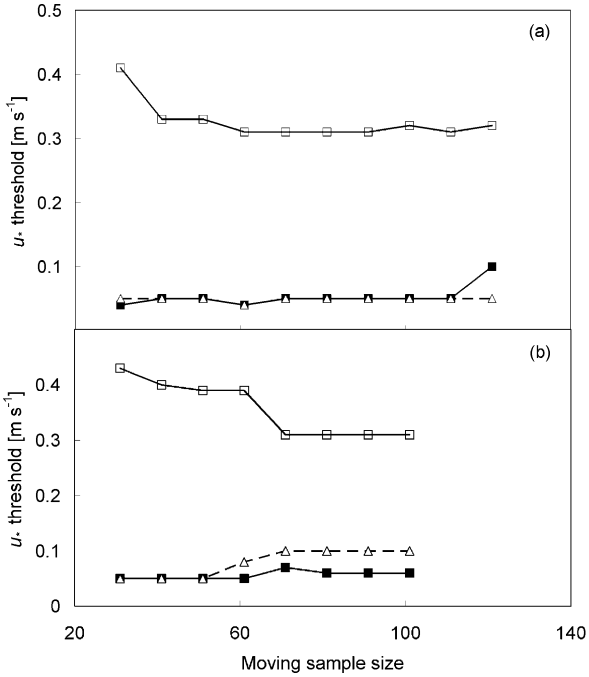

Fig. 4. Evolution of the friction velocity (u_*) threshold with the moving sample size for: (a) Period 1 and (b) Period 2. The modified moving point test algorithm was applied in the search for a higher (empty black square) and a lower (full black square) threshold and by bypassing the higher threshold research (empty triangle and dashed line).

In most of the studies, only a lower threshold was determined by visual examination. In order to analyse the impact of the introduction of a higher threshold, we also applied the Gu algorithm bypassing the u_{*H} research. The evolutions of u_{*L} with n are also shown in Figs. 4a and b. For Period 1, no difference with the preceding u_{*L} value was found, except for $n = 121$. For Period 2, above $n = 51$, there was a significant difference with the preceding value, the new lower threshold rising to 0.1 m s^{-1}. This shows that different lower thresholds can be obtained whether the higher threshold research is bypassed or not.

Nevertheless, the impact of these choices on the global correction remains fairly limited. To demonstrate this, we

Table 1
Values of the moving sample size (n), the mean normalised net ecosystem exchange (NEE_m) and the determination coefficient of the regression NEE–temperature (R^2) for different values of the lower ($u_{*\text{L}}$) and higher ($u_{*\text{H}}$) friction velocity thresholds of Periods 1 and 2

$u_{*\text{L}}$ (m s^{-1})	$u_{*\text{H}}$ (m s^{-1})	n	NEE_m (μmol m^{-2} s^{-1})	R^2
Period 1				
0.04	0.41	31	1.90	0.30
0.05	0.33	41–51	1.90	0.30
0.04	0.31	61	1.88	0.30
0.05	0.31	71–91 + 101	1.89	0.30
0.05	0.32	101	1.90	0.30
0.10	0.32	121	1.90	0.62
0.04	999	61	1.90	0.30
0.05	999	31–51 + 71–121	1.92	0.30
Period 2				
0.05	0.43	31	2.23	0.18
0.05	0.40	41	2.22	0.19
0.05	0.39	51–61	2.22	0.19
0.07	0.31	71	2.22	0.24
0.06	0.31	81–101	2.20	0.21
0.05	999	31–51	2.25	0.17
0.08	999	61	2.30	0.20
0.10	999	81–101	2.32	0.26

$u_{*\text{H}}$ "999" values mean that no higher thresholds values were considered.

computed the mean normalised flux values obtained using the different thresholds. The results are given in Table 1. The maximum difference between the different situations was always lower than 2.1% for Period 1 (from 1.88 to 1.92 μmol m^{-2} s^{-1}) and less than 5.2% for Period 2 (from 2.20 to 2.32 μmol m^{-2} s^{-1}).

We finally chose the thresholds that allowed the best regression between NEE and temperature for each period. To this end, we compared the R^2 of these relationships (see Table 1). For Period 1, the best regression ($R^2 = 0.62$) was obtained for $n = 121$, which is the maximum size recommended by Gu et al. (2005). The corresponding thresholds were $u_{*\text{L}} = 0.1$ m s^{-1} and $u_{*\text{H}} = 0.32$ m s^{-1}. For Period 2, the best regression ($R^2 = 0.26$) was obtained for n being more than 81 and a single threshold. The corresponding threshold value was 0.1 m s^{-1}, as for Period 1.

These values are similar to those observed over grasslands and short crops. Anthoni et al. (2003) determined, by visual examination, a lower threshold value of 0.1 m s^{-1} over a wheat crop at Gebesee. Gu et al. (2005), using the MTP algorithm, found a lower threshold varying from 0.1 to 0.16 m s^{-1} over a tall grass prairie in Oklahoma, from 0.07 to 0.11 m s^{-1} over an oak-grass savanna in northern California and from 0.00 to 0.02 m s^{-1} over an annual grassland in northern California. The higher threshold obtained using the same algorithm on these sites ranged from 0.4 to 0.59 m s^{-1} for the first, from 0.21 to 0.33 m s^{-1} for the second and from 0.09 to 0.27 m s^{-1} for the third.

The percentages of remaining data were 52 and 76% of the total number of nighttime data for Periods 1 and 2, respectively. These percentages were not smaller than those obtained above forests but they generally corresponded to lower thresholds. This is probably because crops present lower roughnesses than forests and are therefore characterised by lower friction velocity values.

In the following sections, nighttime fluxes corresponding to $u_* < u_{*\text{L}}$ are excluded. Values corresponding to $u_* > u_{*\text{H}}$ are excluded from the analyses of flux response to climatic and non-climatic variables but, as these fluxes are not considered to be erroneous, they are included in the summation procedure for computing the annual NEE.

3.3. Response of the turbulent fluxes to the climate

3.3.1. Nighttime fluxes

The evolution of nighttime NEE with temperature is presented in Fig. 5 for Periods 1 and 2 and October. The response of respiration to temperature during Periods 1 and 2 was described by an exponential parametrisation (3). The regression parameters were: $R_{10} = 2.14$ μmol m^{-2} s^{-1} and $T_\text{R} = 305.2$ K, and the determination coefficient was 0.74. The two periods were characterised by different temperature ranges, most of Period 1 corresponding to temperatures lower than 13 °C and most of Period 2 corresponding to temperatures higher than 13 °C. Consequently, the observed response to temperature can also reflect an impact of crop development on the night flux. In October, the month following the harvest, significantly greater fluxes were observed

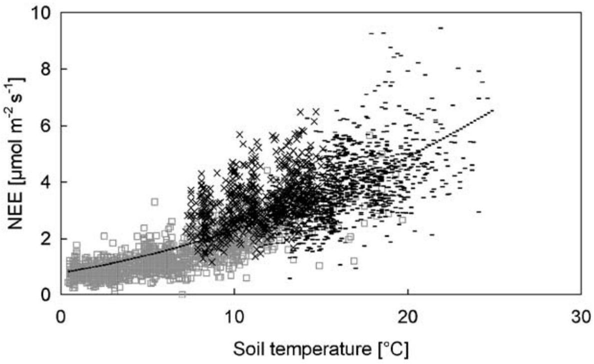

Fig. 5. Response of the nighttime net ecosystem exchange (NEE) to soil temperature for Period 1 (empty grey square), Period 2 (black dash) and October (black cross). The adjusted exponential regression is represented by the line.

than during the other periods. This is due to an additional CO_2 emission resulting from the crop residues left on the ground at harvest time. This impact is quantified in Section 3.5.

The respiration at 10 °C was of the same order of magnitude as those reported in the literature even though the regression was often adjusted for the growing period only. Anthoni et al. (2004) observed an R_{10} of 3.9 μmol m^{-2} s^{-1} for winter wheat during May and June and an R_{10} of 2.5 μmol m^{-2} s^{-1} for potato during June and July. Barcza et al. (2003) reported 3.5 μmol m^{-2} s^{-1} for a semi-natural grass field in western Hungary for the growing period (from March to October). The respiration at 10 °C estimated above the maize crop during full canopy development ranged from 2.3 to 2.7 μmol m^{-2} s^{-1} (Pattey et al., 2001, 2002) and during the second part of the growing season (stage V14–R6) Suyker et al. (2004) observed an R_{10} of 1.3 μmol m^{-2} s^{-1}.

In order to analyse the flux response to soil water content (SWC), in Fig. 6 we plotted the evolution of the residuals of the NEE–temperature parameterisation with this variable. A small but significant decrease of the residuals was observed for SWC higher than 0.29 m^3 m^{-3}. This effect could be explained by a lack of oxygen and a CO_2 accumulation in the soil under high humidity as a result of soil pore spaces filling with water (Glinski and Stepniewski, 1985; Freijer and Leffelaar, 1996; Davidson et al., 2000). About 21% of the period was affected by such a high SWC. As no significant drought occurred during the period under investigation, we cannot draw conclusions about the respiration response to low SWC.

3.3.2. *Daytime fluxes*

The response of daytime fluxes to PPFD evolved with crop development (Fig. 7). During the last 10 days of May, a clear response was apparent. Greater sensitivity was observed in early July and September. In order to reduce the impact of crop development on this response, only measurements made during the stable LAI period (August and September) were selected. Its evolution with PPFD is presented in Fig. 8a. The NEE was modelled using Eqs. (1)–(3) and the parameters were: $\alpha = 0.0557$ μmol μmol^{-1}, $G_s = 27.8$ μmol m^{-2} s^{-1} and $R_d = 3.38$ μmol m^{-2} s^{-1}. The determination coefficient was 0.86. The apparent quantum efficiency of the sugar beet crop was slightly lower than that observed by Anthoni et al. (2004) for winter wheat and potato (0.063 and 0.062 μmol μmol^{-1}, respectively) and by Ruimy et al. (1995) for C_3 crops (0.062 μmol μmol^{-1}). However, these parameters are derived from a hyperbolic regression known to give 20% higher estimations of α than an exponential equation (Aubinet et al., 2001).

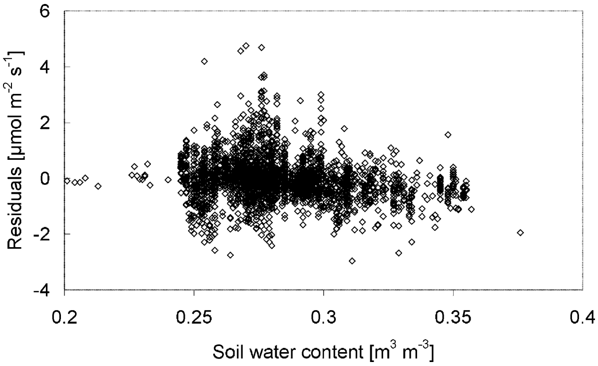

Fig. 6. Evolution of the residuals of the nighttime NEE to temperature response with soil water content for Periods 1 and 2.

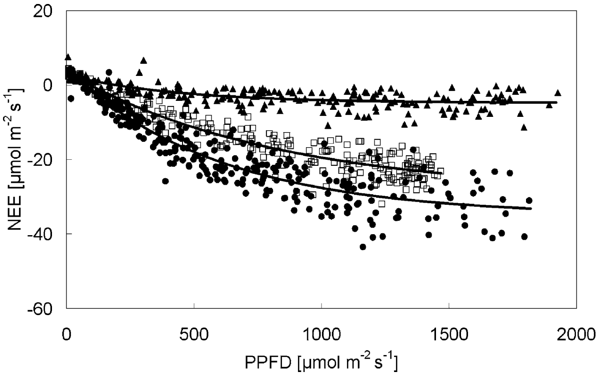

Fig. 7. Response of the daytime net ecosystem exchange (NEE) to photosynthetically active radiation (PPFD) during the last 10 days of May (full triangles), the first 10 days of July (full circles) and the first 10 days of September (empty square) and the corresponding exponential regression.

In order to analyse the possible impact of other climatic variables on the net flux, we present in Fig. 8b–e the evolution of the residuals of the NEE parameterisation (Eqs. (1)–(3)) to air saturation deficit, air temperature, soil water content and diffuse radiation fraction.

The crop did not suffer severe saturation deficit (*D*) at any time, as the maximum observed value was 2.3 kPa in early August and, except for a few half-hours, *D* never exceeded 2.0 kPa (Fig. 1c). However, a small influence of this variable on the flux was observed as the residuals increased with *D* above 1.1 kPa (Fig. 8b). However, the impact of *D* was limited as it corresponded with only 15% of the data. Similar impacts of *D* on NEE were observed by Hirasawa and Hsiao (1999) in a maize crop when $D > 2.0$ kPa and in a semi-natural grass field when $D > 1.5$ kPa (Barcza et al., 2003). In contrast, no clear impact was observed by Suyker et al.

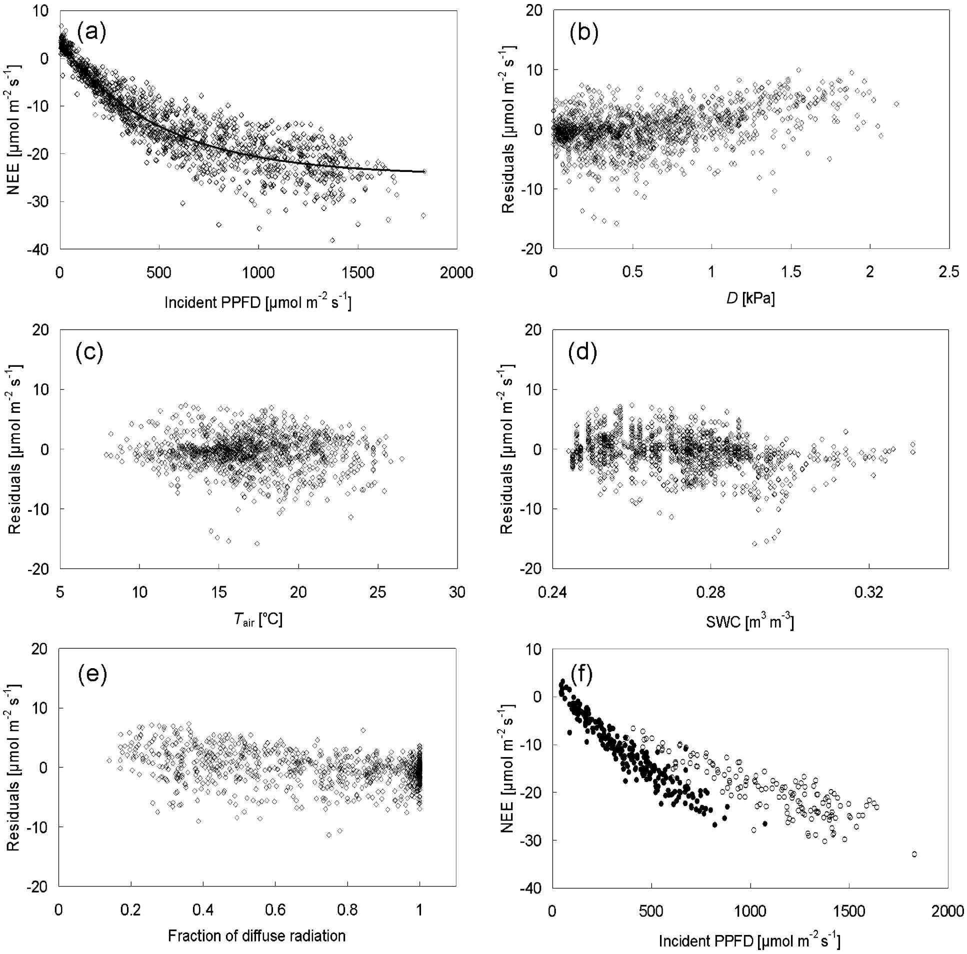

Fig. 8. (a) Response of daytime net ecosystem exchange (NEE) for August and September to incident photosynthetic photon flux density PPFD and evolution of its residuals with (b) saturation deficit (D), (c) air temperature (T_{air}), (d) soil water content (SWC), (e) fraction of diffuse radiation and (f) response of the NEE to incident PPFD during clear (fraction of diffuse radiation: 0.2–0.3) (empty circle) and cloudy (fraction of diffuse radiation: 0.8–0.9) (full circle) periods.

(2004) on an irrigated maize crop. The fluxes corresponding to $D > 1.1$ kPa were removed from the dataset for further analysis in order to avoid any bias regarding the impact of the other climatic variables.

The evolutions of the residuals with air temperature and soil water content are presented in Fig. 8c and d. No dependence of the fluxes on the air temperature appeared. A similar result was obtained with soil temperature (results not shown). However, a dependence of the residuals on soil water content was observed: above a SWC of 0.29 $\mathrm{m^3\,m^{-3}}$, negative residuals were observed, suggesting an increase of the fluxes (in absolute value) at these values. This effect could be due to the respiration decrease, as discussed above. However, only 14% of the assimilation fluxes were obtained under these conditions. These fluxes were removed from the dataset in subsequent analyses.

A clear dependence of the residuals on the diffuse radiation fraction is shown in Fig. 8e. This is confirmed by Fig. 8f which compares the responses of the net assimilation to the incident PPFD during clear (fraction of diffuse radiation = 0.2–0.3) and cloudy periods (fraction of diffuse radiation = 0.8–0.9). The quantum efficiency of the crop is greater during cloudy periods than during clear periods and, at the same incident PPFD, NEE values are greater during cloudy periods than during clear periods. For example, at PPFD = 700 ± 50 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$, the NEE was about -20.2 ± 1.52 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ during cloudy periods but only -13.5 ± 1.37 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ during clear periods.

Gu et al. (2002) discussed the advantages of diffuse PPFD in carbon uptake in a variety of ecosystems (grasslands, croplands and forests). The same observation was made in croplands by Suyker et al. (2004) and

Anthoni et al. (2004). The reason for a greater assimilation during cloudy periods could be related to the impact of other climatic variables such as vapour pressure deficit or leaf or soil temperature or to different degrees of efficiency in canopy light interception. Freedman et al. (1998, 2001) suggested that the vapour pressure deficit could be lower during cloudy periods. As the leaf temperature cannot be measured easily, this variable is unknown here. However, by assuming that leaf temperature is close to air temperature, the vapour pressure deficit can be approximated by the air saturation deficit. It is clear that, under our conditions, the difference between NEE and incident radiation responses during clear and cloudy conditions could not be due to an impact of saturation deficit because data with $D > 1.1$ kPa were removed from the set presented in Fig. 8e. Beside this, Baldocchi (1997) suggested that smaller leaf or soil temperatures may reduce respiration and therefore increase NEE during cloudy periods. As no relationship between NEE and air or soil temperature was observed, this explanation is probably not sound either in this case. Consequently, the main reason for the differences between canopy net assimilation during direct and diffuse PPFD seems to be the differences between diffuse and direct radiative transfer regimes in the plant canopy, coupled with the non-linearity of the photosynthesis, as suggested by Gu et al. (2002).

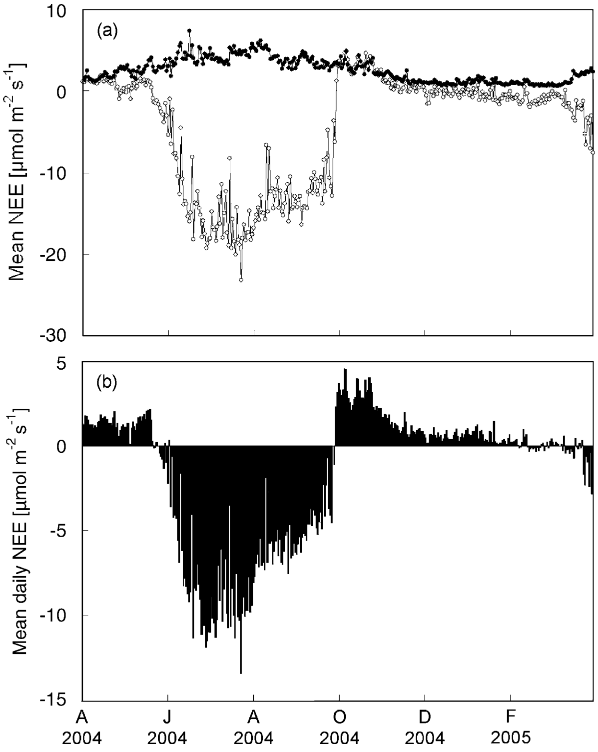

Fig. 9. Evolution from April 2004 to March 2005 of: (a) the mean daytime (empty circle) and nighttime (full circle) net ecosystem exchange (NEE) and (b) the mean daily NEE.

3.4. Evolution of the CO_2 fluxes

3.4.1. Seasonal pattern of the fluxes

The evolution with time of mean nighttime and daytime NEE values is presented in Fig. 9a, and the evolution of the mean daily flux in Fig. 9b. On 1 April, 2 days after sowing, the mean nighttime and daytime fluxes were both 1.5 µmol m^{-2} s^{-1}, confirming that there was no assimilation at the site at this time. The daily flux was, of course, similar during this period. From early May to end of June, the night flux increased continuously, reaching about 4–5 µmol m^{-2} s^{-1}, while the day flux reverted and increased rapidly by negative value, due to leaf development and assimilation onset. It reached about −19 µmol m^{-2} s^{-1}. As a result, the daily fluxes became negative in late May, the crop becoming a carbon sink. In July, daytime fluxes remained stable although the LAI was still increasing, as suggested by the evolution of the plant dry weight during this period (Fig. 1e). From mid July to mid August, the night flux reached 5–6 µmol m^{-2} s^{-1}. From this period until the harvest, it was maintained at 3–4 µmol m^{-2} s^{-1}. The day flux began to decrease regularly in absolute value from early August. The net flux evolved similarly and rose to about −4 µmol m^{-2} s^{-1} just before the harvest. It is noteworthy that throughout this period the LAI remained constant (Fig. 1e). After the harvest, the crop became a carbon source. In the month following the harvest, the emitted daily flux was about twice its spring value because of residue decomposition. After the end of October the net flux fell to about 1 µmol m^{-2} s^{-1}, due to a decrease of the residue decomposition rate as well as to the development of the new crop; winter wheat was sown on 14 October and, although the net flux remained positive, the difference observed between the day and night fluxes during this period suggests that the crop assimilation was already significant.

The maximum observed daily flux was about −11 µmol m^{-2} s^{-1} in early July 2004. This value is of the same order of magnitude as that noted earlier for other C3 crops: Soegaard et al. (2003) observed about −13.5 µmol m^{-2} s^{-1} in winter wheat and −10 µmol m^{-2} s^{-1} in winter barley and spring barley in Denmark, Baldocchi (1994) −12.8 µmol m^{-2} s^{-1} in a wheat crop in Oregon, USA, Anthoni et al. (2003) about −10 to −12 µmol m^{-2} s^{-1} in winter barley in Germany and Hollinger et al. (2005) −8.6 µmol m^{-2} s^{-1} in soybean in Illinois. The maximum daily NEE exchanged by crops of maize, a C_4 plant, was generally greater: Hollinger et al. (2005) observed $-18.5\ \mathrm{g\,C\,m^{-2}\,s^{-1}}$ in IL, USA and Pattey et al. (2001) $-20.5\ \mathrm{g\,C\,m^{-2}\,s^{-1}}$ near Ottawa, Canada.

3.4.2. Crop development influence

In order to investigate the impact of crop development on the fluxes, representative parameters were extracted from the preceding datasets. Assimilation at light saturation, G_s, was used to characterise the crop photosynthetic capacity evolution, while respiration normalised at 10 °C was used to characterise the canopy and soil respiration. These parameters were estimated every 10 days from leaf emergence to the harvest. Data were grouped by 10-day periods, on each period, the NEE response to PPFD was parameterised using Eqs. (1) and (2) from which the parameters R_t and G_s were deduced. Below, we will rename R_t in R_d in order to distinguish respiration estimates based on daytime (R_d) data from those based on nighttime (R_n) data. R_{d10} was then deduced from R_d by normalisation, using relation (4). Another independent estimate of the respiration was obtained by computing the averaged night fluxes (R_n) for the same 10-day periods. R_{n10} was obtained from R_n in the same way as R_{d10}.

Initially, the coherence between the respiration estimations was assessed. To this end, a comparison between R_d and R_n is given in Fig. 10a. The agreement is good, with $R^2 = 0.84$ and a regression slope of 1.00. Such an agreement is remarkable as the two sets of data are independent, and the two estimation methods were subjected to big uncertainties: on one hand, the NEE–PPFD regression intercept is generally affected by a large confidence interval; on the other hand, night data are expected to be prone to large errors due notably to the occurrence of non-turbulent processes. In addition, comparisons between day and night fluxes are sometimes difficult to perform above heterogeneous terrains because the footprint of the two fluxes does not coincide. The good agreement between these two estimations suggests that all these errors were quite limited at our site: the data selection based on night data (see Section 3.3.1) was well-suited to our site, the uncertainty on the PPFD curve intercept was not too large (confidence interval at 0.05: 2.85–3.90 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$) and the site was homogeneous enough.

In order to eliminate any temperature dependence of the respiration, R_{d10} and R_{n10}, estimations were compared in Fig. 10b. The agreement is, of course, weaker but still fairly good ($R^2 = 0.41$). This suggests that the evolution of respiration during the growing season is not only due to a response to the temperature but also reflects a seasonal evolution. Nevertheless, the good agreement between the two respiration estimations confirms the soundness of these parameters. As the uncertainty is larger for R_{d10} than for R_{n10}, in the following sections only the evolution of the latter is discussed.

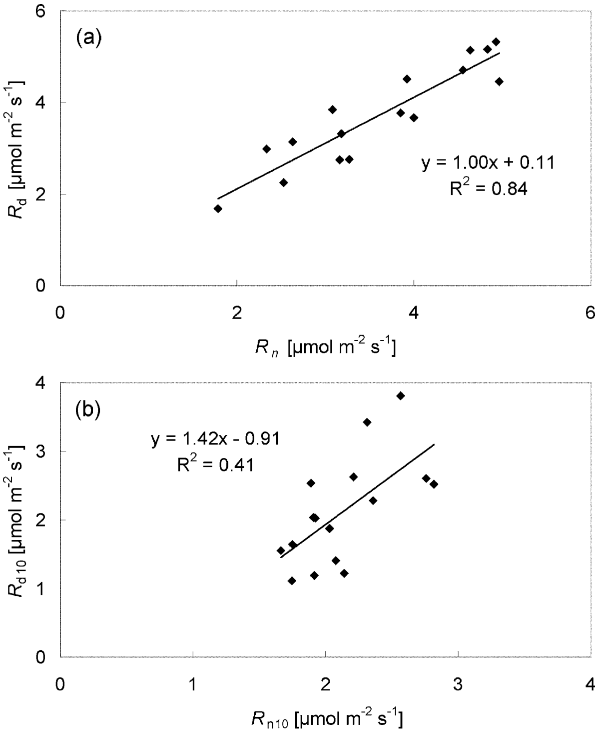

Fig. 10. Comparison of daytime (R_d) and nighttime (R_n) estimates of ecosystem respiration. (a) Ten day average and (b) normalised respiration at 10 °C.

The evolution with time of G_s and R_{n10} are presented in Figs. 11a and b, respectively. During the first 40 days, very low G_s values (lesser than 7 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$) were obtained, due to the limited development of the crop. However, the assimilation was already active, as shown by the well-developed crop NEE response to PPFD in Fig. 7. The larger error bar in the second G_s estimation results from very weak incident radiation during this period. From the end of May, the leaf development provoked a rapid G_s increase: in 20 days it rose from less than 7 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ to a maximum value of 42 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ in mid June. Between mid June and mid July, G_s remained close to its maximum value and the maximum daily fluxes were observed during this period. It is noteworthy that the leaf development was not still completed at this time, the LAI value not yet being maximal. Visual inspection of the field confirmed, however, that the canopy was closed in late June. From late July to the harvest, G_s decreased, falling from about

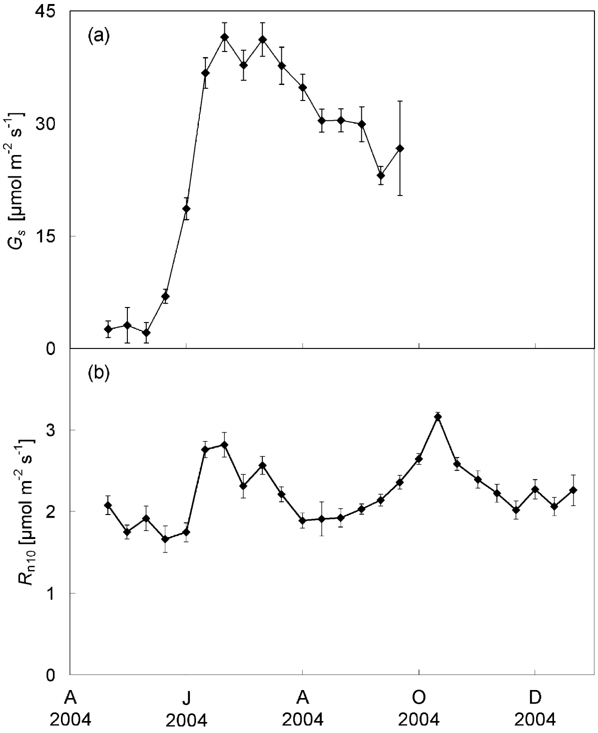

Fig. 11. Evolution of: (a) the assimilation flux at light saturation (G_s) and (b) the normalised nighttime respiration R_{n10} from leaf emergence to December 2004.

38 to 23 µmol m^{-2} s^{-1}. Throughout this period, the LAI remained constant and new leaves were constantly appearing, replacing the old leaves that became senescent. The cause of the G_s decrease is not clear: it is unlikely to be due to meteorological conditions as the parameter is independent of incident PPFD and the fluxes were found to be hardly sensitive to other meteorological variables. It seems therefore to point out a decline in canopy assimilation capacity. However, no diseases had been observed in the canopy and the LAI was constant throughout the period. On the other hand, it could be due to leaf ageing with time (Fig. 2). Complementary measurements of the leaves assimilation performed with a portable photosynthesis system in August and September (results not shown) showed indeed that older leaves were characterised by a lower photosynthetic capacity even if no clear sign of senescence did appear.

At the beginning of the season, the R_{n10} evolution followed that of G_s quite closely: from emergence to early June it was about 1.8–2.1 µmol m^{-2} s^{-1} and then it rose to 2.3–2.8 µmol m^{-2} s^{-1}. The higher values were observed between mid June and mid July, the period during which G_s was also greater. At the beginning of August, R_{n10} fell to its spring value but it began to increase again during August and September, reaching its highest value in mid October, 2 weeks after the harvest. The parallelism between the G_s and R_{n10} evolutions in June and July suggest that the first respiration peak could be triggered by crop development and would correspond mainly to an autotrophic contribution. Winner (1981) reported that the beet tap root grew only after the 12-leaf stage, with only fine roots developing before that stage. As this stage was reached in early June in our case, this suggests that the first respiration peak appeared during the early development of the tap root. The second peak that began in August and culminated in mid October is probably due to leaf and harvest residues decomposition: between mid June and the harvest, each plant lost about 10 leaves at regular intervals and, at harvest, the leaves and beet crowns decomposition produced an additional CO_2. In total, these represent 5.8 kg m^{-2} of fresh matter. The additional respiration was maintained until mid October. Its impact on the total carbon sequestration is estimated below.

3.5. Annual sequestration

The total sequestration by the crop, as well as its sensitivity to the u_* threshold value and to the quality criterion, were assessed. The impact of the crop residues decomposition was then estimated.

