



Variabilité intra-annuelle de l'efficacité de production de biomasse aérienne (aBPE) d'une forêt : comparaison avec une prairie soumise aux mêmes conditions climatiques

Laura Heid

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Thèse

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Par **Laura HEID**

Variabilité intra-annuelle de l'efficacité de production de biomasse aérienne (aBPE) d'une forêt : comparaison avec une prairie soumise aux mêmes conditions climatiques

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Glossaire

Abbreviations	Anglais	Français
aBP	aboveground Biomass Production	Production de biomasse aérienne
aBPw	Wood aboveground BP	Production de biomasse aérienne bois
aBPE	above-ground Biomass Production Efficiency	Efficacité de production de biomasse aérienne
aCP	aboveground Biomass' Component Production	Production de composés de la biomasse aérienne
aCPE	aboveground Biomass' Component Production Efficiency	Efficacité de production de composés de la biomasse aérienne
APG	3-Phosphoglyceric acid	Acide 3-Phosphoglycérique
ATP	Adénosine triphosphate	Adénosine triphosphate
BP	Biomass Production	Production de biomasse
BPE	Biomass Production Efficiency	Efficacité de production de biomasse
CC	Climate change	Changement climatique
CO ₂	Carbon Dioxide	Dioxyde de carbone
CUE	Carbon Use Efficiency	Efficacité d'utilisation du Carbone
DBH	Diameter at Breast Height	Diamètre à 1.30m
EC	Eddy-Covariance	Covariance de turbulence
GES	Greenhouse gas	Gaz à effet de serre
GHG	Greenhouse gas	Gaz à effet de serre
GPP	Gross Primary Production	Production Primaire Brute
NADP	Nicotinamide adenine dinucleotide phosphate	Nicotinamide adénine dinucléotide phosphate
NEE	Net ecosystem exchange	Echange net de l'écosystème
NPP	Net Primary Production	Production Primaire Nette
NSC	Non Structural Carbon	Carbone non structural (sucres, amidons,)
NSCP	Non Structural Carbon Production	Production de composés carbonés non structuraux
O ₂	Dioxygen	dioxygène
PAR	Photosynthetic Active Radiation	Rayonnement Photosynthétiquement Actif
Ra	Autotrophic respiration	Respiration autotrophe
Reco	Ecosystem respiration	Respiration de l'écosystème
Rs	Soil respiration	Respiration du sol
Rsa	Soil Autotrophic respiration	Respiration autotrophe du sol
Rsh	Soil heterotrophic respiration	Respiration hétérotrophe du sol
RubisCO	Ribulose-1,5-bisphosphate carboxylase/oxygenase	Ribulose-1,5-bisphosphate carboxylase/oxygénase
RuBP	Ribulose-1,5-bisphosphate	Ribulose-1,5-bisphosphate
SC	Structural Carbon	Carbone structural (Hemicellulose, Cellulose et lignine)
SCP	Structural Carbon Production	Production de composés carbonés structuraux
SCPcel+l	Structural Carbon Production (Cellulose and lignins)	Production de composés de la biomasse aérienne (cellulose et lignine)
SCPh	Structural Carbon Production (hemicelluloses)	Production de composés de la biomasse aérienne (hémicelluloses)
VOC	Volatile organic component	Composés Organiques Volatils

Chapitre 1 INTRODUCTION

1.1 Contexte de l'étude

Depuis le début de l'ère industrielle, la température moyenne du globe a augmenté d'environ 1°C. Des événements extrêmes (tempêtes, sécheresses,...) ont lieu de plus en plus fréquemment. Ce dérèglement climatique est lié à l'augmentation de la concentration atmosphérique de gaz à effet de serre (GES) d'origine anthropique. L'un des principal responsable est le dioxyde de carbone (Cox et al., 2000).

Le dioxyde de carbone est en effet le gaz à effet de serre le plus produit par l'activité humaine (combustion d'énergie fossile, agriculture,...). Son émission représentait 55% des émissions totales de GES en équivalent C (IPCC, 2013) et sa concentration a augmenté de 2.0 ppm par an depuis 2001, l'amenant à une concentration atmosphérique de 390.5 ± 0.2 ppm en 2011 (IPCC, 2013).

De ce fait, de nombreuses études se sont concentrées sur les flux de CO₂ et sur le cycle du carbone. L'étude des échanges de CO₂ entre atmosphère et milieux naturels, en particulier avec les écosystèmes terrestres qui absorbent environ 28% des émissions (Le Quéré et al., 2012) est devenu un sujet de recherche majeur. Le changement climatique (CC) induit des répercussions sur le comportement de ces écosystèmes terrestres en termes de mitigation des GES, de croissance, de productivité, de biodiversité, d'activité édaphiques et également de gestion des ressources en eau. Ces études permettent une meilleure compréhension du bilan carboné et du fonctionnement des écosystèmes. Elles ont pour but de trouver une solution à l'augmentation de la concentration de CO₂ dans l'atmosphère (en augmentant son stockage) et de modéliser l'évolution future des écosystèmes (mortalité, adaptation, résilience) pour prédire la future configuration de leurs aires de répartitions.

1.2. Bilan CO₂ d'un écosystème terrestre

1.2.1. Définition

Le bilan CO₂ d'un écosystème (NEE, Net Ecosystem Exchange) est la résultante entre le dioxyde de carbone absorbé par cet écosystème (GPP, Gross Primary Productivity correspondant à la photosynthèse moins la photorespiration), celui relargué dans l'atmosphère par la respiration dite « sombre » (Reco, Ecosystem Respiration) et celui s'échappant dans les écoulements d'eau dans le sol sous forme dissoute (Run off). En général, dans la littérature, cette fuite par écoulement est négligée dans le bilan (Clark et al. 2001) (**Figure 1.1**).

1.2.2. Respiration de l'écosystème

La respiration de l'écosystème, Reco, correspond au flux de carbone sous forme de CO₂ rejeté dans l'atmosphère par la chaîne respiratoire de la membrane des mitochondries. Elle est composée de la respiration aérienne (Ra ; plantes, composante autotrophe) et de la respiration du sol (Rs). Cette dernière est scindée en une respiration autotrophe (Rsa ; dont la source est le carbone organique

assimilé par les plantes et fourni à la rhizosphère) et hétérotrophe (Rsh ; décomposition de la matière organique du sol par les microorganismes).

Il existe également une photorespiration ne se déroulant qu'en présence de lumière, au sein des chloroplastes par la fonction oxygénase de l'enzyme RubisCO (Ribulose 1,5 triphosphate Carboxylase/Oxygénase). Elle est, dans notre étude, comprise dans la GPP. Il est difficile de la comptabiliser dans Reco du fait de la méthode d'obtention des différents flux de CO₂ entre les écosystèmes et l'atmosphère. En effet, la seule quantité réellement mesurée parmi ces flux est la NEE par la méthode des covariances turbulentes (Eddy Covariance, technique micro-météorologique basée sur les données de vitesses de vent vertical et de concentrations de gaz à hautes fréquences collectées à l'interface atmosphère-écosystème (Aubinet et al., 2012). La nuit, les valeurs de NEE correspondent à la Reco comme définie ci-dessus. La Reco de jour est obtenue par extrapolation des données obtenues de nuit (ne comprenant donc pas la photorespiration) sur base d'une relation à la température et/ou à l'humidité du sol (Reichstein et al., 2005). La GPP est déduite pour les périodes diurnes en soustrayant les valeurs de Reco de jour aux mesures de NEE faites par Eddy covariance.

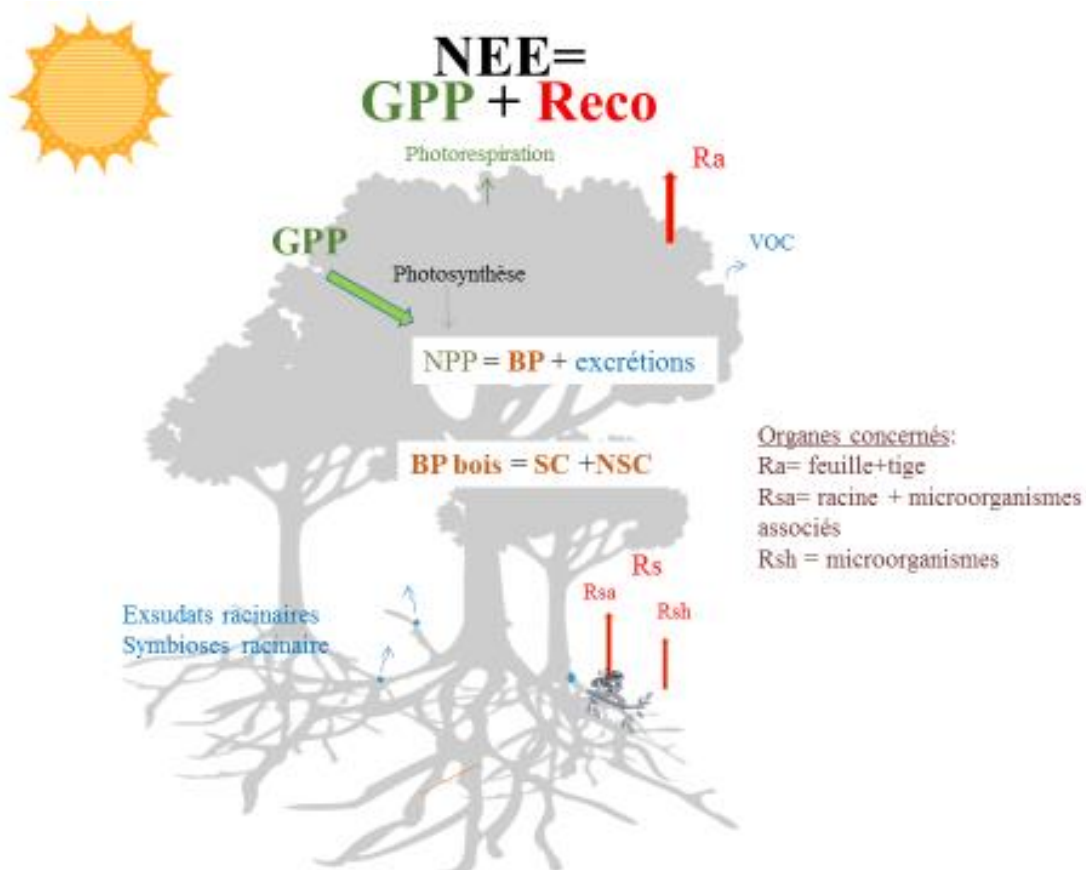


Figure 1.1 Schéma représentant le cycle du carbone dans un écosystème terrestre. (Waring and Schlesinger 1985; Bonan 2008a; Waring and Running 2010)

Reco varie beaucoup spatialement et également temporellement. Ses composantes sont en effet dépendantes de plusieurs facteurs biotiques fluctuants comme la température du sol (corrélation positive ; Raich and Schlesinger, 1992; Lloyd and Taylor, 1994; Davidson et al., 1998; Epron et al., 1999), l'humidité du sol (réduction de la respiration en cas de sécheresse ;(Joffre et al., 2003), la disponibilité en nutriment du sol (nécessaire au fonctionnement des micro-organismes décomposeurs) pour la Rsh, l'indice foliaire et le flux de rayonnement photosynthétiquement actif (accroît l'apport carboné substrat des processus respiratoires), l'âge du peuplement (il semblerait qu'elle augmente chez les peuplements forestiers plus âgés ; (Rocha and Goulden, 2010) ainsi que les pratiques culturales (Toland and Zak, 1994; Peng et al., 2008; Adachi and Tsuda, 2013). De plus, certains facteurs comme l'humidité et à la structure du sol ainsi que la turbulence aérienne, influencent le transport du CO₂ du lieu de production dans le sol jusqu'à son passage à l'air libre (Davidson et al., 1998; Goffin et al., 2015). Cela augmente la variabilité spatio-temporelle de Rs à petite échelle.

1.2.3. GPP (Photosynthèse et photorespiration)

La photosynthèse correspond au carbone prélevé dans l'atmosphère par une plante. L'entrée du carbone se fait sous forme de CO₂ par l'ouverture des stomates. Ces orifices présents dans l'épiderme des parties aériennes d'une plante s'ouvrent ou se ferment suite à des variations de pression de turgescence dans les cellules de gardes. Ces variations sont dépendantes de différents facteurs. En effet, les stomates ne s'ouvrent qu'en présence de lumière (ils sont notamment très sensibles à la lumière bleue ; Assmann, 1993; Zeiger and Zhu, 1998; Assmann and Shimazaki, 1999)), et participent au mécanisme de préservation de l'eau des plantes en se fermant lorsque l'air est trop sec ou que l'eau vient à manquer (Turner and Begg, 1973; Turner, 1974; Assmann, 1993), limitant ainsi l'évapotranspiration mais aussi réduisant l'entrée de CO₂ (Jarvis and McNaughton, 1986; Mott and Parkhurst, 1991; Jones, 1998).

La photosynthèse est composée de deux réactions successives (Whatley et al., 1963; Heineke, 2001; Bendall, 2001; Heineke and Scheibe, 2009). La première, la réaction photochimique, n'a lieu qu'en présence de lumière (Bendall, 2001). Toutes les longueurs d'onde ne sont pas utilisées, uniquement celles comprises dans le rayonnement photosynthétiquement actif (PAR ; 400 -680nm ; McCree, 1971; Gosse et al., 1986)). Cette étape permet la formation d'énergie sous forme d'Adénosine TriPhosphate (ATP) et de pouvoir réducteur sous forme de Nicotinamide Adénine Dinucléotide Phosphate (NADP) grâce à la photophosphorylation de molécule d'eau. Il faut noter que les enzymes participantes aux réactions photochimiques sont sensibles à la température (optimum entre 15-25°C en forêt tempérées, Bonan, 2008 ; Vu et al., 1997; Salvucci and Crafts-Brandner, 2004).

La seconde étape est une réaction chimique, correspondant au cycle de Calvin (**Figure 1.2**) et permettant de fixer le carbone grâce à l'enzyme RubisCO, sans nécessité de lumière. La RubisCO possède une double fonction carboxylase/oxygénase dont la balance dépend du ratio CO₂/O₂, lui-même

fonction de la température. Avec une température élevée, les stomates se ferment (Rodriguez and Davies, 1982), le ratio CO_2/O_2 intercellulaire diminue favorisant ainsi la fonction oxygénase (Brooks and Farquhar, 1985). C'est sa fonction carboxylase qui nous intéresse ici. La fixation se fait soit directement à partir de CO_2 pour les plantes C_3 , soit par l'intermédiaire de l'oxaloacétate pour des plantes en C_4 . Le CO_2 est d'abord incorporé à une molécule (Ribulose bis phosphate, RuBP) pour donner deux molécules d'acide phosphoglycériques (APG). Ces molécules sont alors réduites en Trioses-Phosphate en utilisant de l'ATP et du NADP formés dans la première étape. Certains de ces Trioses-P seront par la suite utilisés pour la synthèse de glucides ou de réserves carbonées sous forme d'amidon qui seront par la suite transformés en glucides (Heineke, 2001; Heineke and Scheibe, 2009). Les principaux glucides formés sont le saccharose, le glucose et le fructose (Hoch et al., 2003), et entreront dans la composition d'énergie et de composés structuraux. Les autres Trioses-P permettent la régénération de la RuBP.

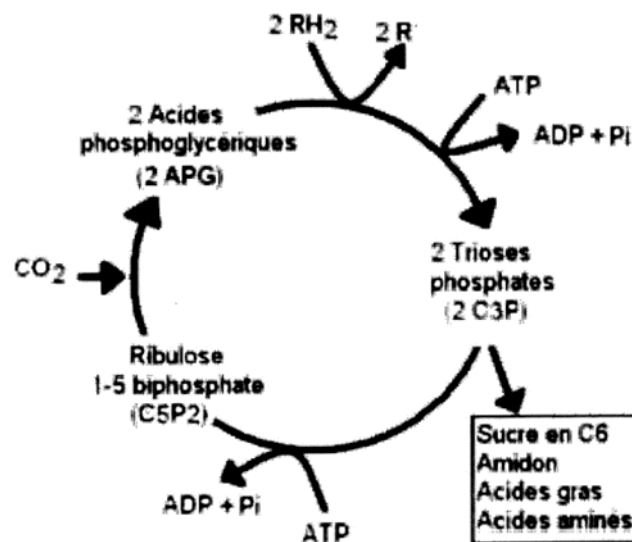


Figure 1.2 Schéma simplifié du cycle de Calvin (source : svtmarcq.over-blog.com)

Il n'est pas possible de quantifier directement la photosynthèse mais en étudiant la production primaire brute (GPP, photosynthèse + photorespiration), on obtient une bonne estimation de sa variabilité temporelle. La GPP caractérise le flux de carbone entrant qui est alloué soit à la formation de la matière organique (c'est la production primaire nette, NPP) soit au processus de respiration autotrophe de la plante (Kira and Shidei 1967; Waring et al. 1998; Ryan et al. 2004). La NPP se décompose elle-même en production de biomasse fixée dans la plante (BP ; croissance, synthèse et formation de réserves) et en divers exsudats et excréctions carbonées (exsudats racinaires, composées organiques volatiles (VOC), symbiontes racinaires,...) souvent considérés dans le bilan carbone comme quantité négligeable par rapport à la quantité allouée à la biomasse (Clark et al. 2001).

1.3. Importance des écosystèmes prairiaux et forestiers

1.3.1. Dans le monde

Plus de deux tiers des écosystèmes terrestres sont répartis entre forêts et prairie.

Les écosystèmes forestiers représentent près d'un tiers des terres émergées, et stockent près de 45% de l'ensemble du C terrestre (Bonan 2008b). Selon la définition de ce qu'est une prairie, leur surface varie entre 20 et 40%, en se basant sur la définition de la FAO (les prairies pâturées et fourragères) elles représentent 26% de la surface terrestre (FAO 2010)

1.3.2. Dans la mitigation des émissions de CO₂

A l'échelle globale, les écosystèmes terrestres peuvent stocker jusqu'à 28% des émissions de C (Le Quéré et al. 2012).

Les émissions liées à l'activité humaine représentent $10.7 \pm 1.2 \text{ Gt C.an}^{-1}$ (Le Quéré et al. 2012).

Dans une synthèse d'inventaire forestier, Dixon et al., (1994) ont estimé que les forêts boréales et tempérées de l'hémisphère nord accumulaient $0.7 \pm 0.2 \text{ Gt C.an}^{-1}$ dans leur biomasse. L'ensemble des forêts pourraient accumuler 2.4 Gt C.an^{-1} (Pan et al, 2011). Lal (2004) a estimé que l'ensemble des prairies permanentes pouvaient séquestrer entre 0.01 et 0.3 Gt C. an⁻¹.

1.3.3. Services écosystémiques

En plus de leur importance dans la mitigation des émissions de CO₂, ces écosystèmes ont également une forte importance socio-économique. Les forêts, tout comme les prairies, constituent l'habitat de nombreuses espèces animales et végétales et ont également un rôle récréatif important. Les forêts, tout comme les prairies, participent également à la filtration de l'eau et de l'air. Si cela n'était pas déjà suffisant, certaines forêts permettent également d'alimenter l'industrie papetière, tandis que d'autre permettent de nous fournir en bois de chauffage, ou tout simplement de fournir de la matière première pour nos meubles et charpentes. Les prairies ne sont pas en reste, permettant de nourrir, été comme hiver, le bétail dont nous dépendons quotidiennement.

1.4. Efficacité de Production de Biomasse

1.4.1 Définition

Afin de quantifier la proportion de carbone assimilé par une plante utilisé pour sa respiration ou pour sa croissance, des grandeurs appelées efficacités ont été introduites. Elles correspondent aux fractions

de GPP dédiées aux processus étudié. L'une d'entre elle est l'Efficacité d'Utilisation du Carbone (CUE) égale au rapport NPP/GPP (Gifford 2003) représentant la part de carbone utilisée pour des processus autres que respiratoire. Or comme décrit précédemment, la NPP inclut aussi bien la BP que toutes les productions d'exsudats racinaires ou de composés tels que les VOC. Vu la difficulté de mesurer ces productions, la BP a souvent été utilisée en tant que proxy pour la NPP ((Gifford 2003; Drake et al. 2011; Goulden et al. 2011) car elle est facile à estimer à partir de données biométriques. Afin de lever toute ambiguïté et cibler en particulier la part de carbone assimilée par la plante dédiée uniquement à la production de biomasse fixée, Vicca et al., (2012) ont introduit l'Efficacité de Production de Biomasse (BPE) et qui correspond au rapport BP/GPP. La BP comprend toute la biomasse produite pendant l'année. On peut estimer sa composante aérienne à partir de la hauteur et de la circonférence de l'arbre pour les forêts. Elle est généralement exprimée en unités de volume de matière sèche par an et par individu. Afin de la rapporter à la GPP, qui est déterminée grâce à la méthode des covariances turbulentes (voir ci-dessous) en unités de masse de carbone par m² de sol, il est nécessaire de prendre en compte la densité de la matière sèche, la concentration en carbone dans la matière sèche et la densité surfacique du nombre de tiges de chaque type d'individus. . Pour les prairies, la quantification de BP provient de chiffre de récolte et est exprimée en unités de masse de matière sèche (MS) par m² de sol. Il suffit de connaître la concentration en carbone de cette MS pour en déduire une biomasse en gC m⁻².

Il a souvent été décrit que l'on pouvait considérer que le rapport de la respiration sur la photosynthèse était constant et par conséquent que la BPE était relativement constante d'une forêt à l'autre, égal à une valeur d'environ 0.47 (entre 0.4 et 0.65 ; Gifford, 2003). La BPE semble également relativement stable en prairie (0.3±0.1 ; Ammann et al, 2007 ; Klumpp et al, 2007) Cette relative stabilité serait liée au phénomène de conservation de masse plutôt qu'à des raisons physiologiques (Oijen et al., 2010). Pourtant dans un rapport bibliographique sur le BPE, DeLucia et al., (2007) ont montré que le ratio de BP/GPP variait substantiellement d'une forêt à l'autre, et que ne pas prendre en compte cette variabilité pouvait amener à de très fortes erreurs lors d'extrapolation spatiale à l'ensemble de la biosphère terrestre. De nombreuses études s'attachent donc à présent à trouver l'origine de ces variations.

1.4.2. Causes de la variabilité de la BPE

Pour les forêts, Vicca et al. (2012) ont mis en évidence que la disponibilité en nutriment était le déterminant primaire du BPE, une faible disponibilité en nutriment entraînant un rapport BP/GPP plus faible. Cette disponibilité en nutriment est considérée dans cette thèse comme la fertilité du sol, lorsqu'elle est couplée à la profondeur du sol. D'autres auteurs mettent également en évidence l'impact positif de la fertilisation du sol sur le carbone assimilé dédié à la productivité du pin de Monterey (*Pinus radiata* D. Don) (Waring 1981; Sheriff et al. 1986). Sheriff et al., (1986) rapportent que le taux d'assimilation nette de carbone par unité de surface foliaire ainsi que l'accumulation de biomasse

aérienne (bois et feuille) sont augmentées dans des proportions différentes par la fertilisation en azote et phosphore. Pour expliquer ces influences, Vicca et al., (2012) ont émis l'hypothèse que les forêts avec une faible disponibilité en nutriment investissent plus de photosynthétats dans l'activité racinaire et symbiotique afin de contrebalancer cette carence par un meilleur taux de prélèvement. Il est difficile de confirmer cette hypothèse car ces composés ne sont en général ni mesurés ou ni pris en compte dans les études de par la difficulté technique existante pour les quantifier. Lehmeier et al., (2013) ont montré chez *Lolium perenne* que le manque d'azote édaphique entraînait la diminution du taux de croissance foliaire et de l'apport d'azote dans la zone de croissance mais augmente son stockage.

DeLucia et al., (2007) ont montré que l'âge semblait avoir un impact négatif sur la BPE, et en corrigeant les valeurs de BPE par l'âge, celles-ci présentaient une meilleur clivage entre différents types de biomes (la BPE étant plus importante pour une forêts de feuillus tempérée que pour une forêt boréale). Cet argument n'est pas confirmé par les résultats de Vicca et al., (2012), qui avancent que cet effet âge serait confondu avec l'effet type de peuplement et climat, les peuplements les plus jeunes étant en majorité situés dans la zone tempérée (Drake et al. 2011).

Ryan et al., (1997) ont mis en évidence qu'il existait également des différences significatives entre les BPE de différentes espèces (*Pinus banksiana*, *Populus tremuloides* et *Picea mariana*) croissantes sur des mêmes sites et ce pour des conditions thermiques variées.

Vicca et al., (2012) ont également montré qu'il existait une dépendance vis à vis de la gestion forestière, le BPE d'une forêt gérée étant supérieur à celui d'une non-gérée. Ce résultat paraît à priori logique vu que les pratiques sylvicoles ont pour objectifs (et ont donc été élaborées) pour maximiser le rendement de production de biomasse (ligneuse pour une forêt, foliaire pour la prairie). Ce comportement pourrait être lié à la diminution du rapport Ra/GPP suite à une éclaircie (favoriser les individus à fort indice foliaire), ou lié au fait que des perturbations anthropiques fréquentes peuvent augmenter la disponibilité en nutriment (en fractionnant la biomasse au sol et permettant ainsi son incorporation plus facilement). Le pâturage semble également avoir un impact fort sur les termes d'allocation dans le cycle du carbone et de l'azote. En effet, Schuman et al., (1999) ont mis en évidence que pour une prairie semi-naturelle le pâturage permettait d'augmenter la quantité de C dans les 30 premiers cm du profil de sol. Ils ont supposés que cela pouvait être lié soit à la meilleure incorporation du C dans le sol lié au piétinement des bêtes (brisure des plantes plus importante, enfouissement amélioré,...) ou alors qu'il pouvait y avoir un transfert du NPP vers les parties souterraines de la plante pour mettre en réserve le carbone et assurer une repousse par après.

Enfin, la concentration en CO₂ atmosphérique entraîne une modification de l'allocation du carbone entre biomasse aérienne et souterraine. En effet, Matamala et al., (2003) ont mis en évidence qu'une augmentation de cette concentration entraîne une plus forte allocation vers les racines.

Le suivi du rapport BP/GPP par rapport à différentes variables (climat, type d'écosystème et gestion, espèce,...) permettrait de mieux cerner l'influence de ces variables sur l'allocation du carbone dans la

biomasse et donc de perfectionner les modèles existants. Par contre il est à noter que pour les écosystèmes forestiers le carbone utilisé lors de la croissance et de la formation de biomasse n'est pas totalement celui assimilé dans l'année. Une partie des feuilles et de la biomasse ligneuse sont élaborées à partir des réserves carbonées formées grâce à l'assimilation de l'année précédente. Toutefois le datage du carbone utilisé demande des techniques de mesures (isotopiques par exemple) qui dépassent le cadre de cette thèse et la quantification de ce carbone provenant des réserves restent actuellement incertaine et représente une faible proportion du carbone total utilisé. Nous mettrons donc ici en relation directement les productions biomasse d'une période (mensuelle souvent) avec l'assimilation simultanée. Nous nous sommes également uniquement concentrés sur la partie aérienne de chaque écosystème. Cette restriction est à la fois technique (difficulté de quantifier la biomasse racinaire) et aussi liée aux objectifs puisque la partie aérienne de l'écosystème représente celle qui peut être exploitée pour une forêt ou une prairie.

1.5. Biomasse aérienne et efficacité de production de ses composants pour l'écosystème forestier

Pour aller plus loin, il est également intéressant d'étudier l'évolution de certains composés formant la biomasse aérienne. Seule la répartition du C dans la production de biomasse aérienne (aBP) en forêt est présentée dans ce manuscrit.

