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PhD Thesis in Forest Biology

Effets du vieillissement et de la fertilité minérale sur l'allocation du carbone entre la croissance, le stockage de réserves et la reproduction chez le chêne et le hêtre

by

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Thesis presented the March 6th 2009 to the jury composed of:

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Réalisation technique

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À ma Famille

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Introduction (Français)

Afin d'éviter toute confusion entre l'allocation et la répartition du carbone (Dickson et al. 1993, Litton et al. 2007), le terme de **Allocation** fera référence dans ce document, à la fraction du carbone assimilé par la photosynthèse et attribué à une *fonction* donnée (par exemple la reproduction, le stockage de réserve ou la croissance) tandis que le terme de **Répartition** fera référence à la fraction du carbone contenu dans un *organe* ou un *compartiment* donné (par exemple, les racines, le tronc, les branches ou partie aérienne et souteraine). L'allocation du carbone peut être étudiée dans un compartiment donné ou dans la plante entière. La répartition du carbone peut être décrite pour une fonction donnée (le stockage de réserve, la croissance…) ou pour le stock total de carbone. Cependant, puisque le fonctionnement carboné de la plante n'est pas statique, l'allocation et la répartition doivent être considérées comme une image prise à un temps donné, d'un équilibre changeant entre plusieurs forces de sources et de puits.

La diminution de la croissance des peuplements forestiers en fonction de leur âge est un phénomène bien connu des forestiers. Il a été notamment mis en évidence de façon formelle lors de l'établissement des premières tables de production de bois d'œuvre en forêt équienne (e.g. Malepeyre 1839, Adrian 1945, Hamilton and Christie 1971, Bouchon 1974, Thill and Palm 1976).

Depuis, ce déclin de la productivité lié à l'âge a été largement étudié, particulièrement au cours de ces 20 dernières années (Kira and Shideï 1967, voir les revues bibliographiques de Gower et al. 1996 and Ryan et al. 1997a). A L'origine de ce déclin, deux types de mécanismes physiologiques peuvent être pris en considération: (1) les mécanismes conduisant à une diminution de l'assimilation du carbone par le couvert (*input*) et (2) ceux conduisant à une modification du coût biochimique des différentes fonctions métaboliques, autrement appelées puits, et/ou à un changement dans la manière dont le carbone est distribué entre ces puits. C'est à cette répartition du carbone entre les différents puits que se réfère le terme d'*allocation* utilisé dans cette étude (voir encadré).
Or, l'attention portée par la communauté scientifique sur ces deux grandes classes de mécanisme est encore aujourd'hui disproportionnée: les études consacrées à ce sujet concernent quasi-exclusivement les effets du vieillissement sur l' assimilation du carbone.

Parmi les hypothèses élaborées concernant la limitation des ressources en carbone assimilé, les avancées récentes réalisées sur cette problématique conduisent à retenir quatre mécanismes principaux : (1) la diminution de la surface foliaire, (2) l'augmentation de la contrainte hydraulique, (3) une diminution de la capacité du couvert à intercepter la lumière et (4) la diminution de la disponibilité en eau et en élément minéraux.

La diminution de la surface foliaire engendre une réduction de la dimension du compartiment photosynthétique. Cette réduction a été mise en évidence à l'échelle du peuplement (Ryan et al. 1997, Bond-Lamberty et al. 2002, Kashian et al. 2005, Leuschner et al. 2006) comme à l'échelle de l'arbre (Nock et al. 2008).
L'augmentation de la contrainte hydraulique avec l'âge fait référence à la diminution de la capacité des arbres hauts à transporter l'eau des racines (site d'absorption) vers les feuilles (site de transpiration/assimilation) (Yoda et al. 1965, Ryan and Yoder 1997a, Bond 2000, Magnani et al. 2000, Delzon et al. 2004, Zaehle 2006). Lors de la croissance en hauteur de l'arbre, la longueur du xylème entre les racines et les feuilles augmente et avec elle, la complexité de la structure hydraulique s'accroît, diminuant la conductivité hydraulique. La diminution de la conductivité hydraulique engendre une augmentation de la tension

xylémienne qui, si elle dépasse un certain seuil variable selon les espèces, engendre la cavitation des vaisseaux et trachéides. L'hypothèse formulée initialement par Ryan et Yoder (1997b), consiste à envisager la diminution de la conductance stomatique comme réponse à la diminution de la conductivité hydraulique. La réduction de la transpiration et du flux de sève induite par la diminution de la conductance stomatique éviterait l'occurrence de potentiels hydriques trop faibles et limiterait le risque de cavitation.
Woodruff, Bond and Meinzer (2004) ont observé que la diminution du potentiel hydrique dans de haut Douglas engendre une diminution de la pression de turgescence dans les cellules et conduit à limiter l'extension cellulaire (Woodruff et al. 2008) et réduire ainsi la capacité de stockage et le flux de sève.