The annual net ecosystem exchange obtained by using the procedure described above was 0.61 ± 0.11 kg C m^{-2}. The uncertainty is computed as the total error resulting from data gap filling using the method recommended by Aubinet et al. (2002). In order to assess its sensitivity on the u_* thresholds, we computed it several times using different thresholds. We conducted three tests, each time varying one threshold while maintaining the others. In the first test, we varied u_{*L} for the two periods and in the two others, we varied u_{*H} during the first and the second period, respectively. For each test, a new NEE to temperature response was estimated and used for data gap filling. Only the data corresponding to $u_* < u_{*L}$ were replaced by the parameterisation. Figure 12 presents the annual NEE evolution versus the varying threshold values for the three tests. As expected, the sequestration was more sensitive to the lower threshold value than to the higher one: it fell in absolute value from 0.62 to 0.59 kg C m^{-2} when the lower thresholds increased from 0 to 0.2 m s^{-1}. This is, however, very limited as it corresponds to 5% of the total sequestration. The sensitivity to the higher threshold was even smaller: the annual NEE varied from less than 3% when u_{*H} varied between 0.2 and 0.5 m s^{-1} during Period 2 and was practically insensitive to u_{*H} variations during

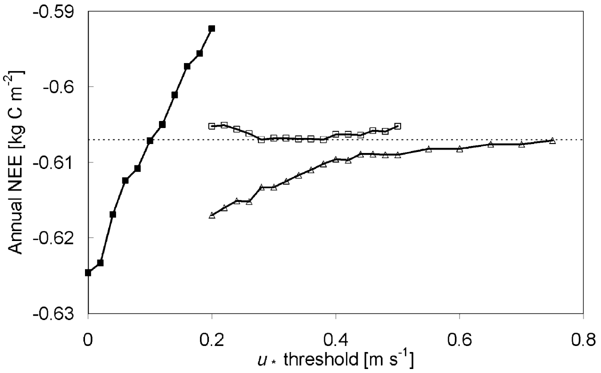

Fig. 12. Evolution of the annual net ecosystem exchange (NEE) with the friction velocity (u_*) threshold value. A black full square corresponds to a variation of the lower u_* threshold of both periods while other thresholds remain unchanged, an empty square corresponds to a variation of the higher u_* threshold of Period 1 while other thresholds remain unchanged and an empty triangle corresponds to a variation of the higher u_* threshold of Period 2 while other thresholds remain unchanged. Dashed line represents the annual NEE corresponding to a lower u_* threshold of 0.1 m s^{-1} for both periods and an upper u_* threshold of 0.32 m s^{-1} for Period 1.

Period 1. The small impact of the threshold values on crop sequestration suggested that the problem of night flux underestimation was very limited at our site. This result is not totally surprising because the problem of night flux underestimation is expected to be less important above short crops than over tall forests. However, this is not always the case: studying a winter wheat crop, Anthoni et al. (2003) observed a decrease in the net annual sequestration from about −0.32 kg C m^{-2} when no threshold was applied to about −0.11 kg C m^{-2} when a 0.3 m s^{-1} threshold was used.

The impact of the data selection in relation to the quality test was also examined. The test led to the removal of 25% of day data and 27% of night data. However, its impact on the annual NEE was limited: the introduction in the annual sequestration computation of data that did not meet quality criteria led to a decrease of 1% in the result. All these results show that the quality of the measurements at our site was high and allowed a robust estimation of the annual sequestration.

3.5.1. Residues decomposition impact

It was shown earlier that the period between 30 September and 25 October was characterised by a larger CO_2 emission due to the decomposition of crop residues left on the ground after the harvest. In order to estimate the impact of these residues, we compared the flux measured during this period with an estimation based on the NEE–temperature parameterisation adjusted for the data of Periods 1 and 2. The results were 0.09 and 0.07 kg C m^{-2} for the measurements and the simulation, respectively. This suggests an impact of the residues decomposition of about 0.02 kg C m^{-2}, representing 3.3% of the total sequestration.

4. Conclusions

Eddy covariance CO_2 fluxes were measured between April 2004 and March 2005 for sugar beet in an agricultural ecosystem in Lonzée, Belgium, in which the crop rotation was 50% cereal and 50% sugar beet and potato. Additional measurements were made of LAI and biomass net primary production.

The response of the nighttime fluxes to turbulence and climatic variables was studied. The u_* thresholds were determined by applying the modified MPT algorithm (Gu et al., 2005). The lower u_* threshold was found to be 0.1 m s^{-1}. The sensitivity of the net ecosystem exchange to lower u_* threshold was found to be less than 5% when varying it from 0 to 0.2 m s^{-1} suggesting that the impact of the night flux error on NEE estimations was limited at the site. However, this result could be crop-dependent and should be re-evaluated in the following years.

Respiration was found to clearly increase with temperature, as expected, and to decrease with increasing soil water content above 0.29 m^3 m^{-3}. This could be explained by a lessening of oxygen availability due to a soil porosity reduction at high soil water contents.

The daytime NEE was found to depend on radiation (PPFD and diffuse to global ratio) and, in a lesser extent, on air saturation deficit and soil water content. The impact of the diffuse to global radiation ratio was attributed to the difference between the light transfer regimes. A decrease of the NEE was observed at saturation deficit values greater than 1.1 kPa. It is probably due to partial stomatal closure. Furthermore, an increase of the NEE was observed when soil water content was larger than 0.29 m^3 m^{-3}. This effect could be due to the respiration decrease observed at high soil water content.

The evolution of assimilation and respiration fluxes was studied. Assimilation was clearly apparent 1 month after leaf emergence and reached its maximum in late June before the canopy was fully developed. From late July onwards, the assimilation fluxes decreased. This decrease was not solely due to a radiation decrease but also to a canopy assimilation capacity reduction probably resulting from the increase of aged leaf relative area. The following crop, winter wheat, was sown in mid October and from February onwards a net assimilation was observed.

Respiration was estimated in two ways: by computing the intercept of the NEE–PPFD response and by averaging nighttime measurements. A good coherence was found between the two estimations, even after normalisation, suggesting that the evolution reflects not only a response to temperature but also a seasonal evolution. Two peaks were observed: the first in July corresponding to the maximum canopy assimilation capacity, which could reflect an autotrophic contribution, and the second from September to October resulting from leaf senescence and harvest residues decomposition.

Annual sequestration was estimated by a summation of the half-hourly fluxes and filling the missing measurements. It was found to be -0.61 ± 0.11 kg C m^{-2} which is unexpectedly high for a crop. It should be noticed that the year of measurement encompassed the whole sugar beet growing season and the first months of the winter wheat cultivation. The contribution of the harvest residues to the annual NEE was estimated to be 3.3%.

These results are accurate under these experimental conditions. However, it must be remembered that carbon sequestration of sugar beet crops depends on many other factors such as variety, sowing date, crop establishments, harvesting date, controls of weeds, disease, pests, soil types, irrigation and fertilizer application rates.

Acknowledgements

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Article 3

Evaluation of different approaches to deduce TER and GPP from eddy covariance measurements above crop

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Abstract

The total ecosystem respiration (TER) and gross primary productivity (GPP) were obtained from the eddy covariance measurements. Two approaches, based on the daytime or night-time measurements, were compared for three successive crops between emergence and harvest (or chemical haulm) at the Lonzée site in Belgium. For both approaches, the differences between assessments obtained using several procedures were evaluated and uncertainties resulting from procedure choices were evaluated on both cumulated and daily values. The choice of the reference temperature produced the most important difference (5–11%) for the both approaches. The differences were systematic but inversed for the day approach compared with the night approach. In both cases, the soil temperature was shown to be a better reference than air temperature. The second cause of systematic differences between assessments was the choice of the relationship between net ecosystem exchange (NEE) and photosynthetic active radiation for the daytime approach (2–5% for the 3-parameter relationships) and the choice of the u* threshold value (0–5%) for the night-time approach. The window size choice produced selective systematic differences that were therefore quite limited on an annual scale (1–11% for both approaches), but could become more important (up to 30%) on a daily scale. The narrow window procedure was able to reproduce particular events such as intense crop development, senescence or water stress. It is therefore recommended for crop analysis. Finally, the error on the regression caused a random error of 1–4 %. The difference between the two approaches was lower than 3–8% on total TER and 1–3 % on total GPP, which is acceptable, taking into account that these estimates were obtained from independent measurements.

Keywords: eddy covariance, TER, GPP, partitioning, uncertainties

1. **Introduction**

The continuous rise of CO_2 atmospheric concentration resulting from anthropogenic activities and the anticipated adverse consequences on the global climate system has led to the need for a better understanding of the global carbon cycle. Since the mid-1990s, the particular interest in the ecosystem contribution to the global carbon cycle has led to net carbon exchange measurements being made worldwide (Baldocchi et al., 2001; Baldocchi, 2003; Valentini, 2003). The measured CO_2 net ecosystem exchange (NEE) is the small difference between assimilated carbon by photosynthesis (gross primary productivity: GPP) and emitted carbon by respiration (total ecosystem respiration: TER). These two components are commonly inferred from the NEE measurements using empirical relationships with climate (e.g., Hollinger et al., 1994; Lee et al., 1999; Falge et al., 2002; Gilmanov et al., 2003; Xu and Baldocchi, 2004; Reichstein et al., 2005; Suyker et al., 2005). Alternatively, neural networks might be used which do not presuppose any prior knowledge of, or assumption about, a relationship between fluxes and climate (Papale and Valentini, 2003; Hagen et al., 2006). In addition to these empirical methods, physiologically based models are also used to partition NEE (e.g., Williams et al., 1996; dePury and Farquhar, 1997; Wang and Leuning, 1998; Owen et al. 2006). In all these methods, TER is assessed from NEE measurements. Apart from this, chamber methods were used (e.g., Norman et al., 1992; Dugas et al., 1997; Lavigne et al., 1997; law et al., 1999; Granier et al., 2000; Dore et al., 2003; Zamolodchikov et al., 2003; Boldstad et al., 2004; Wohlfahrt et al., 2005a) to conduct independent estimations of the ecosystem respiration. Some studies have reported fairly good correspondence (e.g., Granier et al., 2000), whereas others have found that eddy covariance overlooks up to 50% of the respiration measured by chambers (Law et al., 1999; Bolstad et al., 2004).

In this paper, we compared two approaches to obtain TER and GPP from NEE measurements. One approach (the 'night-time approach, TER_N') consisted of deducing TER from night flux measurements; the second approach (as the 'daytime approach, TER_D') deduced TER from the intercept of NEE-photosynthetically photon flux density (PPFD) response during the day. For both approaches, different procedures were compared: the use of a narrow or large window for the adjustment of NEE to climate relationship, and the use of the air or soil temperature as a reference for this response. In addition, the impact on TER_N of an uncertainty in the u_* threshold value and the impact on TER_D of the regression choice to compute the NEE-PPFD responses were assessed. The comparison was performed on three successive crops grown at the CarboEurope-IP crop site of Lonzée, Belgium. Only the uncertainties resulting from the inferring procedure are addressed here; we do not take into account the errors or uncertainties linked to NEE measurements. Crop ecosystems are characterized by a rapid evolution and a large variation of the biologic activity during the growing season. As the overall aim of our work is to assess the crop carbon balance and to understand the assimilation and respiration evolutions in relation to crop development and the vegetation stages, we need reliable daily values for these fluxes. Therefore, the uncertainty analysis we developed here is not limited to total values, but also includes daily values. This differentiates this paper from previous studies, most of which compared TER assessments methods on an annual (Reichstein et al., 2005; Stoy et al., 2006; Richardson et al., 2006; Desai et al., in press) or on a monthly scale (Desai et al., in press) and did not analyse differences produced by models in terms of daily evolution and ecosystem development.

2. **Material and methods**

2.1. Site description

The Lonzée site is an agricultural field, involved in the CarboEurope-IP and IMECC networks, with a 4-year rotational cycle. The climate is temperate maritime with a mean temperature of 10°C and an annual precipitation of about 800 mm. The site has been described by Moureaux et al. (2006).

In 2004, after traditional tillage in late February, a sugar beet crop (*Beta vulgaris* L.) was sown on 30 March and harvested on 29 September. The NEE and the annual sequestration of the sugar beet crop were analysed by Moureaux et al. (2006). The following crop was winter wheat (*Triticum aestivum* L.), sown on 14 October, 2 weeks after the sugar beet harvest. The soil conditions were such that a minimum tillage with a rotary harrow was performed before wheat seedling. The wheat crop was harvested on 3 August 2005, and in late November 2005 a conventional tillage was carried out. No crop was grown during autumn, winter and early spring. The carbon balance of the winter wheat crop between emergence and harvest was studied by Moureaux et al. (in press). In 2006, a seed potato crop was grown on the site. It was planted on 1 May, with the ridging done on 13 May. On 6 August, the first chemical haulm destruction was carried out, following by a second one on 13 August. The potato crop was harvested on 15 September 2006.

2.2. Eddy covariance and meteorological measurement systems

Fluxes of CO_2, water vapour and sensible heat were measured with an eddy covariance system made with a research-grade sonic anemometer (Solent Research R3, Gill Instruments, Lymington, UK) placed at a height of 2.7 m and an infrared gas analyser model Li-7500 (Licor Inc, Lincoln, NE, USA); this was the standard system used in the *CarboEurope-IP* and *Fluxnet* networks (Moncrieff et al., 1997; Grelle and Lindroth, 1996; Aubinet et al., 2000). This system and the complementary measurements were described by Moureaux et al. (2006).

2.3. TER and GPP assessments

The GPP and TER can be deduced from half-hourly NEE measurements. These three fluxes are related thus:

$$\mathrm{GPP} = \mathrm{NEE} - \mathrm{TER} \qquad (1)$$

Following Equation (1), the GPP can be deduced from an NEE measurement and a TER estimate. TER estimates can be obtained by extrapolating to the whole period NEE measurements taken during selected night (TER_N) or day (TER_D) periods. This paper seeks to compare these approaches, evaluate the uncertainties that result from each approach and propose the approach that produces the best GPP and TER estimates. Throughout the paper we use micrometeorological conventions; i.e., upward fluxes are counted as positive and downward fluxes as negative.

The NEE was computed half hourly as the sum of the turbulent flux measured by the eddy covariance system and of the storage flux deduced from a single measurement point. Storage estimates based on single point measurements were comparable with those based on a complete profile, due to the limited height of the measurement system (Moureaux et al. [in press]). The turbulent fluxes were scrutinized using a stationary test (Foken and Wichura, 1996) and only those data that met the quality test, with a deviation below 30%, were used in the present analysis. Stable night-time conditions were identified using a criterion based on the friction velocity (u_*). The impact of the threshold value on the annual fluxes was analysed. Reference u_* thresholds were 0.1, 0.22 and 0.12 m s^{-1} for the sugar beet crop, winter wheat crop and seed potato crop, respectively. They were calculated using a method similar to that described by Reichstein et al. (2002a).

Data gaps were filled using a mean diurnal variation with an 11-day data window approach when meteorological data were missing (Falge et al., 2001). When this was not the case, an empirical NEE-climate relationship was preferred. Daytime gaps were estimated using an NEE (N_e)-PPFD (Q) relationship based on 10-day periods. Three NEE-PPFD relationships were tested for the data gap filling: a Misterlich equation (Dagnelie, 1973; Aubinet et al., 2001), a rectangular hyperbola (Michaelis-Menten, 1913; Falge et al., 2001; Gilmanov et al. 2003) and a non-rectangular hyperbola (Peat 1970; Johnson and Thornley, 1984; Boot and Loomis, 1991; Gilmanov et al., 2003). The differences in NEE between the various methods was less than 0.1%. Finally, we used the Misterlich equation:

$$N_e = -\left(N_s + R_d\right)\left(1 - \exp\left(\frac{-\alpha Q}{\left(N_s + R_d\right)}\right)\right) + R_d \qquad (2)$$

where N_s is the NEE at light saturation, α is the apparent quantum efficiency (i.e., the initial slope of the curve) and R_d the dark respiration.

The TER can be deduced from nigh-time or daytime NEE valid measurements. In the night-time approach, an exponential relationship was established between the night-time NEE which equals the TER and the temperature. The relationship was as proposed by Lloyd and Taylor (1994):

$$\mathrm{N_e} = \mathrm{R_{10}} \exp\left\{\mathrm{E_0}\left(\frac{1}{56.02} - \frac{1}{\mathrm{T_{ref}} - 227.13}\right)\right\} \qquad (3)$$

where R_{10} is the respiration flux at 10°C, T_{ref} is the reference temperature and E_0 is a parameter characterising the respiration sensitivity to temperature. The parameterisation was fitted on data corresponding to mixed conditions. On the assumption that the TER dependence on temperature is the same during the day as it is at night, the TER was computed on the whole day using this parameterisation and $\mathrm{TER_N}$ was then obtained.

In the daytime approach, the respiration was assessed from the intercept of the NEE-PPFD relationship (R_d in Equation 2).

2.4. Description of the computation procedures

First, as CO_2 eddy covariance fluxes are known to be underestimated at night (Goulden et al., 1996, Aubinet et al., 2000), it was important to determine the uncertainty resulting from this error. We considered the night flux error as a systematic error and corrected it by applying the classical u* filtering described earlier. However, as the normalised flux to u* response was not perfectly flat above the u* threshold, an uncertainty remained for TER_N that resulted from the uncertainty for the threshold value. To evaluate it, we compared TER_N computed by using either the best estimate of the u* threshold (u_{*ref}) or this value increased by 0.1 m s^{-1} threshold ($u_{*ref+0.1}$).

Models used to extrapolate TER_N and TER_D can be fitted on long or short periods (large or narrow window). Large window adjustments (subscript LW) were performed for the whole period. In the night-time approach, Equation 3 was fitted on the whole crop data and a unique set of parameters (temperature sensitivity and respiration at 10°C) was obtained. The $TER_{N,\ LW}$ was then computed for the whole period using Equation 3 with this set of parameters. This method is similar to those used, for example, by Hollinger et al. (1994); Saigusa et al. (2005) and Davidson et al. (2006). In the daytime approach ($TER_{D,\ LW}$), $R_{d,10}$ and mean daytime temperature were initially calculated every 10 days. $R_{d,10}$ was deduced from a Misterlich regression (Equation 2) and daytime temperature by a simple average. A Lloyd and Taylor relationship (Equation 3) was then fitted on these data and a unique set of parameters (temperature sensitivity and respiration at 10°C) was again obtained. $TER_{D,\ LW}$ was computed as described earlier. This method was used, for example, by Lee et al. (1999) and Wohlfahrt et al. (2005a).

The problem with the large window procedure is that parameters not only represent a direct response to temperature, but can also reflect indirectly the crop development or soil moisture effects (e.g., Davidson et al., 1998; Reichstein et al.; 2002, Xu and Baldocchi, 2004). To reduce the impact of these factors, they could be incorporated explicitly in the model or implicitly by introducing temporally varying functions of temperature (Reichstein et al., 2005). This is the aim of the narrow window procedure (subscript NW). In the night-time approach ($TER_{N,NW}$), it consisted of using time-varying R_{10} parameters that were re-evaluated every 4 days and temperature sensitivities that were computed on a 15-day basis. This method is similar to those proposed by Reichstein et al. (2005). In the daytime approach the respiration was deduced daily from the intercept of the NEE-PPFD relationship. The daily $TER_{D,NW}$ was the sum of daytime and night-time respiration, where the daytime respiration was the product of the NEE-PPFD intercept (R_d in Equation 2) and the duration of the day (between sunrise and sunset) and the night-time respiration was the product of the intercept, the night duration and a negative exponential function, taking into account the temperature difference between the day and the night. This method was proposed by Gilmanov et al (2003). The intercept value was found to be sensitive to the relationship used for the regression. Gilmanov et al. (2003) recommended a non-rectangular hyperbola relationship (i.e. a 4-parameter equation). We also used this method with a rectangular hyperbola relationship and a Misterlich relationship, both of which are 3-parameter functions.

The impact of the reference temperature choice was also studied. Four methods combining the two approaches (daytime or night-time) with the two procedures (large or narrow window) were applied using either air temperature (subscript TA) or soil (subscript TS) temperature at a depth of 5.5 cm as a reference.

To avoid making this paper too cumbersome, only the most relevant results are presented here. First, the impact of the NEE-PPFD relationship shape on $TER_{D,NW,TS}$ and of the u_* threshold value on $TER_{N,NW,TS}$ and $TER_{N,LW,TS}$ was analysed. The influence of the window size was then tested for both approaches, using TS as a reference temperature. Next, the impact of the temperature reference was assessed for both approaches using the narrow window procedure. Finally, the daytime and night-time approaches, using both the narrow window procedure and the soil temperature, were compared. The uncertainties affecting each method and the method feasibility were discussed. Differences between the methods were evaluated by computing the difference (D) and the quadratic (QD) difference between daily values. A paired t-test was also used to determine the significance of the mean difference on a seasonal scale. The uncertainty associated with TER and GPP parameterisation was computed every half hour as the residual variance of the Lloyd and Taylor fit for the TER and GPP night-time approach assessments, as the standard error of the respiration parameter for $TER_{D,NW}$ and $GPP_{D,NW}$ and as a combination of both for $TER_{D,LW}$ and $GPP_{D,LW}$.

These analyses were performed on three crops (i.e., on periods ranging from emergence to harvest for the sugar beet and winter wheat crops, or chemical haulm destruction for the potato crop). These three periods were referred to as SB04, WW05 and P06, respectively, and corresponded to the periods from 21.04.2004 to 27.09.2004, from 01.11.2005 to 02.08.2005 and from 24.05.2006 to 06.08.2006, respectively. However, for the winter wheat crop, $TER_{D,NW}$ was not computed before 1 April 2005 due to the weak number of possible daily fits. During winter, the crop barely developed and thus the assimilation was weak. In addition, radiation was reduced and the adjustment of a daily NEE-PPFD relationship was then subjected to large uncertainties or even became impossible. The period from 1.04.05 and 2.8.05 was referred to WW05* and the corresponding respiration to TER*.

All the model parameters were determined by non-linear least squares regression, using the Marquardt-Levenberg algorithm (SAS Enterprise, SAS Institute Inc., USA).

3. **Results and discussion**

3.1. Impact of the NEE-PPFD relationship on $TER_{D,NW,TS}$

The same three NEE-PPFD relationships noted earlier were compared for R_d evaluation in the daytime approach: Misterlich (Mist), rectangular hyperbola (RH) and non-rectangular hyperbola (NRH). The TER assessments for the three crops are presented in Table 1. The differences between RH and Mist estimations varied from 1% (0.01 kg C m^{-2}) (WW05) to 4% (0.01 kg Cm^{-2}) (P06), whereas differences between RH and NRH estimations varied from 7% (0.02 kg C m^{-2}) (P06) to 15% (0.10 kg C m^{-2}) (SB04). All the differences were systematic and significant (α = 0.05) (Table 1). This suggested clearly that the R_d value was linked to the regression choice. We were not able to determine which regression gave the best estimate, but practical arguments may prevent the use of the NRH equation. As it was based on four parameters, whereas both the other relationships were based on three, its fit failed more often (64%, 53% and 60% for SB04, WW05* and P06, respectively) than those of the other functions (48%, 19% and 53%, respectively, for the same periods). Gilmanov et al. (2003), who recommended using the non-rectangular hyperbola, did not report this problem. One reason could be that they applied it to gap-filled data series, whereas we exploited only valid measurements and therefore had fewer available data.

In July 2006 the weather was exceptional sunny and dry climatic conditions. Coupled with a superficial root system, these conditions resulted in a level of water-stress in the potato crop that had never been observed in previous crops. Consequently, the fit of a daily NEE-PPFD relationship failed for most of this time period and the interpolation was based on very few data. The large number of interpolation values is shown in Figure 1f in the weak daily variation of this method compared with the other methods (Figs. 1c and 1f). We tested an NRH equation to which we had added a respiration to temperature response in order to improve our TER assessment, as suggested by Gilmanov et al. (2006). This further increased the number of parameters and reduced the number of possible fits (less than 10% of the days). In addition, as Gilmanov at al. (2006) noted, the use of this relationship can overestimate the ecosystem respiration because the NEE decrease could result not only from a respiration increase, but also from an assimilation decrease due to stomatal regulation. Additional measurements carried out at the potato leaf scale with a porometer (Li-6400, Licor Inc., Lincoln, NE, USA) showed a stomatal conductance decrease with increasing vapour pressure deficit (results not shown). We confirm that the use of NEE-PPFD and temperature regression did overestimate TER for the P06 crop and we did not use it again. This model was therefore abandoned.

[kg C m^{-2}]	SB04	WW05*	P06
Mist RH NRH	0.637 0.662 0.562	0.697 0.709 0.625	0.270 0.284 0.264
RH - Mist	D : 0.025 P < 0.001 QD : 0.060	D : 0.011 P = 0.004 QD : 0.043	D : 0.014 P < 0.001 QD : 0.020
NRH - Mist	D : - 0.075 P < 0.001 QD : 0.130	D : - 0.072 P < 0.001 QD : 0.107	D : - 0.006 P = 0.009 QD : 0.020
NRH-RH	D : - 0.100 P < 0.001 QD : 0.135	D : - 0.084 P < 0.001 QD : 0.122	D : - 0.020 P < 0.001 QD : 0.025

Table 1: Total TER values obtained using the daytime approach, a narrow window and the soil temperature. For the three crops (sugar beet (SB04), winter wheat (WW05) and seed potato (P06)), the $TER_{D,NW,,ST}$ was assessed using Misterlich (Mist), rectangular (RH) and non-rectangular (NRH) hyperbola relationships. Differences (D) and quadratic differences (QD) were computed to compare the TER assessments. The P value indicates if the differences are significant.

In conclusion, in view of the difficulties with its fit, the NRH relationship was not retained for further analysis and only parameters deduced from the Misterlich equation were used subsequently. The uncertainty resulting from the equation choice is discussed below.

3.2. Impact of the u_* threshold value on $TER_{N,TS}$

Moureaux et al. (2006) and Moureaux et al. (in press) mentioned that, for SB04 and WW05, the relationship between normalised flux and u_* did not move towards a horizontal asymptote at high u_*, but rather continued to increase, albeit at a limited rate. This suggests that, even above the critical u_* value, the total TER_N of these crops would increase with the u_* threshold. The resulting uncertainty for TER_N cannot be evaluated directly because it also depends on the u_* frequency distribution at the site. It was therefore evaluated by comparing two $TER_{N,TS}$ values, one computed using the best u_* threshold estimate and the other using this estimate increased by 0.1 m s^{-1}. The results, presented in Table 2, showed that the 0.1 m s^{-1} in the u_* threshold induced an increase of 5% (0.03 kg C m^{-2}) for SB04, 3% (0.02 kg C m^{-2}) for WW05 and no increase for P06. A paired t-test concluded that the differences were significant for SB04 and WW05 (Table 2). An analysis of the daily difference evolution (not shown) suggests that this error was systematic and did not vary greatly from day to day. The uncertainties computed here appear similar or slightly smaller than those reported for other sites by Barford et al. (2001), Anthoni et al. (2004) and Xu and Baldocchi (2004). It is worth noting, however, that (i) the uncertainty was computed after applying the u* filtering and therefore does not quantify the night flux error itself, which is far more important (Papale et al., 2006) and (ii) that the impact of this uncertainty on the annual NEE (Anthoni et al., 2004; Moureaux et al., 2006) is one of the biggest uncertainties affecting this variable.

[kg C m^{-2}]		$u_{*,ref}$	$u_{*,ref+0.1}$	$u_{*,ref+0.1} - u_{*ref}$
SB04	NW	0.616	0.648	0.032 $P < 0.001$
	LW	0.622	0.643	0.021 $P < 0.001$
WW05	NW	0.946	0.965	0.019 $P = 0.001$
	LW	0.921	0.940	0.019 $P < 0.001$
P06	NW	0.294	0.294	0.000 $P = 0.963$
	LW	0.300	0.300	0.000 $P = 0.875$

Table 2: Impact of a u_* threshold value underestimation of 0.1 m s^{-1} on the total TER modelled following the night-time approach and the soil temperature. Results corresponding to narrow (NW) and large (LW) windows are presented for the three crops. The differences and the value of P corresponding to a paired t-test are indicated.

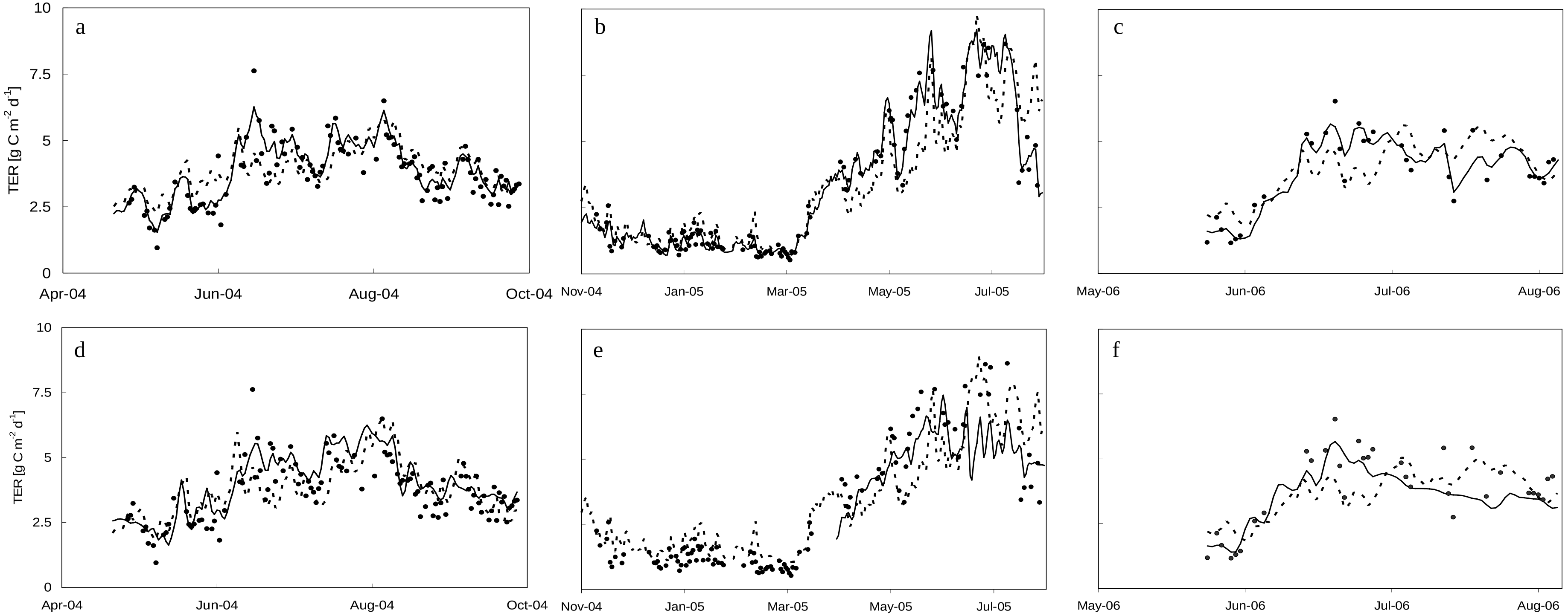

Figure 1: Comparison of the daily evolution of narrow window (continuous line) and large window (dashed line) TER_{TS} assessments for the (a and d) sugar beet crop, (b and e) winter wheat crop and (c and f) seed potato crop. Night-time approaches are shown in Figures a to c and daytime approaches in Figures d to f. The NEE measurements averaged by night are represented by full circles.

3.3. Impact of the window size

Table 3 presents (3a) and compares (3b) different TER estimations computed using various procedures. In particular, a comparison between TER computed with a narrow (NW) and large (LW) window is made for both the night (N) and day (D) procedures. In terms of total TER_{TS}, the window size produced differences varying from less than 0.01 kg C m^{-2} to 0.04 kg C m^{-2}, the differences being significant ($\alpha = 0.05$) only for the daytime approach (Table 3). For both approaches, the difference was not systematic, as confirmed by large differences between the QD and D values. This had already been observed by Stoy et al. (2006) and Richardson et al. (2006), contrary to the report by Reichstein et al. (2005) which predicted systematic ($TER_{N,NW} < TER_{N,LW}$) and greater differences for annual GPP and then for annual TER. They also said that the window size impact would depend on the amplitude between daytime and night-time temperatures. A greater difference between $TER_{N,NW}$ and $TER_{N,LW}$ should therefore be expected when using air temperature instead of soil temperature as a reference. Slightly larger differences between $TER_{N,NW,TA}$ and $TER_{N,LW,TA}$ (not shown) were indeed observed, but they remained lower than 5% and were not significant (paired t-test, $\alpha = 0.05$, results not shown).