1.5.1. Biomasse aérienne

La biomasse aérienne est composée principalement de deux pools de C.

Le premier, le C non structural (NSC) est constitué de composés carbonés facilement réutilisables et très mobile tels que l'amidon et les sucres solubles. Ce sont les composés formés à l'aide des Trioses-P produit par le cycle de Calvin lors de la 2^e étape de la photosynthèse (Figure 1.2). Le NSC a un rôle de réserve et permet de fournir du matériel permettant la croissance et la formation postérieure des molécules présentes dans les parois cellulaires.

Ces molécules des parois cellulaires constituent le 2^e pool de C de l'aBP et représentent le C structural (SC) de la plante. Les parois sont le pool de C le plus large de la biomasse et jouent un rôle important dans le cycle du C des écosystèmes (Hoch 2007). Les parois sont un mélange complexe de protéines et de polysaccharide. Le principal composé formé est la cellulose qui représente environ 45% de la matière sèche du bois (Haigler et al. 2001) et est synthétisée dès le début de la croissance radiale. Le second composé sont les lignines qui représentent environ 30% de la biomasse totale du bois (Boerjan et al. 2003). Elles permettent le processus de lignification qui a lieu en général après la croissance radiale de l'arbre (Cuny and Rathgeber 2014; Cuny et al. 2015) et permettent le renforcement de la structure autorisant ainsi à l'arbre de se maintenir à la verticale et pouvant également avoir un rôle de défense contre les nuisibles (Moura et al. 2010). Pour finir le 3^e composé sont les hémicelluloses qui représentent environ 25% de la biomasse de la plante (Hoch 2007) et a un rôle de pont entre les

différentes fibres de cellulose ce qui permet le maintien de la structure des parois. Les molécules d'hémicelluloses sont les plus mobiles des composants de la paroi cellulaire et peuvent sous certaines conditions jouer un rôle de réserve pour l'arbre (Hoch 2007; Schädel 2009).

1.5.2. Efficacité de production de composés de la biomasse aérienne

La production de SC (SCP) est un terme important du budget C d'une forêt du fait qu'il représente le C stocké sur le long terme dans la biomasse (jusqu'à la mort de l'arbre) et correspond à un stockage « durable » et « utile » (c'est aussi le composé de base de tous les produits d'exploitation tel que papier ou bois d'œuvre,...) dans l'arbre. En calculer l'efficacité de production (aCPE, le rapport entre les aCP hémicellulose et Cellulose + lignine et la GPP) est donc très intéressant et permet d'avoir une idée de l'efficacité de stockage durable du C de l'écosystème. La connaissance de la production de carbone non structurale (NSCP) et de son efficacité (NSCPE) peut aussi se révéler être importante pour comprendre les stratégies interannuelles des feuillus.

1.6 Objectifs et hypothèses

L'objectif de la thèse était d'étudier la dynamique saisonnière de l'allocation du C atmosphérique assimilé au sein de la biomasse aérienne des plantes d'une forêt, et d'une prairie afin de permettre une comparaison entre ces deux écosystèmes.

L'étude des déterminants d'une potentielle variabilité saisonnière est importante. Cela permettrait d'avoir une estimation de l'impact de certaines conditions climatiques pouvant être limitantes (i.e. sécheresse) en termes d'efficacité de production de biomasse selon la période à laquelle elles ont lieu. En effet, les différents déterminants étudiés ici n'étant pas linéaire, l'utilisation de valeurs moyennes issues d'études annuelles entraînerait des erreurs quant à l'estimation de l'aBP.

Nos principales hypothèses de départ sont :

- La densité du bois variant au cours de l'année (Cuny et al. 2015; Rathgeber et al. 2016), il est peut-être nécessaire de prendre en compte ses fluctuations dans l'étude de l'évolution intra-annuelle de l'aBP en forêt. (**Hypothèse 1.1**)
- Le C atmosphérique absorbé n'est pas alloué aux mêmes processus selon la période de l'année, on s'attend donc à ce que le pourcentage de C alloué à l'aBP du bois et de l'herbage varie au cours de l'année (**Hypothèse 1.2**)
- Les NSCP varient généralement peu au cours de l'année pour le hêtre (Barbaroux and Bréda 2002; Zein et al. 2011) contrairement à la aCP en CS variant selon la xylogénèse avec une forte production en début de saison de croissance puis un ralentissement correspondant à la lignification et l'arrêt de la division et croissance des cellules (Cuny et al. 2015) (**Hypothèse 2**)

- Le parcours technique en prairie (mise en pâture, fauchage, fertilisation) impact fortement l'état de cet écosystème. Par conséquent, on s'attend à ce que la variabilité de l'aBPE en prairie dépend plutôt du timing de la gestion que de facteurs environnementaux à l'inverse de celle de la forêt, subissant une gestion beaucoup moins intense (**Hypothèse 3**)

Les trois chapitres suivant sont composés d'articles reposant sur des analyses effectuées sur deux sites localisés au nord-est de la France, en Meuse (55) sur lesquels se trouvent une tour ou un mât de mesure de flux, permettant d'obtenir nos valeurs de GPP. Les flux sont obtenus sur une certaine zone, appelée « footprint » qui est définie par la direction ainsi que la vitesse du vent pour chaque mesure.

Le site « forêt » est une futaie de hêtres (*Fagus sylvatica* L. ; recouvrant 85%) d'une soixantaine d'année gérée par l'Office National des Forêts (ONF). Les principales autres espèces sont des érables sycomores (*Acer pseudoplatanus* L.) et des charmes (*Carpinus betulus* L.). Le sous-couvert est rare dans la partie incluse dans le footprint de la tour de mesure des flux et n'a donc pas été pris en compte. Le site « prairie » est une prairie semi-permanente qui est soumise à une gestion mixte. Elle est à la fois fauchée et pâturée par des bovins. Une fertilisation y a également été effectuée en début d'année d'étude. Les espèces principales sont *Bromus hordaceus* (recouvrant 53.8% de la surface) et *Bellis perennis* (16.8%).

Tous les résultats sont issus d'analyses réalisées sur du matériel collectés en cours de l'année 2014. Nous avons considéré l'année 2014 comme une année typique pour nos sites d'études. Aucun pathogène n'a été trouvé ni aucune éclaircie n'a eu lieu en forêt au cours de l'année d'étude. Le REW n'est jamais descendu sous 0.4 en forêt. Par contre, il semble qu'il y ait eu une seule période, en prairie, pour laquelle il y a eu un risque de sécheresse. En effet, sur une courte période (11 juin au 3 juillet) l'évapotranspiration réelle (ETR) était inférieure à l'évapotranspiration potentielle (ETP) et aucunes précipitations n'ont été enregistrées sur cette période. Ce potentiel déficit hydrique a été pris en compte au cours de l'analyse des données prairiales.

Le **Chapitre 2** de ce manuscrit présentera la variabilité intra-annuelle de l'aBPw ainsi que de son efficacité (aBPE) pour une hêtraie lorraine et consiste en un article accepté dans le journal « Annals of forest science ».

Pour obtenir ces valeurs, un suivi de l'accroissement en diamètre mensuel a été effectué sur plusieurs arbres inclus dans 2 stations d'études. Cet accroissement a ensuite été extrapolé pour obtenir un accroissement moyen pour chaque arbre de chaque station selon son statut de dominance. Des mini-carottes de bois ont été prélevées sur plusieurs arbres représentatifs des différents statuts de dominance et ont permis d'obtenir la concentration en C mensuelle du cerne en cours de formation. Une valeur de densité relative a également été obtenue pour avoir des valeurs d'aBPw au plus proche de la réalité.

Des mesures de flux ont également été effectuée en continu au sommet de la tour à l'aide d'un système d'eddy-covariance. Chaque valeur a ensuite été soumise à un tri permettant d'ôter toutes valeurs

correspondantes à des conditions non optimales pour le calcul des flux ou à des problèmes techniques. Les valeurs manquantes ont ensuite été calculées à l'aide d'une interpolation des valeurs proches sélectionnées sur des critères climatiques similaire aux valeurs manquantes (gapfilling). Les données du flux net de l'écosystème ont ensuite été séparées entre Reco (mesurée de nuit et extrapolée à l'aide de la température à la journée) et GPP (partitioning).

Le **Chapitre 3** permet de mieux comprendre l'allocation intra-annuelle du C au sein de la biomasse aérienne de la forêt en présentant l'évolution des productions de différents composants de l'aBP (aCP, hémicellulose, cellulose et lignine ainsi que NSC) ainsi que leurs efficacités intra-annuelles. Il est également présenté sous la forme d'un article (en préparation). Les étapes d'obtention de ces valeurs sont similaires à celles décrites pour le chapitre 2. Des extractions supplémentaires ont été effectuées sur les mini-carottes prélevées pour permettre d'obtenir d'une part les valeurs d'hémicellulose et d'autre part celles de cellulose et de lignine. Le protocole d'extraction utilisé ne permettait pas d'obtenir la séparation des valeurs de cellulose et des valeurs de lignine. Celles-ci ont donc été étudiées ensemble.

Le **Chapitre 4** introduit l'étude intra-annuelle de l'aBPE en prairie ainsi que la comparaison avec la forêt. Il est également présenté sous la forme d'un article (en préparation).

L'aBP a été obtenue à l'aide de cages d'exclusion, qui ont été déplacées mensuellement sur la parcelle d'étude pour permettre l'obtention de la croissance moyenne sur l'ensemble de la parcelle.

Les flux sont obtenus de la même manière que décrite dans le chapitre 2, mais en utilisant un mât de mesure (moins haut).

Le **Chapitre 5** correspond à une synthèse des résultats de chaque article et d'une discussion pour les confronter à nos hypothèses de travail et mettre ce dernier en perspective.

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Chapitre 2 Variabilité saisonnière de l'efficacité de production de biomasse d'une forêt

Seasonal time-course in beech trees aboveground Biomass Production Efficiency (aBPE).

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2.1 Abstract

Key message In order to record the seasonal changes in wood aboveground biomass production (trunk and branches) in a forest, changes in wood density must be taken into account. A 60 year-old beech forest displayed a large intra-annual variability in its aboveground woody biomass production efficiency. This variation followed a seasonal trend with a maximum during the summer while GPP was rather low.

Context In the current context of land use and climate change, there is a need to precisely quantify the carbon (C) balance of forest ecosystems, and more specifically, of C allocation to tree compartments.

Aims We quantify the seasonal changes in the aboveground biomass production (aBP) of a beech forest growing on two different soil: an alocrisol and a calci-brunisol. In addition, for the alocrisol ecosystem, we assessed the existence and degree of intra-annual variability in the ratio of wood aBP to gross primary production (GPP), i.e. the wood aBP efficiency (aBPE).

Methods The study site is a 60-year-old beech forest in north-eastern France. An eddy-covariance tower records continuously net ecosystem exchange (NEE). To investigate the temporal changes in aBP, mini-cores were drilled and DBH measurements were taken on a monthly basis from 45 trees for both stand studied over 2014.

Results A clear difference in aBP was observed between the two soils with the alocrisol being more productive than the calci-brunisol. For the alocrisol, both woody aBP and GPP changed over the course of the year, reaching peak values during June (6 and 12.5 gC.m⁻².d⁻¹ respectively). Wood aBPE also showed important intra-annual variations, ranging from 0.09 in September to 0.58 in July, the latter corresponding to a lower GPP. Wood density varied throughout the year, and not taking it into account would have led to an overestimation of aBP by as much as 20% in April and Mai.

Conclusion Our study highlights the importance of taking wood density into account for intra-annual studies of aBP. Wood aBPE cannot be considered as constant as it fluctuated from 0.09 to 0.58 throughout the year for an annual value of 0.34. By considering only the error stemming from the calculation of wood aBP, the wood aBPE present a potential error of at least 15%.

Key words Eddy-covariance; GPP; beech forest; carbon allocation; biomass production; tree growth; wood density

2.2 Introduction

As ecosystem management evolves, in the context of climate change, understanding and quantifying terrestrial ecosystem carbon (C) sequestration, growth and the maintenance of ecosystem services have become major research goals. Climate change is linked to increasing concentrations of greenhouse gases (GHG) in the atmosphere (IPCC 2013), carbon dioxide (CO₂) being one of the most important (Cox et al. 2000). CO₂ concentrations have increased by 2.0 ppm per year since the 1980s, and have now reached an atmospheric concentration of 399.4 ± 0.1 ppm (Quéré et al. 2016). This increase, mainly linked to anthropogenic activities, is the first cause of the increase in the GHG effect. That is why long-term CO₂ mitigation is such an important issue, inspiring research focused on CO₂ exchange between the atmosphere and the terrestrial environment, and on carbon allocation and its more or less long-term storage in ecosystem (Trumbore 2006).

In the carbon cycle, gross primary production (GPP) is the difference between production by photosynthesis and release by photorespiration. The net ecosystem exchange (NEE) is the sum of the carbon absorbed via photochemical processes (GPP) and the carbon released into the atmosphere through plant dark respiration and soil organic matter (SOM) decomposition (hereafter Reco). The CO₂ budget of an ecosystem is equivalent to the NEE when dissolved CO₂ escaping in the runoff water is negligible. This is typically the case in beech ecosystems of north-eastern France (Kindler et al. 2011). In assessing how the ecosystem uses absorbed C, another important term is ‘carbon use efficiency’ (CUE), which is defined as the net primary production (NPP) to GPP ratio (Gifford 2003; DeLucia et al. 2007). NPP is not easy to record, since it is the sum of aboveground biomass production (which can be obtained from repeated inventories), belowground biomass increment, mycorrhizal fungus productions, root exudates and the emission of volatile organic compounds (VOCs). These last three types of C release can account for between 2 and 50% of NPP (Kesselmeier et al. 2002) and are difficult to measure or estimate. Consequently, many studies use biomass production (BP, gC.m⁻²), which is available through direct measurements in the field, as a proxy for NPP when estimating CUE (Gifford 2003; Drake et al. 2011; Goulden et al. 2011). Then, to avoid misinterpretation, Vicca et al. (2012) introduced a new term, ‘biomass production efficiency’ (BPE), defined as the ratio between BP and GPP for a given ecosystem. Biomass production includes all the biomass produced during the year (aboveground and belowground, including litter), so BPE represents the fraction of the absorbed C dedicated to the elaboration of organic biomass. At the annual scale, BPE depends on different factors. According to Vicca et al. (2012), the availability of nutrients seems to positively impact BPE. The management regime applied to the ecosystem (Carnioli et al. 2011, 2015) can also influence BPE through its impact on nutrient availability. BPE can also vary with species, as shown by Ryan et al. (1997); indeed in their study on plots with two different climate conditions and hosting different species, they highlighted that BPE differed significantly among species, never between sites. In addition different types of ecosystems have different BPEs; for example, crops usually have a higher BPE (Aubinet et al.

2001) than forests (Malhi et al. 1999; Granier et al. 2000; Vicca et al. 2012; Wu et al. 2013) or grasslands (Ammann et al. 2007; Klumpp et al. 2007). The share of GPP allocated aboveground (aBPE) or belowground (bBPE) varies depending on atmospheric CO₂ concentrations (Matamala et al. 2003, and demonstrated in CO₂ fertilization experiments; Norby and Zak 2011) and on nutrient availability (Sheriff et al. 1986; Giardina et al. 2003).

Annual BPE in forest ecosystems has been investigated and a model simulating inter-annual growth exists for coniferous (Schiestl-Aalto et al. 2015). We still need more knowledge on a larger number of species in order to get a better and larger spatial representativeness. When the intra-annual dynamics of forest BP are investigated, it is important to take into account the time lag between biomass production and trunk radial growth. This lag is due to the increase in wood density during the growing season (Cuny et al. 2015; Rathgeber et al. 2016), which calls into question calculating BPE with BP values estimated from radial growth only. Furthermore, little is known about the impact of soil type, species or climate on intra-annual BPE variations (Steppe et al. 2015), and this reflects remaining uncertainties in the models used to predict the spatial variability and the dynamics of C allocation (Capioli et al. 2013).

The aims of this study were, firstly, to obtain a better understanding of intra-annual carbon allocation in a temperate beech forest by quantifying wood aBPE from GPP and actual aboveground tree carbon sequestration, which was estimated from volume increment, wood density and changes in C concentration. In particular, we wanted to examine the seasonal time course in wood aBPE. To date, wood production had mainly been deduced from tree diameters, meaning that tree wood production was calculated from volume increase (Granier et al. 2008) assuming a fixed density (Delpierre et al. 2016). However, Rathgeber et al. (2016) has assessed different stages in annual ring formation which lead to variations in wood density during the year: the creation of new cells, the enlargement of those cells, deposition of the secondary cell wall, lignification and lastly, death.

In this paper we aim to see if considering the allocation of C to growth constant throughout the year is acceptable. We hypothesize that it is not. Then what are the factors that determine the wood aBPE variation. We also wanted to know whether the intra-annual variation in wood density had an impact on the wood aBP seasonal time course in beech trees.

This study also provided us with an opportunity to compare the wood aBP for two beech stands under the same climatic conditions but on two different soils.

In order to answer those questions we determined GPP, wood density and aBP at a monthly time scale on two forests stand located in north-eastern France.

2.3 Material and Methods

2.3.1 Study site

The study site is located in the state forest of Montiers-sur-Saulx ('Montiers') (48°32'11.85"N - 5°18'48.96"E, Lorraine, north-eastern France), managed by the French National Forest Office (ONF). The stand is even-aged (60 years old) and composed mainly of beech (*Fagus sylvatica* L.; 88% of the stems, with DBH classes and dominance classes similar for the other species). The accompanying tree species are sycamore maple (*Acer pseudoplatanus* L.) and hornbeam (*Carpinus betulus* L.); understory vegetation is scarce. Average tree height is 25m, density is about 800 stems/ha and leaf area index (LAI) is 9. The last thinning occurred in 2010.

The forest is located on a 133 ha topo-sequence, with three main soil types (alocrisol, calci-brunisol and rendisol, RP 2008 denomination). aBP was estimated for two of these soil types (alocrisol and calci-brunisol) and, because of the eddy covariance footprint (described below), only one (alocrisol) was found to be of interest for our study of aBPE. The characteristics of both stand are described in Table 1a. One hectare study plots were set up on both soils where the regular inventories were performed. The alocrisol stand (S1) included 703 trees (64 dominant, 141 co-dominant, 232 intermediate and 263 suppressed) and the calci-brunisol stand (S2) included 739 trees (61 dominant, 87 co-dominant, 263 intermediate and 328 suppressed).

Table 2. 2.1 Panel a: soil characteristics for the alocrisol and the calci-brunisol. Panel b: annual CO₂ fluxes, annual wood aboveground biomass production (aBP) in gC.m⁻².yr⁻¹ and annual wood aboveground biomass production efficiency (aBPE) for the alocrisol and the calci-brunisol and values found for similar ecosystems in the literature

Panel a.

	Alocrisol	Calci-brunisol
pH	< 5	5.2 – 5.4
Depth (<i>m</i>)	>1	<1
CEC (<i>cmol.kg⁻¹</i>)	3.5 – 6.7	7.6 – 17.2
Clay (%)	25 - 35	58

Panel b.

Authors	Forest type	NEE	Reco	GPP	Wood aBP	Wood aBPE
				$(gC.m^{-2}.yr^{-1})$		
This study (Alocrisol)	Temperate deciduous	-549	1089	-1639	555.0±26.9	0.34
This study Calci-brunisol	Temperate deciduous	/	/	/	416.3±26.3	/
Malhi et al, 1999	Temperate deciduous	-584	1141	-1725	189	0.11
Barford et al, 2001	Temperate deciduous and evergreen	-200	1100	-1300	140	0.11
Wu et al., 2013	Temperate deciduous	-277	1624	-1881	261	0.14
Vicca et al., 2012	Temperate	/	/	-1320	227	0.43
Vicca et al., 2012	Temperate	/	/	-1328	361	0.50
Vicca et al., 2012	Temperate	/	/	-1724	677	0.58

The climate is oceanic temperate with total annual precipitation of 1085 mm and a mean annual temperature (MAT) of 9.6°C average over the period 1980-2015 (5°C minimum and 14.1°C maximum MAT respectively, Météo France).

2.3.2 Eddy covariance and meteorological measurement

2.3.2.1 Experimental set-up

The main piece of equipment at the forest site is a flux tower (45m height) set up at the end of 2012 bearing an eddy covariance (EC) system consisting of an enclosed infra-red CO₂/H₂O gas analyzer (IRGA, Li-7200, LI-COR, Lincoln, NE, USA) coupled with a 3D sonic anemometer (HS-50, Gill, Hampshire, UK). This system continuously measures CO₂ exchanges at 35m in height (about 10m above the forest canopy). The flux tower is also equipped with a system to estimate the amount of CO₂ stored in the air between the soil surface and the EC system. This second system measures CO₂ at different heights along the tower (5, 10, 15, 25, 35 m) making it possible to calculate CO₂ accumulation or absorption (positive or negative values) in and below the forest canopy (Storage Flux, F_{sc}) as described in Aubinet et al. (2001).

Supporting meteorological instrumentation includes a vertical atmospheric profile system with six probes to measure air temperature and relative humidity (HMP155, Vaisala, Vantaa, Finland) and six 2D sonic anemometers (Wind Observer 2, Gill, Hampshire, UK) at 5, 10, 15, 25, 35, and 45 m along the tower; a pyranometer for global radiation (CMP21, Kipp&Zonen, Delft, Netherlands); a direct/diffuse Photosynthetically Active Radiation (PAR) sensor (BF5, Delta-T devices Ltd, Cambridge, England) and a net radiometer to measure incident and reflected/emitted components of shortwave (SW) and longwave (LW) radiation (CNR4, Kipp&Zonen, Delft, Netherlands). All the radiation sensors are

installed at the top of the tower. A phenological camera (Stardot netcam SC5) is installed at 35m in height.

2.3.2.2 Flux and meteorological data processing

Half-hourly NEE values correspond to the sum of the CO₂ flux (F_c , measured by the EC system) and the storage flux (F_{sc} , measured by the CO₂ profile system). A last term corresponding to the divergence of the CO₂ horizontal advection (F_a) is neglected because the half hours for which it is significant are not taken into account thanks to the u^* threshold selection (see below). F_c values are obtained by post-processing of the EC system's data using the EddyFlux software (Eddysoft, Meteotools, MPI, Jena) and following the recommendations of Aubinet et al. (1999). The 2D rotation option was selected, as suggested by Finnigan (2004) and Rebmann et al. (2012), and no corrections for high frequency loss were applied since they are quasi negligible because of the short tube for air sampling in the LI-7200 (Burba et al. 2012). In addition, the LI-7200 does not require any post treatment for air density variations because high frequency pressure and temperature are measured in the analyzer and used online for determination of the mixing ratio measurements (Burba et al. 2012).

The quality control of the data consisted of the following: (i) removing aberrant values corresponding to technical problems and inappropriate measurement conditions (liquid water disturbing IRGA or anemometer functioning); (ii) not accepting the half hours with u^* below the threshold (0.35m.s^{-1} on our site, determined following the procedure presented in Longdoz et al. (2008)), to eliminate periods without enough eddies; and (iii) rejecting the data corresponding to inappropriate atmospheric situation for EC (i.e. atmospheric stability and data not fulfilling the Integral Turbulence Characteristic test (ITC) (Beziat 2009)). The non-accepted and missing (failure, maintenance) data were then replaced by values computed following the gap-filling procedure from Falge et al. (2001a; 2001b). The resulting gap-filled NEE is then partitioned between GPP and Reco for the leafy period (using the method of Reichstein et al. (2005)). No GPP was observed during the leafless period and was thus set to 0. The date of the beginning and end of the growing period were set by looking simultaneously to the evolution of the NEE and to leaf development on the pictures taken 3 times a day by a camera placed at the top of the tower (phenocam; Stardot NetCam SC 5MP).

For 2014, the starting date (budburst) was 10 April, complete development 5 May and ending date at 15 November. GPP and Reco were partitioned by extrapolating the Reco dependence on temperature (obtained from night fluxes when $|NEE_{\text{measured}}| = |\text{Reco}|$) and applying them to daytime situations ($|GPP| = |NEE_{\text{measured}}| - |\text{Reco}_{\text{estimated}}|$). Using the dependence of Reco on temperature (fitted over a 10-day interval) is the one preconized by Lloyd and Taylor (1994). We obtained Reco from the following regression equation:

$$\text{Reco} = \text{Reco}_{10} + \exp\left(E_0 * \left(\frac{1}{T_{\text{ref}} - T_0} - \frac{1}{T - T_0}\right)\right) \quad (\text{Eq 1})$$

where Reco_{10} is the ecosystem respiration at 10°C ($\mu\text{mol m}^{-2} \text{s}^{-1}$), T the soil temperature at 10 cm (°C), E_0 the activation energy ($308.56 \text{ KJ mol}^{-1}$), T_{ref} the reference value (10°C) and T_0 the activation temperature (-46.02°C).

Not accounting for soil water content (SWC) in the regression could lead to overestimating GPP; however in our case, no water stress was observed during the study year (2014). Relative extractable soil water (REW), recorded during the whole 2014, never declined below the 0.4 threshold below which water shortage effects begin (Granier et al. 2007).

2.3.3 Biomass characterization

2.3.3.1 Instrumentation and sampling campaigns

Monitoring tree aboveground biomass requires quantifications of leaf biomass production, leaf carbon Monitoring aboveground tree wood biomass implies quantifying wood volume increment and temporal changes in wood carbon content and wood density. In our study, both instrumentation and sampling were designed to measure all these parameters. At each stand, 45 beech trees distributed across the DBH classes (9 in every DBH classes showed on **Figure 2.1** for each stand) to accurately represent the total population, were equipped with manually read dendrometers, to measure diameter at breast height (DBH) once every month during the growing season (6 May, 6 June, 1 July, 29 July, 26 August, 23 September, and 23 November).

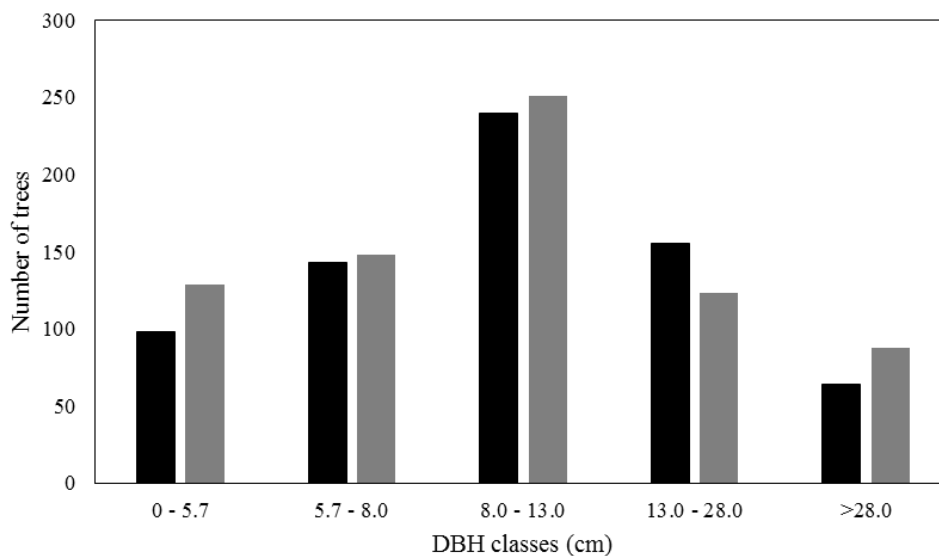


Figure 2.1 DBH distribution of 60 year-old beech trees on two sites: one on an alocrisol (dark bars) and one on a calci-brunisol (grey bars) located in north-eastern France. On each stand 9 trees were selected for each DBH class and were used to get the monthly DBH growth.