Niinemet, Sparrow et Cescatti (2005) ont également récemment montré que la diminution de productivité liée à l'âge pourrait résulter d'une diminution de la capacité du couvert à intercepter la lumière. Ces derniers observent en effet que des individus adultes d'*Agathis australis* (D. Don) Lindl. présentent des feuilles plus inclinées et d'avantage massées en touffes que les jeunes individus, limitant ainsi la capacité individuelle des feuilles à capter la lumière.

Enfin, la diminution de la disponibilité en eau et en éléments minéraux pourrait également participer à la diminution de l'assimilation du carbone avec l'âge du peuplement (Ryan et al. 2004, Simard et al. 2007). Cette diminution peut résulter de la conjonction de deux phénomènes interdépendants : (1) la diminution du stock et/ou de l'efficacité des racines fines responsables de l'absorption de la solution du sol (Vanninen et al. 1996, Idol et al. 2000, Claus and George 2005) et (2) l'appauvrissement progressif des sols au cours des révolutions successives (Vitousek et al. 1989, Simard et al. 2007).

Cependant, la diminution des ressources en carbone assimilé ne suffit pas à expliquer l'intégralité du déclin de productivité observée au cours du développement des peuplements (Ryan et al. 2004, 2006). Ainsi, plusieurs auteurs émettent l'hypothèse que le déclin de productivité avec l'âge n'est pas seulement lié à une limitation de la ressource (carbone assimilé) mais aussi à une modification de l'économie de cette ressource au sein de l'arbre (Becker et al. 2000, Ryan et al. 2006). Cette économie de la ressource au sein de l'arbre est déterminée à la fois par le coût des différentes fonctions métaboliques consommatrices de carbone (puits) et par l'allocation, c'est-à-dire la manière dont la ressource est répartie entre ces puits.

A notre connaissance, peu d'études existent actuellement permettant d'étayer l'hypothèse d'un changement d'allocation du carbone au cours du développement de l'arbre (Becker et al. 2000). Or, il est possible d'envisager que l'équilibre entre les principales fonctions métaboliques de l'arbre que sont la croissance, le stockage de composés de réserve et la reproduction, changent au cours du développement de l'arbre.

Seul l'impact de l'augmentation de la respiration comme cause potentielle du déclin de croissance dans les peuplements âgés a largement été traité par des approches expérimentales (Yoda et al. 1965, Ryan et al. 1994, Murty et al. 1996) et par modélisation (Magnani et al. 2000, Makela and Valentine 2001). Ainsi, l'accumulation de tissus vivants dans les peuplements adultes engendre une augmentation de la respiration et une diminution subséquente de la production nette de carbone (égale à la différence entre photosynthèse et respiration). Même si l'importance de l'augmentation de la respiration dans l'explication du déclin de productivité est encore aujourd'hui sujette à discussion (Ryan and Waring 1992, Ryan et al. 1997b), son existence est néanmoins établie.

La reproduction est généralement considérée comme la fonction caractérisant le stade adulte du développement de l'arbre et l'importance grandissante de la reproduction dans le fonctionnement des arbres vieillissant est généralement admise. Or, à notre connaissance, l'évolution de l'allocation de carbone à la reproduction au cours du développement des peuplements ligneux forestiers n'a fait l'objet d'aucune publication jusqu'à ce jour.

Par ailleurs, même si le rôle des réserves carbonées dans le maintien de l'intégrité physiologique des arbres est admise depuis longtemps (Sinnott 1918, Chapin III et al. 1990), le stock de composés de réserves a longtemps été considéré comme un réservoir passif, accumulant le carbone restant après satisfaction des besoins de la croissance et de la respiration associée (Kozlowski et al. 1991, Körner 2003). Cependant, des études récentes tendent à démontrer que la fonction de stockage représente un puits susceptible de concurrencer d'autres puits de carbone tels que la croissance (Chapin 1990, Silpi 2007). De plus, les réserves sont utilisées dans la plante pour subvenir au fonctionnement métabolique de l'arbre en l'absence de photosynthèse (respiration d'entretien, reprise de croissance et débourrement) mais également pour prévenir le fonctionnement physiologique de l'arbre contre les contraintes environnementales tels que la sécheresse (Bréda et al. 2006), le gel (Morin et al. 2006, Poirier 2008), les défoliations (Lorio 1986, Wargo 1996, Marcais and Bréda 2006), les attaques d'insectes (Rhode et al 1996), les blessures (Bory et al. 1991, Lieutier 2004). Par ailleurs, mettant à profit leur 'pratique' des perturbations environnementales variées, plusieurs auteurs ont suggéré que les arbres adultes doivent

présenter un niveau d'acclimatation à leur environnement plus élevé que les arbres plus jeunes (Reich 2000, Cavender-Bares and Bazzaz 2000, Day et al. 2002, Thomas and Winner 2002). Ainsi, considérant le pool des réserves carbonées comme indicateur de la capacité de l'arbre à survivre, nous pouvons supposer que l'allocation de carbone à la fonction de stockage est susceptible d'augmenter avec l'âge.