As the impact of the window size was limited for total TER_{TS}, its impact on daily values was far more important, differences reaching up to 0.5 to 1.5 g C m^{-2} d^{-1} on certain days (Fig. 1), which could represent uncertainties of up to 30 %. For both $TER_{N,TS}$ and $TER_{D,TS}$, the NW estimations were greater than the LW estimations during intense above-ground biomass development. This period lasted from the second half of June to late July (Moureaux et al., 2006) for SB04, from early April to mid-June (Moureaux et al., in press) for WW05, and from mid-June to early July for P06. This is because, during these periods, the intense crop activity produced an increased respiration flux that was taken into account in the short-term assessment of R_{10} (Equation 3), whereas it was confounded with temperature effect in the long-term assessment (Reichstein et al., 2005).

A noticeable difference was also observed in July 2005 (Figs. 1b and 1e), when the winter wheat was senescent and its activity, including respiration, decreased (Moureaux et al., in press). This decrease was well reproduced by $TER_{NW,TS}$ but not by $TER_{LW,TS}$ which therefore largely overestimated the flux during this period. In the same way, the potato respiration decrease resulting from a drought in July 2006 was again well reproduced by $TER_{NW,TS}$ but not by $TER_{LW,TS}$. During this period, however, the $TER_{D,NW}$ fit failed most of the time, which induced a large number of interpolated data, as discussed in 3.2, thus weakening our confidence in this assessment. These two examples highlight the inability of large window procedures to correctly reproduce the daily TER evolution.

Daily $TER_{NW,TS}$ and $TER_{LW,TS}$ values were compared with measurements of night-time NEE which are representative of TER. Data were u_* filtered, without gap filling, and averaged by night. Only nights with more than five valid measurements were considered. For the three crops and both approaches, the mean quadratic errors between computed TER and night-time NEE were smaller for $TER_{NW,TS}$ than for $TER_{LW,TS}$ (Table 4), confirming that the narrow window procedure is more able to reproduce particular periods as intense crop development, drought or senescence, as confirmed by Reichstein et al (2005), Richardson et al. (2006) and Stoy et al. (2006). Consequently, here we will consider only those estimates computed with the narrow window procedure.

3.4. Impact of the reference temperature choice

Comparisons between TER estimates, computed using either air or soil temperature as a reference, were then made for both the daytime and night-time approaches. The impact of the temperature choice was different for each approach (Table 3): in each case, a systematic difference was observed, but the estimates based on TA were larger than those based on TS for the night-time approach (Table 3), whereas the opposite was observed for the daytime approach. In both cases, the differences were significant (α = 0.05) and ranged between 5% (0.05 kg C m^{-2}) (WW05) and 11% (0.03 kg C m^{-2}) (P06) for TER_D, and between 8% and 9% (0.03–0.05 kg C m^{-2}) for TER_N. The daily differences were fairly constant throughout the season and lower than, or equal to, 0.5 g C m^{-2} d^{-1} in both cases (results not shown).

In both cases, these differences reflected artefacts linked to the extrapolation of measurements from one temperature range to another: in the night-time approach, the procedure included an extrapolation from night to day conditions (i.e., from lower to higher temperatures). Such extrapolations are known to produce large uncertainties but, in this case, the errors would have been less important when using TS rather than TA because the night and day ranges were closer for the former than for the latter.

a. [kg C m^{-2}]	SB04	WW05	WW05*	P06
1. TER$_{N,NW,TS}$	0.616 ± 0.011	0.946 ± 0.011	*0.735 ± 0.010*	0.294 ± 0.010
2. TER$_{N,LW,TS}$	0.622 ± 0.013	0.921 ± 0.017	*0.675 ± 0.012*	0.300 ± 0.011
3. TER$_{D,NW,TS}$	0.637 ± 0.018		0.697 ± 0.015	0.270 ± 0.009
4. TER$_{D,LW,TS}$	0.609 ± 0.013	0.941 ± 0.017	*0.661 ± 0.011*	0.300 ± 0.010
5. TER$_{N,NW,TA}$	0.667 ± 0.011	0.994 ± 0.011	*0.786 ± 0.010*	0.327 ± 0.010
6. TER$_{D,NW,TA}$	0.587 ± 0.018		0.639 ± 0.015	0.246 ± 0.009
b. [kg C m^{-2}]				
2-1: TER$_{N,\mathbf{LW},TS}$ – TER$_{N,\mathbf{NW},TS}$	D: 0.006 P = 0.481 QD: 0.100	D: -0.025 P = 0.120 QD: 0.269	*D: -0.060* *P < 0.001* *QD: 0.173*	D: 0.006 P = 0.403 QD: 0.060
4-3: TER$_{D,\mathbf{LW},TS}$ – TER$_{D,\mathbf{NW},TS}$	D: - 0.027 P = 0.005 QD: 0.125		D: -0.036 P = 0.010 QD: 0.157	D: 0.030 P < 0.001 QD: 0.078
5-1: TER$_{N,NW,\mathbf{TA}}$ – TER$_{N,NW,\mathbf{TS}}$	D: 0.051 P < 0.001 QD: 0.063	D: 0.048 P < 0.001 QD: 0.111	*D: 0.051* *P < 0.001* *QD: 0.073*	D: 0.033 P < 0.001 QD: 0.038
6-3: TER$_{D,NW,\mathbf{TA}}$ - TER$_{D,NW,\mathbf{TS}}$	D: - 0.050 P < 0.001 QD: 0.056		D: -0.058 P < 0.001 QD: 0.063	D: -0.024 P < 0.001 QD: 0.029
3-1: TER$_{\mathbf{D},NW,TS}$ – 1. TER$_{\mathbf{N},NW,TS}$	D: 0.021 P = 0.002 QD: 0.084		D: - 0.038 P = 0.001 QD: 0.130	D: -0.024 P < 0.001 QD: 0.052

Table 3: Values of TER and the corresponding uncertainty resulting from the inferring procedure for the sugar beet crop (SB04), winter wheat crop (WW05) and seed potato crop (P06). The WW05* corresponds to the period beginning on 01.04.05. Italic values correspond to values computed for this period only, whereas they could be computed for the whole WW05 period. Differences and square differences between TER assessments were computed. A P value indicates whether or not the difference is significant.

In Figure 2 we present a comparison made for a few days between half-hourly TER estimates based on TA and TS, respectively. It seems clear that the TA estimate amplitudes and maximal values are not plausible, ranging from 2 to 12 μmol m^{-2} s^{-1}. In contrast, the TS estimate amplitude appears more likely and was found to agree with those obtained from automatic soil chamber measurements taken on the same site at the same time (about 2 μmol m^{-2} s^{-1}). In addition, the mean difference between measured NEE and simulated TER$_{N,NW}$ was found to be smaller when using TS rather than TA (Table 4), confirming that soil temperature constitutes a better reference.

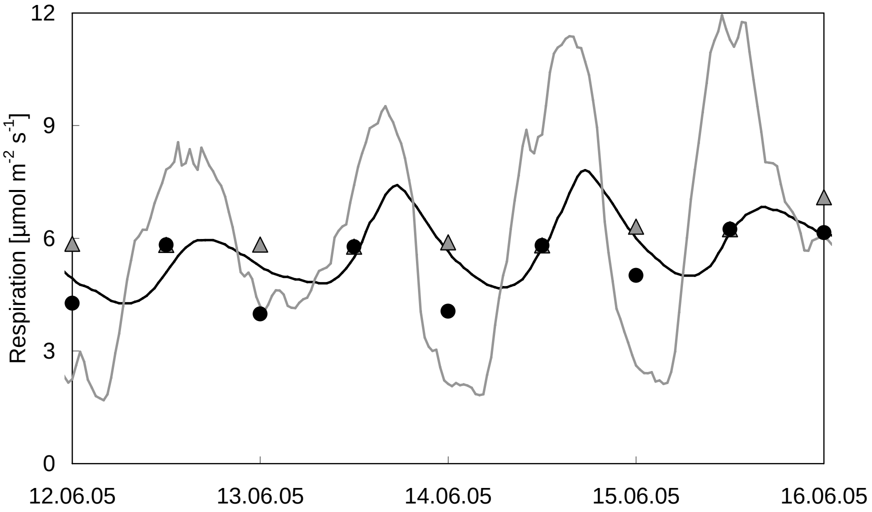

Figure 2: Half-hourly evolution of $TER_{N,NW}$ using TS (black line) and TA (grey line) and half-hourly evolution of measured soil respiration (continuous grey line). The daytime and night-time values of the respiration used in $TER_{D,NW}$ assessments are presented when using TS (grey triangle) and TAIR (black circle)

It should be noted that air temperature is often preferred in synthesis studies (Reichstein et al., 2005; van Dijk and Dolman, 2004), mainly for practical reasons because it is easier to measure and standardize. However, our results suggest that the large differences between the daily estimates of $TER_{N,TA}$ and $TER_{N,TS}$ resulted from a partial compensation of much larger differences that affected half-hourly estimates. This meant we had reservations about the use of TA in the night-time approach.

[kg C m^{-2}]	SB04	WW05	WW05*	P06
$TER_{N,NW,TS}$ - NEE_{night}	0.516	0.370		0.453
$TER_{N,LW,TS}$ - NEE_{night}	0.828	1.053		1.016
$TER_{D,NW,TS}$ - NEE_{night}	0.707		0.876	0.785
$TER_{D,LW,TS}$ - NEE_{night}	0.858	1.049	*1.503*	1.016
$TER_{N,NW,TA}$ - NEE_{night}	0.662	0.481		0.536
$TER_{D,NW,TA}$ - NEE_{night}	0.645		0.961	1.025

Table 4: Mean quadratic differences between TER assessments and night-time NEE measurements. The WW05* corresponds to the period beginning on 01.04.05. Italic values are computed for this period only where they could be computed for the whole WW05 period.

The problem was not the same in the daytime approach because the extrapolation from day to night conditions was based on a different procedure. First, as the method computed only one respiration value per day (namely, R_d), the extrapolation was not based on half-hourly estimates but on daily averages. Two respiration rates were computed each day: one for daytime, R_d , and one for night-time estimated as the product of R_d (Equation 2) and of an exponential function of the difference between night-time and daytime temperatures (Gilmanov et al., 2003). Consequently, daytime respiration did not depend on the reference temperature choice, but the night-time respiration did. In addition, as the difference between daytime and night-time temperatures was larger for air than for soil, night-time respiration should have been systematically smaller when based on the former than on the second temperature. This is illustrated in Figure 2: it shows that daytime estimates of $\text{TER}_{\text{D,TA}}$ and $\text{TER}_{\text{D,TS}}$ were equal, but that night-time estimates of $\text{TER}_{\text{D,TA}}$ were systematically lower than those of $\text{TER}_{\text{D,TS}}$. The daily amplitude of $\text{TER}_{\text{D,TA}}$ appeared to be more in agreement with soil chamber measurements and this could mean that, here, TA would be a better indicator than TS. However, a comparison between TER assessments and measured $\text{NEE}_{\text{night}}$ revealed that this was generally not the case, TS assessments providing lower quadratic differences with measurements than TA in two of the three years (Table 4). The reason is probably that the respiration-TA relationship used to extrapolate day to night conditions is biased. Indeed, this equation puts together two variables that were not measured at the same time: R_d, the intercept of the NEE-PPFD curve, was affected mainly by measurements taken under low radiation conditions and thus most representative of sunrise and sunset conditions, whereas the temperature was computed as an average for the whole day period, encompassing warmer periods. As a result, the relationship would always underestimate the respiration, which explains the results shown in Table 4. This bias was less important when using the soil temperature. We think therefore, that for both the daytime and night-time approaches, the more robust TER estimates are obtained when using soil temperature as a reference.

3.5. Comparison between daytime and night-time approach

The daytime and night-time approaches were compared. For both estimations, we used the narrow window procedure and the soil temperature as a reference. In terms of total value, estimations based on daytime measurements were higher for SB04 and lower for WW05 and P06 (Table 3). The differences were between 0.02 and 0.04 kg C m^{-2} and were significant (α =

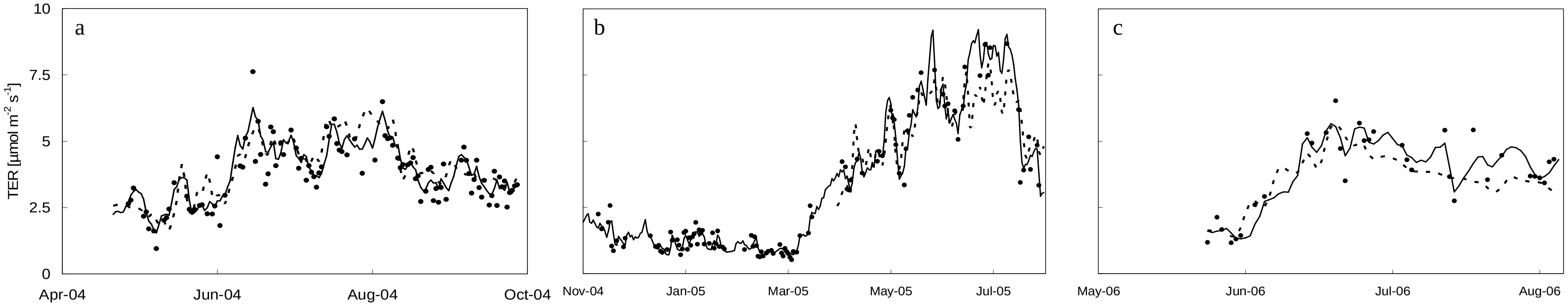

Figure 3: Daily evolution of TER assessed from night-time data (continuous line) and daytime data (dashed line) with a narrow window and the soil temperature for the (a) sugar beet crop,(b) winter wheat crop and (c) seed potato crop.

0.05). Quadratic differences were higher, suggesting that the differences were not systematic throughout the season. This is illustrated in Figure 3 where seasonal evolutions of $TER_{D,NW,TS}$ and $TER_{N,NW,TS}$ are presented for the three crops. The most remarkable differences between the two estimates were observed between mid-June and mid-July in WW05 and from late June to harvest in P06. In both cases, $TER_{D,NW}$ was smaller than $TER_{N,NW}$. The difference for the winter wheat crop was about 2 g C m^{-2} d^{-1} and could not be explained by any climate particularities. This period corresponded to grain development and leaf yellowing. It is worth remembering that the long-term day assessment gave predictions that were similar to the night-time measurements and that only the $TER_{D,NW}$ model provided such small differences. The difference in potato was also about 2 g C m^{-2} d^{-1} and corresponded to the drought period. During this period, there were serious difficulties in assessing the $TER_{D,NW}$ (cf. 3.1) and a large number of values were interpolated.

The fact that the differences between daytime and night-time approaches were not systematic and limited in time contradicts some studies that reported a systematic overestimation of TER and GPP when assessed from night-time data rather than daytime data (Amthor and Baldocchi, 2001; Janssens et al., 2001; Morgenstern et al., 2004; Wohlfahrt et al., 2005b). This overestimation was explained by a reduction of leaf respiration in the light compared with the darkness (Kok, 1948; Brooks and Farquhar, 1985; Pärnik and Keerberg, 1995; Villar et al., 1995; Atkin et al. 1997, 1998, 2000; Schultze, 2003). However, recent findings using stable isotope methodology showed that under most conditions only the light-inhibition of leaf dark respiration is apparent and results in CO_2 refixation in the leaf (Loreto et al., 2001; Pinelli & Loreto, 2003). This suggests that the differences we observed between daytime and night-time based TER are unlikely to be biased.

3.6. Impact on GPP estimations

With the GPP computation method, it was expected that all the uncertainties computed as described earlier would be much smaller than for TER assessments: first, GPP was larger in absolute value than TER, leading to smaller relative errors; second, as GPP was zero at night, it was affected by uncertainties only during the day, whereas TER was affected during both the day and night. However, the differences resulting from the temperature choice (between 0.03 and 0.07 kg C m^{-2}) were of the same order of magnitude, or even greater, for the $GPP_{N,NW}$ than the $TER_{N,NW}$. In fact, the differences between $TER_{N,NW}$ using TA and TS were more important during the day than during the night (Fig. 2). As only the daytime TER$_{N,NW}$ values were used to compute GPP$_{N,NW}$, the error resulting from the temperature reference choice remained important in GPP$_{N,NW}$ assessments. The errors produced by the reference temperature choice were significant (α = 0.05) and systematic (Table 5). The relative differences were less than 5%.

For the other choices, the impact on GPP of each procedure was similar but smaller than for TER. The impact of the window size was between 0.00 and 0.02 kg C m^{-2} for the night-time approach and between 0.00 and 0.02 kg C m^{-2} for the daytime approach. The only significant difference (α = 0.05) corresponded to the WW05 crop for the night-time approach. The window size differences were between 1 and 3% of total GPP values for both approaches (Table 5). As for the TER computation, the size of the window induced a selective systematic error. In terms of daily evolution, the differences between the narrow and large window models using night-time data and the soil temperature were usually less than 10% for the daily values but could reach 30% for TER$_{N,TS}$.

GPP [kg C m^{-2}]	SB04	WW05	WW05*	P06
1. GPP$_{N,NW,TS}$	-1.421 ± 0.009	-1.566 ± 0.008	*-1.430 ± 0.008*	-0.608 ± 0.008
2. GPP$_{N,LW,TS}$	-1.423 ± 0.010	-1.542 ± 0.012	*-1.393 ± 0.009*	-0.611 ± 0.009
3. GPP$_{D,NW}$	-1.434 ± 0.018		-1.403 ± 0.015	-0.592 ± 0.009
4. GPP$_{D,LW,TS}$	-1.417 ± 0.010	-1.547 ± 0.011	*-1.384 ± 0.009*	-0.596 ± 0.008
5. GPP$_{N,NW,TA}$	-1.479 ± 0.009	-1.632 ± 0.008	*-1.495 ± 0.008*	-0.642 ± 0.008
2-1 : GPP$_{N,\mathbf{LW},TS}$ – GPP$_{N,\mathbf{NW},TS}$	D: -0.002 P = 0.764 QD: 0.033	D: 0.024 P = 0.018 QD: 0.168	*D: 0.037* *P < 0.001* *QD: 0.111*	D: -0.003 P = 0.541 QD: 0.040
4-3 : GPP$_{D,\mathbf{LW},TS}$ – GPP$_{D,\mathbf{NW}}$	D: 0.017 P = 0.262 QD: 0.191		D: 0.019 P = 0.362 QD: 0.223	D: -0.004 P = 0.649 QD: 0.081
5-1 : GPP$_{N,NW,\mathbf{TA}}$ – GPP$_{N,NW,\mathbf{TS}}$	D: -0.058 P < 0.001 QD: 0.068	D: -0.066 P < 0.001 QD: 0.119	*D: -0.065* *P < 0.001* *QD: 0.079*	D: -0.034 P < 0.001 QD: 0.039
3-1 : GPP$_{\mathbf{D},NW}$ - GPP$_{\mathbf{N},NW,TS}$	D: -0.013 P = 0.369 QD: 0.179		D: 0.027 P = 0.157 QD: 0.216	D: 0.016 P = 0.087 QD: 0.084

Table 5: Values of GPP assessed using the different procedures for the sugar beet crop (SB04), winter wheat crop (WW05) and seed potato crop (P06). The WW05* corresponds to the period beginning on 01.04.05. Italic values are the GPP computed for this period only, whereas they could be computed for the whole WW05 period. Mean differences and mean quadratic differences between daily values are computed; the P value indicates whether or not the mean difference is equal to zero.

The uncertainty resulting from the choice of the NEE-PPFD relationship was systematic. The differences between RH and Mist $GPP_{D,NW}$ assessments were between 0.01 and 0.02 kg C. With regard to the u* threshold uncertainty, the differences for $GPP_{N,NW,TS}$ were also systematic, the GPP values corresponding to the u_{*ref} being bigger than those corresponding to $u_{*ref+0.01}$. These differences were between 0.00 and 0.02 kg C m^{-2}.

Finally, the differences between the daytime and night-time approaches were not significant ($\alpha = 0.05$) (Table 4) and not systematic. They ranged from 0.01 to 0.03 kg C m^{-2} (Table 5). The relative differences between the total $GPP_{N,NW,TS}$ and $GPP_{D,NW}$ values reached a maximum of 3% (P06).

4. Concluding remarks

In this paper, the TER and GPP assessments provided by two approaches based on independent datasets (night-time and daytime approaches) were compared for three successive crops, between emergence and harvest or chemical haulm destruction.

For both approaches, the impact of the window size used to compute the TER to climate response and those of the reference temperature choice were tested. In addition, the impact of uncertainty on the u_* threshold in the night-time approach and the impact of the regression choice in the daytime approach were tested. Uncertainties resulting from these choices on both cumulated and daily values were evaluated, and the feasibility of each method was discussed.

The daytime approach has two advantages: first, it does not require the use of night-time data and therefore is not affected by the uncertainties affecting night eddy covariance measurements; second, GPP assessments are not sensitive to the choice of the reference temperature. On the other hand, it is more difficult to apply when the vegetation is not well developed or during drought periods, because NEE to PPFD regressions do not always converge or they give wrong parameters during these periods. The use of 4- or 5-parameter regressions was found to exacerbate the problem and it was shown that the most robust regressions (i.e., those that most often gave a good fit with reasonable parameter values) were those that used fewer parameters. This shortcoming could make this method more difficult to apply for the TER and GPP computations in a complete year.

TER_D assessments using the different procedures may differ among themselves in a systematic, selective systematic (i.e., they are systematic on specific periods) or random way. Systematic differences result, in decreasing order of magnitude, from the choice of the reference temperature and of the regression equation (if the choice was limited to the 3-parameter equations). The choice of the reference temperature produced differences between $TER_{D,NW,TA}$ and $TER_{D,NW,TS}$ varying from 0.02 to 0.06 kg C m^{-2}, the former always being smaller than the latter. The choice of the regression also had a systematic effect, the rectangular hyperbola giving estimates 0.01–0.03 kg C m^{-2} larger than the Misterlich equation. The choice of window size produced an error that affected mainly periods of strong vegetation development, drought stress or senescence. Its impact on cumulated values was, ultimately, limited, but it was more noticeable on daily estimates. Finally, the uncertainty resulting from the regression coefficient standard error acted as random and varied from 0.01 to 0.02 kg C m^{-2}. Best estimates using the daytime approach were therefore obtained by choosing soil temperature as a reference and a narrow window procedure. In these conditions, the remaining uncertainty results from the regression parameter and the equation choice. $TER_{D,NW,TS}$ estimates can therefore be quantified as: 0.64 ± 0.02 ± 0.03 kg C m^{-2} for SB04; 0.70 ± 0.02 ± 0.01 kg C m^{-2} for WW05*; and 0.27 ± 0.01 ± 0.01 kg C m^{-2} for P06. $GPP_{D,NW}$ estimates are: - 1.43 ± 0.01 ± 0.02 kg C m^{-2} for SB04; - 1.40 ± 0.02 ± 0.01 kg C m^{-2} for WW05; and - 0.59 ± 0.01 ± 0.01 kg C m^{-2} for P06.

The advantage of the night-time approach is that it can be applied at any time in the season, including periods of stress or intercrops. Its shortcoming is that it depends on night eddy covariance measurements that should therefore be filtered using a u_* criterion before being used. Here, the systematic differences between TER_N estimates are due, in order of decreasing importance, to the reference temperature choice and to the u_* threshold choice. As for TER_D, the window size choice produces selective systematic differences and the uncertainty on the regression produces random errors.

The choice of the air temperature as reference temperature produced an overestimation of TER of 0.03 to 0.05 kg C m^{-2}. It is worth recalling that this overestimation resulted from partial compensation of much more important errors at an hourly time scale, and it is likely that the error would have been much larger at sites where sunny conditions prevailed and the daily temperature amplitude was large. We therefore strongly recommend the use of TS rather than TA to extrapolate night data to day conditions.

The uncertainty resulting from the u_* threshold choice is less important here, as an overestimation of 0.1 m s^{-1} on the threshold choice produced an overestimation of TER of 0.00 –0.03 kg C m^{-2}. In addition, this result depended on the shape of the normalized respiration response to u_* which could vary from one site to another and, at a given site, from one crop to another. We therefore recommend carefully estimating the threshold value for each crop separately and for each long intercrop.

The window size did not produce large differences for the cumulated respiration but, in terms of TER daily values, it did produce systematic differences up to 30%. As a result, it produced the greatest mean quadratic differences, varying from 0.06 to 0.27 kg C m^{-2}. Similarly, as for the daytime approach, the analysis of these daily differences underlined the inability of the large window procedure to reproduce the intense development stages, crop senescence or drought periods.

Finally, the impact of uncertainties on the regression remained quite limited, not exceeding 0.01 kg C m^{-2}. Best estimates using the night-time approach were therefore obtained by choosing soil temperature as a reference and a narrow window procedure. In these conditions, the remaining uncertainty results from the regression parameter and the u_* threshold determination. $TER_{N,NW,TS}$ estimates can thus be quantified as: 0.62 ± 0.01 ± 0.03 kg C m^{-2} for SB04; 0.94 ± 0.01 ± 0.02 kg C m^{-2} for WW05; and 0.29 ± 0.01 ± 0.00 kg C m^{-2} for P06. $GPP_{N,NW,TS}$ are: - 1.42 ± 0.01 ± 0.02 kg C m^{-2} for SB04; - 1.43 ± 0.01 ± 0.01 kg C m^{-2} for WW05; and - 0.61 ± 0.01 ± 0.00 kg C m^{-2} for P06.

The differences between our best estimates for both approaches (daytime or night-time) for TER were between 0.02 and 0.04 kg C m^{-2}, which is the order of magnitude of the uncertainties affecting each of them. For the GPP, they were between 0.01 and 0.03 kg C m^{-2}. This corresponded to relative differences of 3–8 % for TER and 1–3% for GPP. The cumulated differences between the two approaches were not systematic and varied from year to year: TER_D was lower than TER_N (and GPP_D larger than GPP_N) for the last two years, and higher than TER_N (and GPP_D lower than GPP_N) for the first year. This result is all the more satisfying because the two approaches are based on independent datasets. It also gives an order of magnitude of the confidence interval for cumulated TER and GPP estimates. However, it should also be noted that such agreement also results partly from the compensation of larger differences on the daily scale. For example, in the winter wheat crop,

TER_D provided daily values 20% smaller than the night-time approach, whereas the difference between total values was only 12%. This can be quantified by the quadratic difference between the two estimates that varied between 0.05 and 0.13 kg C m^{-2} for TER and between 0.08 and 0.22 kg C m^{-2} for GPP. Hagen et al. (2006) also reported larger relative uncertainties on TER on a daily scale (about 25%) than on an annual scale (less than 10%).

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Article 4

Extrapolating gross primary productivity from leaf to canopy scale in a winter wheat crop

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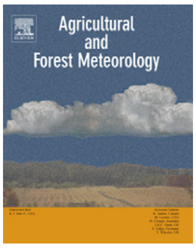

Extrapolating gross primary productivity from leaf to canopy scale in a winter wheat crop

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ABSTRACT

The objectives of this paper are to determine winter wheat gross primary productivity (GPP) by extrapolating to the canopy scale measurements of photosynthetic assimilation made at the leaf scale, to identify the uncertainties inherent in this method and to quantify their impact on GPP predictions. Crop development monitoring and photosynthesis measurements were conducted between 1 May and 19 July 2004 at the Carboeurope site of Lonzée, Belgium, with a portable porometer Li-Cor 6400. The model divided the canopy into 10 layers in which assimilation was computed on the basis of incident radiation and of assimilation to light response curves calibrated in the field. The model also took account of photosynthesis of stems and ears, senescent organ distribution and response of assimilation to leaf to air vapour pressure difference. Model estimates were compared with eddy covariance measurements performed at the site during the same period. The best agreement (regression slope = 1.13, $R^2 = 0.94$) between the two estimates was obtained by postulating a concentration of the senescent organs in the canopy bottom and a stem assimilation rate equal to 63% of the leaf assimilation. This ratio was found compatible with further leaf scale measurements. This led to a GPP of $1570\ \mathrm{g\,C\,m^{-2}}$ during the crop development and maturation periods. The sensitivity analysis revealed that the main sources of uncertainties were linked to the photosynthetic capacity of the stems (an increase of 40% in the initial GPP) and ears (an additional increase of 15%) and to the senescent organ spatial distribution (impact of 7–9%). An overestimation of GPP during spring ($270\ \mathrm{g\,C\,m^{-2}}$) was also observed, due to assimilation reduction at low temperature not be accounted for. Apart from this, the impact of the A–Q curve parameter uncertainties was found to be limited (impact on GPP always lower than 4%).

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Abbreviations: α, quantum yield; A, net assimilation; A_s, net assimilation at saturating light; D_s, air saturation deficit; D_l, leaf to air vapour pressure difference; EAI, ear area index; GLAI, green leaf area index; GPP, gross primary productivity; G_s, gross assimilation at saturating light; PPFD, photosynthetic photon flux density; PsAI, photosynthetic area index; Q, photosynthetic photon flux density; R_d, dark respiration; SAI, stem area index; T_a, air temperature; T_l, leaf temperature; VAI, total vegetation area index; YLAI, yellow leaf area index.

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1. Introduction

Croplands occupy about one-third of the land surface in Europe (FAO Statistical Databases, 2003) and 45% of the land surface in Belgium (MRW-DGA, 2005). They have the potential to mitigate about 16–19 Tg C y^{-1} (Freibauer et al., 2004). Their impact on the terrestrial carbon cycle is therefore significant and this justifies the recent development of CO_2 flux measurements at these sites (e.g., Soegaard and Thorgeirsson, 1998; Anthoni et al., 2004; Suyker et al., 2004). The present study is part of a larger research project whose overall goal is to establish the carbon balance of an agricultural site under a 4-year rotation system, which is typical of the Hesbaye region (Moureaux et al., 2006).

The goal of this research is to evaluate the feasibility of scaling up the assimilation measurements from leaf to crop scale. Scaled-up leaf measurements might provide useful information for validating eddy covariance measurements or refining the description of the various flux contributions to the net ecosystem exchange. The combination of these measurements for establishing the crop carbon balance is described in another paper (Moureaux et al., in press).

In this paper, we concentrate on the scaling up procedure. An extrapolation scheme was developed based on assimilation to radiation responses (*A*–*Q* curves) obtained by porometry measurements performed at the leaf scale during the study and on an evaluation of light absorption by the crop. Continuous micrometeorological measurements performed at the site meteorological station were used as input data, as well as the vegetation element distribution in the crop that was continuously monitored throughout season. The scaled-up results were compared with eddy covariance flux estimations and the differences were discussed. In addition, an uncertainty analysis was developed in order to determine the most important causes of uncertainties that affected the scaled-up GPP. This analysis allowed us to identify the most critical parameters to prioritize during field measurements and scaling up procedures. Although the approach was developed on a specific site and in a specific season, we consider that most of the results presented here could be extrapolated to cereal crops.

2. Material and methods

2.1. Site description

The site is a crop field in Lonzée, near Gembloux in Belgium (50°33′N, 4°44′E). It is described in detail by Moureaux et al. (2006). The climate is typically oceanic temperate. From 1 October to 25 Augustus the overall precipitation and average air temperature at the site were 545 mm and 10 °C, respectively. The soil is a luvisol and the site is flat, with a mean gradient of less than 1.2%. The site is included in the Carboeurope IP, Fluxnet and IMECC networks.

The site was equipped with an eddy covariance system and a meteorological station. The eddy covariance system measured fluxes of CO_2, water vapour and sensible heat. It was placed at a height of 2.7 m and consisted of a research-grade sonic anemometer (Solent Research R3, Gill Instruments, Lymington, UK) and an infrared gas analyser (model Li-7000, LiCor Inc., Lincoln, NE, USA). The eddy covariance system and procedures were those currently used in the Carboeurope IP and Fluxnet networks (Moncrieff et al., 1997; Grelle and Lindroth, 1996; Aubinet et al., 2000). Meteorological measurements were averaged every 30 min. They included air temperature and humidity (RHT2, Delta-T Devices Ltd., Cambridge, UK) at a height of 1.3 m. Global photosynthetically active (PAR Quantum Sensor SKP 215, Skye Instruments Ltd., UK) and global and diffuse photosynthetically active (Sunshine sensor type BF3, Delta-T Devices Ltd., Cambridge, UK) radiation was measured at a height of 2.7 m. Details of the eddy covariance system and meteorological measurements are given in Moureaux et al. (2006).