To estimate C content in trunk wood, some samples (980; seven mini-cores per tree and 35 trees for each of the 7 sampling campaigns) were taken from beech trees located outside of the station, using a Trephor® (Rossi et al. 2006), out of 14 tree trunks on the alocrisol and 21 trunks on the calci-brunisol.

The sampled trees were representative of the healthy growing population (see **Figure 2.1** for the DBH distribution) on the two stands. For the alocrisol, this led to the selection of seven trees from the 13-to-28-cm DBH class plus seven trees with a DBH superior to 28 cm. For the calci-brunisol, in addition seven trees were selected from the 8-to-13-cm DBH class.

In addition to the mini-core sampling, every month from April to November 2014, several micro-cores (1.5-2.0cm long and 2mm in diameter) were taken from 14 dominant ($D > 88$ cm) trees not used for the mini-cores (seven on each stand), in order to assess wood formation and density dynamics. Cores were taken with a Trephor® all around the stem, 10 cm away from each other (Rossi et al. 2006).

2.3.3.2 Processing samples and biochemical analysis

Each mini-core used for C content was placed in liquid nitrogen immediately after sampling and stored in a specific container. They were then stored at -80°C before being freeze-dried. The ring under formation was then cut away from each mini-cores and milled into a powder which was passed through an elemental analyzer (Thermoquest) to determine C and N concentrations.

Monthly wood density (**Figure 2.2**) was determined through an optical process carried out on the micro-cores following procedures described in Harroué et al. (2011) and Cuny et al. (2012). After sampling the micro-cores were rapidly returned to the lab, and successively cleaned, dehydrated and immersed in baths of ethanol, d-limonene and paraffin (Automatic tissue processor STP 121, MM France). They were then embedded in paraffin blocks (Embedding station EC 350, MM France). Finally, thick transverse sections were sliced off (Rotary microtome HM 355S, MM France), stained with cresyl violet acetate and permanently mounted on glass slides with Histolaque LMR® for long-term observation. Wood density was then determined on those glass slides.

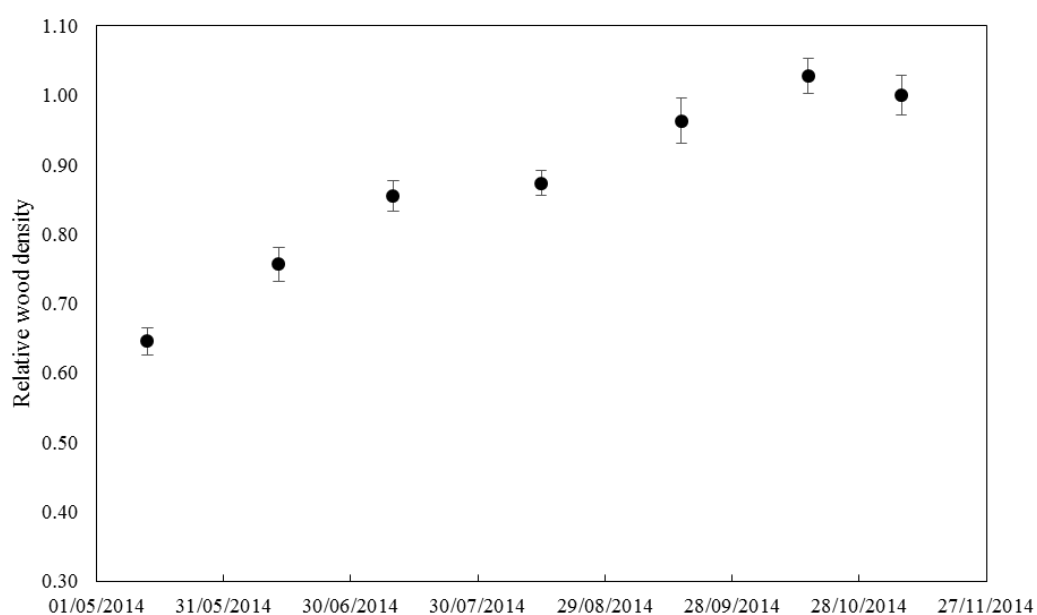


Figure 2.2 Intra-annual changes in wood density in relative value to the one at the end of the year (wood density of 1).

2.3.4 Biomass Production (BP) and efficiency determination

2.3.4.1 Aboveground biomass production

aBP ($\text{gC} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) is the production of aerial wood (aBPw, trunk and branches). aBPw was calculated as the sum of the individual values for all the sampled trees at a station (aBPwi) divided by the station surface area (S in m^2):

$$aBP = aBPw + BPl = \frac{\sum_i(aBPwi)}{S} + BPl \quad (\text{Eq 2})$$

where aBPwi is the difference between two successive estimations of aboveground tree woody carbon biomass (aBw in gC) divided by the number of days separating these estimations (every four weeks during the growing season). aBw was estimated according to the following equation:

$$aBw = DMaw * Caw \quad (\text{Eq 3})$$

where DMaw is the aerial wood dry matter (gDM) and Caw its carbon concentration (gC gDM^{-1}).

One Caw value (Eq 3) was deduced for each month and for each dominance class, by averaging the results of the carbon analysis on the 7 samples per class (see above).

DMaw was determined by summing the dry biomass from each tree woody (i.e. excluding leaves) component:

$$DMaw = DMb_{0-4} + DMb_{4-7} + DMb_{7+} + DMtb + DMw \quad (\text{Eq 4a})$$

with DMb_{0-4} , DMb_{4-7} and DMb_{7+} corresponding to branches with diameters respectively 0-4cm, 4-7cm, and larger than 7 cm; $DMtb$ corresponding to trunk bark; and DMw to trunk wood.

All dry biomass values were estimated separately by using allometric equations combined with transformation from volume to dry biomass, and were specifically parameterized for the Montiers forest (Calvaruso et al. 2017).

$$DMb_{0-4} = R\rho_w \times ((22.3991 + 73.11603 \times e^{(-0.028536 \times age)}) \times D^2 H^{0.911918}) \quad (\text{Eq 4b})$$

$$DMb_{4-7} = R\rho_w \times ((20.20171 - 0.089961 \times age) \times D^2 H^{1.534111}) \quad (\text{Eq 4c})$$

$$DMb_{7+} = R\rho_w \times (5.057486 \times D^2 H^{2.057768}) \quad (\text{Eq 4d})$$

$$DMtb = R\rho_w \times (11.641374 + 0.075737 \times age) \times D^2 H^{0.877139} \quad (\text{Eq 4e})$$

$$DMw = R\rho_w \times (193.387145 - 112.401722 \times e^{(-0.048233 \times age)}) * D^2 H^{0.97556} \quad (\text{Eq 4f})$$

where D is the diameter at breast height (DBH, m), age the age of the tree (years), H the tree height (m) and $R\rho_w$ the relative wood density corresponding to the ratio of wood density actual value on its final value obtained when the wood formation is finished. In Calvaruso et al. (2017), the equations Eq 4b-f were elaborated at the end of the growing season when $R\rho_w$ equalled 1.

For the age factor ('age' in Eq 4), we used only one value per dominance status and per stand. This value was the mean estimated age for seven trees which were cut during a thinning operation at the end of the 2014 growing season and whose rings were counted on the stump.

The relative wood density R_{pw} (Eq 4) (one value per month and per station) corresponds to the relative optical density (ratio of current monthly value to final value when wood formation is completed) measured on the additional trunk micro-cores.

D was measured with manual dendrometers every four weeks during the growing season on 45 trees (see Material section) on each stand (90 trees in total). For the other trees (n = about 1,600), D was measured with a diameter tape in November 2013 and November 2014, and a percentage of the annual increase was allocated to each month to obtain the monthly D estimate. These percentages were determined by status class (see below) rather than for each tree individually. The trees at each station were classified into 3 different dominance status classes (dominant/co-dominant, intermediate, and suppressed); the class-percentage values correspond to the average value for all the trees in the same status class as measured with the band dendrometers. The grouping strategy was based on classes having an average annual diameter growth that was significantly different (p -value < 0.05).

Height H was assumed to be constant throughout the year and was assessed by measuring 230 trees in November 2013 with a Vertex telemeter. For the remaining trees (n =1,370) inside the measurement area, H was calculated via an allometric relationship (Eq 5) fitted to the measurement date in November 2013 (Calvaruso et al. 2017).

$$H = 1.3 + (0.91 * a + 2.3) \times (1 - \exp(-b * \frac{D \times \pi}{3.14159}))^c \quad (\text{Eq 5})$$

where a , b , and c are parameters estimated by regression for each soil type and D corresponds to DBH at the start of the 2014 growing season.

2.3.4.2 Aboveground biomass production efficiency

The wood aboveground biomass production efficiency (wood aBPE) was calculated as the ratio of wood aBP on GPP (with all the variables in $gC\ m^{-2}\ d^{-1}$ and integrated over a given period), as defined in Vicca et al. (2012). Wood aBPE was determined monthly with the monthly wood aBP values and the sum of daily GPP over the corresponding period.

In order to obtain the wood aBPE for the two different stands, the temporal changes representative of each soil type must first be estimated. We partitioned the eddy covariance fluxes between the two sites areas thanks to footprint analyses (see Footprint analysis section below). Unfortunately, half-hour data showing a flux of more than 40% in the calci-brunisol ecosystem were relatively rare (less than 5% of the dataset). It was therefore not possible to extract any specific trend in GPP estimation for the calci-brunisol station. As a result, we only used GPP data representative of the alocriisol station and only characterized the alocriisol aBPE.

2.3.5. Data analysis

2.3.5.1 Statistical test

A linear regression model was used to determine if Reco depended on different factors (air temperature, soil relative extractable water (REW), global radiation and GPP). The effects of mean air temperature and GPP were also tested. We used the same tool to test the relationship between GPP and global radiation, and the residuals of this relationship were then tested against vapor pressure deficit (VPD), air temperature and REW. A statistical test was used to assess whether or not a distinction between the wood aBP at the two stations (on the two different stands) was necessary. As our wood aBP data did not follow a normal distribution, we chose a non-parametrical test (Kruskal-Wallis). The confidence interval were calculated as the standard deviation divided by the square roots of the number of samples.

All the data processing and analysis were carried out with the R 3.0.2 software (R Core Team 2013).

2.3.5.2 Footprint analysis

The Kljun et al. (2004) footprint model, the high frequency anemometer data and the soil type map were all employed to determine the percentage of the CO₂ eddy covariance fluxes coming from the areas located on the alocrisol and calci-brunisol. This operation was repeated for each half-hour.

2.4 Results

2.4.1 Meteorological and flux data

The weather during the year 2014 was comparable in terms of air temperature and precipitation to the 1934-2015 average recorded at a weather station nearby (less than 40km; Table 2). Air temperature dropped once (August 17) and peaked three times (9 June, 19 July, 8 September) and daily global radiation followed an usual distribution with three noticeable drops (5 May, 9 July, 12 August) (**Figure 2.3**).

In 2014, the site presented a negative NEE of -549gC m^{-2} , which indicates that C was being stored in the ecosystem. Cumulated Reco amounted to 1089gC m^{-2} and GPP to -1639gC m^{-2} (Table 2. 2.1b).

The leafy season began on 10 April, as assessed with the phenological camera, and ended on 15 November 2014. The curve representing cumulative GPP for the periods we included (most of the time for 28 days per period) is presented in **Figure 2.4b**. GPP increases to a peak value of $12.9\text{gC m}^{-2}.\text{d}^{-1}$ in June 2014, after which it decreases until November.

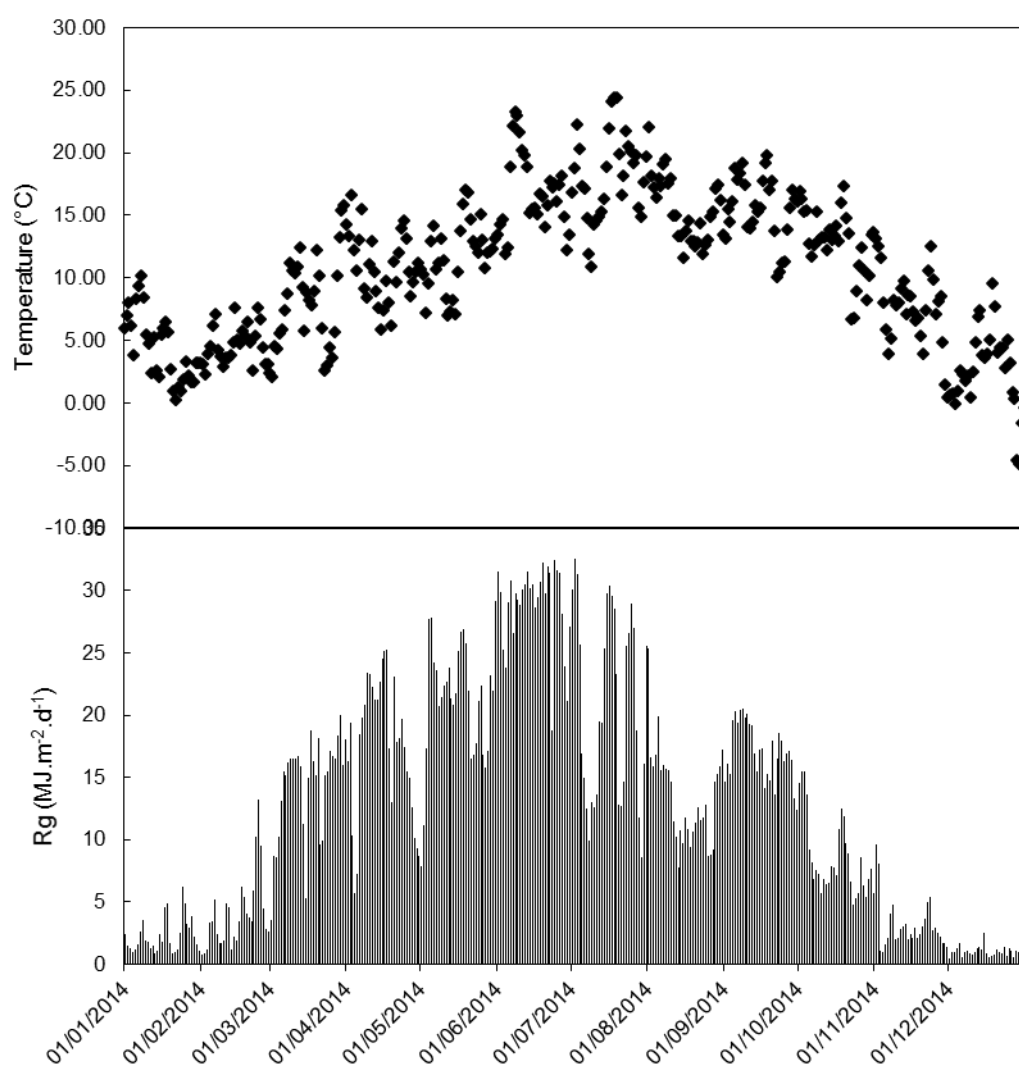


Figure 2.3 Time course of daily mean air temperatures (in °C) and daily cumulated global radiation (in mm) during the year 2014 obtained at the EC tower.

Table 2.2 Average mean annual temperature and precipitation for the 1934-2015 period and for the year 2014, measured at two French weather stations (Ennerville-aux-Bois (a) and Biencourt-sur-Orge (b) Météo France) close to the Montiers site, in brackets are specified the year of occurrence.

Climatic factors	Annual Mean		Minimum		Maximum	
	1934-2015	2014	1934-2015	2014	1934-2015	2014
Temperature (° C) (a)	9.6	10.9	-24.2 (1956)	-13.8	39 (2003)	33.4
Precipitation (mm) (b)	1085	1020	797	-	1351	-

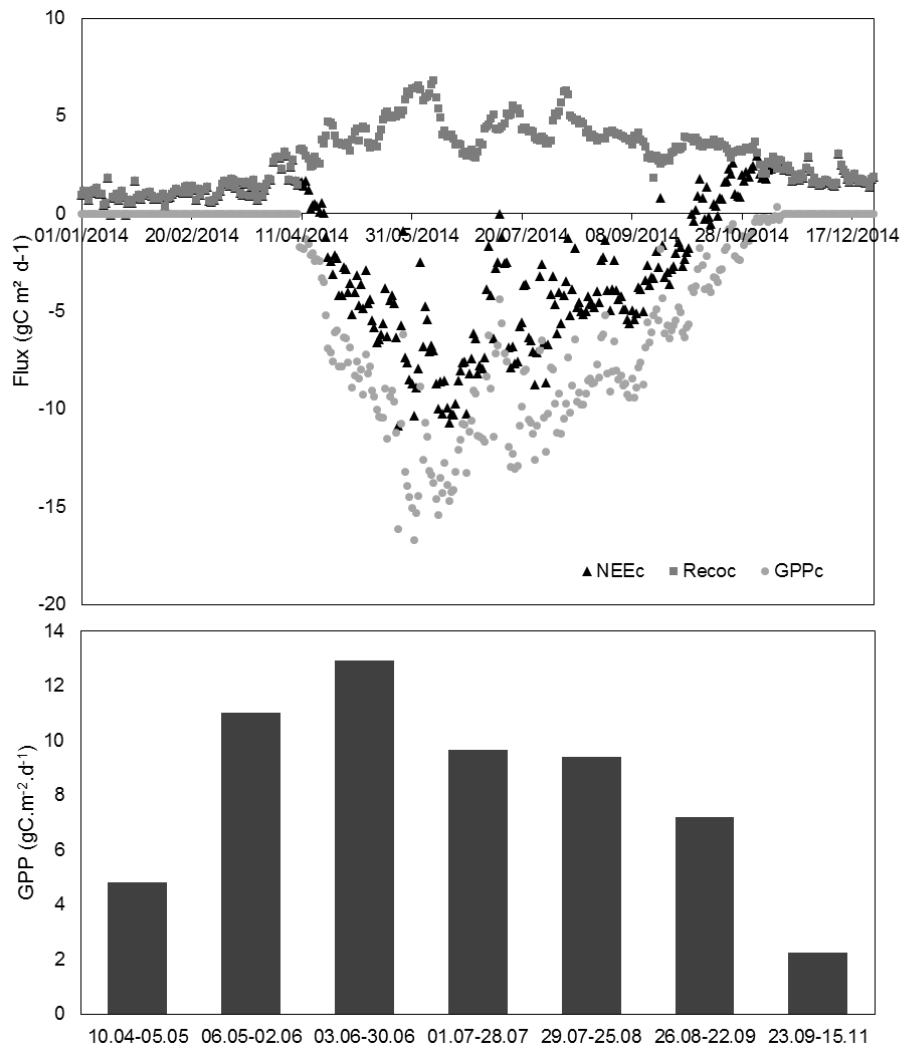


Figure 2.4 Daily changes in NEE, Reco and GPP fluxes during 2014 (a) and in cumulated GPP for the periods corresponding to BP estimates (b)

2.4.2 Biomass

2.4.2.1 Annual Biomass production

In 2014, the alocrisol ecosystem produced more biomass (22% in total aBP, 25% in wood BP) than the calci-brunisol ecosystem.

For the complete year 2014, the aboveground BP as determined from our inventory campaigns and allometric relationships, reached 652.27 gC.m⁻² at the alocrisol station (S1) and 514.15 gC.m⁻² at the calci-brunisol station (S2) with a woody BP corresponding respectively to 555 and 416.3gC.m⁻² (Table 2. 2.1b).

2.4.2.2 Intra-annual evolution of the biomass production

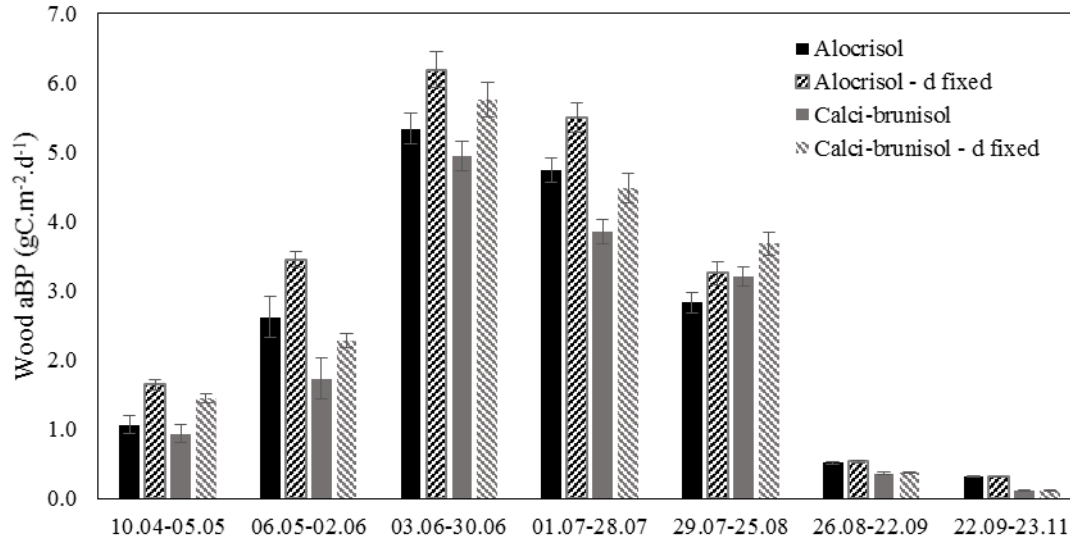


Figure 2.5 Intra-annual changes in woody aboveground biomass production in the year 2014 for the alocrisol station under the hypothesis of a constant density (of 1) or of a variable and recorded density (black and black striped bars) and for the calci-brunisol station under the same hypothesis as previously cited (grey and grey striped bars). Error bars represent confidence interval.

There were large seasonal variations (from 1 in April to 5.7 gC.m⁻².d⁻¹ in June for the alocrisol station) in wood aBP (**Figure 2.5**). Though not symmetrical, the general dynamics at both stations were similar, with the highest aBP during June (5.7 and 4.9 gC.m⁻².d⁻¹ for the alocrisol and calci-brunisol respectively) then a decrease to the end of the growing season.

For nearly every monthly period, the difference between the two stands was significant (p-value<0.05; **Figure 2.5**), with the alocrisol consistently producing more biomass than the calci-brunisol except for the period from 29 July to 25 August.

2.4.2.3 Effects of the density correction

Equations 4a-f include both allometric relationships (Transforming DBH and height to volume) and transform volume to dry biomass. The latter calculation requires accounting for the final wood density value at the end of the 2014 growing season (Eq 4a-f were established at the end of the season). This means that using Eq 4a-f for monthly wood aBP estimates throughout the year 2014 (when wood density was lower than the final value) would lead to an overestimation of woody aBP. Therefore, we used the density measured monthly to calculate corrections for wood aBP. The trend for relative wood density (ρ_w in Eq 4) is presented in **Figure 2.2**. Density increase from 0.7 to 1 with especially clear rises at the beginning and end of the growing season. The degree of overestimation for woody aBP when temporal variations in density are not taken into account can be estimated by comparing the results with and without this correction. Differences between corrected and uncorrected values of aBP range from 4% to 54% (**Figure 2.2** et **Figure 2.5**), the larger percentage corresponding to the first period, when wood density is smallest. If final wood density was used throughout the year for the different periods, the overestimation for total annual aBP would be 20%.

2.4.2.4 Biomass Production Efficiency

The wood aBP of the beech trees represented 34% of the annual GPP (*Table 2. 2.1b*). There was a clear, very large intra-annual variation in woody aBPE which climbed from April to a peak value of 0.6 in July (**Figure 2.6**), then fell by 50% to 0.25 between July and August, then continued to decrease regularly, reaching 0.11 in September. Finally, a single, final rise to 0.24 occurred in November.

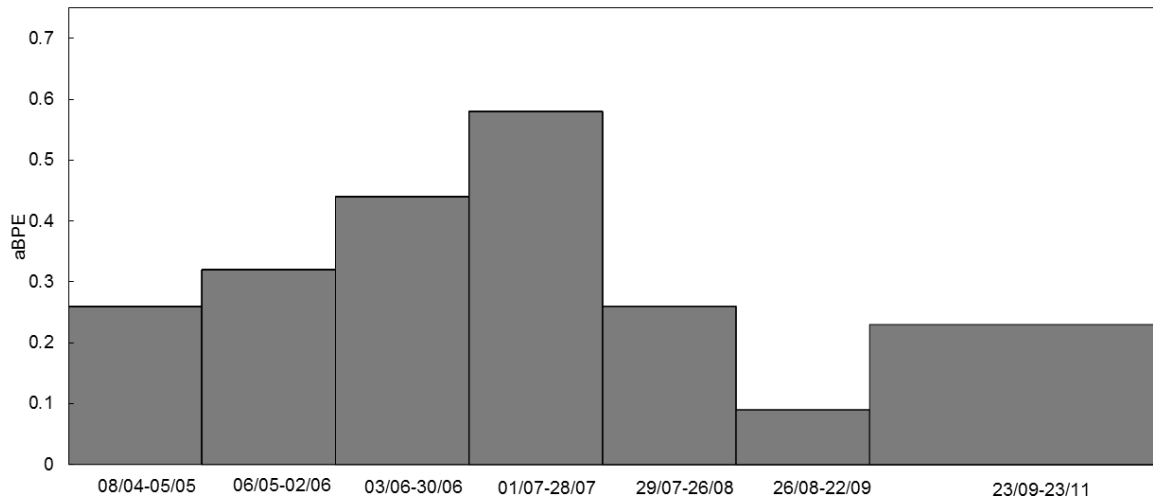


Figure 2.6 Intra-annual changes in woody aboveground biomass production efficiency (aBPE) for the alocrisol (S1) stand, corresponding to the ratio of the cumulated wood aBP obtained in a month to the cumulated monthly GPP calculated

2.5 Discussion

2.5.1 Meteorological and flux data

By Our site was an important C sink during the study year and this is normal for beech forests in north-eastern France (Granier et al. 2008). When no water limitation is recorded, Reco is limited only by C supply and enzymatic activity (T), and GPP is limited by global variation.

NEE (-549 gC.m^{-2}) was in the higher range of what is found in the literature for temperate deciduous forest ecosystems (from -257 gC.m^{-2} to -585 gC.m^{-2} , mean value $-339 \pm 368 \text{ gC.m}^{-2}$, *Table 2. 2.1b*). This NEE value was especially due to a higher-than-usual GPP (-1639 gC.m^{-2} for our alocrisol station compared with 1016 to 1880 gC.m^{-2} and a mean value of $1820 \pm 805 \text{ gC.m}^{-2}$ in the literature (Valentini et al. 1996; Malhi et al. 1999; Granier et al. 2000, 2008)) combined with a relatively standard Reco value (1089 gC.m^{-2} for our alocrisol station compared with 544 to 1425 gC.m^{-2} and a mean value of $1136 \pm 373 \text{ gC.m}^{-2}$ in the literature).

2.5.2 Biomass production

In the literature, annual aBP values range from as low as 140 gC.m^{-2} in a temperate mixed forest (Wu et al. 2013) to 677 gC.m^{-2} for a very fertile temperate forest (Vicca et al. 2012), the mean value being

366±233 gC.m⁻² (Valentini et al. 1996; Knohl et al. 2003; Curtis et al. 2005; Granier et al. 2008; Vicca et al. 2012; Wu et al. 2013). This places our results in the higher range (652 and 514 gC.m⁻² for the alocrisol and the calci-brunisol stations, respectively).