The crop under study was winter wheat (*Triticum aestivum* L., cv Dekan). It was sown on 14 October 2004, following a sugar beet crop (*Beta vulgaris* L.) harvested on 29 September 2004. No ploughing was done between the two crops, but minimum tillage with a rotating harrow prepared the soil for seedling and mixed green residues of sugar beet into a 10 cm layer of soil. The field management schedule is summarised in Table 1. Two herbicide treatments were applied, on 18 March and 11 May. Nitrogen was applied in four fractions (on 22 March and 12 April with a urea ammonium nitrate solution, and on 12 and 30 May with NH_4NO_3). There was only one fungicide treatment, on 19 May. The crop was harvested on 3 August.

2.2. Measurements

Measurements were made at the site at different spatial and temporal scales. They included: regular dry-matter sampling during the growth period, continuous eddy covariance measurements, continuous soil respiration measurements and leaf scale assimilation measurements. We give details below on the measurements used in this study.

2.2.1. Vegetation measurements

Photosynthetic photon flux density (PPFD) absorption by the crop was measured using a ceptometer (Sunscan, Delta-T

Table 1 – Description of the treatments applied in the field during the winter wheat growing season

Date	Treatment
14/10/2004	Sowing
18/03/2005	Weeding (1.5l IP–1.5l Verigal)
22/03/2005	First application of liquid nitrogen (45 units/ha)
12/04/2005	Second application of liquid nitrogen (35 units/ha)
11/05/2005	Weeding (40 g Harmony–25 g Gratil)
12/05/2005	First application of NH_4NO_3 (40.5 units/ha)
30/05/2005	Second application of NH_4NO_3 (81 units/ha)
19/05/2005	Fungicide treatment (1l Opus – 0.5l Amistar)
03/08/2005	Harvest

Devices, Cambridge, UK). Measurements were performed in four different plots every 10 days between 12 May and 15 July 2005. The ceptometer was placed successively above the crop and at the soil surface. In each plot, 20–30 replicates were taken.

The total vegetation, green leaf, stem and ear areas were deduced from sampling. Each week between 22 April and 19 July 2005 all the plants were sampled from a row 30–50 cm long. Their green leaf surface was measured using a picture analyser (WinDIAS, Delta-T Devices, Cambridge, UK). The stem and ear (from 31 May) length and diameter were also directly measured. Green leaf area index (GLAI), stem area index (SAI) and ear area index (EAI) were deduced from these measurements by multiplying the respective average surfaces per tiller by the number of tillers per soil surface unit. For light interception calculations, the surface considered for stems and ears was the cross-section; for the estimation of the CO_2 flux exchange area, the surface considered was the external area. Total vegetation area index (VAI) was calculated by adding the leaf, stem and ear area indexes.

Finally, the leaf stomatal ratio, which is needed to deduce the assimilation from the measurement chamber, was determined by direct counting. Three plants were collected and two leaves were taken from each of them. On each leaf surface, three microscopic cuts were made on which the stomata number was counted.

2.2.2. *Photosynthesis measurements*

Photosynthesis was measured in the field, at the leaf scale, using an open gas exchange system (Li-Cor 6400, Li-Cor Inc., Lincoln, NE, USA) equipped with a modulable light source (6400-02B LED). The leaf was inserted into the chamber and saturated by light (1700 μmol m^{-2} s^{-1}) for about 25 min so that stomatal conductance reached equilibrium. The light was then reduced from saturation point to 500 μmol m^{-2} s^{-1} by steps of 200 μmol m^{-2} s^{-1}, and then to dark (0 μmol m^{-2} s^{-1}) by steps of 100 μmol m^{-2} s^{-1}. At each step, there was a 5-min delay before the measurements were taken in order to make photosynthetic apparatus adjustments to the light regime. The measurements were then repeated three times. Net assimilation (A, μmol CO_2 m^{-2} s^{-1}) to photosynthetic photon flux density (PPFD, Q, μmol m^{-2} s^{-1}) responses (A–Q curves) were deduced from these measurements. Measurements of leaf temperature, leaf-to-air vapour pressure difference (D_l), intercellular CO_2 concentration and stomatal conductance were also performed. The measurement procedure was as prescribed by the system manual (Li-Cor, 2003). Leaf temperature, air humidity and CO_2 concentration in the chamber were kept constant throughout the curve measurement.

Relevant parameters (A_s, the net and G_s, the gross assimilation at saturating light [μmol CO_2 m^{-2} s^{-1}], α, the quantum yield [μmol CO_2 μmol^{-1} photons] and R_d, the dark respiration [μmol CO_2 m^{-2} s^{-1}]) were deduced from the measurements by fitting a non-linear equation on measured A–Q curves. We used the Misterlich equation (Dagnelie, 1991):

$$A = (A_s + R_d)\left(1 - \exp\left\{\frac{-\alpha Q}{(A_s + R_d)}\right\}\right) - R_d = G_s\left(1 - \exp\left\{\frac{-\alpha Q}{G_s}\right\}\right) - R_d \qquad (1)$$

This equation was preferred to the classical rectangular hyperbola because it saturates at a lower PPFD and leads to more realistic saturation assimilation values (Aubinet et al., 2001). As a result, saturation assimilation and quantum yield values were typically 30 and 20% lower when deduced by Eq. (1) than by a classical Michaelis Menten equation. The fitting was obtained by non-linear regression using the Marquart–Levenberg method.

Homogeneity of the A–Q response in the crop was evaluated by repeating measurements at different leaf levels from the same tiller, on different tillers from the same plant and on different plants. The relationship between A and Q curve characteristics and season or climate was also investigated by repeating the measurements on 14 separate days characterised by different meteorological conditions and crop development stages. The impact of senescence on the leaf photosynthetic capacity was assessed by conducting measurements on both green and senescent leaves. Leaf respiration measurements were also performed during the night. The measurement chronology is summarized in Table 2.

2.2.3. *Air humidity characterisation*

In this paper, a distinction is made between the air saturation deficit (D_s) and the leaf to air vapour pressure difference (D_l). Both are defined as a difference between a saturated vapour pressure and actual air vapour pressure. However, in D_s, the saturated vapour pressure is taken at the air temperature while in D_l, it is taken at the leaf temperature. D_s was directly measured at the field scale by the meteorological station while D_l was measured at the leaf scale by the open gas exchange system. No direct D_l evaluation at canopy scale was available. It was thus deduced from D_s and from a leaf energy balance assessment as shown below (Section 3.4).

2.3. *Extrapolation model description*

2.3.1. *General procedure*

A model was developed in order to extrapolate A–Q curves from the leaf scale to the crop scale and to the whole vegetation season. First, the vegetation was divided into 10 layers of equal VAI. In each layer i, the incident PPFD (Q_i), was deduced from the PPFD measurements in taking into account the absorption by the vegetation situated above the middle of the i layer. The leaf gross assimilation (G_i) was then computed for each layer by introducing Q_i into a relationship derived from (1):

$$G_i = G_s\left(1 - \exp\left\{\frac{-\alpha Q_i}{G_s}\right\}\right) \qquad (2)$$

The crop gross assimilation was computed every 30 min by multiplying G_i by the area index of photosynthesizing vegetation in the layer (phototsynthetic area index, PsAI$_i$) and by summing each layer contribution. Finally, daily and yearly GPP were obtained by a summation of the half-hourly values.

2.3.2. *Calibration*

The model calibration required the description of the incident PPFD in each layer, of the PsAI distribution in the crop and a parameterisation of the photosynthetic parameters G_s and α.

Table 2 – Chronology of leaf scale measurements. F1 corresponds to flag leaf, F2 to last but one leaf, F3 to last but two leaf; 'senescent' means that the leaf has begun the death process but still photosynthetizes, and 'necrosed' means that the leaf cells are dead and therefore no more photosynthesis is observed

Date	Strategy	Leaf level	Note
1/05/2005	2 leaves from the same tiller	F2–F3	
5/05/2005	2 leaves from the same tiller	F2–F3	
15/05/2005	2 leaves from the same tiller	F2–F3	
19/05/2005	2 leaves from 2 different tillers of the same plant + exploratory respiration	F2	
28/05/2005	Study of 1 necrosed leaf in comparison with 1 green F1	F1–F3	3 measurements on a necrosed leaf (F3)
9/06/2005	2 leaves from 2 different plants	F2	
10/06/2005	2 leaves from the same tiller	F1–F2	
15/06/2005	2 F2, 1 F3 and 1 F1 from different plants	F1–F2–F3	F3 and 1F2 were damaged
22/06/2005	4 leaves from 2 different tillers	F1-F2	
10/07/2005	1 green F1 + back on the tiller of the 15/05/2005	F1–F2	Tiller of the 15/05/2005: F2 (1 measurement on necrosed part and 1 measurement on green part) + F1
13/07/2005	1 A–Ci + 1 A–Q curves on the same leaf	F1	
14/07/2005	1 green F1 + back on the tiller of the 05/05/2005 + 1 senescent leaf	F1	Tiller of the 05/05/2005: senescent F1
16/07/2005	1 green F1 and 1 damaged F1 + nocturnal measurements	F1	Night: 2 green leaves, 1 necrosed leaf and 2 senescent leaves
23/07/2005	Necrosed and senescent leaves	F1	

When possible (from 12 May to harvest), Q_i was directly estimated from ceptometer measurements as:

$$Q_i = Q_0 \tau^{2i-1/20} \tag{3}$$

where Q_0 is the incident PPFD above the crop (μmol m^{-2} s^{-1}), measured every 30 min by the micrometeorological station and τ represents the transmission factor of the whole crop, estimated as the ratio of the incident PPFD below and above the crop, measured with the ceptometer.

From emergence to 12 May, ceptometer measurements were not available due to the short height of the crop. Q_i was thus deduced from the Beer's law (Monteith and Unsworth, 1990):

$$Q_i = Q_0 \exp(-kV_i) \tag{4}$$

where k is the extinction coefficient and V_i is the cumulated VAI of the layers above the layer i (m^2 m^{-2}). The extinction coefficient k was evaluated by comparing Q_i estimations using the two approaches on two days (10 and 12 May) where both ceptometer measurements and leaf area measurements were available. This gave $k = 0.63$.

The evaluation of the PsAI distribution presents some difficulties that are specific to cereal crops. First, photosynthesizing areas do not relate only to leaves but also to stems and ears. However, the photosynthetic activity of these elements probably differs from those of the leaves. Second, it depends on the yellow organ distribution, which becomes predominant at the end of the season.

Stem and ear photosynthetic activity could not be measured directly as the measurement chamber did not allow photosynthesis measurements on thick elements. The possible impact of these vegetation parts on the GPP was thus assessed by comparing two hypotheses: the first one assuming that their photosynthetic activity was similar to that of the leaves and the second one that it was zero. Finally, a more realistic evaluation of the photosynthetic capacity of stem and ears was proposed by comparing model results with GPP eddy covariance estimates.

For the yellow organ distribution, we assumed a progressive development of the yellow organs from the bottom to the top of the canopy, which is the most realistic scenario in cereal crops. However, as the yellowing progression was not directly measured during the experiment, we evaluated the possible impact of another progression by also testing a homogeneous yellowing distribution.

Finally, the model required a description of G_s and α evolution according to the principal driving factors (time and/or climatic variables) and an evaluation of the vertical distribution of these parameters in the crop. This was obtained only after having thoroughly analysed the measurements made at leaf scale. Consequently, this part is discussed below (Section 3.4).

3. Experimental results

3.1. *Climatic conditions*

The mean daily climatic measurements results are given in Fig. 1. During winter the air temperature (T_a) was always below 10 °C and frost occurred twice: in December and at the end of February/early March. However, T_a never fell below −5 °C (Fig. 1a). Winter was also characterised by low air saturation deficit (D_s, Fig. 1b), low photosynthetic photon flux density (PPFD, Fig. 1c) and well-watered soil (Fig. 1d). In contrast, the end of spring was marked by much drier conditions: at the end of June, T_a reached 25 °C (Fig. 1b), D_s peaked to about 12 hPa (Fig. 1c) and the soil water content fell to 0.12 m^3 m^{-3} (Fig. 1d). These conditions were fairly representative of the regional averages for the previous 10 years, except for the water deficit, which was a bit more pronounced.

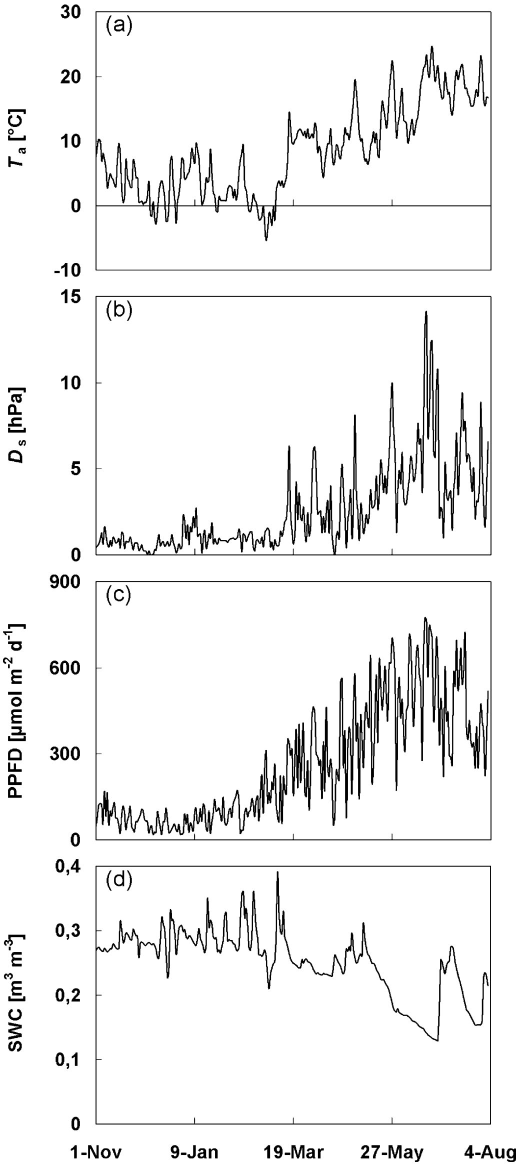

Fig. 1 – Seasonal evolution of climatic variable daily means from 1 November to 2 August: (a) air temperature, (b) air saturation deficit (D_s), (c) photosynthetic photon flux density (PPFD) and (d) soil water content at 5 cm (SWC).

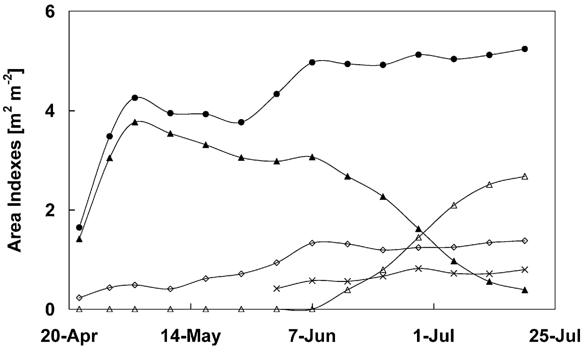

Fig. 2 – Seasonal evolution of the vegetation part area indexes: total vegetation (solid circles), green leaves (solid triangles), stems (open circles), ears (crosses) and yellow leaves (open triangles).

3.2. *Plant development*

Until May–June, the crop had not been submitted to any stress. Emergence occurred 2 weeks after sowing. Tillering (stages 21–30 on Zadoks scale; Zadoks et al., 1974) started in early March and ended in mid-April. At this point the VAI was about 1.6 and it then increased rapidly until early May (Fig. 2). In early May, a decrease in GLAI was observed that corresponded to stem elongation (Fig. 2). During this period, a few tillers on each plant (less than three per plant) exerted their dominance over the others, which regressed and died. The temporary reduction in GLAI was therefore because the growth of the dominant tillers did not compensate for the reduction of tillers per unit of soil surface. Flag leaf emergence occurred in mid-May (stage 37 on Zadoks scale). The subsequent VAI increase was due mainly to stem and ear development (ear emergence occurred in early June, stage 50 on Zadoks scale) (Fig. 2). On 7 June, VAI reached its maximum and then remained fairly constant until the end of July (Fig. 2). However, plant senescence began from early June, with the leaves at the bottom of the plants beginning to turn yellow. This explains the GLAI decline despite a constant VAI. The daily yellow leaf area index (YLAI) in Fig. 2 was not directly measured but was evaluated as the difference between the GLAI value on 7 June and the GLAI value of the day. At the end of July, the GLAI fell to zero and the YLAI reached about 50% of the VAI. The total SAI and EAI remained fairly constant during June and July and constituted about 25 and 15% of the VAI, respectively. At emergence, the ears rapidly reached their maximum size, and their further increase in diameter due to grain development was fairly negligible, which explains the EAI stability in June and July.

Compared with the regional average, crop development followed the standard rate until stage 57 on Zadoks scale (3/4 of inflorescence emerged), but after late May a more rapid development than average was observed, the drought accelerating leaf senescence and ear maturation. The drought effect was probably enhanced by the early sowing and the 'no ploughing' practice. At the end of July, when the ears were mature, precipitation occurred (results not shown), increasing the grain humidity and delaying the harvest date.

3.3. *Assimilation to light responses*

3.3.1. *Homogeneity and impact of senescence*

Thirty-two valid A–Q curves were produced between 1 May and 23 July 2005. As stated earlier (Section 2.2.2), measurements were performed at different plant levels (the three upper leaves) and on leaves at different senescence stages.

For green leaves, no significant differences between A–Q curves were observed between the different plants, between the tillers of the same plant or between the three upper leaves. This accords with the results reported by Veneklaas and Van Den Boogaard (1994), who did not find any effect of leaf age on photosynthesis in two varieties of winter wheat.

Fig. 3 presents three A–Q curves produced under the same meteorological conditions on three leaves at different senes-

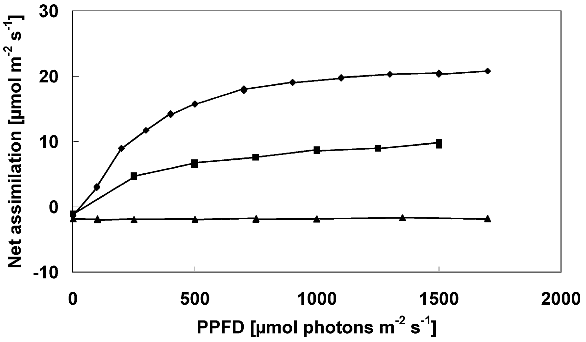

Fig. 3 – Three examples of A–Q curves corresponding to leaves at different senescence stages: green leaves (diamonds), yellow leaves at the beginning of senescence (squares) and dead leaves (triangles).

cence stages. In the case of the green leaf, the classical increase of *A* with *Q* was observed, with saturation reached at about 20 μmol CO_2 m^{-2} s^{-1} at large radiation. The maximal value of A_s observed was 21.4 μmol CO_2 m^{-2} s^{-1} on 28 May 2005. These values are of the same order of magnitude as those reported in the literature: Soegaard and Thorgeirsson (1998) reported 23.7 μmol CO_2 m^{-2} s^{-1} on spring wheat with a non-rectangular hyperbola and Rodriguez et al. (1998) reported 22.8 and 29.4 μmol CO_2 m^{-2} s^{-1} on the leaves of winter wheat using Eq. (1). The latter results were obtained during the tillering phase, which could explain these larger values.

A similar relationship was observed for the yellow leaf but with a lower saturation value, revealing a fall in leaf photosynthetic capacity. Finally, the dead leaf did not photosynthesize, but was still able to respire.

3.3.2. G_s *response to driving variables*

The relationship between the parameters extracted from the different A–Q curves and possible driving variables were analysed. In particular, as shown in Fig. 4, we gathered the distributions of G_s, α and R_d, with time, leaf temperature (T_l) and leaf-to-air vapour pressure difference (D_l). It is clear that G_s declined with the three variables (Fig. 4a–c). In the three cases, the trend was found to be significant ($P = 0.0026$, 0.0060 and 0.0047, respectively). However, these correlations did not each necessarily represent a real dependency because the three variables were not independent from each other. First, D_l is by definition related to leaf temperature and, second, these two variables were correlated with time as dry and hot conditions were observed mainly at the end of the observation period. We supposed that the G_s decline with D_l was probably the most representative of a real mechanism. Indeed, stomatal closure is known to occur under high D_l (e.g., Tewolde et al., 1993; Leuning, 1995), inducing leaf assimilation reduction. In these conditions,

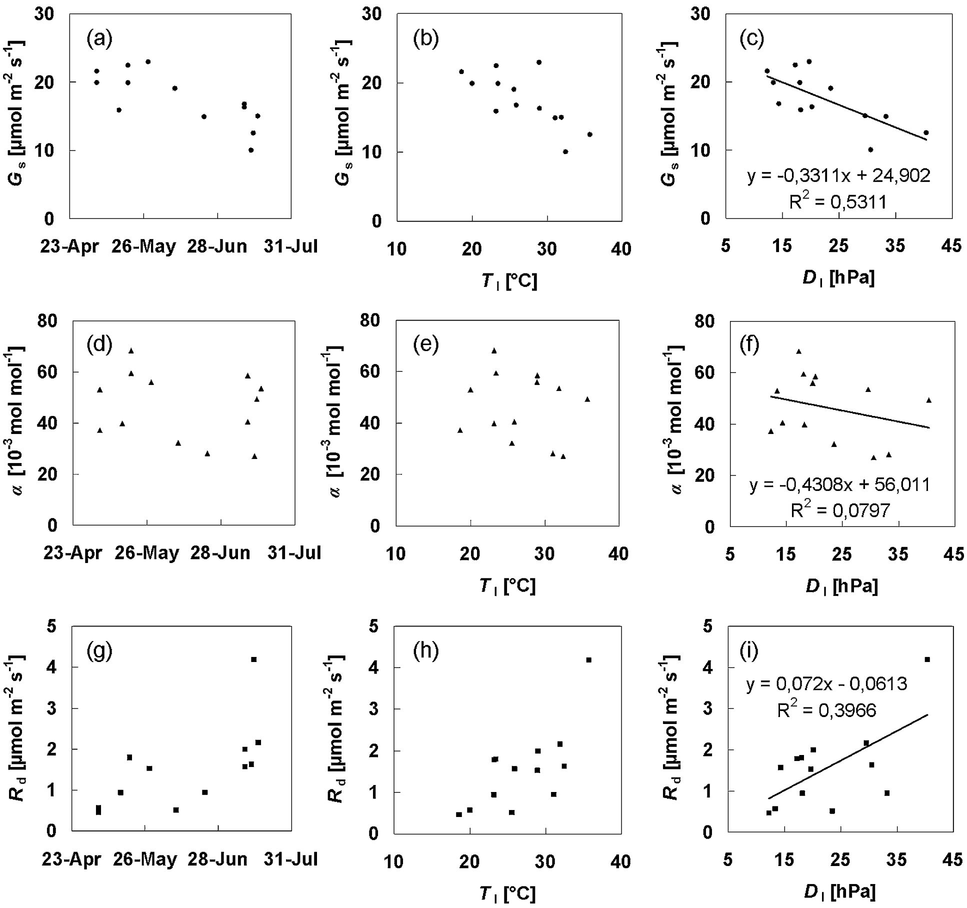

Fig. 4 – Relationship between gross assimilation at saturating light (G_s), dark respiration (R_d) and quantum yield (α) with time, leaf temperature (T_l) and leaf to air vapour pressure difference (D_l).

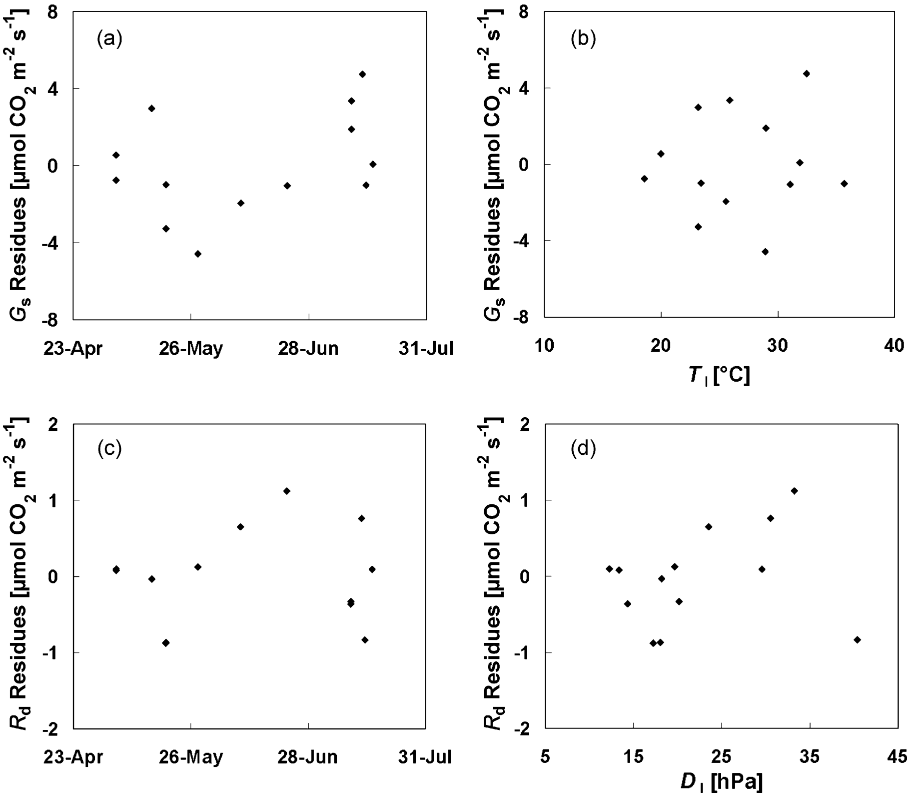

Fig. 5 – Relationship between the residues of the G_s response to D_l with time (a) and leaf temperature (b). Relationship between the residues of the R_d response to leaf temperature with time (c) and with leaf to air vapour pressure difference (d).

the responses of G_s to time and air temperature appear rather as the result of an artefact; indeed, the residues of the linear regression of G_s to D_l were not correlated to time and air temperature (Fig. 5a and b). The absence of correlation between residues and air temperature confirms the suggestion by Schulze and Hall (1982) that assimilation responses to high temperatures have often been confounded with the response to D_l. A modulation of the G_s to D_l response by soil water potential could also be possible, as shown by Xue et al. (2004). However, our measurements were not numerous enough and did not encompass a sufficiently large soil water potential range to allow us to highlight such an effect.

Finally, it should be noted that, due to the porometer regulation, which requires drying the air before pushing it into the chamber, the drought conditions were probably exaggerated by the chamber compared with the ambient air. However, the D_l values measured by the porometer reflect the conditions really underwent by the leaf portion whose assimilation is measured. It is therefore reasonable to think that, if the whole field were subjected to the same conditions, it would undergo the same assimilation decrease. Consequently we consider that the responses to D_l that were observed at leaf scale could be extrapolated at crop scale provided that a convenient estimation of D_l is given.

3.3.3. *α response to driving variables*

Quantum yield did not exhibit any trend with climatic variables or with time (Fig. 4d–f). The α values varied from 0.027 to 0.068 µmol CO$_2$ µmol^{-1} photons, with an average of about 0.046 µmol CO$_2$ µmol^{-1} photons and a standard error always lower than 0.002. These values are of the same order of magnitude as those reported in the literature: values of 0.042, 0.03–0.05 and 0.062 µmol CO$_2$ µmol^{-1} photons were reported, respectively, for winter wheat (Soegaard and Thorgeirsson, 1998), spring wheat (Rodriguez et al. (1998) and on average for C3 crops (Ruimy et al., 1995)). However, this last-mentioned value was derived from a Michaelis Menten regression, which gives larger estimates of this parameter, as stated earlier.

3.3.4. *R_d response to driving variables*

An increase of R_d with time, temperature and D_l was also observed (Fig. 4g–i). Here again, the three trends are significant ($P = 0.0314$, 0.0073 and 0.0211, respectively) but, as the three variables are linked as explained above, some of the correlations are expected to be artificial. In this case, the most probable response is that to temperature, as widely reported in the literatures (see in particular Lloyd and Taylor, 1994; Janssens et al., 2003). We therefore retained leaf temperature as the most important driving variable. Residues of the relationship of R_d to temperature not being found correlated to time and leaf to air vapour pressure difference (Fig. 5c and d), the relationships in Fig. 4 were again interpreted as an artefact and not taken into account.

3.4. *Result synthesis: G_s and α calibration*

The preceding results may be synthesised in order to allow parameterisation of the photosynthesis parameters. First, as the parameters were found not to depend on the leaf position (§ 3.3.1) or age (§ 3.3.2–3.3.4), they were supposed to be similar for all green leaves.

In Section 3.3.1 (Fig. 3), yellow leaves were found to still assimilate, albeit at a lower rate, suggesting a progressive drop in assimilation with the senescence stage. This was, however, difficult to model, mainly because of the high degree of subjectivity in defining the senescence stage. With regard to this difficulty, yellow leaf assimilation was considered as equal to zero.

Following the discussion in Section 3.3, the sole driving variable retained for G_s parameterisation was the leaf to air vapour pressure difference. The relation between D_l and G_s was approximated by a linear model. Least squares regression on the experimental points of Fig. 4c gave:

$$G_s = -0.331 D_l + 24.905 \quad (5)$$

with a R^2 equal to 0.53 and a P value of 0.0047. In order to scale up this relation, D_l should be known at the crop scale. It was stated above that this variable was not directly available but could be deduced from the leaf energy budget. We can indeed write:

$$D_l = e^*(T_l) - e_a \quad \text{with} \quad T_l = T_a + \frac{\text{Hu}}{\rho C_p u_*^2} \quad (6)$$

where e_a is the air vapour pressure and $e^*(T)$ is the saturation vapour pressure at temperature T, T_l (°C) and T_a (°C) are the leaf and air temperatures, respectively, H (W m^{-2}) is the sensible heat, u_* and u (m s^{-1}) are the friction and average velocity, respectively, ρ is the air density (kg m^{-3}) and C_p the air specific heat (J kg^{-1} K^{-1}).

However, D_l cannot be estimated when sensible heat and friction velocity are not available. It could therefore be relevant to evaluate the error made when approximating D_l by D_s. In practice, we found that at our site the differences between leaf and air temperatures were lower than 1 °C for 50% of the daytime and lower than 4.5 °C for 95% of the daytime, so that the difference between D_l and D_s was often small. The impact on the GPP of this approximation will be given in the sensitivity analysis.

Facing with the difficulty to scale up the G_s to D_l response, one could be tempted to replace Eq. (5) by a regression of G_s with the air saturation deficit measured by the meteorological station that could be easier to scale up. However this is not recommended as the air saturation deficit is not representative of the drought conditions to which the leaf was subjected in the porometer chamber. As a consequence this approach would lead to an overestimation of the crop water stress and to an underestimation of the crop GPP. The impact of the error made by doing this will also be evaluated in the sensitivity analysis.

Even if R_d does not appear explicitly in the model, its evaluation was required in order to determine α. Following the discussion in Section 3.3, R_d was parameterised as a function of leaf temperature. We used the Van't Hoff equation (1898) (Lloyd and Taylor, 1994):

$$R_d = R_{d\,25} Q_{10}^{(T_a - 25/10)} \quad (7)$$

where R_{d25} is the dark respiration (μmol m^{-2} s^{-1}) at 25 °C, Q_{10} is the sensitivity of respiration to temperature and T_a is the air temperature (°C). Regression gave R_{d25} = 1.10 (S.E. = 0.22) and Q_{10} = 2.83 (S.E. = 0.75) with a R^2 equal to 0.59.

As no clear relationship of α with climatic and non-climatic parameters was found, it was fixed as a constant. Its value was computed in order to reduce uncertainty for this parameter as much as possible. All the A–Q curves measured on green leaves were gathered and a model combining Eqs. (1), (5) and (7) was fitted on these data. As a result, α was the unique parameter to adjust in a non-linear regression between net assimilation and PPFD, air temperature and leaf to air vapour pressure difference. All variables were measured by the porometer. This regression gave α equal to 0.0452 μmol CO$_2$ μmol^{-1} photons, with a standard error of 0.0009.