Our aBP values were significantly different on the two stands. The alocrisol ecosystem produced more biomass than the calci-brunisol system, as found in Calvaruso et al. (2017). This difference can be linked to the type of soil, its depth and also the stand management history. In our study, this difference in aBP stemmed from very high C production by the dominant and co-dominant trees at the alocrisol station (data not shown). Taken individually, the dominant and co-dominant trees at this station had higher aBP when compared to the trees at the calci-brunisol station, where stem density was greater. Stem density did not compensate for lower C production since, per surface unit, aBP was nearly 3 times higher for dominant and co-dominant trees at the alocrisol station. Consequently, the difference in stand aBP is probably due to the higher aboveground biomass of the dominant and codominant trees at the alocrisol station at the beginning of the study year. The origin of this situation is not known but soil nitrogen concentrations N (gN.m⁻³) could provide an explanation. Nitrogen levels in the soil solutions from the first 10 cm were clearly higher throughout the study year for the alocrisol stand (0.8 - 2.0 mgN.L⁻¹ versus 0.6 to 1.6 mgN.L⁻¹ in calci-brunisol stand; Kirchen, personal communication). This could explain the strong early growth observed on the alocrisol soil (Lawrence 2001; Finzi et al. 2007). The alocrisol also has deeper organic soil than the calci-brunisol; previous droughts could therefore have had more impact on development in the calci-brunisol ecosystem, thus hindering biomass acquisition and growth in 2014. The computed error for the calculation of monthly aBP from DMaw (in gDM) amounted to 15% when adding the errors that could stem from the different corrections applied (wood growth, wood C concentration, and wood density).

At both stands, we found quite a large variation in wood density during wood formation throughout the year. This phenomenon had already been observed (Rathgeber et al. 2016) and corresponds to the thickening of the cell walls. Our results reinforce the importance of including this variation in density when working on intra-annual biomass production, as Delpierre et al. (2016) have already highlighted. Indeed, not taking changing wood density into account and instead using the final value for all intermediate estimations would have led, in our study, to overestimating aBP by as much as nearly 50% for some periods, and by about 20% when these intermediate values were cumulated on an annual basis for 2014. This confirms that dendrometer measurements alone are not sufficient when attempting to understand the monthly dynamics of the C balance in forest ecosystems (Cuny et al. 2015).

2.5.3 Efficiency

Throughout 2014, aBP was consistently lower than GPP for each period. GPP may not be the sole C source for aBP, as the C stored from the previous year could also provide C fuel. However, with our

dataset, we were unable to trace the origins of the C in the biomass produced as this would have required using other techniques such as isotopic tracing (Carbone et al. 2013). The proportion of C in GPP not allocated to aBP could be expelled during Reco, stored in root BP (up to 24% of total GPP; Arneth et al. 1998) or devoted to the production of reproductive organs, but could also be given off in VOCs and exudates. The partitioning of the C between these different fluxes is not known.

Wood aBPE (0.34) is in the upper range of what can be found in the literature, with values from 0.11 for *Quercus alba* L. / *Quercus prinus* L. (Malhi et al. 1999) to 0.38 for a *Fagus sylvatica* L. (Wu et al. 2013) with a mean overall value of 0.22 ± 0.12 for temperate forests (Ryan et al. 1995; Valentini et al. 1996; Granier et al. 2000; Barford et al. 2001; Curtis et al. 2005; Vicca et al. 2012; Wu et al. 2013). Woody aBPE in our study presented a large seasonal fluctuation with a relatively symmetric trend. This shape was different from our aBP curve, thus revealing the occurrence of a discrepancy between the behavior of raw C flux (for biomass production) and the coefficient of allocation (for efficiency). The woody aBPE bell-shaped curve resembled the photoperiod curve; this may indicate synchronization without giving any causality, which should not be overlooked when allocation schemes are established in certain ecosystem models.

June and July are the months when the percentage of assimilated C allocated to aerial wood is the highest. This maximum-efficiency period is when high GPP most enhances wood production.

In addition to variation in annual BP-to-GPP ratio amongst forests (DeLucia et al. 2007; Vicca et al. 2012) that was already studied, we showed that there was also an important variation within a forest throughout the year. This variation is important to take into account in intra-annual studies as using a fixed value in forest models could result to an overestimation or underestimation of the C allocated to biomass depending on the season.

2.6 Conclusion

This study demonstrates the importance of taking wood density into account when conducting seasonal monitoring of an aboveground wood carbon budget, since not doing so could result in an overestimation of woody aBP during some periods of the year of about 20%. Temporal variability in woody aBPE is important: maximum values occur during summer, reflecting trends for several other environmental variables and showing the importance of taking into account the variable allocation coefficient over time in a functioning forest model (Guillemot et al. 2017).

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Chapitre 3 Variabilité saisonnière de la production en carbone structural et non structural et de leur efficacité pour une forêt

Intra-annual variability of structural C component (SCP), non-structural C component (NSCP) and their efficiencies (SCPE and NSCPE) for a forest of north-east of France

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En préparation

3.1 Abstract

In the current context of land use and climate change, there is a need to improve our knowledge of the carbon (C) balance of terrestrial ecosystems and, more specifically, of C allocation in plants.

In this paper, we quantify the seasonal evolution of the aboveground component of the biomass production (aCP) that consist of the structural C production (SCP; which include hemicelluloses, SCPh and cellulose+lignins, SCPcel&l) and the non-structural C production (C_NSC) of a beech forest on two soil types, alocrisol and calci-brunisol. In addition, we assess the existence of the intra-annual variability of the aCP efficiencies (aCPE) -corresponding to the ratio of either aCP to gross primary production (GPP) - for the alocrisol ecosystem.

The study site is a 60-year old beech forest in the north-east of France. An eddy-covariance tower was installed in order to measure net ecosystem exchange (NEE) and obtain the GPP. To investigate the temporal evolution of SCP and NSCP on both soil types, mini-cores were drilled monthly.

A clear difference in aCP was observed between the soil types, with alocrisol being more productive than calci-brunisol. For the alocrisol, all aCP and GPP evolved during the year, reaching peak values during the June period (3.41 gC.m⁻².d⁻¹ for SCPcel&l, 1.67 gC.m⁻².d⁻¹ for SCPh, 0.64 gC.m⁻².d⁻¹ for C_NSC and 12.5 gC.m⁻².d⁻¹ respectively). aCPE also showed an important intra-annual evolution, between 0.02, 0.06 and 0.01 in September for hemicellulose, cellulose and lignin and NSC respectively and 0.16, 0.36 in July for both SCP and 0.11 in April for NSCP, corresponding to a high aCP but a lower GPP.

Key-words: Carbon content, Eddy-covariance, Hemicelluloses, Celluloses, Lignin, NSC

3.2 Introduction

Mitigating the effects of climate change (CC) is becoming crucial at present. Globally averaged, combined land and ocean surface temperatures have risen by 0.85°C between 1880 and 2012 (IPCC 2013), drought and storm are happening more and more frequently. All those changes are induced by the increase in greenhouse gases (GHG) concentration in the atmosphere, the main one being CO₂ (Cox et al. 2000).

Terrestrial ecosystems store up to 28% of the C emissions (Le Quéré et al. 2012) making them quite important in the mitigation of CC. Forests, more particularly, represent 30% of the land surface and store up to 45% of the terrestrial C (Bonan 2008), accumulating from 1 to 3.1015 gC.y⁻¹ (Malhi et al. 1999) and are the one of the most perennial carbon pool. Changes in the C balance of these ecosystems could have a large impact on the atmospheric CO₂ concentrations (Carnioli et al. 2008). Studies are thus more and more focusing on the C storage in plant that can last from a few hours to several decades depending on the C allocation. More detailed studies are needed to get a better understanding of ecosystems behavior in term of C allocation under the changing climate.

In a previous study (Heid et al, in review) we looked into the intra-annual variability of the aboveground biomass production (aBP, stem+branches) of a forest and its efficiency (aBPE, representing the ratio between the C stored into the aBP and the C absorbed through GPP) to store atmospheric C into the aboveground biomass. In this paper we aim at getting a deeper knowledge of the partitioning of the C absorbed through GPP (corresponding to the net ecosystem exchange (NEE) minus the respiration of the ecosystem (Reco)) into specific component of the aBP.

aBP is composed of two pools of C, the nonstructural C pool (C_{NSC}) composed of mobile, easily reusable C compounds (starch, soluble sugars,...) easily used by plants for their growth or reserve and quite fluctuating during the year (Landhäusser and Lieffers 2003), and the structural C (SCP) pool. The latter is the carbon used to build plant cell walls. Cell walls are the largest C pool in biomass and play an important role in the C cycle of ecosystems (Hoch 2007). Plant cell walls are a complex blend of polysaccharides and protein. The main one being cellulose, that represent about 28-30% of dry matter in forage grasses and 42-45% of wood (Haigler et al. 2001).

The second most abundant biomass compound in plant is lignin that represents about 30% of total plant biomass (Boerjan et al. 2003). Lignification happens usually after radial growth in trees (Cuny and Rathgeber 2014) and strengthens the plant structure allowing plants to stand, but also helps with water transport in the xylem and could also have a role in the defense against pests and microorganisms (Moura et al. 2010).

And finally, Hemicelluloses is quite important as it represents about 25% of total plant biomass (Hoch 2007) which is about half of the celluloses content, and helps bind the structure. Hemicelluloses content has been shown to also fluctuate during the year and could also sometime serve as C reserves for the tree (Hoch 2007; Schädel 2009).

The structural C is quite important in the C balance of forests as it represents the C stored into biomass for long period of times (from decades up to centuries, depending on management, and tree health and age) and could be referred to as sustainable C storage. Calculating the aCP efficiency (aCPE, ratio between aCP and GPP) is thus really interesting as it gives an estimation of the “sustainable” C storage efficiency of the ecosystem.

In this study we observed the fluctuation of different components of the aboveground biomass production (aCP) divided into hemicelluloses (SCPh), cellulose+lignins (SCPcel&l) and NSC (C_NSC) production during the year 2014 and tried to see whether there was an influence from different climatic factors or not. For this purpose, the monthly productions for SCPh and SCPcel&l as well as for C_NSC from budburst to leaves senescence for the year 2014 were computed. Several climatic and environmental factors (air temperature, photoperiod, REW) were also studied during the same period. Finally, the aCPE (aCP-to-GPP ratio) were calculated for all component on a monthly bases.

Following what can be found in literature the cellulose and lignin pool should increase during the year as they are both parts of several cell growth phase (Cuny and Rathgeber 2014), while the NSC pool should stay quite stable as is typical for Beech (Barbaroux and Bréda 2002; Zein et al. 2011). We also expect the hemicellulose pool to be variable during the year as shown in the review by Hoch (2007).

3.3 Material and methods

3.3.1 Study sites

The study site is located in the state forest of Montiers-sur-Saulx (‘Montiers’) (48°32'11.85"N - 5°18'48.96"E, Lorraine, North-East of France), which is managed by the French National Forest Agency (ONF). The stand is an even-aged stand (60 years old), composed mainly of beech (*Fagus sylvatica*; 88% of the stems). The accompanying tree species are sycamore maples (*Acer pseudoplatanus*) and hornbeams (*Carpinus betulus*); below canopy vegetation is scarce. The average tree height is 25m, while the forest density is about 800 stems/ha, and the leaf area index (LAI) amounts to 9.

The forest is set on a 133 ha topo-sequence, consisting of three main soil types (alocrisol, calci-brunisol and rendisol, denomination of RP 2008) of the same age (60 years). The aBP was estimated for two of these soil types (alocrisol and calci-brunisol) and only one (alocrisol) was of interest for our study of the aBPE because of the eddy covariance footprint (described below). The characteristics of both soil types are described in detail in Calvaruso et al. (2017). One hectare study plots (‘stations’) were set up on both soils where the regular inventory were performed. The alocrisol station (S1) enclosed 703 trees (64 dominant, 141 co-dominant, 232 intermediate and 263 suppressed) and the calci-brunisol station (S2) enclosed 739 trees (61 dominant, 87 co-dominant, 263 intermediate and 328 suppressed).

The climate is oceanic temperate with total annual precipitation of 1085 mm and a mean annual temperature (MAT) of 9.6°C average over the period 1980-2015 (5°C minimum and 14.1°C maximum MAT respectively, Météo France).

3.3.2 Eddy covariance and meteorological measurement

3.3.2.1 *Experimental set-up*

The main item of the forest instrumental device is a flux tower (45m height), set up at the end of 2012, with an eddy covariance (EC) system consisting of an enclosed infra-red CO₂/H₂O gas analyzer (IRGA, Li-7200, LI-COR, Lincoln, NE, USA) coupled with a 3D sonic anemometer (HS-50, Gill, Hampshire, UK), allowing continuous measurement of the CO₂ exchanges at 35m high (about 10m above the tree canopy). The flux tower is also equipped with a system estimating the CO₂ storage in the air between the soil surface and the EC system. It is composed of CO₂ measurement points at different heights along the tower (5, 10, 15, 25, 35 m) allowing calculation of the CO₂ accumulation (positive or negative) in and below the tree canopy (Storage Flux, F_{sc}) as described in Aubinet et al. (2001).

Supporting instrumentation for meteo characterization consists of a vertical profile with six air temperature and relative humidity probes (HMP155, Vaisala, Vantaa, Finland) and six 2D sonic anemometers (Wind Observer 2, Gill, Hampshire, UK) at 5, 10, 15, 25, 35, and 45 m along the tower; a pyranometer for global radiation (CMP21, Kipp&Zonen, Delft, Netherlands); a direct/diffuse Photosynthetically Active Radiation (PAR) sensor (BF5, Delta-T devices Ltd, Cambridge, England) and a net radiometer to measure incident and reflected/emitted components of shortwave (SW) and longwave (LW) radiation (CNR4, Kipp&Zonen, Delft, Netherlands). All these radiative sensors are installed at the top of the tower. A phenological camera (Stardot netcam SC5) is set-up at 35m.

3.3.2.2 *Flux and meteorological data processing*

The partitioning and gapfilling were made following (Reichstein et al. 2005; Reichstein et al. 2012) and the fluxes obtained were then corrected using (Aubinet et al. 2012). The detail of the data processing is described in Heid et al, in review.

3.3.3 Aboveground biomass production, component of interest production and efficiencies

3.3.3.1 *Components Productions*

3.3.3.1.1 *Instrumentation and sampling campaigns*

The diameter at breast height (DBH) was measured on 45 trees of the site every month during the 2014 growing season. The height of the trees was also measured at the end of 2013 and the age was estimated at the end of 2014. The DBH, the height and the age were used in allometric relationships fitted on our site (Calvaruso et al. 2017). This allowed us to obtain the dry matter biomass production for each monthly diameter measurements that we extrapolated for each trees of the 1ha site. Then a factor was used to transform the DM into carbon aboveground biomass production (aBP).

For more details on the calculation of the aBP and aBPE of the forest refer to Heid et al in review.

3.3.3.1.2 Total C content

In order to obtain the total C content in trunk and branches wood, mini-cores (3.5cm long, 5mm dia.) were taken with a Trephor® (Rossi et al. 2006) from trees located on both soil types. From June to September 2014, the samples were taken monthly on 14 or 21 trees on the alocrisol or the calci-brunisol respectively. The trees were chosen to get a good representation of the population having a significant growth. More information on how the trees were selected are available in Heid et al, (*in review*). During the June and October campaigns, some mini-cores were also retrieved from the first big branches. Then each core was put in liquid nitrogen, freeze-dried, cut in order to obtain only the ring in formation. The rings were then milled into a powder and passed into an elemental analyzer (NCS 2500, Thermoquest, Milan, Italy) for total C content (in gC.gDM⁻¹). This allowed us to get the percentage of total C present in the tree wood biomass.

3.3.3.1.3 Hemicelluloses and Celluloses/lignin content

The powdered ring were then analyzed following the Van Soest Fiber Analysis (Soest 1963; Van Soest et al. 1991) as modified by Schädel et al. (2010b, a). This procedure follows three steps and is based on the weight of each samples and allows to use a low amount of plant material (only 50 mg of plant powder).

The first one is the hydrolysis of starch using a α -amylase solution (SIGMA, A3403). The second step uses a neutral detergent solution to dissolve other NSC and water-soluble cell-wall constituents. After those two steps only the structural C remains in the samples, the non-structural more digestible C (NSC) being washed away during the process. The third and final step allows to separate the hemicelluloses (SCPh) from the cellulose and lignin (SCPcel&l) that will remain in the sample. For this purpose an acid detergent solution is this time used.

The method used is here is detailed in (Schädel et al. 2010a).

In order to obtain the concentration of SCPh and C_Cel+L to total C, the samples were dried using a speed vac and weight after step 2 and step 3 (eq 1 and 2).

$$C_{total} = C_{NSC} + C_{(Hem+Cel\&L)} \quad \text{eq 1}$$

Where C_{total} is the total C, C_{NSC} correspond to the NSC and SCP to the hemicelluloses, the cellulose and lignin, all those values are in gC.kg⁻¹ DM.

$$C_{(Hem+Cel\&L)} = SCPh + SCP_{cel\&l} \quad \text{eq 2}$$

Where SCPh correspond to the Hemicelluloses C content and SCP_{cel&l} the Cellulose+Lignin C content in gC.kg⁻¹ DM

Using the weight obtained before and after each extraction allowed us to calculate a percentage for each C compounds (SC and NSC), on each soil type, for each dominance classes and each sampling date.

3.3.3.2 Production and efficiency determination

The aBP (in $\text{gC.m}^{-2}.\text{d}^{-1}$) was already calculated (Heid et al, in review) and corrected with the C total and relative density for each dates. On those value a correction corresponding to the C% of hemicellulose, cellulose and lignin and NSC in the C total was applied in order to obtain the aCP in $\text{gC.m}^{-2}.\text{d}^{-1}$.

The aCP efficiency (aCPE) were calculated as the ratio of aCP on GPP (with all the variables in $\text{gC m}^{-2}.\text{d}^{-1}$ and integrated on a given period), as defined in Vicca et al. (2012). Efficiencies were determined monthly thanks to the monthly aCP values and the sum of the daily GPP on the corresponding period.

3.3.4 Data analyses

3.3.4.1 Statistical test

A linear model regression was used to determine the dependence of our aCP and aCPE to different factors (mean air temperature, soil relative extractable water (REW), global radiation, and photoperiod). A statistical test was used to assess whether or not a distinction between aCP of the 2 soil types and of the dominance class was necessary

As the dataset did not follow a normal law the non-parametrical Kruskal-Wallis test was used.

All statistical analysis were carried out using R 3.0.2 (R Core Team 2013).

3.3.4.2 Footprint analysis

The Kljun et al. (2004) footprint model, the high frequency anemometer data and the soil type map were all employed to determine the percentage of the CO_2 eddy covariance fluxes coming from the areas located on the alocrisol and calci-brunisol. This operation was repeated for each half-hour.

3.4 Results

3.4.1 Meteorological data

Table 3.1 Average mean annual temperature and precipitation for the 1934-2015 period and the year 2014, measured at the Enerville-aux-Bois (a) and Biencourt-sur-Orge (b) stations, two French weather stations (Météo France) close to the Montiers and Osnes sites.

	Annual Mean		Minimum		Maximum	
	1934-2015	2014	1934-2015	2014	1934-2015	2014
Temperature ($^{\circ}\text{C}$)						
Erneville aux Bois station	9.6	10.9	-24.2 (1956)	-13.8	39 (2003)	33.4
Precipitation (mm)						
Biencourt sur Orge station	1085	1020	797	-	1351	-

The weather during the year 2014 was comparable in terms of air temperature and precipitation to the 1934-2015 average recorded at a state station close by (less than 40km) (*Table 3.1*). Air temperature

presents one drop (August 17) and three peaks (9 June, 19 July, 8 September) and the daily global radiation followed a scattered normal distribution with three main drops (5 May, 9 July, 12 August) (data not shown).

3.4.2 Seasonal variations

3.4.2.1 C partitioning into the aboveground biomass components

Table 3.2 C proportions and content in the biomass and in the different C pools: structural (Hemicelluloses, cellulose and lignin) and non-structural (NSC) for the final ring 2013 and during the formation of the tree ring 2014. All values in between parenthesis (mean $\pm$ standard error) are in gC.kg⁻¹ DM. The kruskal-wallis test p-value is also given to show the significance of the difference between each proportions value for each consecutive date.

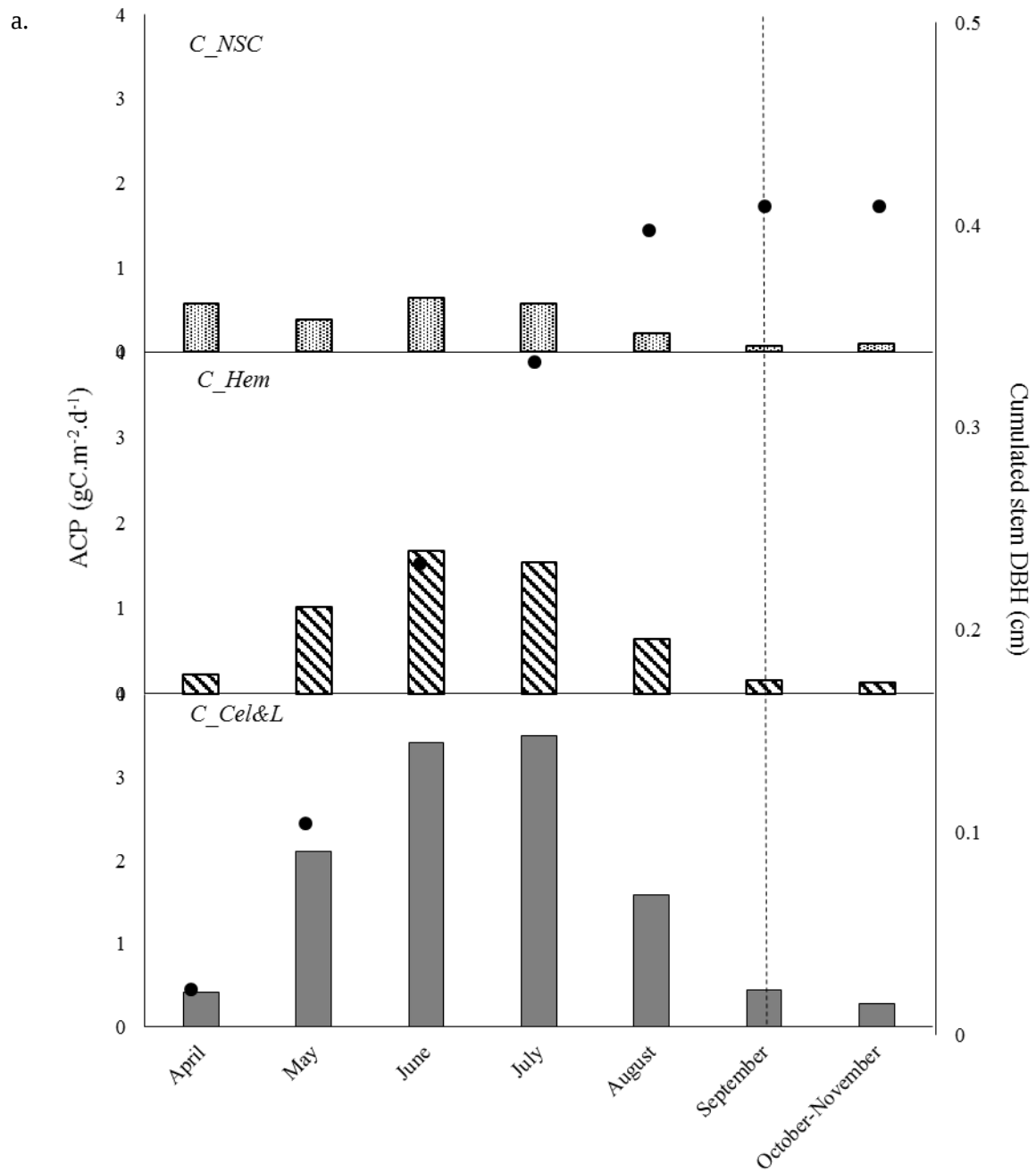
	final ring 2013	02/07/2014		29/07/2014	
C Total (gC.kg⁻¹ DM)	455 $\pm$ 12	448 $\pm$ 11	<0.05	442 $\pm$ 10	<0.05
SCPcel&l	66% (302 $\pm$ 6)	58% (259 $\pm$ 13)	<0.05	64% (283 $\pm$ 10)	<0.05
SCPh	27% (123 $\pm$ 2)	31% (137 $\pm$ 8)	<0.05	27% (119 $\pm$ 4)	<0.05
C_NSC	7% (30 $\pm$ 1)	12% (52 $\pm$ 1)	<0.05	9% (40 $\pm$ 1)	<0.05

	29/08/2014		01/10/2014	
C Total (gC.kg⁻¹ DM)	447 $\pm$ 21	NS	472 $\pm$ 14	<0.05
SCPcel&l	67% (298 $\pm$ 5)	NS	68% (319 $\pm$ 10)	NS
SCPh	26% (117 $\pm$ 3)	NS	22% (104 $\pm$ 3)	<0.05
C_NSC	7% (32 $\pm$ 0)	NS	10% (49 $\pm$ 2)	<0.05

Both soil type showed a similar repartition in term of C content in the tree ring during the year as no significant difference was found between them (p -value =NS ,data not shown). In 2014, the C proportions in each compounds varied between each dates (p -value<0.05) at the exception of the values in August which did not differ significantly from July. A general observation is that the SCPh and C_NSC were declining from 2 July to 29 August (from 137 $\pm$ 8 to 117 $\pm$ 3 gC.kg⁻¹ DM and from 52 $\pm$ 1 to 32 $\pm$ 0gC.kg⁻¹ DM for each component at each dates respectively) while SCPcel&l was increasing (from 259 $\pm$ 13 to 298 $\pm$ 5gC.kg⁻¹ DM) and C total was stable (between 442 $\pm$ 10 and 448 $\pm$ 11gC.kg⁻¹ DM). Between 29 August sample and the 1 October one, there was a strong increase in C total and in C_NSC, nearly recovering the amount present in the 2 July sample.

There was also a significant difference between the different components proportion in the 2013 final ring and the 2014 final ring (corresponding to 1 October value) for all components and also the C total except for the SCPcel&l compartment. The SCPh proportion was more important in 2013 than in 2014 and conversely the C_NSC proportion was higher in 2014 than 2013.

3.4.2.2 Daily aboveground component production (aCP))



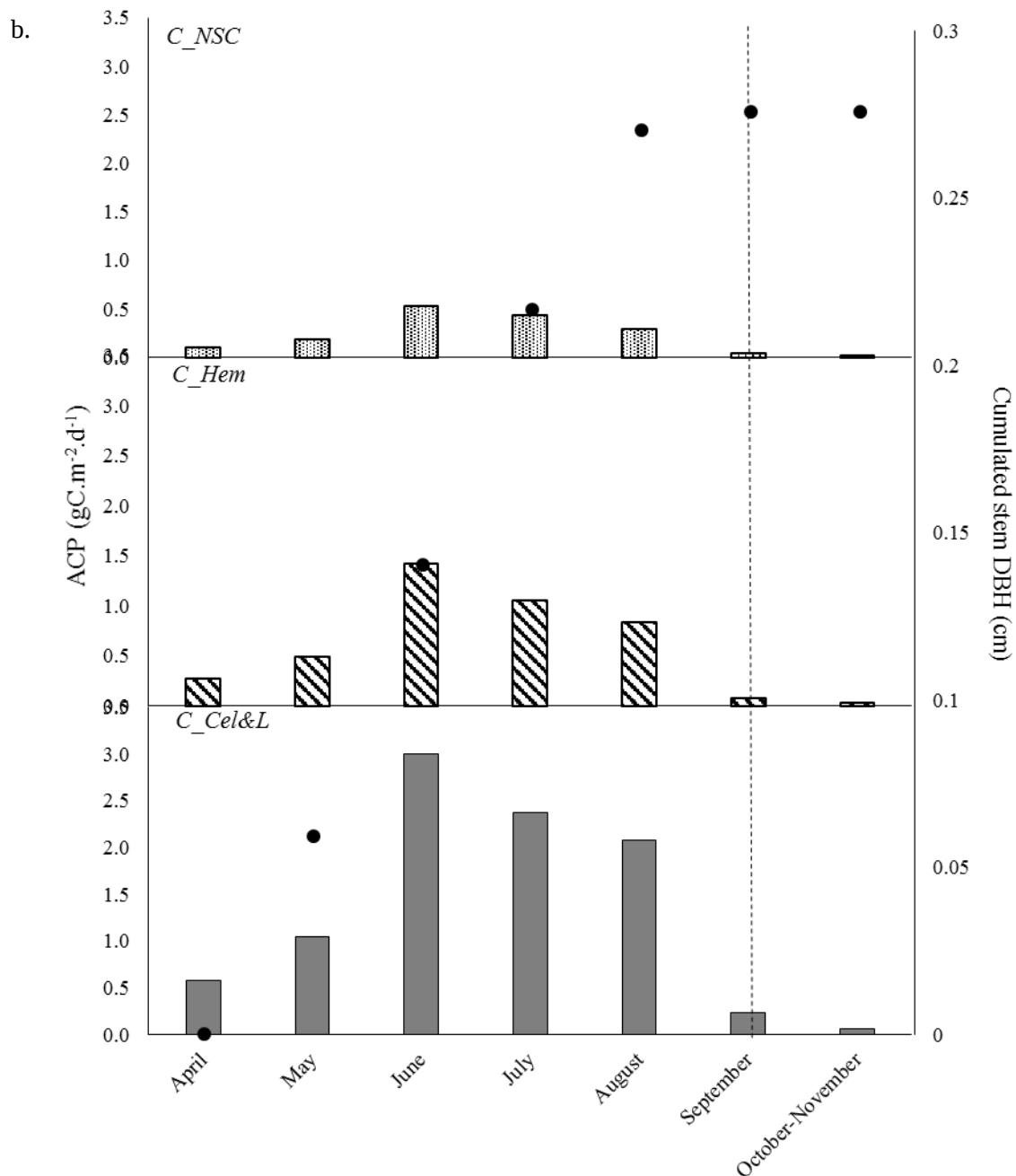


Figure 3.1 Daily mean aCP value for each month: hemicelluloses (SCPh; Striped bars), cellulose and lignins (SCPcel&l; grey bars) and NSC (dotted bars) productions (gC.m⁻².d⁻¹) during the year 2014. The black dots represent the cumulated stem DBH for each month in cm. The vertical dotted line represent the end of the growth in diameter. For (a) the alocrisol and (b) the calci-brunisol.

There is a quite large fluctuation in aCP throughout the year 2014 (Fig 1). The production for SCPh, C_Cel+L and C_NSC differed from date to date ($p\text{-value} < 0.05$). They also differed significantly between each soil type ($p\text{-value} < 0.05$). The evolution dynamic was different between both soil types. The SCP on both soil started with a similar value in April (period starting after the budburst the 10 April), but in May the alocrisol doubled the production of the calci-brunisol (1.02 and 2.11gC.m⁻².d⁻¹ for SCPh and the SCPcel&l respectively against 0.5 and 1.05 gC.m⁻².d⁻¹ for both component respectively

on the calci-brunisol) and was then quite stable between June and July before diminishing starting August. A peak was reached in June for the calci-brunisol, and the production started to decline already in July, slightly earlier than for the alocrisol. The C_NSC production was always more important on the alocrisol than the calci-brunisol, and was quite stable from April to July (at the exception of a lower value of $0.38 \text{ gC.m}^{-2}.\text{d}^{-1}$ in May) and declined by half in August ($0.22 \text{ gC.m}^{-2}.\text{d}^{-1}$) on the alocrisol. It was more fluctuant on the calci-brunisol, and the production reached a peak value during the month of June and July (0.52 and $0.43 \text{ gC.m}^{-2}.\text{d}^{-1}$ respectively) before diminishing again. All productions were at their lowest at the October-November period, which includes the end of the growing season the 15 November. It is interesting to note that the DBH growth slowed down for both soil in August and reached a plateau in September, while there was still some aCP happening.

Both SCP_h and SCP_{cel&l} productions seemed to be influenced by the mean air temperature. Indeed when computed together a bell shaped curve appears for both soil. Starting from 10.58°C the CIP increased until peaking around 10.77°C and decreasing afterwards. A significant exponential correlation was found with the mean photoperiod calculated for each period for both SCP. There was also a linear correlation with both minimum REW and mean REW for both SCP. No significant relationships were found between both SCP and other environmental factors (R_g , VPD).

Table 3.3 Statistical results of the correlations between monthly productions or efficiencies and environmental factors. The type of fit and the R^2 are given when significant correlations existed.

		Alocrisol					
		Productions			Efficiencies		
Fit		Hemicelluloses	Cellulose+Lignins	NSC	Hemicelluloses	Cellulose+Lignins	NSC
Mean							
Photoperiod	Exponential	0.80	0.79	0.62	NS	NS	NS
Mean air							
Temperature	Binomial	0.81	0.84	0.77	NS	NS	NS
REW min	Linear	0.73	0.76	NS	0.71	0.74	NS
Mean REW	Linear	0.76	0.80	NS	0.78	0.82	NS
		Calcibrunisol					
		Productions					
Fit		Hemicelluloses	Cellulose+Lignins	NSC			
Mean							
Photoperiod	Exponential	0.92	0.92	0.88			
Mean air							
Temperature	Binomial	0.79	0.79	0.81			
REW min	Linear	0.77	0.76	0.82			
Mean REW	Linear	0.74	0.73	0.82			

3.4.2.3 Aboveground component production efficiency (aCPE)

The efficiency was computed only on the alocrisol ecosystem because GPP was only determined for this soil type.

In order to obtain the aCPE for the two different soil types, estimations are required of the GPP temporal evolution representative of each soil type. The partitioning of the eddy covariance fluxes between the contributions of soil types areas was performed with the footprint analyses (see Footprint analysis section). The half-hour data including more than 40% of flux coming from the calci-brunisol ecosystem were relatively rare (less than 5% of the dataset). In addition, a comparison between the fluxes coming quasi exclusively (more than 70% of the footprint) from each of the soil type under relatively similar environmental conditions (global radiation between 200 to 300 J.m⁻².s⁻¹, air higher than 15°C, no edaphic drought...) did not show any significant difference in GPP values. In these conditions, it was not possible to extract a specific behavior for the GPP estimation of the calci-brunisol. All the GPP data obtained were then considered as representative of the alocrisol and used to characterize the alocrisol production efficiencies.

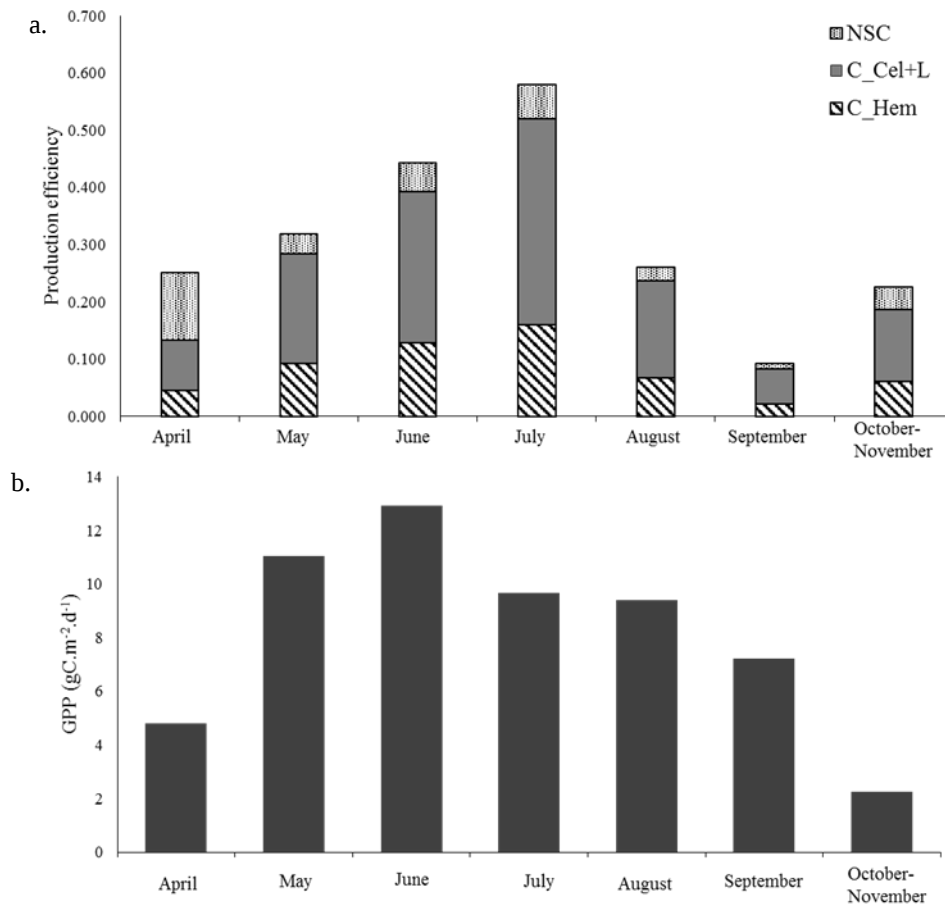


Figure 3.2 (a) Monthly values of the hemicelluloses (SCPh; Striped bars), cellulose+lignins (C_C+L; grey bars) and NSC (dotted bars) efficiencies on the alocrisol for the year 2014. (b) Monthly cumulated value of the GPP measured on the alocrisol for the same period of time.

There was an important intra-annual variation in the production efficiency of both Hemicelluloses and Cellulose and lignins following the variation in total aboveground biomass production efficiency (aBPE corresponding to the sum of all aCPE), with an increase from April-Mai value of 0.05 and 0.09 respectively to a peak in July value of 0.16 and 0.36 respectively (**Figure 3.2a**). Again similarly to the aBPE the efficiencies dropped from about 50% from July to August (0.07 and 0.17 for SCPh and SCPcel&l respectively), followed afterwards by a slight increase at the end of the year. The C_NSC aCPE had a slightly different pattern, mainly at the beginning of the growing period, indeed its value was at its highest point in April (0.11) and fluctuated between 0.03 and 0.06 the rest of the year.

There was a slight increase in the efficiencies for the October-November period compared to September (+ 50% for all efficiencies).

As showed in table 3, a linear relationship was found with both the min REW and the mean REW. No significant correlations were found between the aCPE and the other environmental factors tested (Rg, mean Ta, VPD, photoperiod).

3.4.3 Annual balance

For the complete year 2014, the hemicelluloses production represented 184.5 gC.m^{-2} , i.e. 27% of the wood aBP on the alocrisol and $115.1 \text{ gC.m}^{-2}.\text{y}^{-1}$, i.e. 28% of the wood aBP for the calci-brunisol, while the cellulose and lignin production represented 399.9 and $257.7 \text{ gC.m}^{-2}.\text{y}^{-1}$, i.e. 60% and 62% of the wood aBP on the alocrisol and the calci-brunisol respectively. The C_NSC amounted to 71 and $43 \text{ gC.m}^{-2}.\text{y}^{-1}$, i.e. 13% and 10% of the wood aBP on the alocrisol and calci-brunisol respectively.

On the alocrisol, 9% of the C uptaken through photosynthesis was dedicated to the Hemicelluloses and 20% to the cellulose and lignin pool, and 4% to the NSC.

Table 3.4 Annual values of the aboveground wood productions, and the different component productions ($\text{gC.m}^{-2}.\text{y}^{-1}$) on both soil type, and annual fluxes ($\text{gC.m}^{-2}.\text{y}^{-1}$) and component production efficiencies for the alocrisol. The p-value are also shown for the productions.

Alocrisol	Calci-brunisol	P-value
-----------	----------------	---------

<i>Productions ($gC.m^{-2}.y^{-1}$)</i>			
Aboveground wood biomass (stem + branches)	555	416	<0.05
Hemicelluloses	151.7	115	<0.05
Cellulose+Lignin	331	257	<0.05
NSC	71	43	<0.05
<i>Fluxes ($gC.m^{-2}.y^{-1}$)</i>			
NEE	-549	/	/
Reco	1089	/	/
GPP	-1639	/	/
<i>Annual Production efficiencies</i>			
Hemicellulose	0.092	/	/
Cellulose+Lignin	0.202	/	/
NSC	0.043	/	/

3.5 Discussion

The weather for the year 2014 can be qualified as typical for the region when compared with the 1934-2015 period. No sign of water stress was found on the alocrisol or the calci-brunisol as REW never went below 0.4. The last thinning happened in 2010. In view of these elements, interference of exceptional or extreme events are avoided.

3.5.1 C partitioning

During the year 2014, the cumulated C content in the tree rings was variable for each component (SCPh, SCPcel&l and C_NSC).

The hemicellulose pool decreased while the cellulose and lignin one increased continuously. A few studies indicated that hemicelluloses acted as C reserves that could be used for the growth (Kozłowski 1992) even though this has been contradicted in a more recent thesis (Schädel 2009). Although Hemicelluloses are quite mobile molecule (Hoch 2007). The cellulose and lignin increase could be

linked firstly to the processes of the creation of a new cell and its enlargement and the creation of the secondary wall that involves celluloses at the beginning of the growth and secondly, later in the year to the process of lignification which are part of the major phases of xylem cell formation (Cuny and Rathgeber 2014; Rathgeber et al. 2016).

Several studies found that the NSC pool remained quite stable during the year in beech trees (Barbaroux and Bréda 2002; Zein et al. 2011) contrary to what we found. On this site the NSC content of the tree ring decreased from 2 July to 29 August, which could be explained by the trees actually using this pool of easily accessible and mobile C to build the cell walls preferentially.

There was also a difference between the 2013 final ring and the 2014 one (corresponding to 1 October sample). The latter showed a more important C total ($472 \pm 14 \text{ gC.kg}^{-1} \text{ DM}$ against $455 \pm 12 \text{ gC.kg}^{-1} \text{ DM}$ in 2013).

The C allocated within the different component is also different, the NSC pool being more important in 2014 compare to 2013 ($49 \pm 2 \text{ gC.kg}^{-1} \text{ DM}$ against $30 \pm 1 \text{ gC.kg}^{-1} \text{ DM}$). Conversely, the hemicelluloses pool is lower in 2014 ($104 \pm 3 \text{ gC.kg}^{-1} \text{ DM}$ against $123 \pm 2 \text{ gC.kg}^{-1} \text{ DM}$ for each year respectively).

The total C proportion granted to the cellulose and lignin pool did not vary between both year (68% in 2014 against 66% in 2013). There was a significant difference in the partitioning towards the hemicelluloses and NSC pool. Indeed, while the proportion allocated towards the hemicelluloses decreased in 2014 (22% against 25%), the one allocated to the NSC increased (10% against 7%). An explanation for this result could be that as the 2013 final tree ring was sampled the 2 July, few month after bud break, and thus some of the C reserves could have been used for leaf development as is typical in temperate broadleaved species (Landhäusser and Lieffers 2003) even though this remobilization of NSC has been shown to be really low in Beech trees (Barbaroux and Bréda 2002; Zein et al. 2011).

3.5.2 aCP

All productions followed the same shape as the total C (aBP; results presented in Heid et al, in review) even though there was a slight shift in the period during which the decrease starts between both soil - starting already in July on the calci-brunisol contrary to the alocrisol on which the decrease started in August. The productions were significantly different ($p\text{-value} < 0.05$) for each period on both sites, on the calci-brunisol, the values were always inferior to the alocrisol. This difference was independent of the C ratio in the biomass for each C component as the SCPh, SCPcel&l and C_NSC were the same on both site (Table 2). The same explanation can be made as were in Heid et al, in review about the difference in aBP between both soils. Since the meteorological conditions are the same on both stations, this difference cannot be due to factors like temperature or radiation. The same can be said about management, which has been realized in the same way on both stations. This difference in aCP comes from a really high production by the dominant and co-dominant trees on the alocrisol (data not shown).

Taken individually, the alocrisol trees of this class have a far more important biomass production when compared to the calci-brunisol ones, but the latter have a larger stem density. This last factor does not compensate, since, on a surface unit basis, the aBP is nearly 3 times higher for dominant and co-dominant alocrisol class.

Both SCP_h and SCP_{cel&l} reached their maximum in June at the maximum of daily photoperiod (15h) and start decreasing afterward. All aCP have a binomial relationship to temperature, all increasing until a maximum value of mean Ta (around 10.8°C) and decreasing afterwards, implying that there is a mean Ta optimum to allow the production.

The radial growth rate started decreasing already during the July period (data not shown), explaining the decrease in August and the really low value in September and October-November. Even though the radial growth rate decreased, C is still taken up by the trees (as shown in Fig 2b) and the components are still produced at the same rate as during the radial growth in July for the alocrisol. The growth stopped in September but there is still aCP in September and October-November. A similar result was assessed by Cuny et al. (2015) on conifers, implicating the beginning of the lignification process.

Our annual SCP_h (151.7gC.m⁻².y⁻¹ and 115.1gC.m⁻².y⁻¹ for the alocrisol and calci-brunisol respectively) represented 27 and 28% of the total wood biomass production which is similar to result found in literature (25%) (Hoch 2007; Schädel 2009). The SCP_{cel&l} (331.5 and 257.7gC.m⁻².y⁻¹ for the alocrisol and calci-brunisol respectively) represented 60 and 62% of the aboveground wood biomass production, which is lower to what can be found in literature (42-45% for the Celluloses and 30% for the lignin in wood BP which amount to 72-75% of wood BP) (Haigler et al. 2001; Boerjan et al. 2003). Although we did found a similar SCP_{cel&l} to SCP_h ratio (2.2) as Schädel et al. (2010a).

The NSC we found representing between 13 and 10% of the total wood biomass production on each soil respectively is quite high compare to what is found in literature (around 2.5%; Hoch et al. 2003).

3.5.3 aCPE

As far as we know, there is actually in the literature no other research presenting both aCP and GPP in a same study. Same goes for the calculation of the different aCPE that we calculated here.

Again, the aCPE follow the aBPE seasonal evolution. During 2014, the aBP was always lower than the GPP for each period. The latter may not be the unique C source for aBP, as the C storage from the previous year could also be used as C fuel. However, determining the origin of the C in the biomass is not possible with our dataset, and would have required other techniques such as isotopic tracing (Carbone et al. 2013). These phenomena introduced some uncertainties into our estimation of aboveground biomass production efficiency (aBPE = aBP/GPP) and corresponding aCPE.

The aCPE presented a large seasonal fluctuation with a relatively symmetric evolution (quasi bell-shaped curve) which is different from aCP curve. Although no significant correlation was found with the photoperiod the efficiencies bell-shaped curve are relatively similar to this factors evolution. No

clear influence of any climatic driver can be inferred from our dataset. June and July are the more efficient period to product hemicelluloses and cellulose and lignin, while April is the one for the NSC. This could be as the beech starts its growth right at bud burst (10 April in this study) so C uptaken through photosynthesis is preferably assimilated towards this C pool, before being used to build the other structural components. The higher value in efficiency in October-November in all aCPE is linked to a constant aCP but a lower GPP, as the leaves were starting to yellow during this period.

In 2014, there were 9% of the C taken up from the atmosphere that was stored into hemicelluloses form and 20% into cellulose and lignin, meaning potentially 29% of the atmospheric C has been stored in a long term C storage sink.

3.6 Conclusion

In this study we found that on our site for the year 2014, the C proportion allocated to the different C component of the aBP varied annually. As expected the proportion of cellulose and lignin increased during the year and the proportion of Hemicellulose varied throughout the year. Although our NSC was quite fluctuating between each month.

We also showed that those components production are also variable throughout a year, and seem to depend of the daily photoperiod and the mean air temperature. Also, an optimum value seems to exist for the mean Ta. On an annual basis, both our cellulose and lignin and NSC productions were different from what could be expect in literature, with what was lacking in cellulose and lignin going to the NSC pool.

The efficiencies followed closely what was found for the aBPE and responded to the photoperiod and other environmental driver the same way. During the year 2014, our site stored in its structural component pool 29% of C potentially coming from the atmosphere. More studies would be needed to assess more precisely exactly which part of the C stored into this long term C storage pool in trees is actually coming from the atmosphere and which comes from previous C tree reserves. A more precise phenological monitoring would also be of high interest.

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Chapitre 4 Variabilité saisonnière de l'efficacité de production de biomasse aérienne d'une prairie : Comparaison avec un écosystème forestier soumis aux mêmes conditions climatiques.

Intra-annual variability of the aboveground biomass production efficiency (aBPE) of a French grassland: comparison with a forest ecosystem under the same climatic conditions.

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En préparation

4.1 Abstract

With the evolution of ecosystem management and the climate change we are facing, there is a need to improve our understanding of carbon (C) balance and more specifically C allocation in the plants (biomass, storage, exudates). The lack of knowledge on the use of the C assimilated and on the temporal variability of the processes involved leads to significant uncertainties in the prediction of ecosystem behavior by models.

In the present study, we quantified the seasonal variation of both gross primary production (GPP, obtained through eddy covariance measurements) and aboveground biomass production (aBP, the C fixed into the biomass obtained based on inventory campaign) for a permanent grassland under mixed practices (i.e. grazing and mowing) located in North East of France. This provides material for estimation of the intra-annual evolution of the aBP efficiency ($aBPE = aBP/GPP$ which is the fraction of the C assimilated fixed in the aboveground biomass) in order to estimate the grassland role as a C sink and its potential importance into C sequestration. The grassland aBPE is compared to a 60 years-old beech forest located just 4 km away and under the same climatic conditions. The potential factors responsible for the divergence between the aBPE variability of these two ecosystems are identified.

In 2014, the grassland had an annual net ecosystem exchange (NEE) of -484 gC.m^{-2} slightly inferior to the forest one (-549 gC.m^{-2}). The difference is mainly linked to GPP (-1538 and -1639 gC.m^{-2} respectively). The mean annual aBPE of the grassland was also lower than in the forest (0.25 vs. 0.37 respectively), mainly linked to a quite large difference in aBP (400 vs. 603.7 gC.m^{-2} respectively).

Concerning the dynamics of biomass growth, our results show that the growth peak was more important in the forest (up to $6 \text{ gC.m}^{-2}.\text{d}^{-1}$) when it was only half of it for the grassland. The intra-annual aBPE variability was larger in the forest, which could be caused by the forest's aBPE being mainly impacted by climate whereas the grassland one's is impacted by management.

Key words *Grassland, Eddy covariance, Forest, aboveground BPE, management*

4.2 Introduction

In last decades, increasing greenhouse gas emissions (GHG) have led the globally averaged combined land and ocean surface temperature increases by 0.85°C between 1880 and 2012 (IPCC 2013), changes in rainfall and related biomass production. In addition, management practices have led to increasing biomass production (for wood production, fodder supply...) in order to provide for our expanding demography.

The CO₂ balance of an ecosystem with atmosphere is assessed by the Net Ecosystem Exchange (NEE), which is the sum between the ecosystem's respiration (Reco, C released in the atmosphere) and the Gross Primary Production (GPP, C taken up from the atmosphere). The NEE is the term that determines whether an ecosystem acts as C sink or source depending on the species, climate and soil type, and whether it can play an important role in the global C sequestration in soil and vegetation (up to 2000 Gt, Singh et al. 2015). In terrestrial ecosystems, the atmospheric C is absorbed through photosynthesis (a part of the GPP) and then stored into the plants either into the form of reserves or allocated to biomass production (BP). Within total terrestrial ecosystems, forests (temperate, boreal and tropical) cover 28% of the area and store 46.3% of the C (Singh et al. 2015) when the grassland/savannah cover 34% (Noble et al. 2000) and store 25.6% (Singh et al. 2015). While forests store the carbon mainly aboveground (wood) (from 30 to 50% of the GPP allocated belowground (Ryan et al. 2004)), grasslands C storage resides mainly in the belowground (floor and soil, Jones and Donnelly 2004). Both ecosystem types represent more than half of the terrestrial land cover and store up to three fourth of the global C, making them important actors for C mitigation.

The actual policy implemented to face climate change (FCCC 2015) is to reduce the net emission of carbon dioxide (CO₂) in the atmosphere and one possibility is to optimize the carbon (C) sequestration in the plants and soil biomass. In order to do this, a better understanding of the effects of climate change on production and C sequestration is necessary. Also, indicators giving a better understanding on the growth and C allocation (aboveground/belowground, different biochemical compounds) are necessary to determine more efficient management practices.

One of these indicators is the biomass production efficiency (BPE) defined by Vicca et al. (2012) as the ratio between BP and GPP. It assesses which the part of the carbon collected through photosynthesis is used for biomass production and, by analogy the aboveground BPE (aBPE – corresponding to the ratio between aboveground BP (aBP) and GPP). Their seasonal variability presents important uncertainties (Campioli et al. 2013). BPE has been shown to vary positively with nutrients availability (Vicca et al. 2012), management practices (Campioli et al. 2011), type of ecosystems (Malhi et al. 1999; Aubinet et al. 2001) and species (Ryan et al. 1997).

We have already presented the aBPE variability for a temperate forest in a previous study (Heid et al., under review, Chapitre 2), and found that this efficiency had a temporal evolution relatively similar to

the photoperiod. Some studies have also investigated the annual aBPE of forests (Steppe et al. 2015), but the comparison of different agricultural ecosystems in order to determine effective production and C sequestration systems have not been performed yet.

Here we would like to assess the aboveground biomass production (aBP) and its efficiency (aBPE) for two agricultural production systems (grassland and forest) growing under the same climatic conditions (i.e. nearby plots). This allowed us to compare the climate and management impact on the aBP and aBPE for the 2 ecosystems according only to their inherent characteristics throughout the year.

4.3 Material and method

4.3.1 Study sites

The grassland site is located at Osne-le-Val (Haute-Marne, Champagne-Ardenne, East of France) and is managed by a local farmer. The plot is a 8.5 ha permanent grassland managed under mixed practices. Only 5.1 ha are actually mowed (subplot 1), but the entire stand is grazed by bovine. Twenty-six species were count, *Bromus hordaceus* covers the most of the surface (53.8%) followed by *Bellis perennis* (16.8%). The soil is a calcisol presenting a pH varying from 7.1 to 8 depending on the depth. An organic and mineral fertilization was made in November 2013 followed by a mineral one in March 2014 (Table 4.1). On the 5th of June 2014 the 5.1 ha of the subplot 1 was mown (Table 1). The cattle (see composition on Table 1) entered into the other part of the grassland (3.3 ha, subplot 2) on the 13th of April and the subplot 1 was opened to them on the 12th of July. The animals stayed on the field until the 6th of November 2014.

Table 4.1 Technical management event on the studied grassland during 2014

Dates	Events
30/03/2014	Fertilization : N (36 kg/ha); P2O5 (16kg/ha); K2O (29kg/ha)
13/04/2014	Pasture (on subplot 2)
05/06/2014	Mowing (subplot 1)
12/07/2014	Pasture (8 cows, 8 calves, 1 heifer, 1 bull; on sublots 1 and 2)
16/07/2014	1 cow added
06/11/2014	End of pasture

The forest site is located in the Montiers-sur-Saulx state forest (Meuse, Lorraine, East of France) managed by the French national forest office (ONF) and situated a few kilometers away from the grassland site (**Figure 4.1**). The plot is composed mainly by beech trees (*Fagus sylvatica*). They are about 60 years old and around 25m high. The LAI is of 9 and the soil is an alocrisol. For more detail, see Heid et al., (under review).