4. Model results

4.1. Seasonal flux evolution

The general evolution of GPP estimated with our model is presented in Fig. 6a, along with those provided by eddy covariance measurements (Moureaux et al., in press). For this presentation, we used the best model estimate obtained by adjustment of the eddy covariance data for the development and maturation periods. As a result, the summed GPP were equal for the two estimates for these periods. They were 1570 g C m^{-2}. Except in early spring, scaled-up and eddy covariance estimates of GPP matched each other quite closely (slope of the regression = 1.13, R^2 = 0.94). This high level of

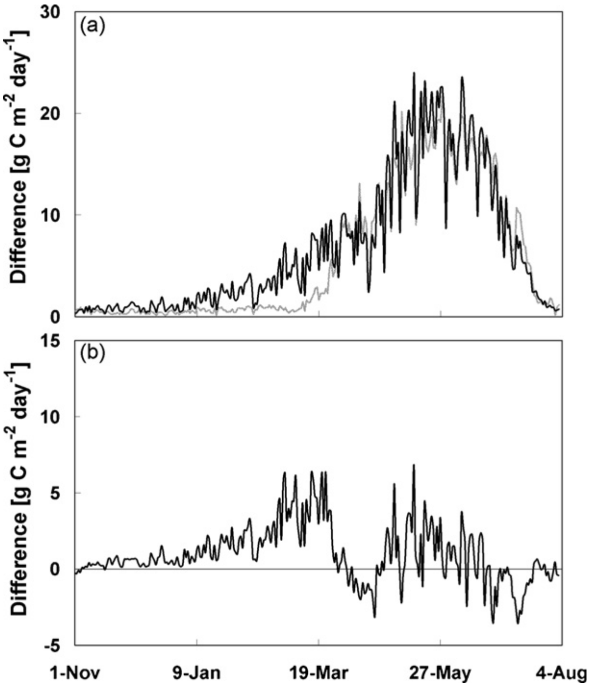

Fig. 6 – (a) Seasonal evolution of the winter wheat crop daily GPP estimated with the scaling up model (solid line) and with eddy covariance measurements (grey line); (b) seasonal evolution of the difference between the model and the measurements.

agreement related not only to the seasonal trend, but also to day-to-day variations, as observed particularly at the end of the season. Before early March, the assimilation was slightly positive in both cases and increased sharply from early March until early May, which corresponds to the phase of intense crop development. Maximal values were reached in May, after which the GPP fell abruptly until the end of the season, when it reached zero. The disagreement between the two estimates that appears in winter and spring is discussed later.

4.2. *Sensitivity analysis*

4.2.1. *Stem and ear assimilation*

First, in order to assess the possible impact of ear and stem contributions to GPP, the model was run three times using three hypotheses to estimate the PsAI: (A) only the leaves are photosynthesising (i.e., PsAI = GLAI); (B) stems and leaves photosynthesise at equivalent rates (PsAI = GLAI + SAI); (C) stems, leaves and ears photosynthesize at equivalent rates (PsAI = GLAI + SAI + EAI). Before May, the three runs gave the same results as the stems and ears were not well developed (cf. Fig. 2). Paired t tests performed on the data after the beginning of May showed that the differences between the three runs were significant (cf. Fig. 7) ($P < 0.0001$). From mid-May until the end of the season, the three situations clearly differed, with maximum values of 21, 28 and 36 g C m^{-2} day^{-1} for situations A, B and C, respectively. In addition, the maximum was reached later in the last two situations (8 June) than in the first (12 May), as the stem and ear development occurred later in the season while the green leaf area was already decreasing due to crop senescence. Cumulated GPP was highly sensitive to this parameter as the inclusion of the stems in the photosynthetically active organs led to an increase of 40% in the initial GPP estimation and the inclusion of the ears to an additional increase of 15%. Compared with the eddy covariance GPP estimations, the extrapolation scheme underestimated the GPP in situation A and overestimated it in situations B and C. This suggests that the stem and ear contributions to assimilation are clearly important but that these organs probably present a lower photosynthetic capacity than the leaves. The best agreement with eddy covariance measurements was obtained by taking hypothesis B and assuming a stem photosynthetic capacity equal to 63% of that of leaves. Further measurements made in 2007 on the same field confirmed that the stems photosynthesize but at a lower rate. It was used in the following simulations. This result clearly needs to be confirmed by further A–Q curves made on stems in the field.

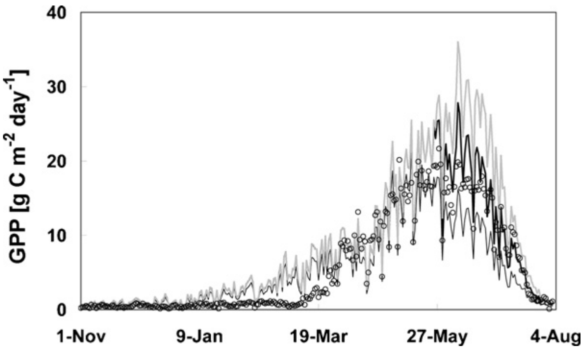

Fig. 7 – Comparison between the GPP seasonal evolutions simulated using three PsAI scenarios: (A) only leaves (thin line); (B) leaves and stems (solid line); or (C) leaves, stems and ears (grey line) are photosynthesizing. Open circles correspond to eddy covariance measurements.

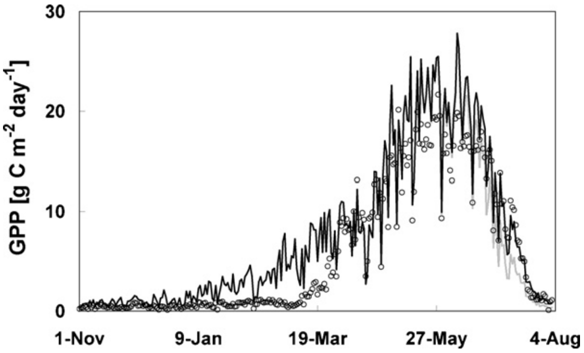

Fig. 8 – Comparison between the GPP seasonal evolutions simulated postulating a homogeneous (grey line) or a bottom (solid line) distribution of yellow organs, assuming that leaves and stems photosynthesize. Open circles correspond to eddy covariance measurements.

4.2.2. *Spatial distribution of yellow parts*

In the preceding model, yellowing was supposed to progress from the crop bottom to the top (bottom distribution). However, even if highly probable, this hypothesis was not checked experimentally. Its impact was therefore tested by comparing the preceding simulations with those of a model submitted to a similar yellowing in all the crop layers. The difference between the two models was about 7–9%, depending on the situation. The impact of the yellowing distribution was significant only after early June (the paired t test gave $P < 0.0001$), the GPP being always higher for the bottom rather than the homogeneous repartition (Fig. 8). This is because, with the bottom distribution, a larger part of the upper leaves, which take greater advantage of sun radiation, remained photosynthetically active for a longer time. The difference in yellowing distribution did not severely affect the maximum daily assimilation values (27 and 28 g C m^{-2} day^{-1} for homogeneous and bottom distributions, respectively). A comparison of these trends with eddy covariance GPP showed that the bottom distribution gave a more realistic evolution of the GPP at the end of the season, confirming the former hypothesis.

4.2.3. *Regression parameters*

In order to study the sensitivity S of annual GPP to the model parameters (P), we used the following definition:

$$S = \frac{\Delta G/G}{\Delta P/P} \tag{8}$$

where Δ represents an absolute variation and the parameter P may represent saturation gross assimilation, dark respiration or quantum yield. This ratio is dimensionless. The impact of each parameter uncertainty on the annual GPP was therefore

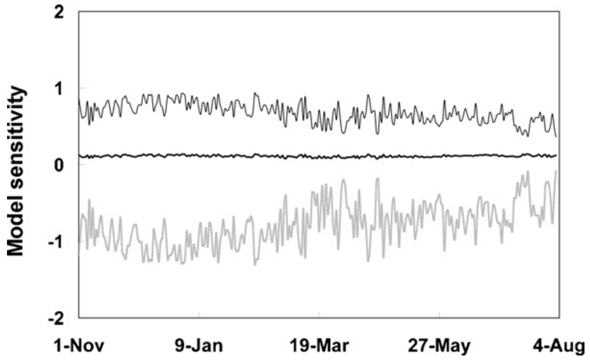

Fig. 9 – Seasonal evolution of the model sensitivity to parameter uncertainties: G_s (grey line), α (thin line) and R_d (thick line).

computed by multiplying the former with the corresponding sensitivity.

The normalized sensitivity of annual GPP to G_s, α and R_d were about −0.65, 0.6 and 0.11, respectively (Fig. 9). As the uncertainties on these parameters (Standard Errors) were 5, 2 and 10%, respectively (§ 3.4), their impact on the annual GPP was about 4%, slightly larger than 1 and 1%, respectively.

Surprisingly, the sensitivity to G_s was negative, meaning that an increase of this parameter caused a GPP decrease. This can be explained by the calibration procedure: as α was deduced from a regression after G_s had been fixed, a greater G_s value would induce a lower α value. This had more impact on the GPP than the G_s increase itself, as radiation was not saturating for most of the canopy most of the time. The fact that the parameters are estimated in reference to α explains that the sensitivities are larger in absolute value in winter and spring than in summer. Indeed, during these periods, leaves were rarely saturated by light and therefore their assimilation rate was determined more by quantum efficiency than by other parameters.

The last point of this sensitivity analysis concerns the impact of the way the response of G_s to air humidity is parameterised. We found, on the one hand, that the error made by approximating D_l by D_s in the scaling up procedure led to a GPP overestimation of 20 g C m^{-2}. On the other hand, the error made by replacing Eq. (5) by a G_s to D_s regression led to a GPP underestimation of 70 g C m^{-2}. The impacts of these errors on GPP went thus in the same way as predicted but their importance were limited. This is because the drought condition underwent by the crop were quite smooth and limited in time. These impacts could be more important in crops subjected to more arid conditions.

4.3. *Comparison with eddy covariance measurements*

The preceding analysis suggested that more realistic assimilation estimations were obtained when assuming that stems assimilate at a lower rate than leaves (63%) and that the yellowing progressed upwards from the lower parts of the canopy. The evolution of the GPP extrapolated from leaf scale measurements using these hypotheses and deduced from eddy covariance estimations is presented in Fig. 6a, as well as the difference between them (Fig. 6b).

We will now focus on these differences. First, it seems clear that before April the scaled-up GPP estimates were systematically higher than the eddy covariance estimates. This is because the extrapolation scheme does not take account of the photosynthesis response to low temperatures. Clearly, the eddy covariance deduced estimate was more realistic here: negative air temperatures were observed between mid-February and early March, which hindered any photosynthetic activity. This effect cannot be taken into account by the extrapolation scheme because no leaf scale measurements were performed during this period. The overall impact of this overestimation on total GPP was 270 g C m^{-2}.

From April until harvest, the average difference between the two GPP estimates was zero as a result of the stem photosynthetic capacity adjustment. The root mean squared difference between the two estimates was 1.9 g C m^{-2} d^{-1} which is about 16% of the daily average GPP. It was mainly negative in April and July and positive in June and May, suggesting that the extrapolation scheme overestimated the GPP in the latter months and underestimated it during the former months. Underestimation in July could be due to neglecting the photosynthetic contribution of the ‘yellow’ organs. Indeed, in this scheme, only the green organs were taken into account in the photosynthetic area, whereas we showed earlier (Fig. 3) that senescent organs could still assimilate, albeit at a lower rate. The overestimation in May and June was positively correlated with the GPP itself and with radiation, and was not related to D_l.

5. Conclusion

A model was developed in order to scale up assimilation measurements from leaf to canopy scale in a winter wheat crop. The model was based on porometer measurements made in the field during the growth period. These measurements showed an increase in assimilation with PPFD of dark respiration with temperature and a decrease in saturating assimilation with leaf to air vapour pressure difference. The model correctly reproduced the GPP during the development and maturation period, but not during winter because it did not take account of the photosynthesis reduction at low temperature. An analysis was developed in order to determine the most important causes of uncertainty affecting these results.

The most important cause of uncertainty resulted from the assimilation of stems and ears. A model considering only assimilation by leaves underestimated the GPP by 23%, whereas a model considering stems as organs assimilating at the same rate as leaves increased the GPP by about 600 g C m^{-2}, leading to a 14% overestimation GPP. These two estimates bracketed the eddy covariance estimate, suggesting that the reality lay between these two extreme hypotheses. The best agreement with the eddy covariance estimate was obtained by assuming a stem assimilation equal to 63% of leaf assimilation, which was found compatible with further leaf scale measurements. More generally, this result shows that a correct determination of stem and ear assimilation is critical when scaling up wheat (and, more generally, cereal) assimilation from leaf to canopy scale.

The second cause of uncertainty was linked to the yellow organ distribution. In particular, it was shown that a model with a homogeneous repartition of the yellow organs gave GPP estimates 7–9% lower than the model, postulating a bottom yellowing distribution. This suggests the importance of better evaluation of yellow organ progression and photosynthetic capacity in the field. Measurements with a chlorophyll meter would be an option for clarifying this area of assimilation. Hanan et al. (2005) reported a similar problem, showing that their land surface model (SiB2) overestimated crop photosynthetic uptake at the end of the season because they had not taken into account the physiological senescence.

The third cause of uncertainty is linked to the winter period. From January to March, the scaling up overestimated the GPP because the assimilation reduction at low temperatures was not taken into account by the model. The resulting error was about 10% of the GPP. Such an underestimation is specific to winter species and would not be so critical for spring species that do not have to contend with low temperatures for long periods. The problem could be easily solved by performing some A–Q curves in winter conditions and introducing an assimilation response to low temperature in the model.

Finally, the impact of the A–Q curve parameter uncertainties was found to be the weakest, not exceeding 4%. Rodriguez et al. (2000) reported that for well-irrigated conditions a simple approximation based on a light response curve avoiding the calculation of the coupling between photosynthesis and stomatal conductance could be used. This study confirmed that this is possible once a careful identification of photosynthesizing organs and monitoring their evolution has been performed at the site.

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Article 5

Carbon balance assessment of a Belgian winter wheat crop (Triticum aestivum L.*)*

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Carbon balance assessment of a Belgian winter wheat crop (*Triticum aestivum* L.)

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Abstract

The carbon balance of a winter wheat crop in Lonzée, Belgium, was assessed from measurements carried out at different spatial and temporal scales between November 2004 and August 2005. From eddy covariance measurements, the net ecosystem exchange was found to be $-0.63\,\mathrm{kg\,C\,m^{-2}}$ and resulted from the difference between gross primary productivity (GPP) ($-1.58\,\mathrm{kg\,C\,m^{-2}}$) and total ecosystem respiration (TER) ($0.95\,\mathrm{kg\,C\,m^{-2}}$). The impact of the u_* threshold value on these fluxes was assessed and found to be very small. GPP assessment was partially validated by comparison with an estimation scaled up from leaf scale assimilation measurements. Soil respiration (SR), extrapolated from chamber measurements, was $0.52\,\mathrm{kg\,C\,m^{-2}}$. Net primary productivity, assessed from crop sampling, was $-0.83\,\mathrm{kg\,C\,m^{-2}}$. By combining these fluxes, the autotrophic and heterotrophic components of respiration were deduced. Autotrophic respiration dominated both TER and SR. The evolution of these fluxes was analysed in relation to wheat development.

Keywords: agricultural crop, autotrophic respiration, carbon balance, eddy covariance, GPP, heterotrophic respiration, NEE, TER, winter wheat

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Introduction

The aim of this study was to assess the carbon (C) balance of a Belgian winter wheat crop from measurements carried out at different spatial and temporal scales. It is not necessary to recall the role of carbon dioxide (CO_2) in the global climate change (IPCC, 2007) and the impact of terrestrial ecosystems on the global CO_2 balance. Besides this, crops cover about one third of the European land surface (FAOSTAT, 2003) and one quarter of Belgian land surface (MRW-DGA, 2005). The CO_2 exchange between crops and atmosphere is therefore a major driver of atmospheric CO_2 fluctuations at an annual scale and, possibly, at an interannual scale. In addition, preceding studies (Smith *et al*., 2000; Freibauer *et al*., 2004; Lal, 2004; Smith, 2004) suggested that crops had a significant potential to store C and that some changes in crop management could induce greenhouse effect mitigation. All of this justifies the necessity to better quantify the crop C balance components and to better understand their response to climate and to cultural management.

Over the past decade, networks using the eddy covariance method have been established worldwide to continuously measure the CO_2 exchanges between terrestrial ecosystems and the atmosphere (Baldocchi *et al*., 2001; Baldocchi, 2003; Valentini, 2003). This method allows a direct evaluation of the net CO_2 exchange of terrestrial ecosystems (NEE) and an extrapolation to the gross primary productivity (GPP) and to the total ecosystem respiration (TER) (e.g. Falge *et al*., 2002; Gilmanov *et al*., 2003, 2007; Reichstein *et al*., 2005; Suyker *et al*., 2005). However, it does not give other terms of the ecosystem C balance. In particular, it does not allow discriminating between below- and aboveground contributions or between autotrophic (resulting from plant activity – roots and aboveground parts) and heterotrophic (due to the decomposition of organic materials by soil microorganisms) components of TER.

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Therefore, the net primary productivity (NPP), which represents the C stored in the plants, cannot be deduced from the sole eddy covariance method.

Despite their obvious importance, few crop C balance analyses were carried out until now (e.g. Anthoni *et al*., 2004a; Suyker *et al*., 2004; Hollinger *et al*., 2005; Suyker *et al*., 2005), only one concerning a winter wheat crop (Anthoni *et al*., 2004a). In this study, Anthoni *et al*. combined eddy covariance NEE measurements, NPP assessments and simulations using a soil C balance model.

The objectives of the present study are (i) to assess the C balance of a winter wheat crop (i.e. to evaluate the crop NEE, GPP, TER and NPP), (ii) to discriminate the ecosystem respiration between its auto and heterotrophic contributions and (iii) to study the evolution of the C balance components with climate and season. To these ends, different flux measurements made at different spatial and temporal scales were combined: crop scale fluxes using the eddy covariance method, leaf scale assimilation using a porometer, soil plot scale respiration using soil chambers and dry matter (DM) and C content using biomass samplings. At the crop scale, NEE was measured every half hour using the eddy covariance method. GPP and TER were inferred from these measurements. At the leaf scale, leaf net assimilation was measured once a week and scaled up to provide a second GPP assessment (Hoyaux *et al*., in press). At the soil plot scale, soil respiration (SR) was measured every half hour with an automatic system and once a week with a manual system. The SR of the whole crop was modelled using these measurements. At the plant scale, crop development was monitored and samples were taken weekly or fortnightly to assess NPP. The fluxes obtained using these methods were combined to evaluate the different terms of the C balance and, when relevant, comparisons between the methods were made.

The approach is here applied to winter wheat, which is justified by its relative importance in Belgium (winter wheat accounts for 23% of Belgian crop area, Statistics Belgium, 2005); however, most of the procedure described here could be applied to any other crop.

Materials and methods

Site description

The studied site is an agricultural field in Lonzée, Belgium. This site is included in the CarboEurope-IP ecosystem network and has been described in detail by Moureaux *et al*. (2006). The climate is temperate maritime. The mean annual temperature is about 10 °C and the annual precipitation is about 800 mm. The site is a quadrilateral area of ca. 12 ha located on fairly flat plateau. The site provides a fetch of 240 m in the southwest, which is the main direction. In this direction, the adjacent crop was planted with sugar beet. The second main wind direction is northeast, with a fetch of 200 m. This site of the field is bordered by a potato crop. A footprint analysis of our site was carried out using the forward Lagrangian stochastic trajectory model by Rannik *et al*. (2003). The site evaluation approach is described in detail in Göckede *et al*. (2005). It appears that, excepted for one sector and for strongly stable conditions, more than 80% of the flux contribution is from the target area, which corresponds to representative results for the target land cover type. The remaining sector corresponds to 5% of wind occurrence and more than 77% of flux contribution is from the target area, even during stable conditions (M. Göckede, personal communication).

In 2005, winter wheat (*Triticum aestivum* L.) (Dekan variety) was grown. The seed was sown on 14 October 2004, 2 weeks after the sugar beet harvest. As the soil conditions were appropriate, a minimum tillage with a rotary harrow was performed on 10 cm before sowing the wheat. Between mid-April and late May, 201.5 kg mineral nitrogen per hectare was applied in four stages. No farmyard manure had been applied since 1996. The crop was harvested on 3 August 2005.

General methodology

Throughout this paper, micrometeorological conventions are used (i.e. fluxes towards the surface are counted as negative and fluxes away from the surface as positive). The presented fluxes related to the period from 1 November 2004 to 2 August 2005. As plant emergence occurred about 10 days after the crop had been sown, we consider that assimilation began on 1 November. However, as the crop was harvested on 3 August the study period ended on 2 August.

The computation methodology used to assess the C balance terms is presented in Fig. 1. Flux measurements were performed at four spatial and temporal scales: crop sampling at the plant scale; eddy covariance at the ecosystem scale; diffusive fluxes at the leaf scale; and SR at the soil plot scale. Using these approaches, the NPP, NEE, net assimilation and SR, respectively, were measured. From the NEE, two fluxes were inferred: the TER and the $\mathrm{GPP}_{\mathrm{EC}}$. Similarly, aboveground autotrophic respiration ($R_{\mathrm{aa,LS}}$) and GPP ($\mathrm{GPP}_{\mathrm{LS}}$) were deduced from net assimilation. All these fluxes were combined to obtain the total autotrophic respiration (R_{a}), the belowground autotrophic respiration (R_{ab}), the heterotrophic respiration (R_{h}) and an independent assessment

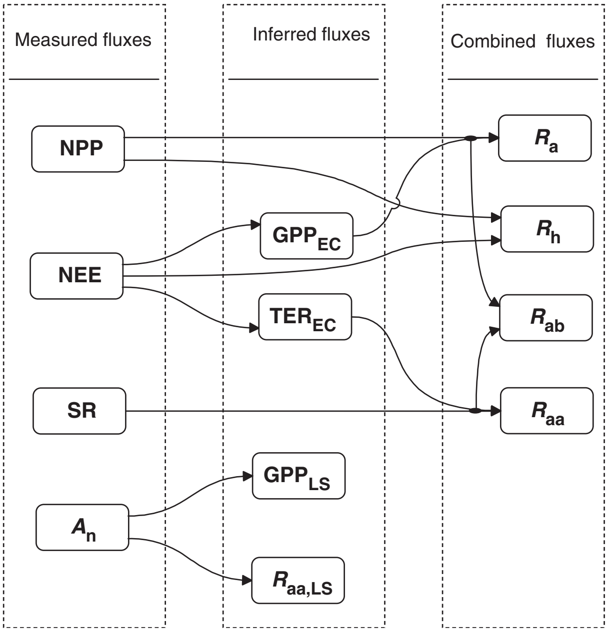

Fig. 1 Flow chart showing the computation methodology.

of R_{aa}. The ways in which the fluxes were combined are described in the following sections.

Measured fluxes

Crop sampling and biometric measurements. In order to monitor crop development, growth stage observations were performed once a week on several winter wheat plants. In addition, DM and C content, as well as vegetation area indexes, were measured.

From mid-March to harvest, aboveground crop samples were collected in four zones. Sampling was performed fortnightly from mid-March to mid-April and weekly thereafter because of faster crop development. Until early May, sampling was performed on three 1-m-long rows; the sample area was then reduced to three 0.5-m-long rows because the samples were becoming too voluminous. Where relevant, the total aboveground DM was divided into three parts: ears; dead and yellow leaves and stems and green leaves.

As wheat roots can reach a depth of up to 2 m, it was not feasible to collect all the belowground biomass. In order to estimate their DM, we used the ratio between belowground and total biomass described by Baret *et al.* (1992). This ratio evolved exponentially with growth degree-days. It was 0.6 at emergence and <0.1 at maturity. This last value was confirmed by Hay (1995) who reported a ratio of about 0.1 at harvest.

Grain yield was measured at harvest by gathering grains from four zones measuring 2.05 m × 50 m. After grain harvest and straw removal, the remaining aboveground DM was measured by taking eight samples from three 0.5-m-long rows.

The ear, leaf and stem C content was measured on crop samples obtained from mid-March to harvest. The root C content was not measured but it was assumed that the C percentages of above- and belowground plant parts were the same. These measurements allowed the NPP to be estimated by multiplying the DM by the C percentage. The C percentage of crop residues was also measured. By adding the residue and root C content, the amount of C returned to the soil was assessed.

The green leaf area index (GLAI) was measured using a camera and a picture analyser (Windias, Delta-T Devices, Cambridge, UK). These measurements were carried out once a week between mid-April and mid-July. During the same period, stem and ear lengths and diameters were also measured and the stem and ear area indexes were deduced by assimilating them to a cylinder and a parallelepiped, respectively.

Eddy covariance measurement. Fluxes of CO_2, water vapour and sensible heat were measured with an eddy covariance system made with a research-grade sonic anemometer (Solent Research R3, Gill Instruments, Lymington, UK) placed at a height of 2.7 m and an infrared gas analyser model Li-7500 (Li-Cor Inc., Lincoln, NE, USA); this was the standard system used in the CarboEurope-IP and FLUXNET networks (Grelle & Lindroth, 1996; Moncrieff *et al.*, 1997; Aubinet *et al.*, 2000). This system and the complementary measurements were described by Moureaux *et al.* (2006).

Turbulent fluxes were subjected to a stationarity test (Foken & Wichura, 1996) and only the data that met the quality test with a deviation lower than 30% were used for the net exchange computation. The impact of the quality criterion on annual NEE had already been found to be very limited (Moureaux *et al.*, 2006). In addition, stable night-time conditions were identified using a criterion based on the friction velocity (u_*). The impact of the threshold value on different fluxes was analysed. The fluxes were computed with u_* threshold values ranging from 0 to $0.3\,\mathrm{m\,s^{-1}}$. Using visual analysis, the threshold appeared to be between 0.2 and $0.3\,\mathrm{m\,s^{-1}}$. The results presented in this paper correspond to a threshold of $0.22\,\mathrm{m\,s^{-1}}$.

Throughout this paper, the NEE is considered as the sum of turbulent flux and storage flux. The latter flux was computed using a single concentration measurement at a height of 2.7 m. A comparison was performed between storage fluxes computed from a single point and from a four-point profile during stationary periods. On average, the storage computed from the four-point profile was 6% lower than those computed from a single point.

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Eddy covariance data quality was also assessed by analysing the energy balance. The sum of turbulent fluxes [i.e. sensible (H) and latent heat (LE) fluxes] was compared with available energy [i.e. the difference between net radiation (R_n) and soil heat flux (G)]. The relationship we found was: $(H + \mathrm{LE}) = 0.94(R_n - G) - 14.61$ with a r^2 of 0.82. This attests a fairly good energy balance closure compared with what is usually found on other sites: in a comparison of the energy balance closure of 22 FLUXNET sites, Wilson *et al.* (2002) reported slope, intercept and r^2 ranging, respectively, between 0.53 and 0.99, −32.9 and 36.9 $\mathrm{W\,m^{-2}}$, and 0.64 and 0.36 without any effect of vegetation height. The imbalance at our site could be due to the neglecting of heat storage in the air below the measurement height and in the canopy, to the neglecting of energy consumed by photosynthesis or to the loss of high-frequency fluctuations for water vapour. Including the first two terms, as well as the ground heat storage above the plate in the energy balance of a maize crop and a soybean crop, Meyers & Hollinger (2004) increase indeed the regression slopes of 3% to 6%. Losses of high-frequency fluctuations were corrected for CO_2 according to the procedure described by Aubinet *et al.* (2001). However, these losses are more important for water vapour (Baldocchi, 2003). In conclusion, although the energy balance closure test provides only an indirect validation of CO_2 measurements, the good degree of energy balance closure suggests the good quality of CO_2 measurements all the more that most of the causes of errors we identified in the energy balance are specific to energy fluxes and do not affect CO_2 fluxes.

Data gaps were filled using parameterization or mean diurnal variation approaches. Where there were missing meteorological data, the mean diurnal variation was applied using an 11-day data window (Falge *et al.*, 2001). Elsewhere, gaps were filled using the empirical NEE–climate relationship. Daytime gaps were estimated using an NEE–photosynthetically photon flux density (Q) relationship based on 10-day periods. The relationship used was the Misterlich equation (Dagnelie, 1973; Aubinet *et al.*, 2001):

$$\mathrm{NEE} = -(N_s + R_d)\left(1 - \exp\left(\frac{-\alpha Q}{(N_s + R_d)}\right)\right) + R_d, \quad (1)$$

where N_s is the NEE at light saturation, α is the apparent quantum efficiency (i.e. the initial slope of the curve) and R_d the dark respiration.

Night-time gaps were estimated using a respiration–soil temperature relationship (Lloyd & Taylor, 1994):

$$\mathrm{NEE} = R_{10} \exp\left\{E_0\left(\frac{1}{56.02} - \frac{1}{T_{S5} - 227.13}\right)\right\}, \quad (2)$$

where R_{10} is the respiration flux at 10 °C, T_{S5} is the soil temperature expressed in Kelvin and measured at a depth of 5.5 cm and E_0 is a parameter characterizing the respiration sensitivity to temperature. The parameterization was fitted on data for the whole period corresponding to mixed conditions.

Leaf scale measurement. Leaf scale measurements and their extrapolation at canopy scale have been described by Hoyaux *et al.* (in press). At the leaf scale, assimilation response to photosynthetically photon flux density (A–Q curve) was measured using an open gas-exchange system (Li-Cor 6400, Li-Cor Inc.) equipped with an adjustable light source (6400-02B LED). Net assimilation was measured for radiation ranging from 1700 to 0 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$. During the measurement, CO_2 and H_2O concentrations and leaf temperature were maintained at constant values. Net assimilation measurements were performed once a week between early May and late July on different leaves. Homogeneity of the A–Q response in the crop was evaluated by repeating measurements at different leaf levels from the same tiller, on different tillers from the same plant and on different plants. The relationship between A–Q curve characteristics and season or climate was also investigated by repeating the measurements on 14 separate days characterized by different meteorological conditions and crop development stages. The impact of senescence on the leaf photosynthetic capacity was assessed by conducting measurements on both green and senescent leaves. In total, about 30 A–Q curves were collected.

A Misterlich relationship, similar to Eqn (1), was fitted on each of the curves:

$$A_n = -G_{s,L}\left(1 - \exp\left(\frac{-\alpha_L Q}{G_s}\right)\right) + R_{d,L}, \quad (3)$$

from which the leaf gross assimilation at saturating light ($G_{s,L}$), the leaf apparent quantum efficiency (α_L) and the leaf dark respiration ($R_{d,L}$) were deduced.

The dependence of these three parameters on climatic and nonclimatic factors was examined. First, no significant differences between A–Q curves were observed between the different plants, between the tillers of the same plant or between the three upper leaves. This accords with the results reported by Veneklaas & Van den Boogaard (1994), who did not find any effect of leaf age on photosynthesis in two varieties of winter wheat. Then, $G_{s,L}$ was found to depend linearly on vapour pressure deficit, and $R_{d,L}$ to increase exponentially with temperature, but no clear dependence of α_L was observed. These relationships were established from measurements carried out between May and mid-July and extrapolated to the whole period. The vegetation area index was deduced from biometric measurements (see 'Crop sampling and biometric measurements'). As they were not known before mid-April, they were assumed to evolve linearly with time between sowing and the first measurement. The measurement results and the leaf-to-crop scaling up procedure are described in more detail in Hoyaux *et al*. (in press). The model assumed that wheat senescence began in the lower part of crop. A sensitivity analysis also showed that the contribution of stem and ear assimilation to the GPP was important. Unfortunately, as the porometer measurement head was not designed for thick plant elements, it was not possible to evaluate it experimentally. It was, therefore, assessed by fitting the cumulated $\mathrm{GPP_{LS}}$ on the eddy covariance estimate (Hoyaux *et al*., in press). Therefore, the cumulated $\mathrm{GPP_{LS}}$ and $\mathrm{GPP_{EC}}$ cannot be considered as independent. However, their relative evolutions are independent and will be compared below. Finally, the leaf-to-crop scaled up dark respiration was associated to the autotrophic respiration of the aboveground parts of the crop ($R_{\mathrm{aa,LS}}$).