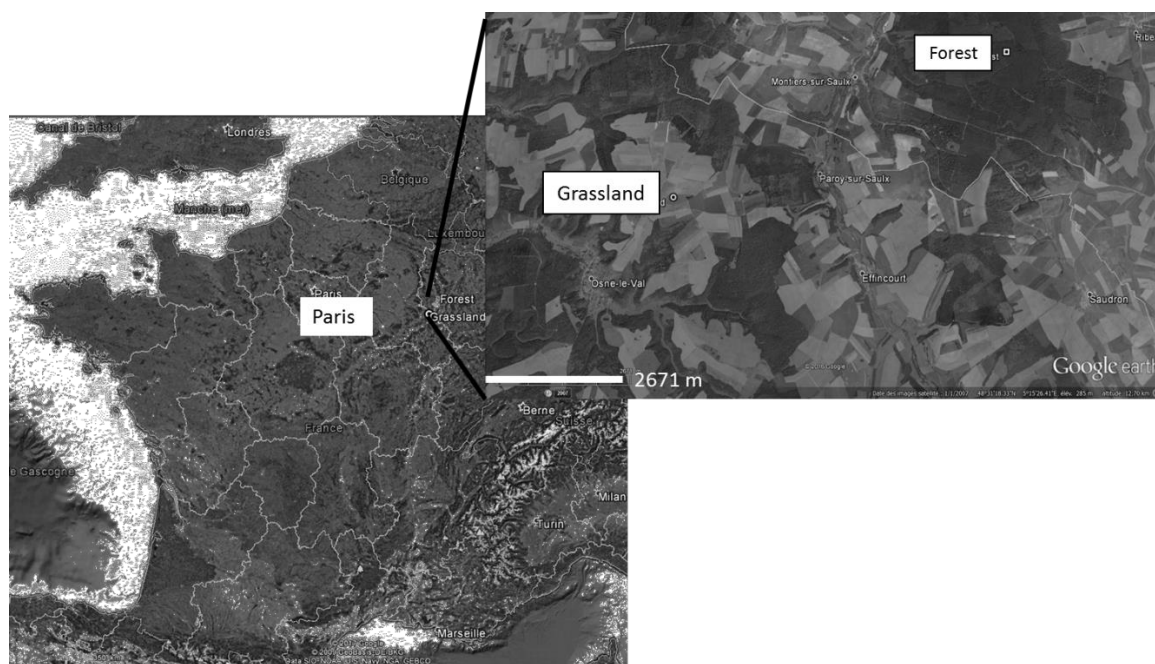


Figure 4.1 Site localisation

Because of their geographical proximity, the meteorological conditions are similar. The climate is oceanic with, on average over 20 years, an annual precipitation of 1085mm and a mean annual temperature of 9.6°C (6.7°C and 15.7°C for MAT minimum and maximum respectively, Meteo France, table 2).

4.3.2 Grassland Eddy covariance and meteorological measurement

4.3.2.1 Experimental set-up

The Net Ecosystem CO₂ Exchange (NEE) corresponds to the CO₂ flux measured with an Eddy Covariance (EC) system consisting of an enclosed infra-red CO₂/H₂O gas analyzer (IRGA, Li-7200, LI-COR, Lincoln, NE, USA) coupled with a 3D sonic anemometer (HS-50, Gill, Hampshire, UK). The EC system is set-up on a 3m high mast, inside a fence in the subplot 1.

Supporting meteorological instrumentation consisted of a vertical profile with two air temperature and humidity probes (HMP155, Vaisala, Vantaa, Finland) and two 2D sonic anemometer (Wind Observer 2, Gill, Hampshire, UK) at 2 different heights (50cm and 1m from the ground). The other radiative sensors - pyranometer (CMP21, Kipp&Zonen, Delft, Netherlands), a direct/diffuse Photosynthetically

Active Radiation (PAR) sensor (BF5, Delta-T devices Ltd, Cambridge, England), Normalized Difference Vegetation Index (NDVI), Photochemical Reflectance Index (PRI) sensors (SKR1800, Skye, Alliance Technologies,) and net radiometer (CNR4, Kipp&Zonen, Delft, Netherlands) - are installed at the top of the mast.

The experimental set-up is the same for the forest ecosystem (see Heid et al., Chapitre 2) but the measurements are made above the canopy at 35m high and CO₂ storage in the canopy air is quantified to be added to eddy covariance flux to obtain NEE.

4.3.2.2 Flux and meteorological data processing

In order to calculate the net fluxes of CO₂ for grassland, the same post-processing as for the forest (Heid et al, Chapitre 2) was applied, at the exception of the u^* threshold selection, not implemented for grassland dataset as the value was really low and selection had no significant impact. The raw fluxes were post-processed using Aubinet et al. (2012), and were gap-filled and partitioned between GPP and Reco following Reichstein et al. (2005, 2012).

4.3.3 Aboveground Biomass Production and efficiency

4.3.3.1 Grassland

4.3.3.1.1 Experimental set-up

In order to assess the aBP, a protocol similar to Klumpp et al. (2011) was followed. The aBP was obtained using 12 grazing exclusion cages (0.64m²) placed on the 5.1ha part of the site. The grass was cut at ca. 4 cm from the ground on the future location of each cages, just before their installation. After few weeks (exact duration pointed below), the cages were removed and the grass that had regrown under them was cut at 4 cm. The collected material was dried and weighed, allowing us to get the aboveground biomass production of the location over the period between 2 successive harvests (named “partial growing period” in the text). The cages were dispatched at 12 intersections of a grid pattern around the flux mast. After each sampling, the cages were shifted from a few meters, always around the intersection points. They were set from the 23rd of February 2014 and removed the 6th of November 2014, and the material collections took place on 6 dates throughout the year giving 5 partial growing period (22 February-16 April; 16 April-23 Mai; 05 June-24 July; 24 July-11 September and 11 September-6 November).

4.3.3.1.2 Samples processing

A sub-sample of each cage was thinly milled in order to perform C and N analyses and obtain their percentage for each period. The mean dry matter produced by all the cages (deduced from dry weight) was multiplied by the average C percentage and divided by the total surface of the cages to give us the aboveground biomass production in gC.m⁻² for each partial growing period. These values were then

divided by the number of day between each sampling date to obtain mean daily aBP ($\text{gC.m}^{-2}.\text{d}^{-1}$). These latter were then integrated temporally (summation) to get the total annual aBP ($\text{gC.m}^{-2}.\text{y}^{-1}$).

4.3.3.1.3 Computation of weekly aBP

The aBP temporal evolution is defined by only 5 values of aBP for partial growing period. In order to improve this temporal resolution and to allow the research of correlations with different possible impacting factors, we determined the weekly aBP ($\text{gC.m}^{-2}.\text{w}^{-1}$) as the difference between 2 values of aboveground biomass (aB, gC.m^{-2}) one week apart was estimated using a predefined binomial equation from (Carrère et al. 2012). This relationship, validated on several French grasslands, provides the value of aB from degree-day T ($^{\circ}\text{C}.\text{d}^{-1}$, summation of the degree above zero for the average daily temperature since the 22nd of February 2014):

$$aB = (-1e^{-0.6T^2} + 0.0074T - 2.0571) * c \quad \text{Eq 1}$$

where c is a correcting factor for adjusting the aB predicted values to the data. Here, c was calculated for each partial growing period in order to achieve aB and then aBP value that match with field campaign data.

This calibration gives good results (equ 1, $R^2 = 0.95$).

4.3.3.2 Forest Experimental set-up

The aBP of the forest was determined by summing aBP of individual trees located in an experimental plot and then dividing the sum by the plot surface (1-ha). Individual tree aBP was obtained by difference of two successive aB estimation deduced from the measurements of the increase of diameter at breast height (DBH), the wood density evolution, the C concentration, the tree height and age (see allometric relationship in Heid et al; Chapitre 2) The height of every trees on three 1-ha plots was measured at the end of 2013 and the age (considered identical for all the trees in the same diameter class) was estimated at the end of 2014 by counting the rings of 30 trees that were cut at the beginning of 2015. The diameter at breast height (DBH) was measured on 45 trees every month during the 2014 growing season. For the other trees, we extrapolated the average value obtained on trees of the same dominance class. The C concentration and wood density was also considered as identical for all the trees and deduced from mini-cores sampling and laboratory analyses (see Heid et al., Chapitre 2).

4.3.3.3 Aboveground biomass production efficiency

The aboveground biomass production efficiency (aBPE) is calculated as the ratio of aBP on GPP both in gC.m^{-2} and over the same period (annually, weekly or partial growing period) as defined in Vicca et al. (2012). To obtain the GPP over these periods, the daily GPP values are simply summed.

4.3.4 Data analyses

All statistical analyses were carried out using R 3.0.2 (R Core Team 2013).

4.4 Results

4.4.1 Meteorological data

Table 4.2 Average of the mean annual temperature and the annual precipitation over the 1934-2015 period measured at the Enerville-aux-Bois (a) and Biencourt-sur-Orge (b) stations, two French weather stations (Meteo France) located 32km and 15km away from our grassland site respectively. The corresponding values for the studied year measured on the grassland site.

	Annual Mean		Minimum		Maximum	
	1934-2015	2014	1934-2015	2014	1934-2015	2014
a. Temperature (° C)	9.6	10.9	-24.2 (1956) -13.8		39 (2003)	33.4
b. Precipitation (mm)	1085	1020	797	-	1351	-

The weather during the year 2014 didn't stand out from the average climatic conditions recorded in a nearby state station over the 1934 to 2015 period (*Table 4.2*).

In 2014, the daily mean air temperature reached a minimum of -4.8°C in December and a maximum 24.4°C at the end of July (*Figure 4.3c*). In addition to the normal seasonal evolution, there are large day to day throughout the year (in particular for CO_2 fluxes interpretation: at the beginning of April, beginning of June and around the 20 June).

The global radiation, measured on the forest site, peaked, as planned, at the end of June reaching a value of $31,5 \text{ MJ.m}^{-2}.\text{d}^{-1}$ (*Figure 4.2a*). There also were a lot of variations with two important drops in radiation, a first narrow one in Mai (from 14 to $6 \text{ MJ.m}^{-2}.\text{d}^{-1}$) and then a larger in July from 16 to $3 \text{ MJ.m}^{-2}.\text{d}^{-1}$), in between several other less important fluctuations.

As no direct SWC values are available for the site, we used precipitation, ETP and ETR to see whether there were some drought episodes or not. There were 2 periods (April and June) during which no precipitation was registered (*Figure 4.2b*). For one of these periods the ETR was inferior to the ETP (from the 11 June to the 3 July, *Figure 4.2c, d*) showing the potential existence of an edaphic drought episode implying that the SWC should be taken into account for the analysis. For the rest of the year, there have been no apparent lack of water for the ecosystem functioning.

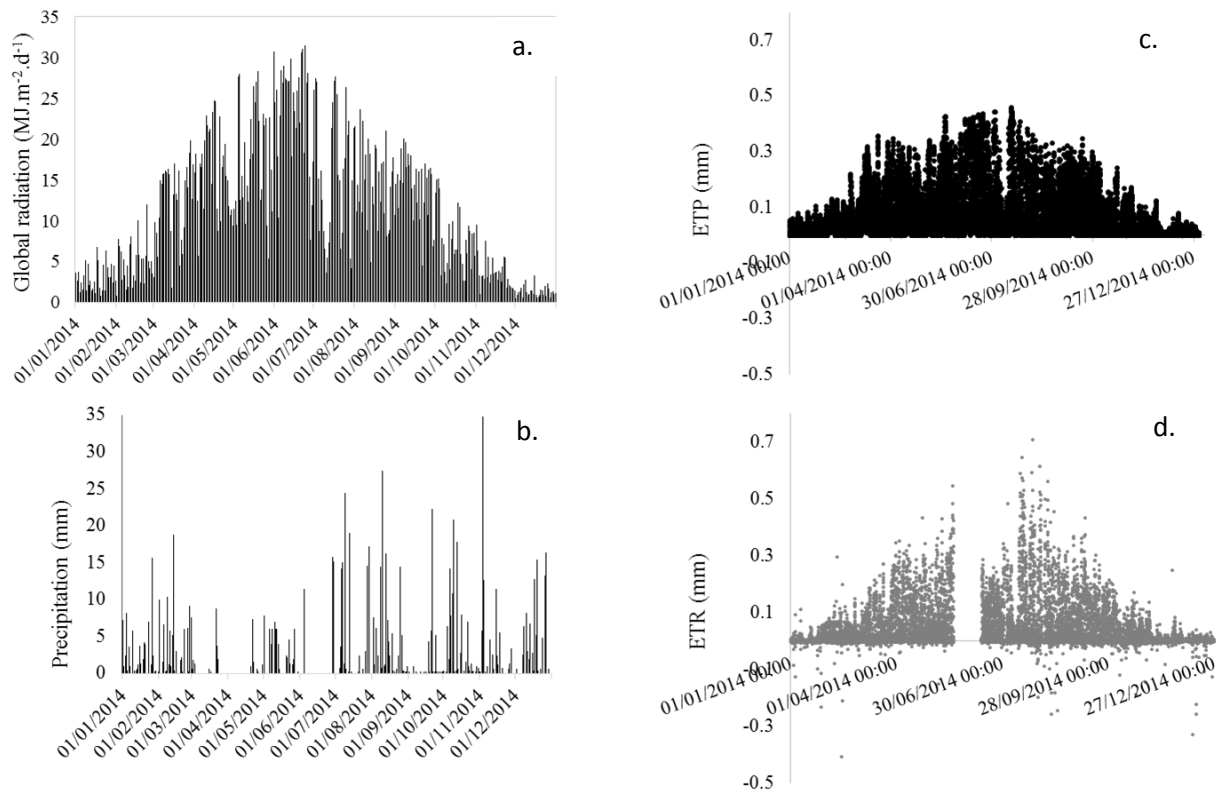


Figure 4.2 Evolution of the daily global radiation in $\text{MJ.m}^{-2}.\text{d}^{-1}$ (a), daily precipitation in mm (b) half-hourly potential evapotranspiration (ETP, c) and half-hourly real evapotranspiration (ETR, d) both in mm. The gap in ETR in June is due to a probe failure.

4.4.2 Total annual values

4.4.2.1 Flux (NEE, GPP, Reco)

Table 4.3 Summary of the 2014 annual fluxes (GPP, Reco and NEE), aboveground biomass production (aBP) and its efficiency (aBPE) for the grassland and forest ecosystems.

a.	NEE	GPP	Reco
Grassland Fluxes (gC.m^{-2})	-484	-1538	1054
Forest Fluxes (gC.m^{-2})	-549	-1639	1089

b.	aBP (gC.m^{-2})	aBPE
Grassland	400	0.25
Forest	652.27	0.39

In 2014, the grassland site presented a NEE of -484 gC.m^{-2} (storage in the ecosystem) corresponding to a Reco of 1054 gC.m^{-2} and a GPP of -1538 gC.m^{-2} (Table 4.3a). For the forest site, the NEE was larger (-549 gC.m^{-2}) corresponding to -1639 gC.m^{-2} and 1089 gC.m^{-2} for GPP and Reco.

4.4.2.2 Aboveground Biomass Production and Efficiency

The aboveground biomass production on the grassland in 2014 amounted to 400gC.m^{-2} (Table 4.3b) and to 652.27 gC.m^{-2} for the forest.

These productions represent respectively, 25% and 39% of the GPP, meaning that only these fractions of the carbon assimilated and stored was allocated to the aBP and then resulting in an efficiency of 0.25 for the grassland (Table 4.3b) and 0.39 for the forest.

4.4.3 Intra-annual variability

4.4.3.1 Flux

Reco fluctuated between $0.19\text{ gC.m}^{-2}.\text{d}^{-1}$ in December and $8.27\text{ gC.m}^{-2}.\text{d}^{-1}$ in July. During the year, Reco flux showed several peaks mainly linked to the air temperature increases, at least for the peak in beginning of April, beginning of June and around the 20 July and August (peak number 2, 3, 4, 5 and 6, corresponding to the peak mentioned previously in the meteorological part) (**Figure 4.3b**). The different technical management events are also chronologically classified for future flux interpretation. Peak one seems to happen right after fertilization, while peak 7 happens at the end of the pasture.

The GPP in absolute value increases in spring, with maximal values at the end of Mai ($-15\text{ gC.m}^{-2}.\text{d}^{-1}$), decreases at the beginning of June (corresponding to the mowing) with a minimal plateau and a regrowth during the summer, and finally falls in autumn/winter (after October; **Figure 4.3a**). The GPP decrease at the onset of June lasts for several days, making the NEE positive (source of CO_2) before it increases again (from -1 on the 30th of June to $-10\text{ gC.m}^{-2}.\text{d}^{-1}$ on the 14th of July). During this period, the precipitations were quite low with a ETR lower than the ETP (Figure 2c, 2d) all along the course of the year and considering the general trend, the GPP shows a number of fluctuations in addition to the June-July plateau. An April decline (number 1 on **Figure 4.3a**) matches with the incoming of the cattle in the subplot 2 of the grassland. A peak recorded in August (n°2; 09/08/2017) seems to correspond to a slight increase in the global radiation (**Figure 4.2a**) and a last peak at the beginning of September (n°3).

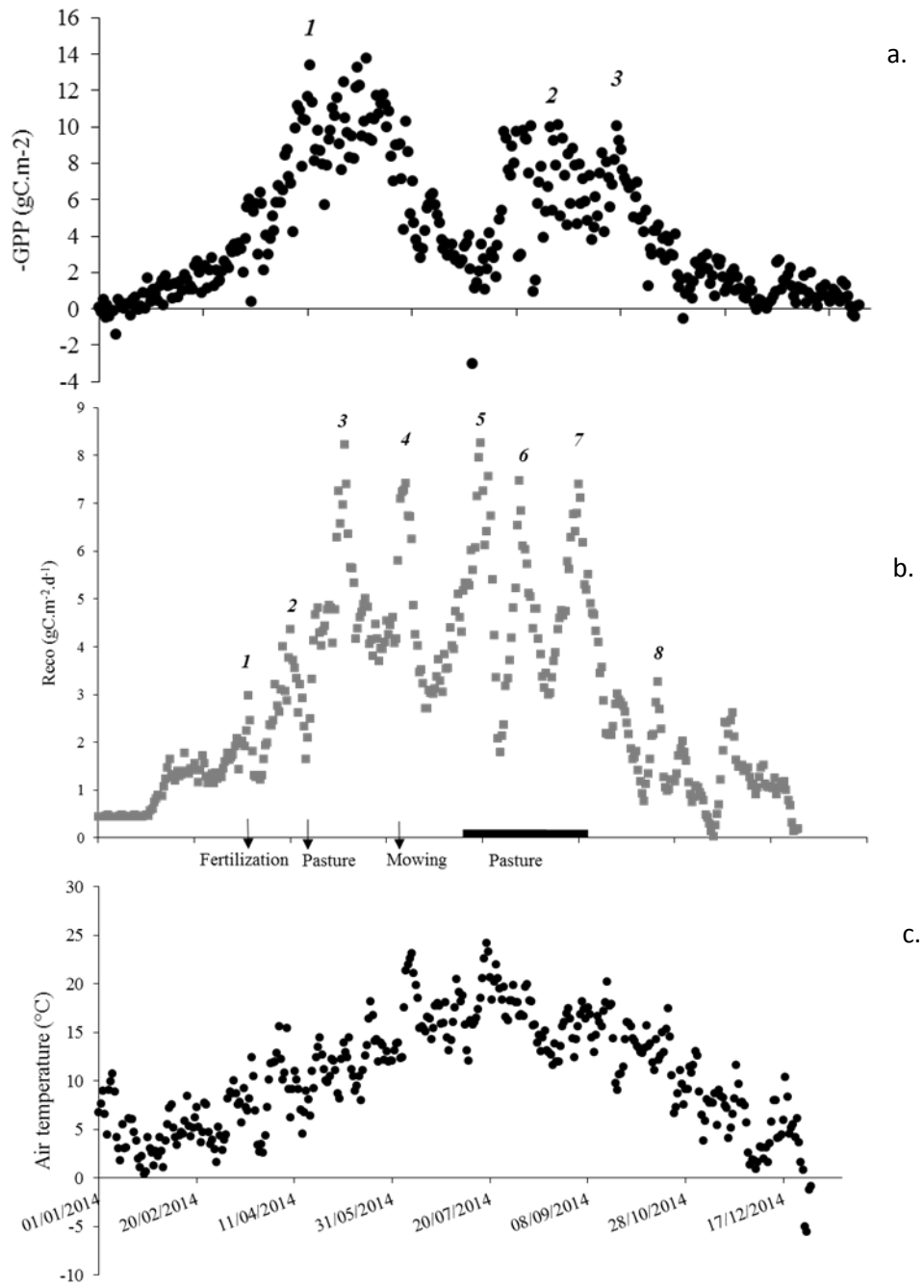


Figure 4.3 Daily evolution of absolute GPP ($\text{gC.m}^{-2}.\text{d}^{-1}$) (a), daily Reco ($\text{gC.m}^{-2}.\text{d}^{-1}$) (b) and the daily mean air temperature ($^{\circ}\text{C}$) (c). The Reco peaks are numbered and the technical management events are also mentioned.

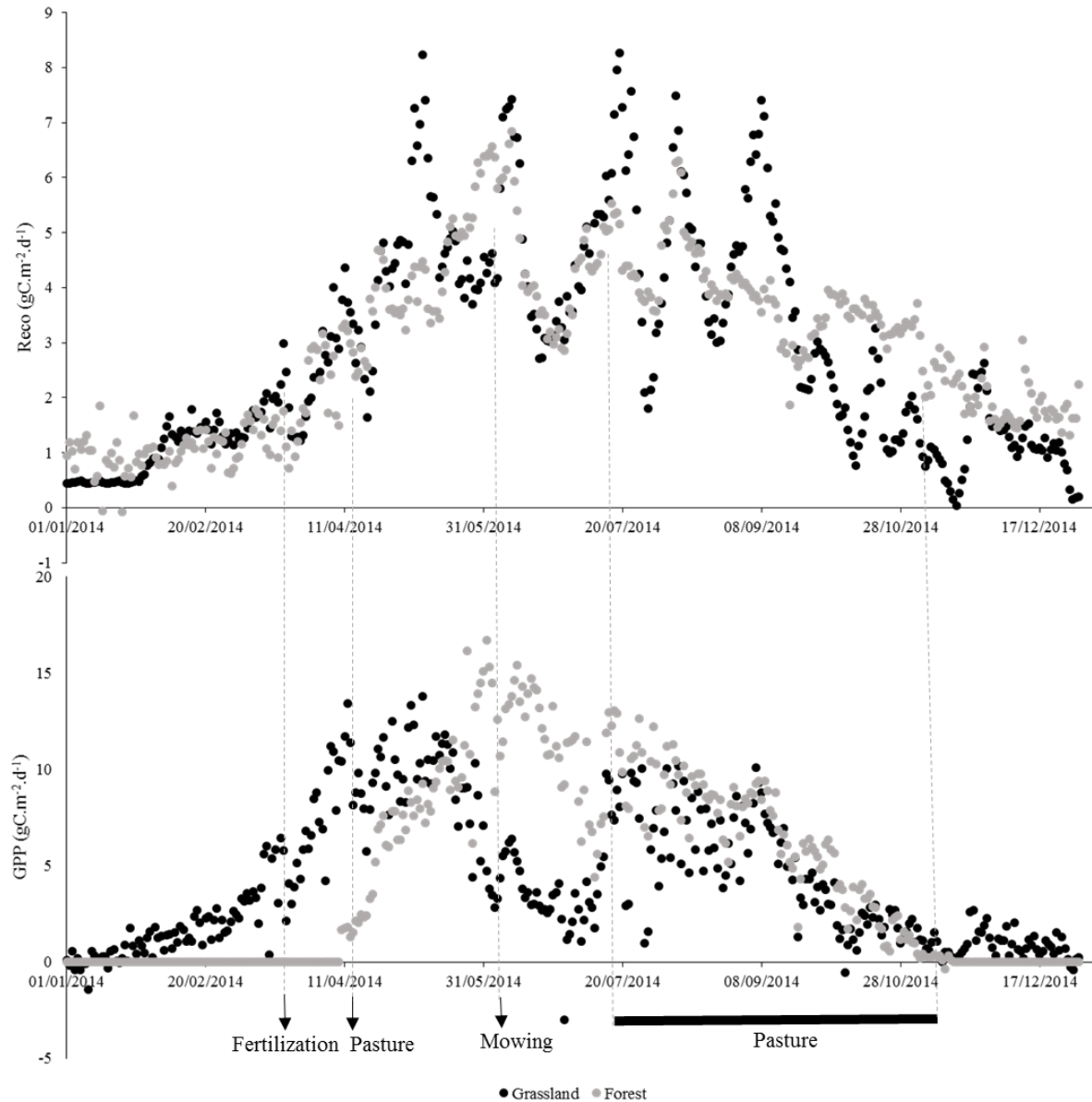


Figure 4.4 Evolution of the daily Reco (a) and absolute value of GPP (b) for the forest (grey dots) and grassland (black dots) sites.

The Reco evolution throughout the year shows higher variability in the grassland than in the forest (**Figure 4.4a**), with some peak happening simultaneously on both sites. Generally the peaking values in Reco seemed slightly higher for the Grassland than for the Forest with respectively top values of 8.3 $\text{gC.m}^{-2}.\text{d}^{-1}$ against 4.8 $\text{gC.m}^{-2}.\text{d}^{-1}$ in Mai, 8.4 $\text{gC.m}^{-2}.\text{d}^{-1}$ against 5.5 in July and finally 7.3 $\text{gC.m}^{-2}.\text{d}^{-1}$ against 4.2 $\text{gC.m}^{-2}.\text{d}^{-1}$ in September. After the end of September the Forest Reco values are generally higher than the Grassland ones until the end of the year.

The GPP started increasing already in February in the Grassland and only in April for the Forest, when leaves appeared (**Figure 4.4b**). While the forest GPP continued to increase and reached its maximum at the end of Mai (16.7 $\text{gC.m}^{-2}.\text{d}^{-1}$), the grassland one declines following the harvest in mid Mai. This last

rise at the end of July to reach the forest curve and then both GPP curves show relatively the same pattern and timing from the beginning of August.

4.4.3.2 Aboveground Biomass Production

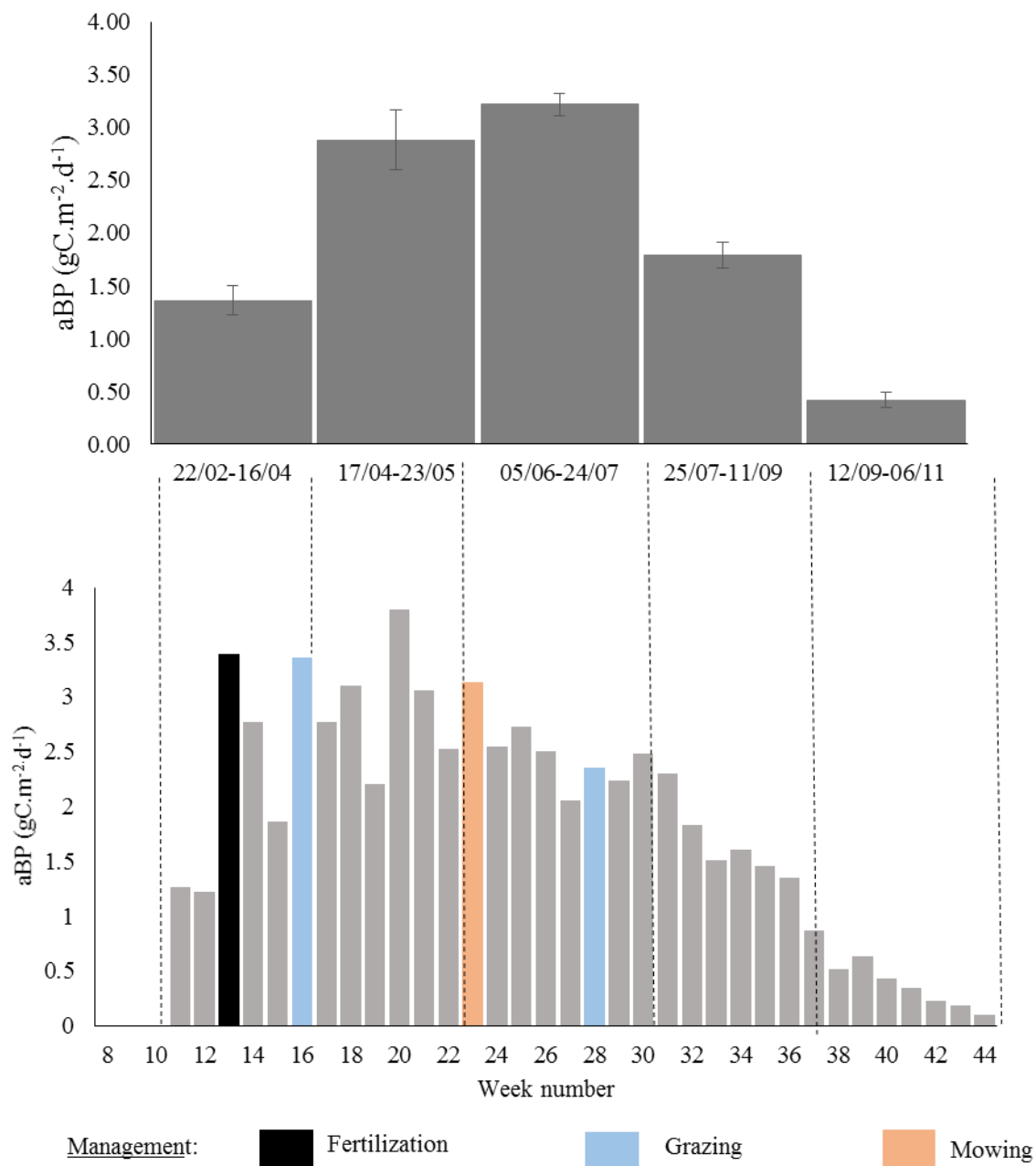


Figure 4.5 Evolution of the aboveground biomass production (aBP) in $\text{gC.m}^{-2}.\text{d}^{-1}$. Panel (a) shows the partial growing period values and panel (b) the weekly estimations.

The partial growing period aBP valued varied significantly throughout the year following a bell-shaped curve, from 1.4 $\text{gC.m}^{-2}.\text{d}^{-1}$ for the February-April period, to the highest value (3.2 $\text{gC.m}^{-2}.\text{d}^{-1}$) during the June-July period and back to a minimum of 0.4 $\text{gC.m}^{-2}.\text{d}^{-1}$ in the September-November period (**Figure**

4.5a). The weekly estimated values showed a less smooth pattern, with large fluctuations around the bell-shape curve starting with a value of 1.2 for week 11 (10th – 16th March) following by a general increase with large oscillations (peak at week 13) up to 3.8 gC.m⁻².d⁻¹ on week 20 (12th – 18th Mai) and then a decrease with some fluctuations until the lowest value reached on week 44 (27th October to 2nd November) (**Figure 4.5b**). The management practices are identified by colored bars on the figure 6b and happened during week 13 for the fertilization, weeks 16 and 28 for the entry of the animal on the different subplots, and on week 23 for the mowing. Each of the practice seems to correspond to a slight peak in aBP compare to the neighboring values.

No relationship was found between weekly aBP and the precipitation or the mean air temperature but with the global radiation. The best fit was obtained with a linear function ($R^2 = 0.52$, p-value<0.05).

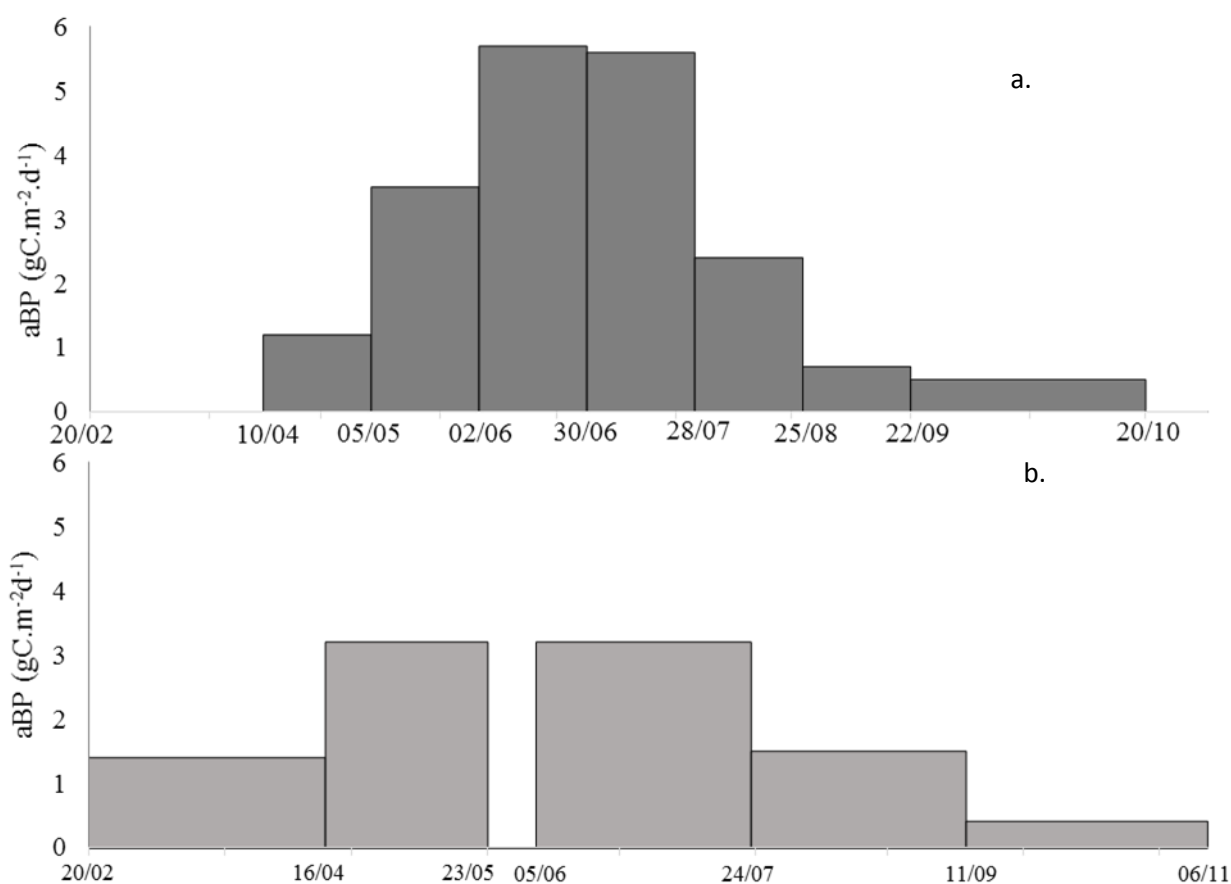


Figure 4.6 Evolution of the aBP deduced from sampling campaigns data for forest (a) or grassland (b), in gC.m⁻².d⁻¹.

The evolution of aBP for both sites presents the same overall shape (**Figure 4.6**) with broader amplitude for the forest. The maximum aBP is then more important for forest (6 gC.m⁻².d⁻¹ against 4 gC.m⁻².d⁻¹ for the grassland), but reached earlier in the grassland (Mai against June for the forest).

4.4.3.3 aBPE

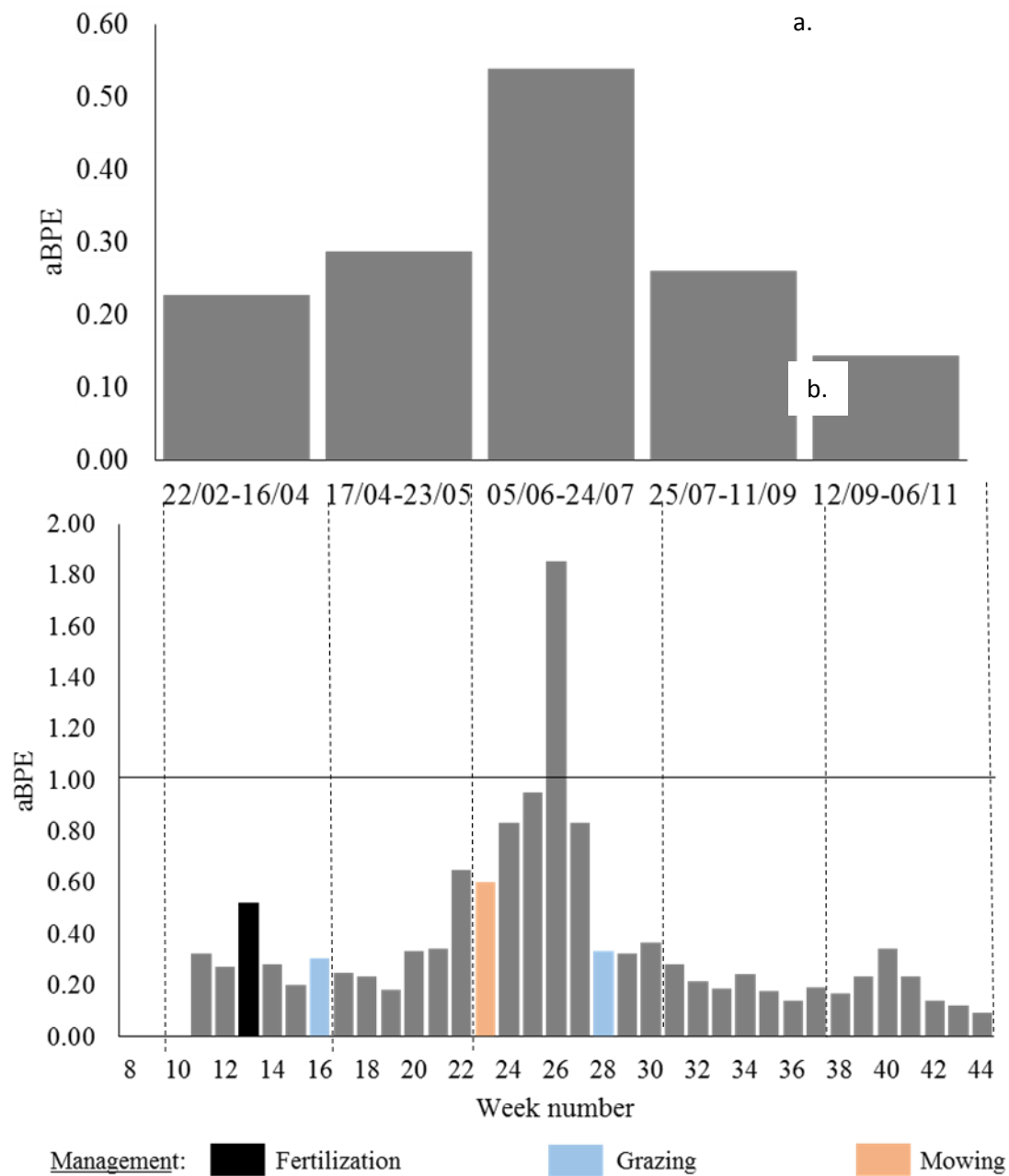


Figure 4.7 Evolution of the aboveground biomass production efficiency deduced from partial growing period data (a) and weekly estimations (b). The management practices are enlightened with the black, orange and blue bars corresponding respectively to fertilization, mowing and entry of the cattle on the different subplots.

The aBPE values compiled from partial growing period data are quite similar for the two first and the fourth periods (0.23, 0.3 and 0.28 for respectively the February-April, April-Mai and July-September periods; figure 8a). A peak (0.52) appears for the June to July period and the lowest value (0.12) occurs at the last period of the season. The weekly evolution is relatively similar presenting few weeks with high values (from week 22 to 27, 26 May to 6 July) surrounded by aBPE staying around the annual mean (between 0.18 and 0.34). There are few exceptions in this surrounding like the week 13 (24th-30th

March: **Figure 4.7b**, during the fertilization) having an aBPE of 0.52. The highest value (1.86) was reached at week 26 (23rd-29th June), three weeks after the mowing. This value higher than 1 is only possible if there are other sources of C outside of the one assimilated through photosynthesis. In general, the weeks can be divided into two groups, one corresponding to aBPE under 0.4 and the other with aBPE above 0.5. This classification presents a significant gap (0.1) between the two groups with the higher one that could be linked to the management practices (fertilization week and one the month after mowing).

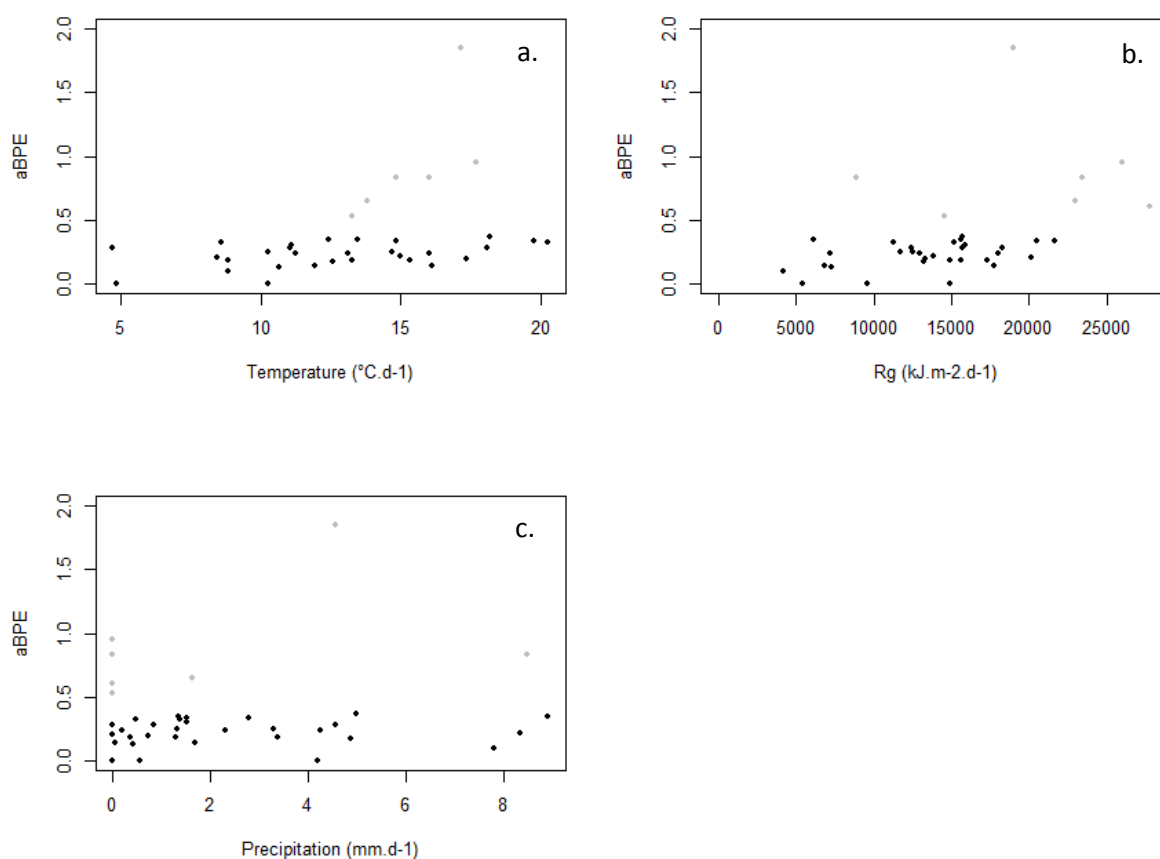


Figure 4.8 Relationship between weekly aBPE and different meteorological factors: air temperature in °C (a) , global radiation in kJ.m⁻².d⁻¹ (b) and precipitation in mm.d⁻¹ (c). The grey and black dots correspond respectively to the groups with aBPE above 0.5, and below 0.4.

As shown in **Figure 4.8**, there is little impact of meteorological factors (air temperature, global radiation or precipitation) on aBPE for the group with values <0.4, while for aBPE > 0.5 they seem to increase with increasing air temperature.

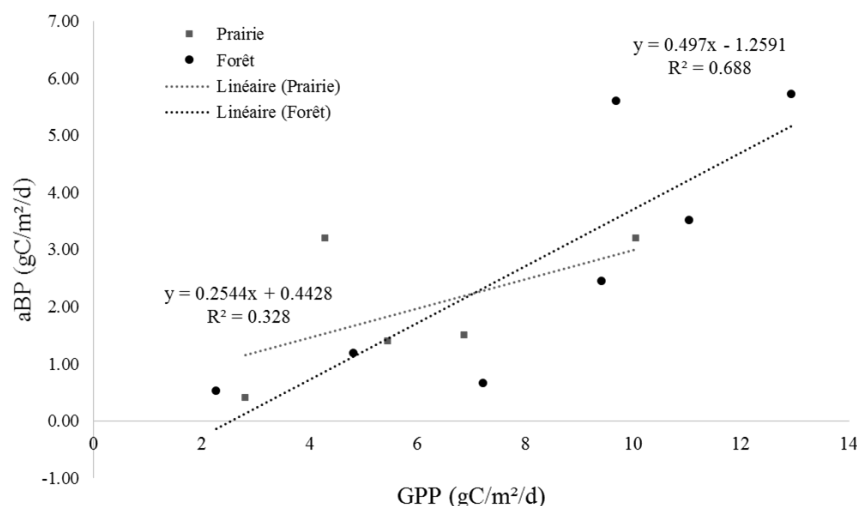


Figure 4.9 Linear relationship between aboveground biomass production and GPP, both in $\text{gC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ for the grassland (grey, $R^2 = 0.33$) and the forest (black, $R^2 = 0.69$).

The comparison of the forest and grassland aBPE can be performed through the temporal evolution and the linear relationships between aBP and GPP. For these lasts the slope represents the efficiency and the degree of correlation its temporal stability. **Figure 4.9** shows that the correlation and the slope are higher for the forest than for the grassland ($R^2=0.68$ and $R^2= 0.33$ respectively).

The evolution of the efficiencies for the two ecosystems presents the same dynamics, at the exception of the peak in April for the forest (**Figure 4.10**) corresponding to the remobilization of the carbon from the reserves for leaves formation. After the April period, the forest aBPE corresponds totally to wood growth efficiency. The maximum aBPE during the summer is a little bit higher for the grassland.

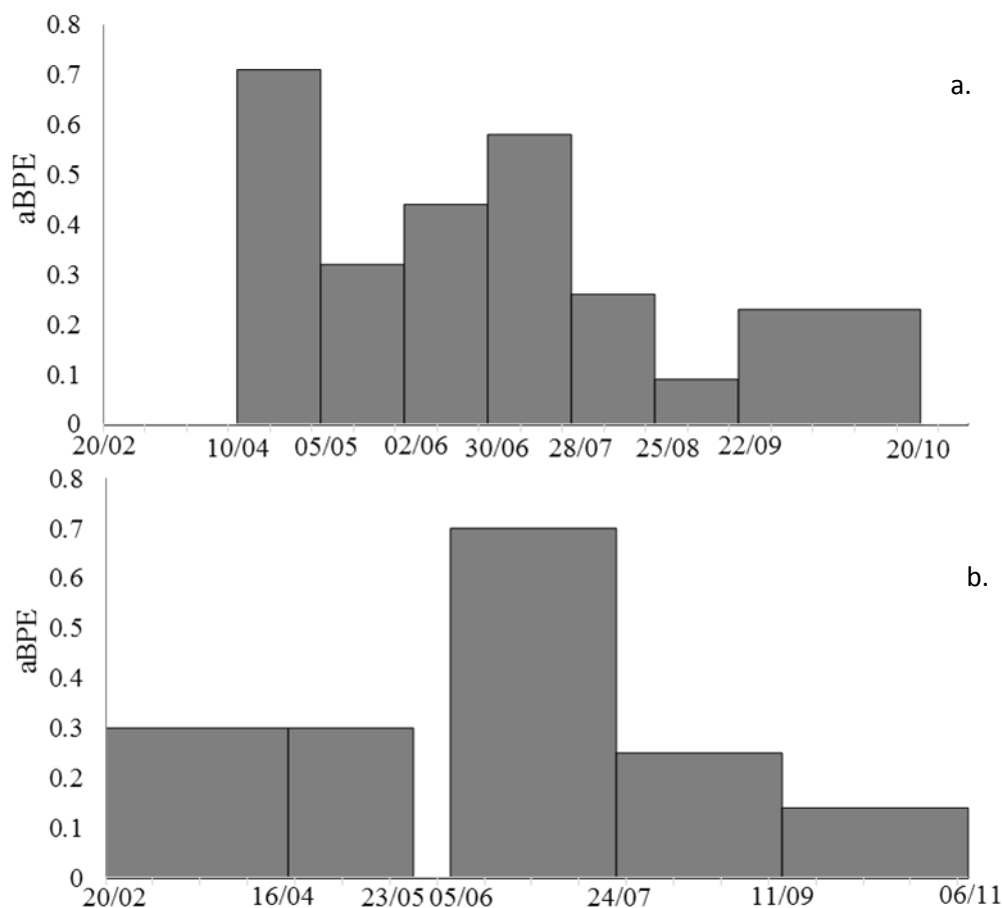


Figure 4.10 Evolution on the respective period of measurements of the aBPE for the forest (a) and the grassland (b).

4.5 Discussion

4.5.1 At Annual scale

4.5.1.1 Fluxes

The studied grassland site has acted as a sink of C for the year 2014 with a NEE of -484 gC.m^{-2} which is in the range of what can be found on similar ecosystems (temperate grassland with different management) from $+340$ to -2662 gC.m^{-2} (mean value $= -394 \pm 868 \text{ gC.m}^{-2}$; Novick et al. 2004; Ammann et al. 2007; Prescher et al. 2010; Zenone et al. 2013).

The GPP (-1538 gC.m^{-2}) was quite low compare to other studies (up to -4527 gC.m^{-2} ; mean value $= -1805 \pm 1240 \text{ gC.m}^{-2}$ (Ammann et al. 2007; Klumpp et al. 2007) as was Reco (1054 gC.m^{-2} compared to range from 266 gC.m^{-2} to 1736 gC.m^{-2} , mean value $= 1116 \pm 564 \text{ gC.m}^{-2}$) (Ammann et al. 2007; Byrne et al. 2007).

The fact that grassland and forest have relatively similar annual fluxes under comparable meteorological conditions is a first significant result. The forest is a very slightly better C sink than the grassland, as it is storing 549 gC.m^{-2} for the same year. The annual Reco is relatively similar for the two ecosystems

(1089 and 1054 gC.m⁻² for the forest and grassland) and in consequence, the annual GPP was slightly higher in the forest (-1639 gC.m⁻²) than in the grassland (-1538 gC.m⁻²).

4.5.1.2 *aBP*

The grassland aBP (400 gC.m⁻²) is in the range (335 to 644 gC.m⁻²; mean value= 464±130 gC.m⁻²) of what is found in literature for temperate grassland grazed by cows (Flanagan et al. 2002; Ammann et al. 2007; Byrne et al. 2007; Zenone et al. 2013).

It is lower compared to the 652.27 gC.m⁻² for the forest in 2014. This difference is not linked to climate as both sites are very close together. Even if the soil type from the grassland (calciisol) is slightly less fertile than the forest one (alocrisol), this property shouldn't disadvantage the growth of the grassland as the latter is fertilized manually. The quantity of C available for aBP doesn't seem a good explanation as the GPPs are relatively equivalent. The difference could simply arise from the nature of the cover type with their own physiology and C cycle processes.

4.5.1.3 *aBPE*

The annual aBPE (0.25) of our grassland site is higher compared to the two other ones presented for temperate grassland with similar management (0.16 to 0.23 (Ammann et al. 2007; Klumpp et al. 2007)). However, there are few values for comparison and the Osne aBPE remains close to the others. In fact, in view of the fluxes, aBP and aBPE results. In Ammann et al. (2007), the aBP (401 gC.m⁻²) is similar but the GPP (-2056 gC.m⁻²) is slightly inferior, in Klumpp et al. (2007) both GPP and aBP were higher (-4527 and 1049 gC.m⁻² respectively). The Osne grassland seems to be representative of a typical European temperate grassland with management based on both grazing and mowing.

The efficiency is lower in the grassland than in the forest (0.25 vs. 0.39). The forest stores the C more efficiently in its above ground biomass than the grassland when the GPP was relatively similar for both ecosystems with forest GPP having only few percent more (6%). The only significant difference was in the aBP (50% more for the forest). There is clearly a large difference in the C allocation factor to the aboveground biomass with forest making the choice to foster the development and storage in trunk and leaves compared to grassland. If we assume a relatively small contribution of the mycorrhizal fungi productions, root exudates, and volatile organic compounds emissions to our ecosystem C cycles, this induces a larger C storage in the belowground for the grassland. This behavior is coherent with Schuman et al. (1999) who found an increase of soil C in grazed pasture either through the direct transfer of assimilated C to the roots or by C incorporated into the soil thanks to the physical impact of the cows weight, breaking the leaves when walking and inserting that into the soil. Peichl et al. (2012) also found that for newly afforested former grassland, the belowground biomass was half the one of a nearby grassland after 5 years, whereas the aboveground biomass was superior. The soundness of our reasoning

can only be tested by field campaign measurements with soil organic matter sampling and technic like ingrowth cores or rhizotron with camera and scanner.

The storage of C in wood biomass, where it can stay beyond 100 years depending of the management practice, is also more durable than the storage into grasses where it stays only until it is digested (following grazing or harvest) or decomposed (few months). The strategy consisting in a reduction of the allocation to aerial components for the grassland comparing to forest seems to be in an optic of long term C storage, a more suitable mitigation purpose.

4.5.2 Intra-annual

4.5.2.1 Fluxes

The Reco of the grassland is quite variable during the year and is mainly link to climate (temperature, peaks number 2, 3, 4, 5 and 6 on Figure 3b) but also slightly by management (mostly by pasture as the cattle respiration might also be measured at the EC mast, peak 1 and 5 mainly on figure 3b). Those impacts were also assessed for alpine grasslands (Zeeman et al. 2010).

Due to these impacts of the management practices, Reco is more variable in the grassland during 2014 than in the forest. The amplitude of the peaks in grassland Reco is also more important than for forest. This shows a higher sensibility of Reco to climate and perturbations for grassland perhaps coming from the soil respiration, as the C is mainly allocated and present in the belowground component.

As expected, GPP was correlated to global radiation and impacted by the mowing (Novick et al. 2004; Prescher et al. 2010). The GPP after the mowing was really low for around one month, which is unusual. (Jaksic et al. 2006) report an impact of about 2 weeks after harvest on fluxes when global radiation was at its highest point. The long time needed to recover here could have been linked to a low water deficit ($ETR < ETP$, Fig 1c&d) at the same period.

The GPP on both sites has a similar range, and the main difference in the dynamics is linked to the harvest on the grassland. The photosynthesis is also starting earlier for the grassland (end of February) than in the forest (beginning of April) as the tree leaves only started to grow at the end of March. The loss of GPP due to mowing is nearly compensated by the lengthening of the growing season.

4.5.2.2 aBP

Global radiation is the main driver of the aBP variability explaining 52% of it. There is a higher aBP value during the week when the fertilization took place comparing to the surrounding. This reflects the combination of weekly aBP partitioning inside a partial growing period using the temperature relationship (Eq.1) and the fertilizer application performed during the hottest week of the period by the farmer. This explanation is still valid to illustrate the higher aBP during the harvest week compared to the following ones belonging to the same partial growing period. The grazing effect can't be estimated in our study as exclusion cages were used to avoid the impact of the animal on the aBP.