SR measurement. SR was assessed from a combination of automatic continuous and manual SR measurements, carried out between April and the harvest. Five automatic closed dynamic chambers (Norman *et al*., 1992; Longdoz *et al*., 2000; Davidson *et al*., 2002) were placed 1 m from each other in a representative part of the crop. Each chamber measured SR every half hour. The SR extrapolation to the whole vegetation period was performed by parameterizing the SR climatic response for a selected measurement period and applying the resulting equation to the whole period. The SR responded mainly to temperature and soil water content (Raich & Schlesinger, 1992; Raich & Potter, 1995; Davidson *et al*., 1998; Duiker & Lal, 2000; Mielnick & Dugas, 2000; Han *et al*., 2007). For the parameterization, a multiplicative model was chosen:

$$\mathrm{SR} = R_{\mathrm{s},10}\exp\left(E_{0,\mathrm{S}}\left(\frac{1}{56.02}-\frac{1}{T_{\mathrm{S5}}-227.13}\right)\right) \\ a\left[1-\exp\left(-b\left(W_{\mathrm{s}}^{2}-c\right)\right)\right], \tag{4}$$

where $R_{\mathrm{s},10}$ was the normalized SR at 10 °C, $E_{0,\mathrm{S}}$ was the soil temperature sensitivity parameter, a, b and c were parameters of regression, and W_{s} was the soil water content.

The parameters describing the SR response to temperature and soil water content [E_0, a, b and c in Eqn (4)] were obtained by fitting Eqn (4) on data measured between early May and mid-July. Data from April and from late July were not used because they corresponded to specific crop development stages (i.e. tillering and senescence stages). As the SR spatial variability was large, the $R_{\mathrm{s},10}$ estimate deduced from the automatic soil chambers was not considered as sufficiently representative of the crop. It was thus deduced from manual measurements. These additional measurements were carried out once a week with a portable system (Licor 6200, Licor Inc.) at 24 locations in the crop. The manual SR values were divided according to both temperature and humidity responses and averaged in order to obtain $R_{\mathrm{s},10}$ parameter.

Inferred fluxes

GPP. GPP can be inferred from eddy covariance measurement ($\mathrm{GPP_{EC}}$) or from leaf scale measurement ($\mathrm{GPP_{LS}}$). In both cases, they were considered to be zero during the night. During the day, $\mathrm{GPP_{LS}}$ was computed by extrapolation at the crop scale of the first term of the right side of Eqn (3) (cf. 'Leaf scale measurement') and $\mathrm{GPP_{EC}}$ was computed as

$$\mathrm{GPP} = \mathrm{NEE} - \mathrm{TER}. \tag{5}$$

The way this term was evaluated is described below.

Respiration terms. TER was inferred from night-time NEE measurements. A comparison between the different inference methods, the impact of the reference temperature choice and an evaluation of the uncertainties associated with each of them will be discussed in another study (Moureaux *et al*., submitted). The method we finally retained was that described by Reichstein *et al*. (2005): the ecosystem respiration was parameterized as a function of temperature using the Lloyd and Taylor relationship [Eqn (2)] and it was assumed that the temperature dependence of TER was the same during the day and the night. The respiration at a reference temperature R_{10} [Eqn (2)] was estimated on a 4-day basis and the temperature sensitivity parameter, E_0, was estimated on a 2-week basis. Soil temperature measured at a depth of 5.5 cm was used as a reference to describe the evolution of the night-time NEE. The impact of u_* threshold on TER assessments was analysed.

A first evaluation of aboveground autotrophic respiration was obtained from leaf scale measurements ($R_{\mathrm{aa,LS}}$). The Lloyd and Taylor equation was fitted on the dark respiration, $R_{\mathrm{d,L}}$, respiration was extrapolated to the whole period (November–August) and was then scaled up to the whole crop. Leaf respiration was estimated from air temperature, sensible heat and aerodynamic resistance measurements (Hoyaux *et al*., in press).

Combined fluxes

Ecosystem respiration can be partitioned into autotrophic (R_{a}) and heterotrophic (R_{h}) contributions. Autotrophic respiration can be further divided into its aboveground (R_{aa}) and belowground (R_{ab}) components. These terms were assessed from eddy covariance, SR and crop sampling measurements as follows:

Autotrophic respiration was computed as the difference between the NPP and GPP_{EC}:

$$R_a = GPP - NPP, \tag{6}$$

its above-soil component as the difference between the TER and SR:

$$R_{aa} = TER - SR, \tag{7}$$

and its below-soil component by deducing R_{aa} from R_a:

$$R_{ab} = R_a - R_{aa}. \tag{8}$$

Finally, heterotrophic respiration was deduced from the NPP and NEE:

$$R_h = NEE - NPP. \tag{9}$$

As explained above ('Leaf scale measurement'), leaf scale GPP was not used in this procedure. Moreover, as the NPP was measured weekly or fortnightly from mid-March to harvest, the combined fluxes based on the NPP were computed using the same time intervals. Because no sampling was performed in winter, the NPP was linearly interpolated between sowing and the first measurements.

Results

Biometric measurements

We divided the crop development into five periods between key winter wheat crop stages: (i) from sowing to 'full' tillering [main shoot and one or two tiller(s)]; (ii) from 'full' tillering to early stem elongation; (iii) from early stem elongation to booting; (iv) period of inflorescence emergence and grain development (milk and dough development); and (v) period of ripening. Figure 2 presents the evolution of the GLAI and of total, stem, green leaf, dead leaf and ear DM.

During the first period (mid-October 2004 to mid-March), corresponding to autumn and winter, crop development was weak and the cumulated total biomass reached $0.054\,\mathrm{kg\,m^{-2}}$ DM.

The second period (mid-March to mid-April) corresponded to a temperature increase and a stronger development of the vegetative parts. The total DM increased to $0.27\,\mathrm{kg\,m^{-2}}$, including $0.095\,\mathrm{kg\,m^{-2}}$ for green leaves. The GLAI was $1.5\,\mathrm{m^2\,m^{-2}}$ during the third week of April.

During the third period (mid-April to late May), an intense increase of vegetative DM was observed, from 0.27 to $1.12\,\mathrm{kg\,m^{-2}}$, resulting from a stem biomass rise and flag leaf opening. The GLAI doubled in 1 week and reached its maximal value ($3\,\mathrm{m^2\,m^{-2}}$) in late April. Thereafter, the GLAI did not increase because of the senescence of older leaves and a selection made from tillers. Indeed, during this period, dominant tillers developed while other died. As a result, the dead leaves biomass increased to $0.065\,\mathrm{kg\,m^{-2}}$.

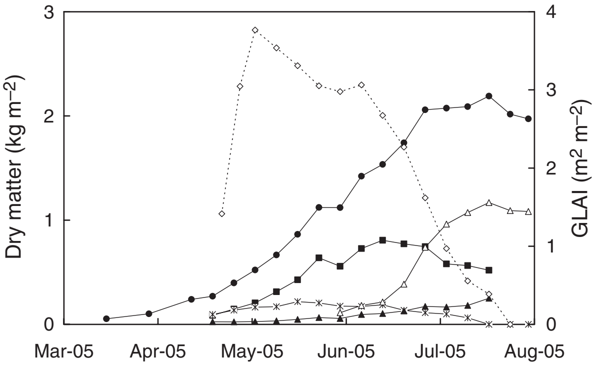

Fig. 2 Evolution over time of total (full circles), stem (full squares), green leaf (crosses), dead leaf (full triangles), ear (empty triangles) dry matter and green leaf area index (GLAI, empty squares).

Inflorescence emerged in late May, after which the grains developed. During the milk development stage (up to late June), ear and stem biomasses increased. However, green leaf biomass decreased and, at this stage, only flag and penultimate leaves remained green. Other leaves yellowed or died. The GLAI decreased to $2.3\,\mathrm{m^2\,m^{-2}}$ but the DM increased to $2.06\,\mathrm{kg\,m^{-2}}$. During the dough development stage (up to mid-July), only ear and dead leaf biomasses increased. The stems, leaves and roots DM was transferred to the ears. Total DM remained practically stable, reaching $2.09\,\mathrm{kg\,m^{-2}}$ at the end of the period. The penultimate leaves died and only the flag leaf remained partly green. The GLAI decreased to $0.6\,\mathrm{m^2\,m^{-2}}$.

Finally, during the ripening, the DM decreased slightly to $1.97\,\mathrm{kg\,m^{-2}}$. This decrease at the end of crop growth had been observed by Schiettecatte (1993) and de Ghellinck (2003). The ear DM did not change significantly. At this stage it represented 55% of aboveground DM, as reported by de Ghellinck (2003). Green leaf biomass and GLAI fell to zero.

On 3 August, $0.88\,\mathrm{kg\,m^{-2}}$ DM grain and $0.42\,\mathrm{kg\,m^{-2}}$ DM straw were harvested. Crop residues and roots biomass represented $0.67\,\mathrm{kg\,m^{-2}}$ DM and were buried in the soil. The grain yield was comparable to the mean winter wheat yield in the region ($0.86\,\mathrm{kg\,m^{-2}}$ DM, De Proft & Bodson, 2007) but slightly lower than the average yield of the parcel under study.

Fluxes

The NPP was obtained by multiplying the DM by the average C content. It ranged from 0.42 to 0.45 kg C kg^{-1} DM, with a mean of 0.43 kg C kg^{-1} DM. This value was close to those reported by Bolinder *et al.* (1997).

The evolution of the NPP (Fig. 3) was therefore similar to that of DM described in 'Biometric measurements' (Fig. 2). At harvest, the NPP was -0.85 kg C m^{-2} distributed in 0.46 kg C m^{-2} for ears (i.e. 55% of plant C content), 0.31 kg C m^{-2} for leaves and stems and 0.08 kg C m^{-2} for roots. The harvested grains represented 0.38 kg C m^{-2} and the harvested straw 0.18 kg C m^{-2}. The C left on the crop was 0.20 kg C m^{-2} for residues and 0.09 kg C m^{-2} for roots. Main important causes of NPP uncertainties are crop heterogeneity and possible biased root contribution assessment. In this study, the measurement method does not allow determining a standard error on NPP. Indeed, instead of measuring dry biomass for each tiller, we split samples into ears, stems and leaves sub samples in order to follow the development of these different organs.

As, we define the NPP as the stored C, root exudates and turnover are not included in these values but they are included in belowground autotrophic respiration. Swinnen *et al.* (1995a, b) measured root exudates on a winter wheat crop by labelling. They found that maximum exudates occur at the tillering stage and that the total amount of exudates C was around twice the C contained in the roots at the harvest. About 94% of root exudates and decay are estimated to be respired before the harvest (Sauerbeck & Johnen, 1977).

The sensitivity of the cumulated NEE, TER and GPP to the u_* threshold value is given in Fig. 4. It appears that, for u_* thresholds varying from 0 (no threshold) to 0.3 m s^{-1}, the NEE varied from -0.67 to -0.62 kg C m^{-2}, the TER from 0.78 to 0.98 kg C m^{-2} and the GPP$_{\mathrm{EC}}$ from -1.47 to -1.58 kg C m^{-2}. However, it is reasonable to assume that the uncertainty about the u_* threshold was not so large. We fixed the u_* threshold value at 0.22 m s^{-1}, and estimated its uncertainty at <0.1 m s^{-1}. On this basis, the cumulated NEE, TER and GPP$_{\mathrm{EC}}$ were -0.62, 0.95 and -1.57 kg C m^{-2}, respectively, and the uncertainties on these fluxes were 0.01, 0.05 and 0.03 kg C m^{-2}, respectively. The impacts of the temperature and of the model chosen to infer TER and GPP were analysed in a further study (Moureaux *et al.*, submitted). It appears that, for the above-determined threshold, TER was between 0.92 and 1.00 kg C m^{-2}, and GPP between -1.55 and -1.57 kg C m^{-2} (i.e. in the same range as induced by the u^* threshold uncertainty). Further details and the impact of these choices on daily values were detailed in Moureaux *et al.* (submitted).

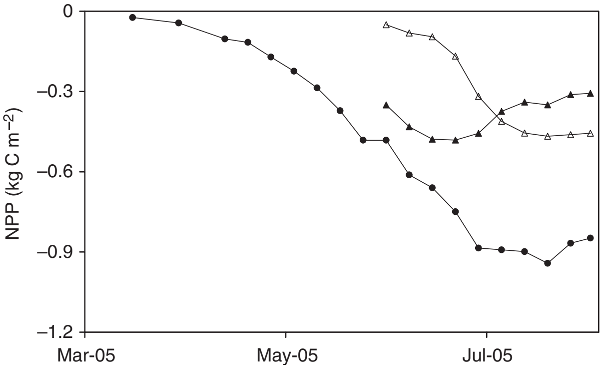

Fig. 3 Evolution over time of total (full circles), stem and leaf (full triangles) and ear (empty triangles) carbon content.

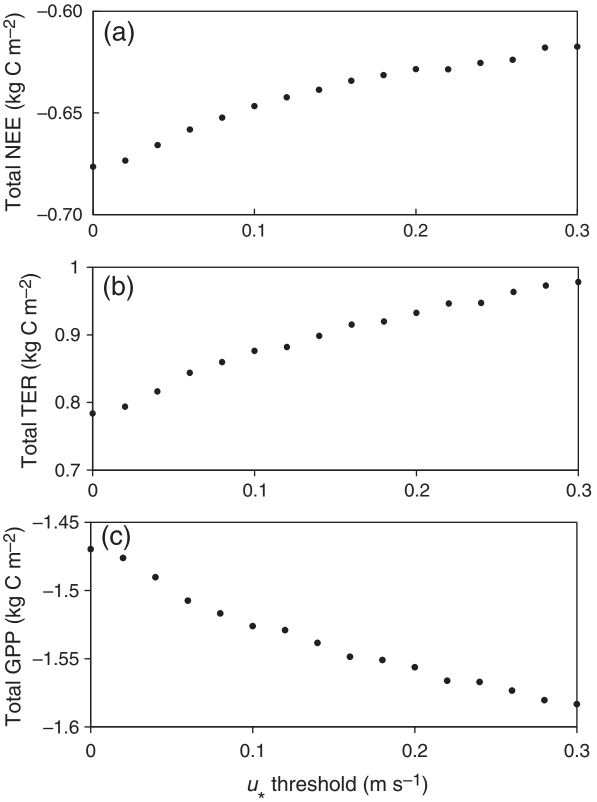

Fig. 4 Evolution with u_* threshold value of (a) total net ecosystem exchange, (b) total ecosystem respiration and (c) total gross primary productivity.

The evolution over time of the daily NEE, TER and GPP$_{\mathrm{EC}}$ are given in Fig. 5. From November to early March, they were small. Until late January, the NEE was always positive, suggesting that respiration dominated assimilation because of the weak crop development. It was 2 g C m^{-2} day^{-1} in early November and decreased to about 1 g C m^{-2} day^{-1} 10 days later, following the temperature evolution. Between November and late

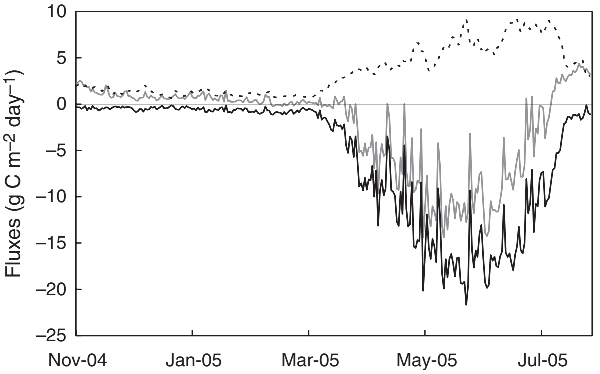

Fig. 5 Evolution over time of daily net ecosystem exchange (grey solid line), total ecosystem respiration (dashed line) and gross primary productivity (black solid line).

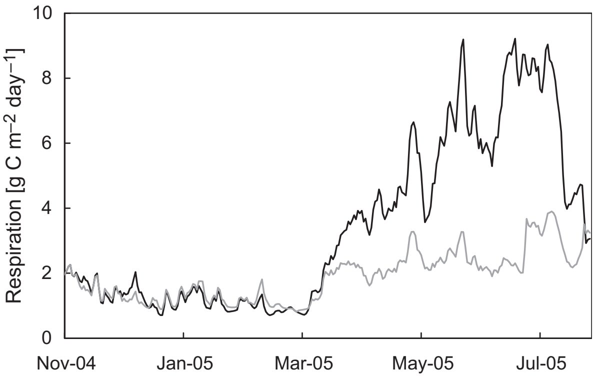

Fig. 6 Evolution over time of daily total ecosystem respiration (black line) and soil respiration (grey line).

January, the TER and GPP_{EC} remained stable at about 1.3 and $-0.3\,g\,C\,m^{-2}\,day^{-1}$, respectively. Later, both TER and GPP decreased slightly, with the NEE reaching about $0\,g\,C\,m^{-2}\,day^{-1}$.

From mid-March, both the TER and GPP_{EC} increased in absolute values. The GPP increase resulted from the crop development that occurred when temperature rose. The daily GPP_{EC} values increased until mid-May, when they reached about $-19\,g\,C\,m^{-2}\,day^{-1}$; they remained stable during the maximal LAI period, from mid-May to mid-June, and then decreased due to the GLAI decrease, falling to about $-1\,g\,C\,m^{-2}\,day^{-1}$ in late July and until harvest. The TER increased rapidly from mid-March and reached about $4\,g\,C\,m^{-2}\,day^{-1}$ in early April, which corresponded to the winter wheat tillering. Thereafter, the TER increase was weaker. Maximal TER values, exceeding $8\,g\,C\,m^{-2}\,day^{-1}$, were observed initially during a short period in late May, and then for a month between mid-June and mid-July. The first period occurred at the booting phase but was of short duration and corresponded to a temperature increase. The second peak took place at the grain development stage (milk and dough development). At the end of this peak period, in mid-July, the TER values decreased from 8 to $4\,g\,C\,m^{-2}\,day^{-1}$ and remained stable during the ripening. The TER repartition between its different components is analysed below.

The NEE evolution results from the combination of the GPP and TER. In mid-March, as the GPP increase was in absolute values larger than those for the TER, the NEE became negative. It became a CO_2 sink from late March and reached its maximal absolute values (about $-12\,g\,C\,m^{-2}\,day^{-1}$) between the end of May and mid-June. Subsequently, it decreased in absolute value and the crop switched again to become a source in mid-July. The NEE remained positive during the ripening stage and reached maximum daily values $>4\,g\,C\,m^{-2}\,day^{-1}$ in late July. Just before harvest, the NEE was about $3\,g\,C\,m^{-2}\,day^{-1}$.

The time evolution of daily SR computed with the parameterization described above is presented in Fig. 6 along with daily TER assessments. The aboveground autotrophic respiration also appears in Fig. 6 as the difference between these two curves. Over the whole period, SR was $0.52\,kg\,C\,m^{-2}$, while the aboveground autotrophic respiration was $0.43\,kg\,C\,m^{-2}$. The heterotrophic and autotrophic components of SR were 0.23 and $0.29\,kg\,C\,m^{-2}$, respectively. During winter, the SR was close to the TER, generally about $1\,g\,C\,m^{-2}\,day^{-1}$, suggesting a very low R_{aa}. At some times, the SR was slightly greater than the TER, which could result from the uncertainties for both variables.

In mid-March, both the SR and TER increased. However, the SR increase was quite limited, reaching $2\,g\,C\,m^{-2}\,day^{-1}$ rapidly but then remaining quite stable, between 2 and $3\,g\,C\,m^{-2}\,day^{-1}$, until late June. This suggests that the main cause of the TER increase at this period resulted from the aboveground autotrophic component and is related to crop development. Indeed, R_{aa} increased from mid-March until mid-June and was then, for a fortnight, greater than $6\,g\,C\,m^{-2}\,day^{-1}$. These maximal values occurred at the flowering stage. In late June, after R_{aa} maximal values, the SR increased and was between 3.5 and $4\,g\,C\,m^{-2}\,day^{-1}$ until mid-July (i.e. during the dough development stage and a soil water content increase).

During ripening, after mid-July, R_{aa} and SR both fell to $2\,g\,C\,m^{-2}\,day^{-1}$. Here again, the TER evolution resulted mainly from the aboveground autotrophic component decrease following crop senescence. Just before harvest, SR values larger than TER were also observed.

The evolution of R_a, R_{ab} and R_h is presented in Fig. 7. As these variables were inferred from the NPP (Fig. 1), which was estimated fortnightly, we present the evolu-

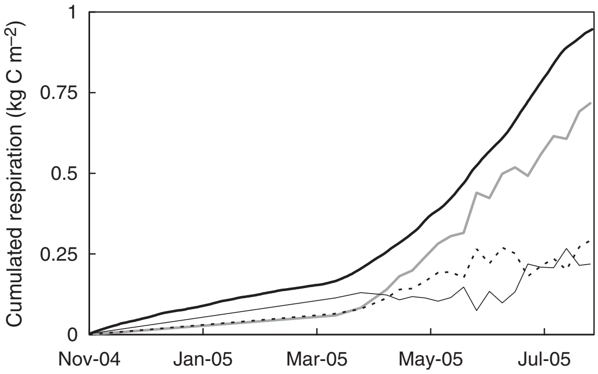

Fig. 7 Evolution over time of cumulated total ecosystem respiration (black bold line), autotrophic respiration (grey bold line), belowground autotrophic respiration (dashed line) and heterotrophic respiration (thin black line).

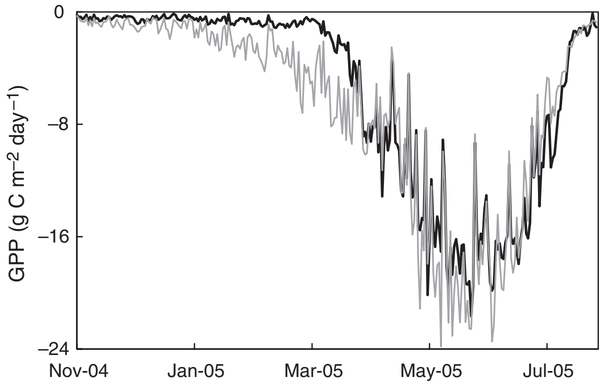

Fig. 8 Evolution over time of daily gross primary productivity inferred from eddy covariance measurement (black line) and scaled up from leaf scale measurement (grey scale).

tion of the cumulated values, along with the cumulated TER assessments.

From November to March, the autotrophic respiration constituted about one-third of the TER and resulted only from the belowground component, the R_{aa} contribution being very small, as shown earlier. The heterotrophic component increased regularly during this period and accounted for about two-thirds of TER; it then reached $0.11\,\mathrm{kg\,C\,m^{-2}}$ in mid-March. At this point, R_{a} and R_{ab} increased sharply, while R_{h} remained quite weak. R_{ab} reached about $0.2\,\mathrm{kg\,C\,m^{-2}}$ in late May, constituting about 50% of the autotrophic respiration during this period. The cumulated heterotrophic respiration was smaller than the cumulated autotrophic SR during this period. In June, both R_{ab} and R_{h} remained low until harvest. The low R_{ab} value suggests that the soil autotrophic respiration decreased as soon as the wheat was developed and inflorescence emerged. From late June to harvest, the cumulated R_{h} was about $0.2\,\mathrm{kg\,C\,m^{-2}}$ and remained stable. During this period, the cumulated R_{h} and R_{ab} were of the same order of magnitude and contributed equally to SR.

Discussion

Data quality

Although the different C balance terms were computed using different methods, each of them affected by specific uncertainties, the results presented here appeared fairly consistent and in good agreement with the literature.

Firstly, the NPP estimate, obtained by DM sampling, was clearly enclosed between the NEE and GPP estimates from eddy covariance, as expected. The C use efficiency (NPP/GPP ratio) was 0.54, which is within the range predicted by the literature (between 0.3 and 0.6 for crops, Amthor & Baldocchi, 2001).

A second validation can be obtained by comparing the leaf scale and eddy covariance GPP estimates. We showed earlier that, although the cumulated $\mathrm{GPP_{LS}}$ and $\mathrm{GPP_{EC}}$ were linked, the day-to-day evolutions of these fluxes remained independent. It appears clearly in Fig. 8 that, between mid-March and harvest, the seasonal trends and the day-to-day evolutions (notably the strong day-to-day variations in early April and at the end of May/early June) followed each other closely, providing a further validation of these estimates. The differences appearing before mid-March result from an error in the leaf scale estimate, which does not take the photosynthesis response to low temperature into account. This is discussed in detail by Hoyaux *et al.* (in press).

In addition, the maximal daily and cumulated flux values are of the same order of magnitude as in the literature. The maximal NEE daily values ($-12\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$) were close to those found for other winter wheat crops by Baldocchi (1994) ($-13.3\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$), Anthoni *et al.* (2004a) and Soegaard *et al.* (2003) (about $-10\,\mathrm{g\,C\,m^{-2}\,day^{-1}}$). Finally, the cumulated $\mathrm{GPP_{EC}}$ was slightly larger than that reported by Falge *et al.* (2002) on other wheat crops (-1.40 and $-1.10\,\mathrm{kg\,C\,m^{-2}}$).

Finally, it is worth noting that the uncertainty of these fluxes resulting from the choice of the u_* threshold is limited. In particular, the $0.01\,\mathrm{kg\,C\,m^{-2}}$ uncertainty for the NEE is small compared with those reported by Anthoni *et al.* (2004b) for winter wheat and potato (0.06 and $0.03\,\mathrm{kg\,C\,m^{-2}}$, respectively) and suggests that the C balance factors were not very sensitive to the night flux underestimation at our site.

However, some inconsistencies appear in the data. First, the estimates of aboveground autotrophic respiration deduced from leaf scale measurements were found to be unrealistic, due to an excessive sensitivity to temperature (results not shown). These results were therefore not used here. Second, some inconsistencies were observed between the SR and TER estimations, the former being larger than the latter in winter and at the end of the season. This probably results from uncertainties in the SR computation, the model not being validated during these periods. However, the impact of this error on the cumulated flux was small in both cases: during the first period, the error was small as winter fluxes were very low and the second period was very short in time. Finally unrealistically negative respiration values were sometimes found, in late May (R_h) and in late June (R_{ab}) (Fig. 7). This is because these terms were computed as a difference between two fluxes estimated with two independent methods [see Eqns (6–9)] each of them affected by a large uncertainty. In consequence, the uncertainty of the difference results from the accumulation of the uncertainties on each flux and is larger than for other fluxes. The most important causes are probably the uncertainties on the NPP resulting from crop heterogeneity and the biased root contribution assessment. However, even if the short-term evolution of autotrophic and heterotrophic SR components should be considered with caution, their average evolution and annual totals remain reliable.

C balance terms

The results presented above can be combined to establish the C balance of the crop. We will present it first for particular periods of crop development and then for the whole growth period.

During autumn and winter, the TER was twice as great as gross assimilation, due to the low development stage of the crop. As a consequence, the field behaved as a source and emitted $90\,\mathrm{g\,C\,m^{-2}}$ between November and mid-March. One-third of the TER was due to belowground autotrophic respiration and the two remaining thirds were due to heterotrophic respiration. The latter was boosted by the decomposition of sugar beet residuals from the preceding crop that were spread on the field after harvest.

In mid-March (tillering) both the $\mathrm{GPP_{EC}}$ and TER increased, the $\mathrm{GPP_{EC}}$ reaching a maximal value in early May and remaining stable until the end of May (booting end). During this period of intensive crop development, the GPP reached $-85\,\mathrm{g\,C\,m^{-2}}$ and the TER about 40–45% of GPP. Consequently, the NEE was about $-49\,\mathrm{g\,C\,m^{-2}}$ during this period. As the heterotrophic respiration was small at this time, the TER resulted mainly from autotrophic respiration, to which above- and belowground components contributed one half each. Similar ratios had been observed during the same period by Lohila *et al*. (2003) on a barley crop. Moreover, an increase of root respiration and rhizodeposition was already observed on winter wheat at the tillering stage by Swinnen *et al*. (1995a).

After flowering, in early June, the GPP began to decrease but the TER remained fairly constant until mid-June and then increased for a month. The cumulated GPP between early June and mid-July reached $-61\,\mathrm{g\,C\,m^{-2}}$ but the TER now exceeded 50% of the GPP so that the NEE was about $29\,\mathrm{g\,C\,m^{-2}}$. The aboveground autotrophic component reached 70% of the TER and SR resulted mainly from the heterotrophic component, R_{ab} being almost zero during this period. Decreases in assimilation after inflorescence emergence had already been observed in winter wheat crops by Geisler (1983), Johnson *et al*. (1981) and Anthoni *et al*. (2004a). It is worth noting that the amount of assimilated C after flowering was still significant. It was nearly exclusively used to build grain. Indeed, the ear C content increased from 0.08 to $0.47\,\mathrm{g\,C\,m^{-2}}$ during the considered period. This resulted both from C assimilation and from C translocation from stems, leaves and roots. A similar nitrogen accumulation in grain was also observed during this period (Destain *et al*., 1997).

An earlier TER increase (after inflorescence emergence) had been observed by Baldocchi (1994) and Denmead (1976), while Lohila *et al*. (2003) reported maximal value after flowering. The R_{ab} decline could be explained by the translocation of photosynthesis products from the roots to the grain that occurs after flowering in cereals. As a result, the supply of easily degradable C into the soil and, consequently, the rhizosphere respiration gradually declines (Lohila *et al*., 2003). However, this explanation is hypothetical because the R_{ab} decline could also result from an artefact linked to uncertainties about the NPP, as discussed above.

Finally, after mid-July, during ripening, both the GPP and TER decreased. As the GPP decrease was sharper than the TER decrease, the crop reverted to a source, as at the start of the season. However, unlike this early period, the three respiration terms, R_{aa}, R_{ab} and R_h, contributed about 45%, 30% and 25%, respectively, to the TER. The net exchange between mid-July and harvest in mid-August reached $7\,\mathrm{g\,C\,m^{-2}}$.

A similar TER decrease during ripening was observed by Lohila *et al*. (2003) on a barley crop. This suggests that the respiration process is linked to plant activity. Respiration is known to be linked to photosynthetical activity (e.g. Landsberg & Gower, 1997; Waring *et al*., 1998; Janssens *et al*., 2001; Kuzyakov &

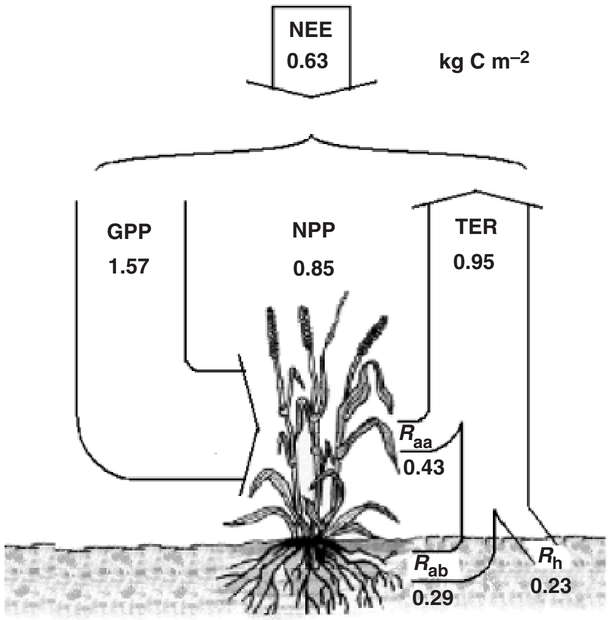

Fig. 9 Carbon balance of the winter wheat crop during the cultivation period. Cumulated fluxes are given in kg C m^{-2}.

Cheng, 2001) and is, therefore, expected to fall when all organs have yellowed and died. The measurements made at leaf level on the same crop confirmed that the respiration rates of dead leaves were smaller than those of other leaves (Hoyaux *et al*., in press).

From these results, the C balance of the winter wheat crop can be deduced for the whole cultivation period (Fig. 9). In total, the crop assimilated -1.57 kg C m^{-2} and the ecosystem emitted 0.95 kg m^{-2}. The TER to GPP$_{EC}$ ratio was, therefore, 0.61, in agreement with ratios for maize crops [between 0.55 and 0.66 (Meyers *et al*., 2001; Law *et al*., 2002; Suyker *et al*., 2005; Verma *et al*., 2005)] and soybean crops [between 0.55 and 0.65 (Law *et al*., 2002; Suyker *et al*., 2005; Verma *et al*., 2005)]. The net ecosystem was then -0.63 kg m^{-2}. The NPP was -0.85 kg C m^{-2} (i.e. 54% of the GPP, as already discussed). The C of harvested ears and straw was 0.57 kg C m^{-2}. As a result, over the period in question, the net ecosystem assimilation was greater than exported C. The ecosystem could then be considered as a C sink.

TER can be divided into its above- and belowground component: R_{aa} reached 0.43 kg m^{-2} and the SR was 0.52 kg m^{-2}, corresponding to 45% and 55% of the TER, respectively. The SR to TER ratio was lower than that reported for grasslands [0.75 at Carlow (Gilmanov *et al*., 2007), 0.85 for a New Zealand grassland (Hunt *et al*., 2004)], or forests [between 0.68 and 0.88 (Wofsy *et al*., 1993; Goulden *et al*., 1996; Davidson *et al*., 1998; Law *et al*., 1999, 2001; Granier *et al*., 2000; Saigusa *et al*., 2005)]. However, our ratio was computed only in relation to the crop growth period and could thus be smaller than if considered over a whole year, as in other studies.

The heterotrophic respiration was 0.23 kg C m^{-2} and the total autotrophic respiration was 0.72 kg C m^{-2}, which corresponds to 76% of the TER, confirming that autotrophic processes govern crop ecosystem respiration (Falge *et al*., 2002). R_{aa}, the aboveground contribution of autotrophic respiration, was 0.43 kg C m^{-2} (i.e. 60% of R_a). The belowground part can be deduced and was 0.29 kg C m^{-2}. R_{ab} was the autotrophic component of SR and represented 56% of the SR, which is greater than the 45% reported by Shi *et al*. (2006). There, SR, like TER, was dominated by autotrophic process.

Conclusions

The C balance was assessed for a winter wheat crop. Using the eddy covariance measurements, the NEE, TER and GPP were -0.63, 0.95 and -1.57 kg C m^{-2}, respectively. In order to partition TER into its above- and belowground components, SR measurements allow assessing belowground respiration: 0.52 kg C m^{-2}. We observed that this term was quite constant after the tillering stage (i.e. after important root development) and that the TER increase results from the increase of the autotrophic aboveground respiration. Combining NPP and GPP, the autotrophic respiration of the crop was found 0.72 kg m^{-2} s^{-1}. The autotrophic respiration dominates then the TER (76%) and the autotrophic part of the SR was 56%.

The main uncertainties in establishing the C balance are related to R_{ab} and R_h assessments, which are linked to the NPP uncertainties. To improve the NPP estimate, the root C content has to be measured. This involves a large amount of work (soil sampling up to a depth of 2 m depth and sorting roots) and many repetitions to take crop heterogeneity and root evolution into account. A better way to discriminate between autotrophic and heterotrophic contributions could be to measure SR in excluded and nonexcluded roots zones. However, this method presupposes that heterotrophic SR in roots-excluded soil is not influenced by microbial population shifts that might occur from root C inputs. Experiments with this aim are in progress.

The results presented here are of course dependent on the crop type, on climatic conditions and on crop management. In particular, let us recall that the winter wheat crop was not ploughed before sowing because of appropriate soil conditions and that, in June, the amount of precipitation was particularly small, while temperature was high compared with mean averages. This led to an early yellowing of the crop compared with other winter wheat crops growing on adjacent fields after a traditional tillage (Tourneur *et al*., 2006). However, the yield of the study crop was comparable with the regional mean, although slightly (<5%) lower than the studied parcel potential yield.

Further studies would be necessary in order to study the impact on the different terms of the C balance of extreme climatic events (mild winters, harsh droughts) of management practices (ploughing/no ploughing, nitrogen fertilizer dressing, disease, pest and crop protection, sowing date, variety choice) or of soil conditions.

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Article 6

Carbon sequestration by a crop during a four year rotational cycle

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Abstract

A production crop managed in a traditional way was followed during a complete sugar beet / winter wheat / potato / winter wheat rotational cycle, from 2004 to 2008. Eddy covariance, automatic and manual soil chamber, leaf diffusion and biomass measurements were performed continuously in order to obtain daily Gross Primary Productivity (GPP) and Total Ecosystem Respiration (TER) and seasonal Net Ecosystem Exchange (NEE), Net Primary Productivity (NPP), GPP, TER, autotrophic respiration, heterotrophic respiration and, finally, Net Biome Production (NBP). performed continuously in order to obtain daily GPP and TER and seasonal NEE, NPP, GPP, TER, autotrophic respiration, heterotrophic respiration and, finally, NBP.

Results show that GPP and TER were subjected to an important interannual variability that was due to differences between crops but also to climate variability. A significant impact of intercrop assimilation and of some farmer interventions (ploughing, crop residue left) was also detected and quantified.

Seasonal budgets showed that, during cropping periods, the TER/GPP ratio varied between 40 and 60 % and that TER was mainly dominated by autotrophic component (65 % of TER and more). Autotrophic respiration was found closely related to GPP during growth period.

Whole cycle budget showed that NEE was negative and the rotation behaved as a sink of 1.59 kgC.m^{-2} on the four year rotation. However, if exportations are deduced from the budget, it turned out to a slight source of 0.17 (+/- 0.14) kgC.m^{-2}. The main causes of uncertainty on this result were due to eddy covariance measurements (uncertainty on the u_* threshold determination) and to biomass samplings. The positive NBP also suggests that the crop soil carbon content decreases. This could be explained by the crop management, as neither farmyard manure nor slurry was applied on the crop since more than 10 years and as cereal straw was systematically exported for livestock. In addition, this result was strongly influenced by the particular climatic conditions in 2007 that increased the fraction of biomass that returned to the soil to the prejudice of harvested biomass and mitigated thus the source intensity. If 2007 had been a “normal” year, this intensity would have been twice as large.

1. Introduction

The impact of agriculture lands on climate is multiple and significant. First, compared to forested sites, agricultural lands are characterised by larger albedo, lower soil roughness and soil humidity variations which influences sensible and latent heat exchanges (Bonan, 2002). Crop management techniques may also influence the local and regional climate. Overgrazing, land use change, deforestation contribute to minder precipitations (Bonan, 2002) while irrigation contributes to increase air humidity, cloud density and precipitation. In addition, crops constitute the most important biospheric source of CO_2 (Cole, 1996; Mosier *et al.*, 1998; Pattey *et al.*, 2007) as resulting from plant respiration and soil organic matter decomposition.

Recently, changes in agricultural practices have been considered as possible ways to mitigate climate change by increasing carbon storage in their crop soils (Smith *et al.* 2000; Vleeshouwers et Verhagen, 2002; Freibauer *et al.*, 2004; Smith, 2004). Soil organic carbon content of agricultural ecosystems was indeed found to depend on land use, cultural management fertiliser application, harvest features, residues management and, on the other hand on microclimate, soil tillage, etc… (IPCC, 1997).

However, relations of CO2 exchanges between crop and atmosphere and their response to climate, crop management activities as well as their difference from crop to crop remain largely unknown. The overall aim of this work is thus to quantify and understand the evolution of CO2 exchanges in a crop rotational cycle. More particularly, they are to:

- Measure net carbon fluxes exchanged by the crops and estimate the overall carbon sequestration by the crop during the rotational cycle.
- Compare the budgets of different crops.
- Analyse the impacts of climate and of management activities on these fluxes and on the global carbon sequestration.
- Identify the respective importance of assimilation and respiration in the carbon balance and better bound the physiological processes that control the mechanisms of the net flux response to climate.

In this aim, a production crop managed in a traditional way was followed during four years, from 2004 to 2008. Different measurements (eddy covariance, automatic and manual soil chambers, leaf diffusion, biomass sampling) made at different spatial (leaf, soil chamber, whole crop) and temporal (half hour, week, fortnight) scales were performed regularly, treated and extrapolated at the crop scale and either at the day, the season or the whole rotational cycle. The results of this analysis are presented and discussed below.

2. Material and methods

2.1 Site description

The study site is a cropland situated in Lonzée, about 45 km SE of Brussels, Belgium (50°33'08'' N, 4°44'42'' E, 165 m asl). It is a node of the *Carboeurope,* and *Fluxnet* networks since 2004, a core site of the *IMECC* infrastructure and an inferential measurement site of the *Nitroeurope* network since 2007. The climate is temperate maritime. The mean temperature is about 10°C and the annual precipitation is about 800 mm.

The cropland is a quadrilateral area of *c.* 12 ha located on a fairly flat plateau with a maximum slope of 1.2 % in a WSW direction. The site provides a fetch of 240 m in the SW which is the main wind direction. The farm is located 400 m WSW from the measurement point. There are no other buildings or roads in this direction for more than 1000 m. The second main wind direction is NE, with a fetch of 200 m. This side of the parcel is bordered by a road with very light traffic, beyond which croplands extend more than 900 m. The soil is a Luvisol (FAO classification). A footprint analysis of our site was carried out by Göckede (pers.comm.), using a forward Lagrangian stochastic trajectory model (Rannik et al., 2003) and following the procedure described in detail by Göckede et al. (2005). It appears that target area contribution to flux amounted in all conditions to more than 80% in all sectors, excepted one, corresponding to 5% of wind occurrence, where it amounted to 77% in stable conditions.

2.2 Crop history

The land has been cultivated for more than 70 years. For at least the past 6 years, the crops have been cultivated following a 4 year rotational cycle with sugar beet, winter wheat, seed potato and again winter wheat. Before the period under study, 180 kg.ha^{-1} mineral N and 60 kg.ha^{-1} organic N (sugar lime) had been applied in 2003, 156 kg.ha^{-1} mineral N, 14 kg.ha^{-1} phosphorus and 42 kg.ha^{-1} potassium in 2002, and 180 kg.ha^{-1} mineral N in 2001. No farmyard manure had been applied since 1996. Before the cycle beginning, in February 2004, the soil was ploughed at about 30 cm.

All the crop management activities during the rotational cycle are listed in Table I. The cycle began with sugar beet (*Beta vulgaris* L.) sowing on 30 March. Nutrient applications were performed in April and May 2004. At the harvest, on 29 September, roots were lifted and exported while beet crowns and leaves were left on the field.

Date	**Action**	**Material / Product**
1-Feb-04	Ploughing	
30-Mar-04	Soil preparation	Canadian cultivator, Rotary harrow
	Sowing	Sugar beet
1-Apr-04	Application	liquid nitrogen (156 units .ha $^{-1}$)
	Weeding	3l Pyramine
24-Apr-04	Weeding	0,2 Premium + 0,2 Fumesin + 0,5 Goltix
3-May-04	Weeding	0,3 Premium + 0,2 Fumesin + 0,5 Goltix + 0,25 Matrigon
12-Apr-04	Weeding	0,5 Premium + 0,25 Fumesin + 0,75 Goltix + 0,5 Matrigon
12-May-04	Application	Boramax : Magnesia + Boron (200kg.ha^{-1})
23-May-04	Weeding	0,5 Premium + 0,25 Fumesin + 0,5 Goltix + 0,25 Matrigon
31-May-04	Weeding	Venzar
7-Aug-04	Fungicide treatment	0,3 Virolex + 0,5 Capitan
29-Sep-04	Pulling (lifting ?)	
14-Oct-04	Soil preparation	Rotary harrow
	Sowing	Winter Wheat, cv. Dekan, 150 kg.ha^{-1}
28-Mar-05	Weeding	1,5l IP + 1,5l Verigal
22-Mar-05	Application	liquid nitrogen (45 Units.ha^{-1})
12-Apr-05	Application	liquid nitrogen (35 Units.ha^{-1})
11-May-05	Weeding	40g Harmony + 25g Gratil
12-May-05	Application	NH_4NO_3 (40,5 Units.ha^{-1})
30-May-05	Application	NH_4NO_3 (81 Units.ha^{-1})
19-May-05	Fungicide treatment	1l Opus + 0,5l Amistar
3-Aug-05	Harvest	
28-Aug-05	Stubble breaking	

23-Nov-05	Ploughing	
11-Apr-06	Application	Asparagite (0N/0P/25K +10% calcium oxide + 30% sulphuric oven-dry)
1-May-06	Planting	Potatoes - cv. Spunta
2-May-06	Application	liquid nitrogen (117 Units.ha^{-1})
	Weeding	4l Defi + 1l Linuron (Pre emergence treatment)
13-May-06	Definitive ridging	
14-May-06	Weeding	(4l Defi + 1l Linuron (Pre emergence treatment)
1/9/15/20/27 Jun-06 3/8/13/19 Jul-06	Insecticide + Fungicide Spray	
6-Aug-06	chemical haulm destruction	Purivel
13-Aug-06	chemical haulm destruction	Reglone
15-Sep-06	Pulling (lifting ?)	
19-Sep-06	Stubble breaking	
13-Oct-06	Sowing	Winter Wheat, cv. Rosario
16-Mar-07	Weeding / Insecticide spray	Weeding (Cossack 300g/ha +1l/ha Actirob) Insecticide (Cytox 0,2l/ha)
17-Mar-07	Application	liquid nitrogen (40 Units.ha^{-1})
12-Apr-07	Application + Spray	liquid nitrogen (60 Units.ha^{-1})+Growth regulator (1l Cycocel)
19-Apr-07	Fungicide Spray	1l Opus
8-May-07	Application	Third application of nitrogen (350 kg Nitrate 27) (94,5 Units.ha-1)
23-May-07	Insecticide + Fungicide Spray	Fungicide (Fandango 1,25l/ha + Daconil 1l/ha) Insecticide (Cytox 0,2l/ha)
5-Aug-07	Harvest	
10-Sep-07	Application	Slimes (10t.ha^{-1})
20-Sep-07	Stubble breaking	
5-Jan-08	Ploughing	

Table 1: Schedule of management activities during the rotational cycle.

In 2005, winter wheat (*Triticum aestivum* L., cv. Dekan) was grown. The seeds were sown on 14 October 2004, 2 weeks after the sugar beet harvest. As the conditions were appropriate, before the winter wheat sowing, the soil has been managed using a power take-off rotary harrow working on 10 cm combined with a subsoiler made up of loosening shares with a 30 cm tillage depth. Between mid-April and late May, mineral N was applied in four stages. The crop was harvested on 3 August 2005. Grain and straw were both harvested and exported while other crop residues were incorporated in the soil. A deep ploughing was operated on 23 November 2005.

In 2006, potato (*Solanum tuberosum* L., cv. Spunta) was cultivated for seedlings. They were planted on 1 May 2006 and earthed up on 13 May 2006. Nutrients were applied in April and May 2006. Chemical haulm was applied in two steps, on 6 and 13 August 2006. The crop was harvested on 15 September 2006.

On 19 September 2006, a stubble breaking was operated and winter wheat (*Triticum aestivum* L.) (cv. Rosario) was sown on 13 October 2006 after a similar soil treatment as in October 2004. Between mid March and mid May mineral N was applied in three phases. The crop was harvested on 5 August 2007. Here again both grain and straw were exported and crop other crop residues were left on the soil. A stubble breaking operated in end September after application of a total herbicide on 7 September and of 10 t ha^{-1} sugar beet mill slimes (corresponding to about 0.07 kg C.m^{-2}, Destain et al., 1997) on 10 September 2007. A deep ploughing was operated in January 2008.

2.3 Eddy covariance system and meteorological station

Fluxes of CO_2, water vapour and sensible heat were measured with an eddy covariance system made with a research-grade sonic anemometer (Solent Research R3, Gill Instruments, Lymington, UK) placed at a height of 2.7 m and an infrared gas analyser model Li-7000 (Licor Inc, Lincoln, NE, USA); this was the standard system used in the *CarboEurope-IP* and *Fluxnet* networks (Moncrieff et al., 1997, Grelle and Lindroth, 1996; Aubinet et al., 2000). This system has been described in more details by Moureaux et al. (2006). Data from the sonic anemometer were gathered at a sampling rate of 20 Hz using the EDDY Software (Kolle, Max-Planck-Institute for Biogeochemistry, Germany). This software was also used to determine online and post-processed fluxes.

Micrometeorological measurements were made on a half-hourly basis. They included air temperature and humidity (RHT2, Delta-T Devices Ltd., Cambridge, UK) at a height of 1.3 m, soil temperature (PT100) at a depth of 3, 5.5, 9, 26 and 56 cm and soil humidity (ThetaProbe, Delta-T Devices Ltd., Cambridge, UK) at a depth of 5, 20 and 50 cm. Global (CM21, Kipp en Zonen, Delft, NL), net (Q*7.1, REBS, Seattle, WA, USA), global photosynthetically active (PAR Quantum Sensor SKP 215, Skye Instruments Ltd., UK) and global and diffuse photosynthetically active (Sunshine sensor type BF3, Delta-T Devices Ltd., Cambridge, UK) radiation were measured at a height of 2.7 m. Rainfall and mean atmospheric pressure (MPX4115A, Motorola, Phoenix, AR, USA) were also measured at the site.

2.4 Biometric measurements

In order to monitor crop development, growth stage observations were performed once a week or once a fortnight, according to crop development rate. In addition, vegetation area indexes were measured as well as dry matter (DM) and carbon (C) content, Net Primary Productivity (NPP) was deduced from these measurements.

In each crop, dry mass (DM) and carbon content were studied separately. DM was obtained by weighing the samples after drying in an incubator. Incubator temperature and drying duration were 80°C and 15 days for sugar beet and 90°C and 2 days for the other crops. Carbon content was estimated by gas chromatography after complete combustion, purification and gas reduction. In each case, the sample was divided in four duplicates.

In the sugar beet crop, 3 lines of 2 meter long each were taken at each sampling. As soon as the root was developed enough, it was separated from the rest of the plant and DM and carbon content of the two parts were followed separately. Details of the procedure are given by Moureaux et al. (2006). In the potato crop, 12 to 20 plants were taken at each sampling. Samples were separated in four parts: mother tuber, daughter tubers, roots and aerial parts. In winter wheat crops, plants were sampled on a surface of 0.5 to 1 m^2. Samples were divided into two parts: ears and stems / leaves. In 2005, in addition, separation between green and yellow organs was made. As winter wheat roots can grow down to 1.5 m deep, it was not possible to collect all the below-ground biomass in these crops. Root biomass was thus evaluated by using a ratio between below-ground and total biomass described by Baret et al. (1992). Details of the procedure are given by Moureaux et al. (2008).

Exportations were measured using the same procedure as for NPP. In the winter wheat and the sugar beet, sampling was made on four different parcels of 6 lines of 150 meter each in the sugar beet and of 2 m X 50 m and 2 m X 30 m area in the winter wheat in 2005 and 2007, respectively. In the potato, they were estimated on the basis of the last NPP sampling that was made on two parcels. Indeed, values given by the farmer were underestimated as not taking below grade potatoes into account.

Vegetation area index was also deduced in each crop from light absorption measurements, using a Ceptometer (Sunscan, Delta T Devices, Cambridge, UK). Measurements were performed weekly during the period of vegetation development. The green leaf area index (GLAI) was also measured in each crop by directly measuring the leaf surface of sampled plants with a camera and a picture analyser (Windias, Delta-T Devices, Cambridge, UK).

2.5 Data treatment and uncertainty evaluation

This study is focused on day average evolution and/or seasonal cumulated values of Net Ecosystem Exchange (NEE), Gross Primary Productivity (GPP), Total Ecosystem Respiration (TER), Net Primary Productivity (NPP), autotrophic and heterotrophic respirations and exportations,

Half hourly NEE measurements were estimated as the sum of the turbulent flux and of the change storage in the air below the measurement point. Measurements were computed using the standard Carboeurope computation procedure (Aubinet et al., 2000). Classical corrections (high frequency, density effects) were applied. In addition, the data were filtered in order to remove those taken during periods of low turbulence (u_* filtering) or those that did not fill the stationarity criteria (Foken and Wichura, 1996). Data gaps were filled using mean diurnal variation (Falge et al., 2001) when meteorological data were missing and parameterisation when they were available. All these procedures were described in more detail by Moureaux et al. (2006) and (2008).

Respiration components were computed using two methods. In the first, an estimate of cumulated autotrophic respiration (AR) was obtained as the difference between GPP and NPP and an estimate of cumulated heterotrophic respiration (HR) as the difference between NPP and NEE. In the second method, HR was obtained by extrapolation of chamber measurements taken in field parcels that were maintained without vegetation and AR was deduced by subtracting HR from TER. Soil respiration measurements were taken using home made manual (Longdoz et al., 2000) or automatic (Suleau et al., submitted) chambers. Data were obtained during two campaigns, from June to July 2006 and from March to August 2007, in 2 m X 4 m non planted areas situated in the middle of the planted field. In 2006, manual measurements were performed on 32 points every four days. In 2007 they were performed every half hour at four locations, using the automatic chambers. Extrapolation of these measurements to the whole rotational cycle was performed using an exponential temperature response (Q_{10} equation).

Errors in eddy covariance measurements were avoided as much as possible by applying corrections and quality tests. The main corrections applied in this case concerned the high frequency losses by the IRGA pumping system and the filtering of night fluxes. However, some uncertainty could subsist, due notably to a wrong evaluation of the u_* criterion used for night flux filtering. The resulting uncertainty was evaluated by Moureaux et al. (2006) as lower than 5 % on cumulated NEE. An evaluation of uncertainty due to all fluxes variations that were not controlled by climate fluctuations (i.e., footprint fluctuations, mesoscale movements) was estimated by applying the daily differencing approach (Richardson et al., 2006) to Lonzée data. The cumulated error due to this was about 2 g C.m^{-2} on each cropping season and 2 g C.m^{-2} on the cumulated intercrop periods. Thanks to a low percentage of missing data, uncertainties due to data gap filling was limited to about 2 g C.m^{-2}.yr^{-1} and did not exceed 5 g C.m^{-2}.yr^{-1} on the whole rotational cycle.

GPP and TER were deduced by extrapolation of NEE measurements. Two approaches were compared by Moureaux et al. (sub.) and each of them was optimised. Both computed first TER and deduced GPP by summation of TER and NEE. TER computation was based in both cases by extrapolation to the whole day of respiration estimates. The first approach was based on night eddy flux measurements while the second used the intercept of day flux response to radiation (PPFD). We used here the first approach as it is applicable to the whole rotational cycle, including intercrop periods. The uncertainty on TER and GPP was estimated as: $\varepsilon = \frac{1}{2}\sqrt{\sigma_1^{\,2} + \delta_{12}^{\,2} + \sigma_2^{\,2}}$ where σ_1 and σ_2 correspond to the uncertainties relative to each method and δ_{12} to the mean squared difference between TER or GPP annual estimates by the two methods.

Finally, for the NPP computation, the product of dry mass and carbon content was first computed for each sample. NPP was then computed as the mean of the four samples and its uncertainty as the standard error of the mean.

3 Results and Discussion

3.1 Climate evolution

With 10.7 °C, 11.0 °C, 11.4 °C and 11.5 °C, respectively, the years 2004 to 2007 were all characterised by an annual mean temperature higher than average (9.8°C), 2006 and 2007 corresponding in addition to the two warmest years ever observed in Belgium (Institut Royal Météorologique, 2008). This was due notably to very warm conditions in July 2006 and to temperatures well above seasonal averages between September 2006 and May 2007. In particular, only four days with an average temperature below zero was observed during winter 2006-2007. During the first two years, the average monthly temperature varied between 2 - 3 °C in winter and 17-18 °C in summer, minima lower than -5°C and maxima larger than 23°C being sometimes observed (Figure 1a). Average monthly radiation varied between 40 and 500 µmol.m^{-2}.s^{-1}. June - July 2006 and April 2007 were characterised by larger radiation than average while August 2006 and the period from May to September 2007 by radiation lower than average (Figure 1 b). Average air vapour pressure deficit peaked to 20 hPa, with day maxima up to 30 hPa (Figure 1c), and soil water content varied between 0.15 and 0.40 m^{3}.m^{-3} (Figure 1d). Three drought periods characterised by more than ten days with large saturation deficit were recorded in end June 2005, June - July 2006 and April 2007. These periods were also characterised by a sharp soil water content decrease.

3.2 Evolution of GPP and TER

In all figures and Tables and in most of the discussion below, the results are presented with the micrometeorological sign convention, considering that the positive sign is associated to upward fluxes and the negative flux to downward fluxes. However, in the next section for the sake of clarity in the discussion, both TER and GPP will be considered in absolute value.

Temporal evolutions of GPP and TER measured between 1 April 2004 and 31 March 2008 are given on Figure 2. Arrows indicate farmer interventions that had an impact on fluxes: sowing (S), harvest (H), ploughing (P), chemical haulm application (C), Round up and slime application (A) and shallow tillage (T).

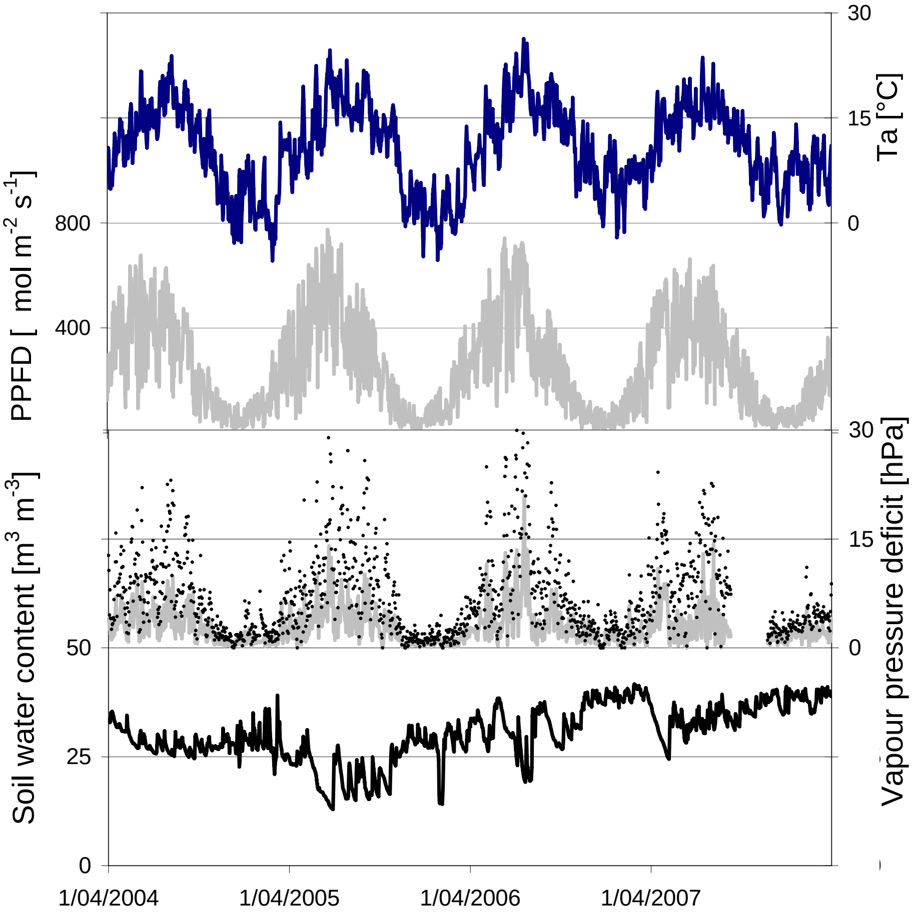

Figure 1 : Evolution of main daily averaged meteorologic variables from 1 April 2004 to 31 March 2008. Figure 1a : Temperature and Photosynthetic Photon Flux Density. Figure 1 b : Average (curve) and maximal (poins) Vapour pressure deficit and soil water content.

3.2.1 Differences between crops

Daily GPP and TER were both subjected to seasonal variability reaching maximal (absolute) values (respectively 15 gC.m^{-2}.d^{-1} and 5 to 10 gC.m^{-2}.d^{-1}) during spring and summer and minimal values (respectively lesser than 3 gC.m^{-2}.d^{-1} and 1 gC.m^{-2}.d^{-1}) in autumn and winter.

These fluxes are also subjected to a large inter-annual variability that is due either to climate variations or to differences between the crops. First, the cultivation period duration (between emergence and harvest) differed from one crop to another: it was limited to 75 days for seed potato and extended to 147 days for sugar beet and to 275 and 287 days for the two winter wheat crops. In the latter case however the vegetation period includes a vegetative slow growth period of about 150 days and a full vegetation development period on the rest of the growing season. In addition, full vegetation periods were not synchronous as apparent on Figure 3: they began in April for winter wheat and much later, in mid to end June, for the sugar beet and the seed potato. In the two latter crops the assimilation prolonged until the harvest in end September for the sugar beet or until the chemical haulm which was operated in early August for the seed potato. On the contrary, in winter wheat, assimilation was slowed down well before the harvest, the leaf senescence progressing from bottom to flag leaves and stems during the grain filling and until the crop maturation. As a result, the crop development period included a two to three week period corresponding to plant senescence.

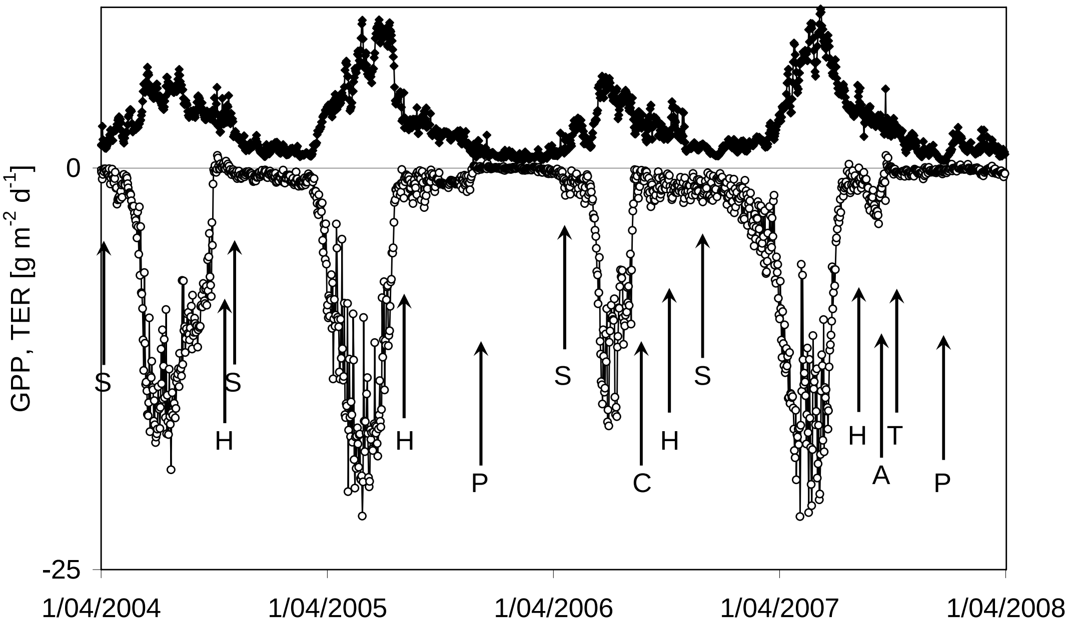

Figure 2 : Evolution of daily averaged GPP (open symbols) and TER (closed symbols) from 1 April 2004 to 31 March 2008. The different arrows represent the main management interventions : S : Sowing, H : Harvest, P : Deep ploughing, T : Tillage, A : Slimes application, C : Chemical haulm.

Amplitudes of daily GPP and TER also depend on crops. Higher values of both fluxes were observed in the winter wheat (16 gC.m^{-2}.d^{-1} and 8 gC. m^{-2}.d^{-1}, respectively), slightly smaller values in sugar beet crop (15 gC. m^{-2}.d^{-1} and 5 gC. m^{-2}.d^{-1}, respectively) and again smaller values in the seed potato crop (10 gC. m^{-2}.d^{-1} and 5 gC. m^{-2}.d^{-1}, respectively). The smaller values in the potato could partly be explained by a smaller LAI (about 3) compared to other crops (LAI about 4). However, this explanation does not hold for sugar beet that had similar LAI than winter wheat. The difference should thus probably due to a lower photosynthetic capacity of the beet. GPP values in winter wheat are in good agreement with those found in a similar crop by Anthoni et al. (2004) in Thuringia (> 15 gC. m^{-2}.d^{-1}) but larger than those found by Soegaard and Thorgeirsson (1998) (10 gC. $m^{-2}.d^{-1}$ at Tisby). However, in the latter case, the smaller value is probably explained by the higher latitude (59°N) of the site. No such data were found for potato and sugar beet. TER in the winter wheat was always larger than observed by Anthoni at Gebesee (< 5 gC. $m^{-2}.d^{-1}$) (Anthoni et al., 2004).