The evolution of aBP throughout the year was similar on both sites but the grassland aBP variation showed a lower amplitude than the forest one (approximately half lower, Fig 7). There was also a weaker link between GPP and aBP (fig 10) in the grassland that could be explained by the interferences of the management.

4.5.2.3 aBPE

The grassland weekly aBPE is rather stable throughout the year with a few peaking values. The highest one happening on week 26 being superior to 1 (1.86) implies that not only the C uptaken through GPP was used but also C coming from another source (probably remobilization of roots or leaves reserves). This value corresponds to a GPP at its lowest value (between 3 and 2.2 $\text{gC.m}^{-2}.\text{d}^{-1}$ in absolute value) but an aBP ($2.5\text{gC.m}^{-2}.\text{d}^{-1}$) relatively similar to the surrounding weeks.

The variation in aBPE doesn't seem related to any climatic factor but more dependent on the management technical event. The fertilization seems to have an immediate (and short) impact on the efficiency (increase), whereas the mowing seems to have higher and longer one (increase too). This last impact is difficult to quantify as the efficiency is already above 0.5 a week before the site was mowed. The fluxes seem to be the main responsible for the higher values of aBPE after mowing, as the aBP is quite stable during this period. In opposition, the aBP seems responsible for the fertilization impact.

The aBPE from both sites varies within the same range (0.1 to 0.7 throughout the year). The first main difference was the April period when the forest presents a higher aBPE (0.7) compared to the grassland (0.3). This is completely explained by the budburst happened and the used of the C reserve of the beech to produce some biomass. In these conditions, the ratio aBP/GPP doesn't represent the allocation of the GPP to the biomass production because of the existence of another C source. The aBPE was also more temporally variable in the forest than in the grassland (at the exception of the peak in June/July following the harvest). This could be explained by the greater influence of climatic factors on the aBPE in the forest compared to the latter seeming more impacted by management. This interpretation should be temperate by the fact that temporal resolution is lower in the grassland data. A new experiment with an increase of this resolution could improve the precision on this analysis.

The aBPE of the grassland showed a stronger correlation ($R^2=0.74$) to the GPP than for the forest one ($R^2=0.56$) (data not shown), this could be explained by a relative saturation of the aBP in the grassland, with a more stable value during the year even if growing conditions are less advantageous.

4.6 Conclusion

Both our study sites acted as a C sink for the year 2014, with the forest storing more C than the grassland. The C fixation is also more important in the aboveground biomass in forest compared to grassland. In terms of mitigation, the forest is more efficient as more C is stored in component more sustainable when only aBP is taken into account. The same kind of analyses should be performed on belowground BP to complete our results or perhaps to inverse this conclusion. Indeed, several studies showed that the grassland were storing up to the same amount (or more) of C in their belowground biomass than in their aBP (Hungate et al. 1997; Schuman et al. 1999; Peichl et al. 2012). Schuman et al. (1999) found that for grassland less than 10% of the C was found in the aBP and around 90% was in the roots whereas trees generally allocate around only 1/3rd of the C to the roots (Cairns et al. 1997).

We found that aBPE in the grassland is mainly impacted by management (mainly fertilization) whereas the forest seems more influenced by climate. It would be interesting to study the evolution of aBPE under different management practices for grassland (intensivity, type of cattle, not grazed...) and for forests (more intensive thinning) to disentangle the effect of anthropogenic action and climate on the efficiency. This could bring information about when the management impact overshadows the climatic/phenologic one.

This study also allowed to show the limit of the use of aBPE as an indicator of uptaken C storage, as the C don't forcefully come from the GPP but from C stored previously. The experiment that could respond to the C origin and to the influence of climatic factor should be made in a controlled environment, with labeling, in order to assess properly which part of the C used to build biomass comes from the actual GPP.

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Chapitre 5 Discussion générale

5.1 Rappel

L'objectif principal de la thèse était d'étudier la dynamique saisonnière de l'allocation du C atmosphérique assimilé au sein de la biomasse aérienne des plantes d'une forêt, et d'une prairie, permettant ainsi une comparaison des deux écosystèmes terrestres représentant plus de 60% de la surface du territoire mondiale.

Dans un premier temps nous avons mis en évidence que la production de biomasse aérienne ainsi que de son efficience présente une variabilité saisonnière significative pour une hêtraie tempérée en Lorraine (Montiers-sur-Saulx). Nous avons ensuite affiné le schéma d'allocation du C au sein de la biomasse aérienne en quantifiant les productions et efficacités pour le C structural (SC comprenant l'hémicellulose, la cellulose et la lignine) et pour le C non-structural (amidon, sucre soluble,...) à l'échelle mensuelle. Nous avons, pour finir, étudié, toujours pour la même année, la variabilité saisonnière de l'aBP et de l'aBPE d'une prairie (Osne-le-Val) placée dans les mêmes conditions pédoclimatiques que la hêtraie, ce qui nous a permis d'effectuer une comparaison entre écosystèmes des comportements et des influences vis-à-vis des facteurs abiotiques.

5.2 Bilan carbone de la hêtraie de Montiers-sur-Saulx

5.2.1 Bilan annuel 2014

Pour l'année 2014, qui était une sans conditions extrêmes, le site forestier est un puit de carbone ($549 \text{ g m}^{-2} \text{ y}^{-1}$) relativement important pour une hêtraie comparée à des écosystèmes similaires. Cela est liée principalement à une GPP plus élevée que la moyenne (Valentini et al. 1996; Malhi et al. 1999; Granier et al. 2000, 2008) Le LAI particulièrement important (proche de 9) du couvert forestier est probablement une des causes de ce comportement mais la provenance de cette abondance foliaire reste incertaine et vraisemblablement partagée entre les effets de la gestion sylvicole, le climat et la fertilité du sol en lien avec l'espèce.

Assez logiquement, cela entraîne une production de biomasse aérienne totale plus élevée que pour la majorité des forêts étudiés, quel que soit le sol (Valentini et al. 1996; Knohl et al. 2003; Curtis et al. 2005; Granier et al. 2008; Vicca et al. 2012; Wu et al. 2013). Par contre, les productions en hémicelluloses trouvés en 2014 pour notre forêt sont semblables à celles trouvées dans la littérature (Hoch 2007; Schädel 2009) et il semble y avoir une production plus faible en cellulose et lignines que normalement attendu bien que le ratio de concentration d'hémicellulose par rapport à cellulose et lignines soit similaire à ce qui a été trouvé par Schädel et al. (2010). La hêtraie de Montiers-sur-Saulx semble plutôt investir le carbone assimilé dans une production de NSC important (Haigler et al. 2001; Boerjan et al. 2003; Hoch et al. 2003). Il est vrai qu'au vu de la quantité importante de feuille à produire au printemps suivant (LAI entre 8 et 9), la mise en réserve doit être conséquente. Plus de données seraient nécessaire pour mieux comprendre cette singularité.

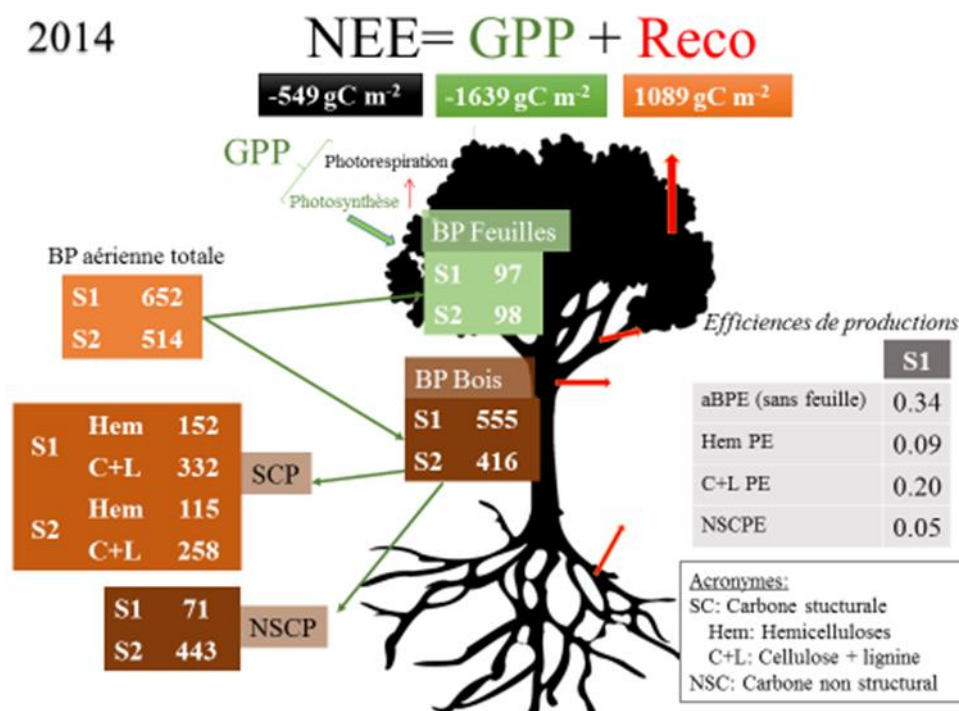


Figure 5.1 Synthèse des différents résultats trouvés sur la forêt pour l'année 2014 et décrits dans les chapitres 2 et 3. Les productions ainsi que les flux sont en $\text{gC.m}^{-2}.\text{an}^{-1}$.

L'aBPE de notre site (0.34) est également plus élevée que la moyenne (0.22 ± 0.12 ; Ryan et al. 1995; Valentini et al. 1996; Granier et al. 2000; Barford et al. 2001; Curtis et al. 2005; Vicca et al. 2012; Wu et al. 2013) ce qui dénote une tendance à soit réduire l'engagement des ressources vers la respiration autotrophe, l'exsudation ou l'émission de composé volatile, soit privilégier le compartiment aérien par rapport au souterrain. La forte anthropisation de la hêtraie de Montier-sur-Saulx pour un site forestier, avec des éclaircies assez massives, semble atteindre son objectif de maximiser la formation de matériaux exploitable économiquement. Une étude complète regroupant des mesures des croissances des différents compartiments sur les sites de tour à flux pourrait nous éclairer sur les déterminants qui régulent ce genre de choix stratégiques d'allocation. Il faut noter aussi une étonnante grande proportion du carbone consacré à la biomasse dirigé annuellement vers sa composante structurale soit 85%, les 15% restant étant alloué au CNS.

5.2.2 Variabilité intra-annuelle pour 2014

Nos résultats soulignent et quantifient l'importance primordiale de prendre en compte la densité du bois dans l'analyse de l'évolution intra-annuel de l'aBP, ce qui avait déjà été mis en évidence par Delpierre et al. (2016), confirmant également notre **Hypothèse 1.1**. En effet, les équations allométriques (utilisées pour calculer l'évolution de biomasse intra-annuelle) sont fréquemment ajustées sur une coupe ayant lieu en fin de croissance, à une période où la densité est maximale, alors que la densité varie énormément au cours de l'année (Rathgeber et al. 2016). Leur adoption pour calculer les biomasses intra-annuelles

amène donc des surestimations conséquentes et masquer la variabilité saisonnière. Nous avons trouvé dans notre étude une surestimation mensuelle pouvant aller de 4 à plus de 50% pour l'aBP

Une forte variabilité en termes d'aBP a été observée pendant l'année d'étude (**Chapitre 2**), les productions passant du simple au quadruple entre le début de la saison de croissance et le maximum de croissance quel que soit le sol étudié en accord avec notre **Hypothèse 1.2**. Les impacts d'événements climatiques extrêmes auront donc des effets très différents sur la croissance suivant la période à laquelle ils arrivent avec les mois de juin et juillet représentant la période la plus sensible. La variabilité en termes de production des composés structuraux est encore plus importante (**Chapitre 3**). En effet, la dynamique est semblable à celle de l'aBP mais avec une production de cellulose et lignines qui est multipliée par 6 et celle d'hémicellulose par 8. Par contre, la variabilité de la production en carbone non structural est beaucoup plus faible (notamment pour l'alocrisol), commençant avec une forte valeur en avril qui reste relativement stable jusqu'en juillet avant de diminuer. Ces résultats viennent ainsi confirmer notre **Hypothèse 2**. Cette faible variabilité implique que la mise en réserve du carbone, et par conséquent le redémarrage de la saison suivante, est moins susceptible d'être vulnérable vis-à-vis de l'occurrence d'un événement perturbateur qui arriverait dans un moment de forte allocation.

Une différence a également été mise en évidence entre les aBP des deux types de sol présents sur le site, L'aBP de l'alocrisol est à tout moment supérieure à celle du calci-brunisol. Nous avons mis en évidence que cette différence semblait être liée, en termes instantanés, à la composition des sites. L'alocrisol a plus d'arbres de classes dominante et co-dominante, classes qui ont des croissances élevées, que le calci-brunisol. Ce point mériterait plus d'attention pour déterminer d'où provient cette différence de répartition entre classe de dominance sur les 2 sols gérer de façon similaire et soumis aux mêmes conditions météorologiques.

En termes d'efficacités de la production de la biomasse aérienne par rapport au carbone assimilé, on retrouve également une forte variabilité au cours de l'année. Cette évolution possède une phénologie qui suit une courbe en forme de cloche avec un maximum en juillet. Nous ne pouvons pas mettre en évidence autre chose qu'une covariance temporelle avec d'autres facteurs (rayonnement, température) qui ont typiquement la même dynamique phénologique.

Peu d'études ont effectué des suivis intra-annuels sur les efficacités de production des composés carbonés spécifiques. Leur variabilité ne semble pas être liée à un facteur environnemental mais plutôt à la xylogénèse, avec une augmentation de la part allouée aux carbone structural qui correspond à la période de formation des parois puis à leur lignifications (Cuny and Rathgeber 2014; Rathgeber et al. 2016).

5.3 Bilan carbone de la prairie d'Osne-le-Val (Chapitre 4)

5.3.1 Bilan annuel 2014

Le site prairial semble avoir un comportement tout à fait représentatif des écosystèmes similaires en ce qui concernent les flux de carbone que ce soit au niveau du CO₂ (Novick et al. 2004; Ammann et al. 2007; Prescher et al. 2010; Zenone et al. 2013), ou de la production de biomasse aérienne (Flanagan et al. 2002; Ammann et al. 2007; Byrne et al. 2007; Zenone et al. 2013).

En revanche l'efficacité de cette production est légèrement plus forte que sur d'autres prairies tempérées ayant une gestion similaire (Ammann et al. 2007; Klumpp et al. 2007). Là encore plusieurs raisons peuvent être invoquées mais la possibilité d'une allocation plus faible vers le compartiment souterrain paraît la plus plausible et pourrait être testée avec des techniques telles que les carottes de croissances.

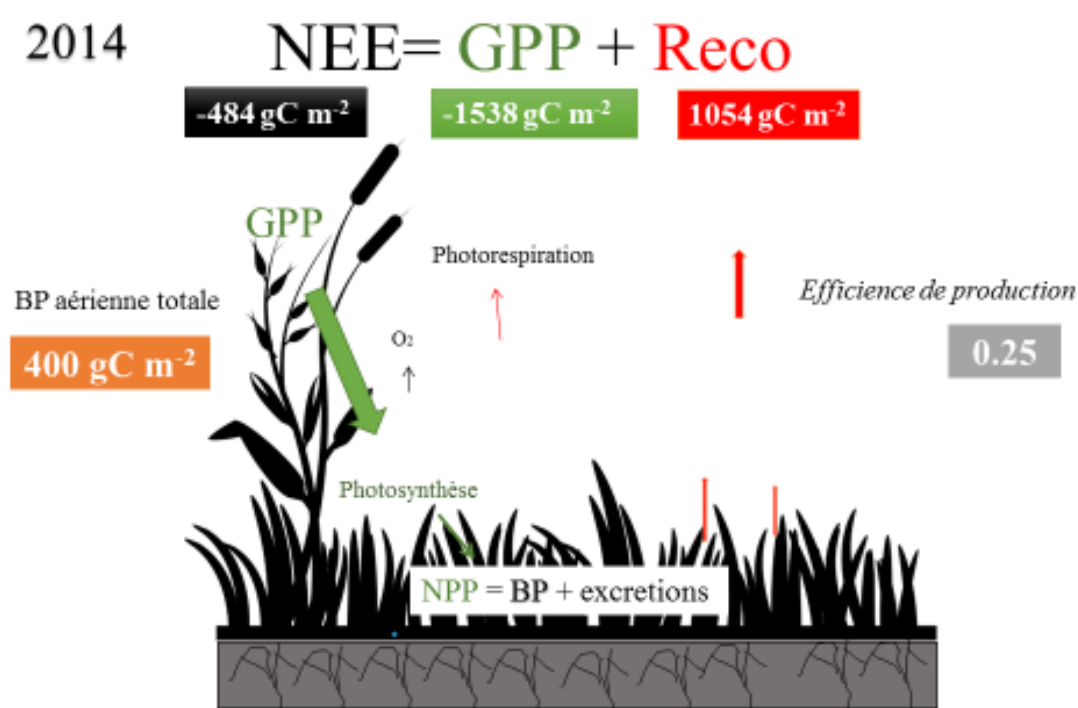


Figure 5.2 Synthèse des différents résultats trouvés sur la prairie pour l'année 2014 et décrits dans le chapitre 4. Les productions ainsi que les flux sont en $\text{gC.m}^{-2}.\text{an}^{-1}$.

5.3.2 Variabilité intra-annuelle pour 2014

L'aBP possède une tendance générale (large amplitude de variation du simple au triple) qui est principalement expliquée par le rayonnement global ($R^2=0.52$). En, plus de cette tendance, des fluctuations de production plus brusques semblent être dues aux interventions techniques liées à la gestion, notamment la fertilisation ainsi que la fauche qui stimule la production.

L'efficacité de l'aBP présente une nette augmentation au début de l'été juste après la fauche. Il apparaît donc qu'après des interventions anthropométriques, l'allocation du carbone soit plutôt dirigée vers la

production de la partie herbeuse aérienne pour revenir vers une situation qui permette de nouveau une assimilation importante. Cette constatation doit être confirmée avec des données à plus haute fréquence.

5.4 Comparaison entre les écosystèmes forestier et prairial (Chapitre 4)

5.4.1 Valeurs annuelles

La forêt et la prairie présentent des flux assez similaires pour l'année 2014 pour des conditions climatiques similaires. La forêt est quand même un puit de C légèrement supérieur, lié à un GPP plus importante probablement à cause de la fauche qui réduit ce flux sur une période significative. Cela implique aussi une production de biomasse aérienne plus importante en forêt qu'en prairie (un tiers en plus).

De même, l'efficacité est également beaucoup plus faible en prairie qu'en forêt (environ la même proportion que pour l'aBP). Il existe donc une forte différence dans le pourcentage d'allocation du carbone vers la biomasse aérienne qui est bien plus importante en forêt par rapport à la prairie. L'allocation à la biomasse souterraine pourrait par conséquent être plus importante en prairie ce qui serait cohérent avec l'étude de (Schuman et al. 1999). Le fait de devoir construire une structure ligneuse nécessite probablement une quantité et un pourcentage plus important qui n'est pas compensée par le fait de devoir reconstruire totalement sa composante après la fauche.

Des études supplémentaires sont nécessaires pour tester cette hypothèse précisément.

Il est possible de faire une estimation du stockage à moyen terme en prairie et en forêt. En ôtant de la valeur de GPP (C prélevé depuis l'atmosphère) la Reco (C relâché dans l'atmosphère par les plantes et micro-organismes), on obtient le C stocké effectivement dans les plantes (aérien et souterrain). Cette valeur vaut 550gC.m^{-2} en forêt, en prairie il est nécessaire d'ôter en plus l'aBP (stockage à court terme) pour obtenir une valeur pouvant être comparée. La valeur obtenue est de 84gC.m^{-2} , 6 fois moins environ qu'en forêt. La forêt semble donc être un écosystème plus intéressant pour le stockage de C à moyen terme.

5.4.2 Comportement intra-annuel

La GPP présente des évolutions et des ordres de grandeurs relativement proches sur les 2 sites à l'exception d'une chute de sa valeur après la fauche. La photosynthèse débute environ un mois plus tôt en prairie qu'en forêt. Il est étonnant de voir que malgré les grandes différences structurelles ce sont des éléments anthropiques et phénologiques qui impliquent les différences.

L'évolution de l'aBP est similaire pour les 2 sites, mais les amplitudes de variations sont plus faibles en valeur absolue pour la prairie que pour la forêt, ce qui peut être lié au fait que la biomasse présente en début d'année est plus grande en forêt. Les variations de l'aBP en valeur relative n'est par conséquent pas si différentes pour les deux écosystèmes.

L'efficacité varie entre les mêmes bornes quel que soit l'écosystème, mais il existe des fluctuations bien différentes en forêt et en prairie. Les différences sont expliquées par leur origine liée à une certaine phénologie en forêt alors que les principales variations d'efficacité en prairie sont liées aux opérations de gestion (fauche).

De ce fait, la variabilité de l'aBPE en forêt semble plutôt liée au climat alors que celle de la prairie semble plutôt être liée aux interventions anthropogéniques, allant dans le sens de notre **Hypothèse 3**.

5.4.3 Incertitudes de calcul

Il est important de rappeler qu'il existe des incertitudes liées aux estimations de l'aBP en forêt notamment. En effet, les valeurs obtenues peuvent présenter une erreur pouvant aller jusqu'à 15% en considérant les erreurs liés aux différentes corrections utilisées (extrapolation de la croissance en diamètre, concentration en C du bois, densité).

Pour le calcul de la GPP des erreurs ont également pu apparaître lors du calcul de la Reco de jour et du gapfilling, mais ces erreurs sont difficiles à estimer précisément.

5.5 Conclusion générale et ouverture

En regardant nos résultats pour chacun des écosystèmes étudiés de façons brutes (c'est-à-dire en n'utilisant que les valeurs, sans prendre en considération l'environnement global), la forêt est bien plus efficace que la prairie pour stocker le C dans sa biomasse aérienne. Le stockage dans le bois a également une durée de vie bien plus importante que celui dans les plantes herbacées. La forêt a alors une importance et une utilité toute trouvée dans la politique mise en place actuellement de mitigation des causes du changement climatique.

Comme déjà discuté plus haut, notre étude ne permet pas d'indiquer avec certitude que le C stocké dans la biomasse aérienne provient à 100% du C qui a été prélevé par les plantes depuis l'atmosphère pour l'année 2014. Et il est faut donc rester prudent dans les conclusions.

Une autre incertitude est liée à l'absence de données sur le C stocké dans la partie souterraine des écosystèmes et émis dans les exsudats ou composés complexes, qui pourraient éventuellement contredire nos résultats.

Mais est-il réellement possible d'affirmer qu'un type d'écosystème est plus efficient dans le stockage à long terme du C atmosphérique qu'un autre et de comparer ? Il faut relativiser ce résultat car une grande partie du stockage du C à très long terme se fait dans le sol dans des structures stables et pas uniquement dans les parties aériennes. De plus la mitigation de l'effet de serre lié à ce stockage de C n'est pas le seul service écosystémique et une étude globale du rôle des écosystèmes doit prendre en considération les apports spécifiques de chacun d'eux comme leurs apports socio-économiques leur contribution à la biodiversité végétale, bactérienne ou mycorhizienne, leur participation à la production et à la qualité de

l'eau. Rien qu'en considérant l'aspect financier, alors que notre forêt est gérée pour la production de bois de chauffage principalement, la prairie elle permet à la fois de produire du fourrage sec et frais pour des animaux destinés à la consommation humaine.

Si de notre point de vue, la forêt est plus efficiente dans la mitigation des effets du changement climatique, il serait aberrant de transformer les prairies en forêt.

Un dernier point est que cette étude ne concerne qu'un seul type de forêt et qu'un seul type de prairie, soumise à un type de gestion et sous un climat donné, et ne permet en rien de généraliser sur l'ensemble des écosystèmes prairiaux et forestiers.

Il serait intéressant d'étudier l'évolution de la production de biomasse racinaire intra-annuelle en prairie et en forêt, présentant des gestions et des espèces différentes, ainsi que la mise en réserve du C et l'utilisation que les plantes en font pour obtenir un bilan plus précis.

Une autre information qu'il est possible de retirer de cette étude est qu'une modification de la gestion pourrait entraîner un changement dans l'allocation et le stockage du C, par exemple des fauches trop répétées peuvent appauvrir le sol et entraîner une diminution de la biomasse sur le terrain en plus de diminuer la qualité du fourrage.

Et pour finir pour un stockage durable du C, l'utilisation du bois devrait être privilégiée en construction (meuble ou charpente).

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Résumé

L'étude du cycle du carbone (C) dans les écosystèmes terrestres (forêt, prairie) est fondamentale afin de comprendre leur fonctionnement, leur rôle dans le cycle du carbone ainsi que les répercussions du changement climatique sur ces écosystèmes. L'objectif général de la thèse qui est de faire un suivi intra-annuel de l'allocation du C au sein de différents écosystème terrestre (forêt et prairie), se place dans ce contexte.

Il s'agit dans un premier temps d'obtenir des efficacités de production de biomasse aérienne (aBPE, rapport entre les quantités de carbone stockées dans la biomasse aérienne et absorbées) pour des intervalles de temps réduits, du mois à la semaine selon l'écosystème (forêt et prairie, respectivement). Dans un second temps, une estimation plus précise de l'allocation du carbone en forêt a été effectuée, en suivant la formation de certains composés structuraux (hémicelluloses et cellulose+lignine). Un possible lien entre la variation de cette allocation selon les conditions climatiques a été étudiée. Les efficacités correspondantes ont également été calculées mensuellement pour avoir une idée plus précise du stockage durable du C dans cet écosystème. Une comparaison avec la prairie a été réalisée en termes d'aBPE afin d'analyser les capacités respectives des 2 écosystèmes à s'adapter aux changements climatiques et à jouer un rôle dans la mitigation des gaz à effet de serre.

Dans le cadre de l'Observatoire Pérenne de l'Environnement (OPE), deux écosystèmes voisins situés à Montier-sur-Saulx et Osne-le-Val ont été instrumentés dans le but de mesurer en continu les échanges de CO₂ à l'interface couvert-atmosphère, ainsi que les conditions micrométéorologiques dans lesquelles ces échanges se produisent. De plus, un suivi régulier du développement des écosystèmes (biomasse, surface foliaire, état de sénescence) a également été réalisé

Abstract

The study of the carbon (C) cycle is important in terrestrial ecosystems (forest, grassland) in order to understand their behavior, their role in the C cycle and also the impact of climate change on them. The general study of this thesis which is to monitor the intra-annual allocation of C into different terrestrial ecosystem (forest and grassland), lays within this context.

Firstly we calculated aboveground biomass production efficiencies (aBPE, ratio between the quantity of C stored into the aboveground biomass and absorbed) intra-annually, weekly or monthly depending on the ecosystem (grassland and forest respectively). Secondly a more precise assessment of the C allocation in forest was made by analyzing the formation of structural C compounds (hemicelluloses and cellulose + lignins). A possible link between the variability of these allocations and climate was studied. The corresponding efficiencies were then calculated monthly in order to have a better idea of the sustainable C storage in this ecosystem. A comparison with a grassland in term of aBPE was then realized in order to analyze the adaptation capacity of each ecosystem to climate change and to play a role in the mitigation of GHG.

Two neighboring ecosystems located in Montiers-sur-Saulx and Osne-le-Val were equipped, as part of the Observatoire Pérenne de l'Environnement (OPE), to measure continuously the CO₂ exchange between land cover and atmosphere and the micrometeorological conditions in which these exchanges happen. A regular monitoring of those ecosystems development (biomass, leaves area, senescence) was also made.