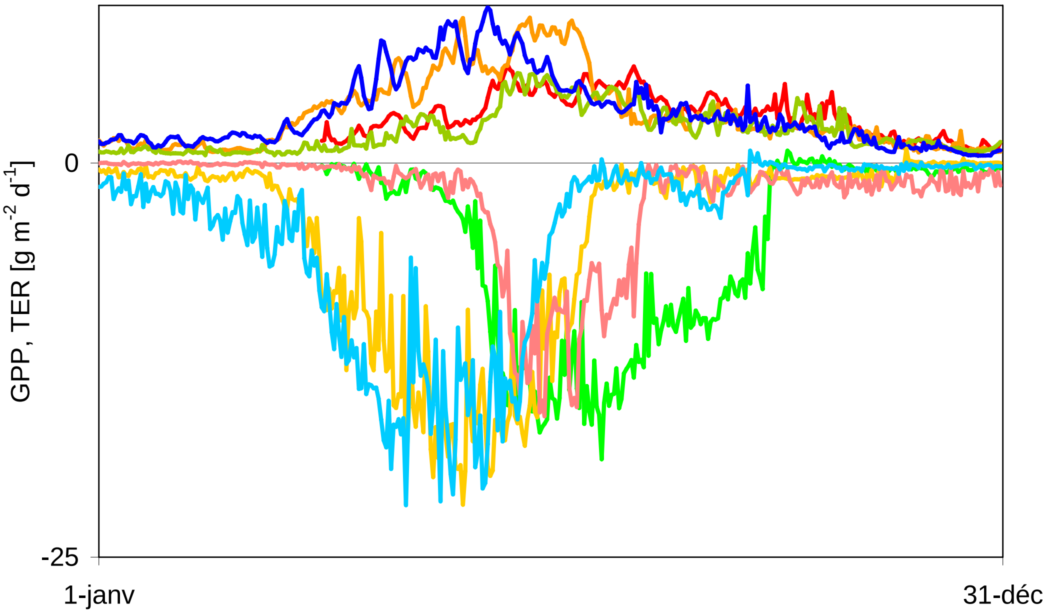

Figure 3 : Evolution with day of year (DOY) of daily averaged GPP and TER. Positive values correspond to TER, negative values to GPP. Legend : Green : Sugar beet 2004, Yellow / orange : Winter wheat 2005, Red / pink : Potato 2006, Blue : Winter wheat 2007.

Seasonal decreases in GPP had also different origins: in the winter wheat, they resulted from the leaf senescence that carries out in end June and July, while, in the sugar beet, it was due to both a radiation reduction in August and September and a reduction of sugar beet leaf photosynthetic capacity (Moureaux et al., 2006). In the potato crop, the small values observed in July are also due to the water stress undergone by the crop during this period. This is confirmed by half hourly NEE measurements taken during this period that exhibit an asymmetrical daily response which points out an afternoon stomatal closure in response to a large air vapour pressure (Figure 4). Such behaviour is relatively exceptional in Belgium and was observed only at this moment of the whole rotation cycle.

3.2.2 Impact of intercrops

Figure 2 suggests also a non negligible contribution to TER and GPP during intercrops. After winter wheat harvests, in autumn 2005 and 2007, weeds and wheat volunteers developed in the field, which induced an increase of both GPP and TER. The carbon uptake resulting from these plants was 1 to 2 gC. m^{-2}.d^{-1} but it did not compensate the TER (2 to 3 gC. m^{-2}.d^{-1}) so that the field remained a net source. These fluxes were stopped, in November 2005 by a ploughing and in September 2007 by a total weed killer application and a shallow tillage.

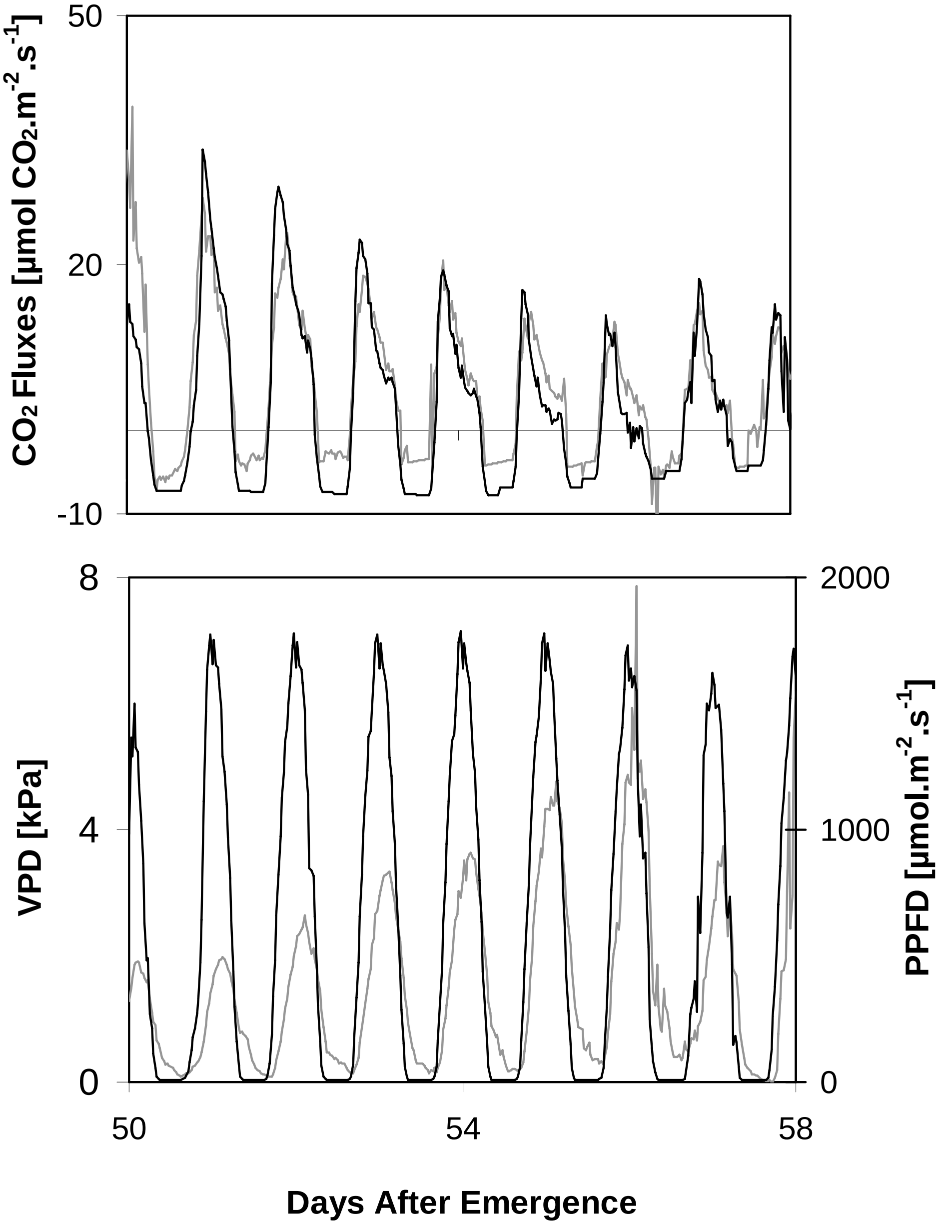

Figure 4 : Time evolution of half hourly NEE (Figure 4 a), PPFD (Figure 4 b, black curve) and VPD (Figure 4 b, grey curve) during the drought period in July 2006.

In autumn 2006, after the potato harvest, a sizeable GPP was also observed. It was first due to assimilation by weeds and after to the next crop development. GPP and TER were similar as in the other intercrops and, during this period again, the field remained a net source of about 1 to 2 gC. m^{-2}.d^{-1}. During the following winter, winter wheat assimilation was larger, due the especially mild conditions. The usual leaf development limitations due to frost and low temperature were indeed not observed on this year.

3.2.3 Impact of crop management

Some impacts of crop management on GPP and TER are also apparent in Figure 2: after the sugar beet harvest, in autumn 2004, no TER decrease was observed as should have been expected due to autotrophic respiration suppression. This is because this suppression was compensated by an increase of heterotrophic respiration due to the leaving on the field of crop residues (beet crowns and leaves, about 0.38 kgC.m^{-2}) after the harvest. The additional emission associated to the residues was clearly observable during about three weeks. Moureaux et al. (2006) estimated it to amount to 0.02 gC.m^{-2}, which corresponds to only 5 % of the carbon left.

In November 2005 a deep ploughing (30 cm) was operated. Its effect was to stop immediately both the assimilation and the respiration of the weeds that had developed in the field since the harvest. However, as both the uptake and the emission of CO_2 were suppressed the effect on NEE was not observable. The carbon emission from soil due to the ploughing itself was very limited, not exceeding 2 to 3 gC. m^{-2}.d^{-1} during one or two days following the intervention. Continuous eddy flux measurements made by Anthoni et al. (2004) on a winter wheat in Thuringia also suggested this effect to be limited. In addition, Baker and Griffis (2005), who compared flux exchanged by fields subjected to shallow or conventional tillage showed that the emission difference was of the same magnitude. This result doesn't of course take the indirect and long term effects on soil structure and soil quality into account.

In September 2007, the farmer intervention was operated in three steps: first an application of herbicide was operated on 7 September, followed by a spread of sugar beet mill slimes on September 10th, and a shallow tillage on 21 September. The herbicide application induced a progressive decrease of GPP but didn't change the TER. As a result, the net emission increased during this period. The stubble breaking finished to stop weed assimilation but had again no detectable effect on TER. Other shallow tillages, operated in mid October 2004 and 2007 had a small effect on the flux, increasing TER by 1 to 2 gC. m^{-2}.d^{-1} but this increase did not persisted beyond the day of the intervention.

3.2.4 *Impact of interannual climate variability*

The impact of interannual climate variability may be emphasized by comparing the two winter wheat crops. 2005 and 2007 were indeed characterised by very different climates that induced large differences: the exceptionally mild conditions in winter 2006-2007 boosted the wheat assimilation during winter time and provoked an earlier vegetative development but also an earlier senescence and maturation than in 2005 (Figure 3). Between November and March, the GPP was three times as high in 2007 as in 2005 (205 gC.m^{-2} compared to 68 gC.m^{-2}). However, the drought that occurred in April 2007 had a negative effect on the assimilation that was not immediately detectable on the GPP evolution but perturbed the crop development and led finally to a reduced crop productivity compared to 2005. An analysis of these interannual differences is in progress.

3.2.5 *Relative role of autotrophic and heterotrophic respiration*

The evolution of heterotrophic respiration computed with the second approach (i.e. extrapolation of soil chamber measurements on bare areas) is presented on Figure 5 (grey curve). The extrapolation was performed by using a simple exponential response to temperature (Q_{10} equation). The regression coefficients of this relation were: R_{10} (i.e., respiration normalised at 10°C) = 0.91 μmol m^{-2}s^{-1} and Q_{10} (i.e., temperature sensitivity) = 1.5 and the Rsq was 0.75. In addition, the time evolution of autotrophic respiration deduced by difference between HR and TER is presented on Figure 6a along with those of GPP and the relation between ten-day-averaged values of AR and GPP on Figure 7.

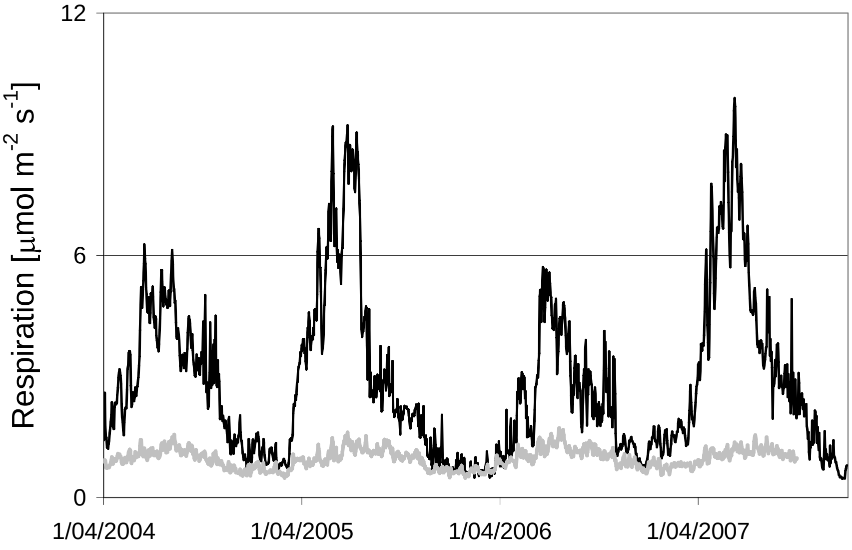

Figure 5 : Time evolution of daily averaged TER (black curve) and HR (grey curve).

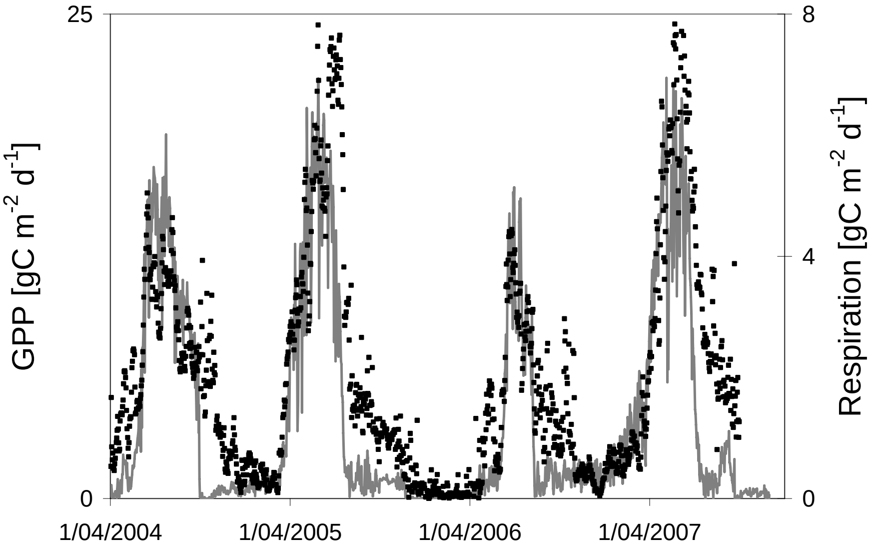

Figure 6: Time evolution of daily averaged AR (points) and GPP (grey curve).

Despite that this HR computation method is quite crude, as based on a limited set of measurements, on a single temperature response and on the hypothesis that temperature sensitivity is constant over the whole rotational cycle, it gives estimates that agree fairly well with other independent estimates during both cropping and intercrop periods. First, Figure 5 shows that during the intercrop periods, HR estimates are close to TER measurements, which was expected as the autotrophic component is small at these moments. In addition, during the three first cropping periods, cumulated HR values computed with this method was found to agree very well with estimates based on the first method (i.e. difference between NEE and NPP) (Table 2). The discrepancy between the two estimates on the fourth year is due to another problem and will be discussed below.

The HR temperature sensitivity we found was lower than the expected value of 2 and much lower than long term temperature sensitivities observed usually in crops (Reichstein et al., 2005). As a result, the annual HR fluctuations are of limited amplitude (Figure 5) and the TER increase observed in summer appears rather to be related to an AR change. This suggest that the large temperature sensitivities usually observed in crops do not indicate a direct response to temperature but rather an indirect response associated to leaf assimilation and plant growth. This was already stressed, notably in forests by Janssens and Pilegaard (2003) and in crops by Han et al. (2007) and Moyano et al (2007).

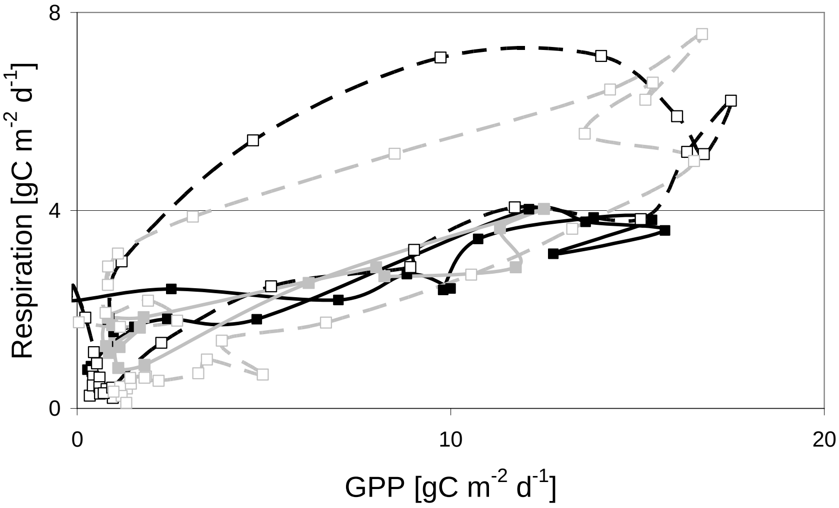

Figure 7 : Relation between AR and GPP. Each point corresponds to a ten day average. Closed symbols / Continuous line : sugar beet in 2004 (black) and potato in 2006 (grey). Open symbols / Dotted lines: winter wheat in 2005 (black) and 2007 (grey). In the winter wheat the chronological order is counter clockwise.

During the growth phases of each crops (Figure, 7, excluding the end of winter wheat season), the ratio AR / GPP appears to be practically constant, similar for the four crops and equal to 0.3. Amthor (2000), Cannell and Thornley (2000) suggested indeed this ratio to vary between 0.4.and 0.6, Monje and Bugbee (1998) and Gifford (1995) found it to remain fairly constant during the development in winter wheat.

At the end of the winter wheat season, the AR / GPP ratio increased due not only to the GPP decrease following the leaf senescence but also to an AR increase. The cause of the latter increase is not clearly identified. It probably results from specific processes at work during the dough development phase. In particular, photosynthesis product translocation and grain growth are possible causes (Amthor, 2000). Such an increase was not observed in the sugar beet and the potato crops suggesting that it is linked to a specific winter wheat development stage.

	SB - 2004	**WW - 2005**	**PS - 2006**	**WW - 2007**	**IC**	Total
Exportation	Roots: 0.63	Grain : 0.37 Straw : 0. 19	Tuber : 0.29 (0.03)	Grain : 0.31 Straw : 0.14		**1.88**
Importation		Grain : -0.006	Mother tuber : - 0.04	Grain : -0.006	Slimes : - 0.07	**- 0.12**
GPP	-1.42 (0.08)	-1.58 (0.13)	-0.60 (0.05)	-1.68 (0.12)		
TER	0.62 (0.08)	0.95 (0.13)	0.29 (0.05)	0.95 (0.12)		
NEE	-0.80 (0.04)	-0.63 (0.03)	-0.31 (0.02)	-0.73 (0.04)	0.88 (0.04)	**-1.59**
NPP	-1.01 (0.09)	-0.88 (0.05)	-0.36 (0.01)	-0.76 (0.05)		
AR	0.41 (0.12) *0.44*	0.70 (0.14) *0.70*	0.24 (0.05) *0.20*	0.92 (0.13) *0.70*		
HR	0.21 (0.09) *0.18*	0.25 (0.05) *0.24*	0.05 (0.01) *0.09*	0.03 (0.05) *0.26*		
NBP	**-0.17 (0.10)**	**-0.07 (0.06)**	**-0.06 (0.03)**	**-0.28 (0.06)**	**0.81 (0.06)**	**0.17 (0.14)**

Table 2 : Carbon budget of the rotation. Legend : SB : sugar beet (from emergence (21 April) to lifting (29 September)), WW : winter wheat (from emergence (1 November) to harvest (3/5 August)), PS : potato seeds (from emergence (24 May) to chemical haulm (6 August)), IC : intercrops (cumulated on the whole cycle). AR and HR values in normal (italic) fonts were computed using the first (second) approach. Values between parentheses correspond to the uncertainty. For more detail, see text.

3.3 Crop budgets

3.3.1 Terms of the budget

The carbon balances of each crop are presented on Table 2 as well as an evaluation of the uncertainties on each term. First, the values of all cumulated fluxes depend mainly on vegetation period lengths. In particular, the lowest values were observed for the seed potato whose vegetation period was 75 day long. Winter wheat and sugar beet, that had longer full growth period lengths (about four and three months, respectively), obtained the largest GPP and TER.

The ratio TER / GPP varied between 40 % in potato and sugar beet and 60%, in the winter wheat. The higher percentage in the winter wheat results on one hand from a higher daily respiration rate during the crop development, on the other hand from the additional respiration observed during dough development, as discussed above. TER/GPP ratios reported in the literature are generally much higher than found here because they are based on a complete year and include intercrop periods during which TER remained important while GPP was generally low. On the eight sites that we listed in the literature, only one fertilised barley field, reported by Gilmanov et al. (2003), had a TER/GPP ratio lower than 60% (42%), all the others varying between 60% and more than 100% (Suyker et al., 2005, Falge et al., 2002, Gilmanov, 2003). If we had computed this ratio on the same length scale, we would have obtained comparable values, between 61% and 73%.

The NPP / GPP ratios, obtained by comparing biomass carbon content and eddy covariance measurements were 70% for sugar beet, 60% for seed potato and the 2005 winter wheat crop and 45% for the 2007 winter wheat crop. The three first results appear in good agreement with those of Cannell and Thornley (2000) (between 40% and 60% for crops), Monje and Bugbee (1998) and Gifford (1995) (60% for winter wheat). However, the ratio obtained in winter wheat in 2007 appears too small in comparison to 2005 measurements and to literature values. We suspect this is due to a NPP underestimation and identified two possible causes. The first one is the non account in NPP computations of the tillers that decayed during the stem elongation phase. During this phase, a lower than expected NPP increase was observed, which could be explained by the degeneration of dominated tillers. As these tillers were especially numerous in 2007, due to the mild temperature underwent by the crop during winter, the non account of this term in the NPP could have a larger impact than in 2005. The second cause could be an underestimation of root biomass. As it was evaluated on the basis of a partitioning coefficient (Baret et al., 1992), which was validated on normal conditions, it did not take into account a possible enhancement of root development during the mild winter or the drought underwent by the crop in spring 2007. Both hypotheses are in agreement with the fact that, despite a larger GPP, the crop harvest was lower in 2007 than in 2005. They suggest in addition that, in 2007, a larger part of the biomass was not harvested and left to the field.

Cumulated autotrophic and heterotrophic respiration components computed by the two approaches are also presented in Table 2. The agreement between the two approaches is satisfactory for the three first crops, in view of the uncertainty inherent to each method. The differences between the predictions by the two approaches are indeed always lower than 40 gC.m^{-2}, which corresponds typically to less than half the uncertainty affecting each approach. The two methods diverge in 2007 for the reason discussed above: due to the NPP underestimation the first approach leads to abnormally high AR estimates and unrealistically low HR estimates. The second approach appears to give more coherent results. For all crops the AR / TER ratio is larger than 0.65, suggest a clear dominance of AR compared to HR during crop development period. Here again these ratios are larger than found in the literature, the reason being again that they are evaluated on the crop vegetation season and not on a whole year.

3.3.2 Global budget

In order to establish the global rotational cycle budget, NEE was also evaluated during the intercrops. During these periods, the field behaved mainly as a source, emitting 0.83 kgC.m^{-2} on the cumulated period. The emission was fairly constant, varying between 1 and 1.5 gC.m^{-2}.d^{-1}, excepted in October 2004 when NEE was increased to 3 gC.m^{-2} d^{-1}, due to the decomposition of crop residues left on the soil after the sugar beet harvest. The cumulated NEE on the four years amounted thus to -1.64 kgC.m^{-2}. If we consider that all the grain and straw is rapidly consumed and resituated to the atmosphere in a short term, we could define the NBP as the difference between NEE and net exportation (exportations minus importations). The exported carbon by the harvest amounted to 1.88 kgC.m^{-2} that distributed into 0.63 kgC.m^{-2} sugar beet roots, 0.37 + 0.31 kgC.m^{-2} winter wheat grain, 0.24 kgC.m^{-2} seed potato tuber and 0.14 + 0.19 kgC.m^{-2} wheat straw. Carbon importation also resulted from slime application, in September 2007 (0.07 kgC.m^{-2}) and from potato mother tuber sowing (0.04 kgC.m^{-2}). Importation resulting from other crop sowing was neglected, amounting to lesser than 0.01 kgC.m^{-2} in the winter wheat and the sugar beet.

On the whole, the net biome production of the whole rotational cycle could be evaluated to 0.17 kgC.m^{-2}. In average, the crop behaved thus as a slight source of about 43 gCm^{-2}.yr^{-1}. The uncertainty on the cumulated NBP is estimated to be 0.14 kgC.m^{-2}, i.e., the same order of magnitude as the value itself, so that the source character of the rotational cycle is just significant.

Any comparison of our results with literature is delicate as published results don't correspond to the same rotational cycle or to the same time scale. On one hand, one find local carbon budget studies, similar to ours that are based on multi year eddy covariance measurements and exportation assessment. However, excepted one incomplete rotational cycle (two year of winter wheat crop, Anthoni et al., 2004) most of the other studies concern maize-soybean rotational cycles, which are more common in Northern America (Verma et al., 2005, Hollinger et al., 2005). On the other hand, studies performed at a decennial scale analyse the evolution of crop soil organic carbon (SOC) using models or carbon inventories. If methane and volatile organic compound emission contributions to the soil carbon balance are neglected, NBP can be compared to SOC evolution.

Two of the multi year eddy covariance measurements show the crop to behave as a source with a NBP varying between 25 and 10 $gCm^{-2}.yr^{-1}$ (Verma et al., 2005, Anthoni et al., 2004) while the third one appears as a sink (30 $gCm^{-2}.yr^{-1}$ on a six year maize – soybean rotation, Hollinger et al., 2005, 2006a), a debate remaining however in the latter case (Hollinger et al., 2006b, Doberman et al., 2006) to determine if the sink character is significant.

SOC evolution studies conclude generally that SOC decreases in average in crops, i.e. that they behave as sources but with a variable intensity. Vleeshouwers and Verhagen (2002) using the CESAR model predicted an average emission by European arable crops of 84 gCm^{-2} yr^{-1}, under a business as usual scenario during the Commitment period 2008-2012. Goidts and Vanwesemael (2007) estimate the average decrease on carbon soil content of Southern Belgium crops between 1955 and 2005 to be about 12 $gCm^{-2}.yr^{-1}$ and, more specifically, between 7.6 to 32 $gCm^{-2}.yr^{-1}$ in the region of our study (loam region). They suggest that it is due to a decrease in mass of farmyard manure and slurry applied on cropland along with a change in the types of crops cultivated. Dawnson and Smith (2007) also indicate a SOC decrease in UK and explained it as due to a decrease in farmyard manure and slurry application. They also noticed the impact of a more efficient removal of agricultural products from fields. On the contrary, Gervois et al. (2008) consider that this last effect was compensated by increased yield that induced increased litterfall and estimated the European cropland to have behaved as a sink during 20th Century.

Globally the results we found are in coherence with most predictions at local (Anthoni et al., 2004, Verma et al., 2005) or regional (Vleeshouwers and Verhagen, 2002, Goidts and

Vanwesemael, 2007, Dawnson and Smith, 2007) scale. The emission of 42 gCm^{-2}.yr^{-1} by our rotation could indeed be explained by the crop management which includes a systematic exportation of winter wheat straw for livestock and didn't apply any farmyard manure or slurry since more than ten years. The soil carbon content decrease we observed corresponded to about 1 % per year of the initial carbon content.

Finally, this result is strongly linked to the particular climatic conditions undergone by the crops during the rotational cycle. It is indeed largely influenced by the large NBP in 2007, which is supposed to be due to a larger than usual carbon accumulation in non harvested biomass, as a result of the particular climatic conditions. Indeed, if 2007 had been similar to 2005, the cycle NBP would have been more positive (~ 0.38 kg C.m^{-2}) which would have accentuated the source character of the crop rotation (~ 90 gC.m^{-2}.yr^{-1}) and made it more significant. Models suggest generally that the impact of climate change on SOC is much lower than those of agricultural management (Vleeshouwers and Verhagen, 2002, Gervois et al., sub.). However, generally they only include the direct impact of temperature on respiration and don't take crop development modifications, as observed here, into account. They could thus underestimate this effect. Our results suggest that, by inducing an increased tiller biomass, the particular climate conditions in 2007 have increased the biomass of residues left to the field and have thus increased the carbon storage in soil. It remains however to be determined what is the residence time of the carbon stored thanks to this process.

4 Conclusions

This study allowed studying the carbon balance of a rotational crop. It showed that both TER and GPP are submitted to large seasonal and interannual variations, mainly due to differences between crop development and to climate. In particular a clear impact of a drought was observed on the seed potato crop in 2006 but, in the absence of measurements on a similar crop in normal conditions, it was not possible to quantify it. Besides this, the impact on winter wheat of the exceptionally mild conditions in winter 2007 and of the drought in spring 2007 was to increase the fraction of biomass that returned to the soil. Impact of farmer interventions were also observed: CO$_2$ emission during ploughing was found to be limited in intensity (1 to 2 μmol.m^{-2}.s^{-1}) and duration (not more than 1 day). However, this does not preclude about its impact at longer term, notably through soil structure or microbial activity modification. A significant impact of sugar beet residue abandonment on the field after the harvest was also clearly during the three weeks that followed the harvest. However, as only a small fraction of residues was respired during this period, it this effect was prolonged during the following months. It was however not possible to separate it from the other contributions to the flux. Assimilation during intercrops was also found significant, although not sufficient to offset the respiration during these periods.

A separation of TER between its autotrophic and heterotrophic components was also performed and showed that the former was clearly dominating (65 % and more) during the cropping season. A strong correlation between AR and GPP was also found during the growing season. In the winter wheat, the response of AR to GPP was characterised by a hysteresis: at the end of the season, larger AR were observed while GPP decreased due to leaf senescence. This AR increase was interpreted as due to specific processes that take place during the dough development.

Budget of the rotational cycle showed that NEE was negative during cropping periods but positive during intercrops. On the whole, NEE was negative, the ecosystem assimilating -1.64 kg C.m^{-2}. The NBP, computed by combining NEE, exportations at the harvest and importations was finally positive, about 0.17 kg C.m^{-2}. This suggests that, if the carbon exported at the harvest was immediately released in the atmosphere, the rotational cycle would then behave as a source. Another consequence is that, at the rotation scale, the crop soil looses carbon. This result is just significant as the uncertainty is about the same as the flux itself. However, it is always on the source side of zero. In addition, the source intensity was mitigated by the particular climatic conditions of 2007. The exceptionally mild temperatures in winter and the drought in April 2007 induced a larger than usual tiller biomass that degenerated during the elongation phase and returned to the soil, leading to a larger aerial litter biomass as usual. Consequently, if 2007 had been a “normal” year, similar to 2005, the source intensity of the rotation would have been much larger and more significant. However, caution must be taken before extrapolating this result at a larger scale as this result is probably a result of the specific management of the site. Indeed, neither farmyard manure nor slurry was applied on the side since more than ten years and cereal straw were systematically exported for livestock, which could explain the decrease in soil carbon content.

The main causes of uncertainties affecting these results were associated to eddy covariance or biomass sampling measurements. In eddy covariance, the main cause of uncertainties came from the u_* threshold determination. Indeed, as no clear plateau appeared in the relation between normalised night flux and temperature, NEE was sensitive to the threshold choice. Moureaux et al. (2006) showed that an uncertainty of 0.1 m.s^{-1} on the threshold, induced an uncertainty of 17 gC .m^{-2}.yr^{-1} on the NEE. Besides this, random uncertainties introduced by data gap filling, by footprint fluctuations or mesoscale movements appeared very small, of the order of 2 gC.m^{-2}.yr^{-1} each. This uncertainty appeared finally lower to those associated with the biomass sampling and that resulted from crop heterogeneity.

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