En plus du phénomène bien connu de diminution de la productivité, le vieillissement est également caractérisé par une augmentation de la sensibilité des arbres aux perturbations environnementales (Mueller-Dombois 1993). Ainsi, l'âge est considéré comme l'un des facteurs prédisposant du processus complexe de dépérissement et de mort prématurée des arbres (Manion and Lachance, 1992). Or, les symptômes de dépérissement ont largement été observés dans les peuplements forestiers au cours des deux dernières décennies (Ogden 1988, Innes 1992, Manion and Lachance 1992, Bréda et al. 2006) et ont souvent été attribuées aux perturbations induites par les changements récents des conditions environnementales. Ainsi, seule une connaissance approfondie des processus physiologiques accompagnant le vieillissement de l'arbre peut permettre d'identifier les dysfonctionnements susceptibles d'engendrer un dépérissement prématuré des arbres adultes. Les études s'intéressant à l'âge comme facteur de dépérissement sont cependant rares. Elles ont néanmoins permis de montrer l'augmentation de la sensibilité de la croissance radiale au climat au cours du développement de l'arbre (Penninckx 1999, Rozas 2005, Esper et al. 2008, Yu 2008).

Par ailleurs, différentes études ont montré que les déséquilibres nutritionnels pouvaient être un facteur prédisposant au dépérissement des peuplements forestiers sur sol acide (Zoettl et al. 1989, Huettl et al. 1990, Le Goaster et al. 1990, Kandler, 1993). L'acidification des sols résulte de l'augmentation de la charge en protons provenant de sources internes à l'écosystème forestier – le prélèvement par la végétation, la nitrification ou la dégradation de la matière organique – ou de sources externe à l'écosystème. L'augmentation récente des dépôts atmosphériques acides et azotés est la principale source externe de protons accélérant les processus d'acidification et de lessivage des sols (Bonneau et al. 1983, Weissen et al. 1990) et perturber la nutrition et la production des peuplements forestiers (Nys 1989, Landmann and Nageleisen, 2001). Par ailleurs, nous avons vu qu'au cours du vieillissement, la nutrition minérale des arbres pouvait être altérée (Vitousek et al. 1989, Vanninen et al. 1996, Idol et al. 2000, Claus and George 2005, Simard et al. 2007). L'occurrence de ces deux facteurs prédisposant dans un grand nombre de massifs forestiers a conduit les forestiers et les écologues à envisager l'amendement comme pratique de remédiation au dépérissement observé sur sol acide depuis la fin des années 1970 (Van Praag et Weissen 1986, Mohamed et al. 1993, Bonneau 1995, Misson et al. 2001). Dans ce contexte, plusieurs programmes de

recherche ont vu le jour en Europe et notamment le programme DEFORPA (dépérissement des forêts attribué à la pollution atmosphérique, 1983) coordonné par M. Bonneau, en France. Les résultats des études passées concernant les effets de l'amendement sur les écosystèmes forestiers ne sont pas tous convergeant et la controverse à propos des programmes d'amendement à grande échelle des forêts Européennes est encore vive (Ven Breemen 1985).

L'amendement calcique permet d'augmenter le pH et le taux de saturation du sol et de diminuer l'acidité (diminution des concentrations en aluminium notamment) (Mohamed et al. 1993, Misson et al. 2001). Il permet également de corriger les déséquilibres nutritifs liés aux prélèvements par la végétation (Mohamed et al. 1993, Belkacem et al. 1992, Huber 2006). L'effet de l'amendement sur l'activité biologique du sol a également pu être mis en évidence. Ainsi, le nombre de vers de terre augmente après amendement (Kreutzer 1995, Robinson et al. 1996) stimulant la dégradation de la matière organique. Ainsi, l'amendement induit une amélioration générale de la fertilité minérale des sols et réduit les risques de déséquilibre entre éléments minéraux (Lebourgeois 1995, Becker et al. 1996).

Par ailleurs, plusieurs études effectuées à partir d'essais de fertilisation menés en milieu forestier montrent les effets suivants :

1. un effet positif sur la croissance aérienne (Larsen et Buch, 1995, Bakker *et al.*, 1999) ;
2. une augmentation du contenus en composés de réserves dans les racines (Wargo et al. 2002) ;
3. une augmentation du rapport [biomasse aérienne : biomasse racinaire] (Ericsson, 1995, Bakker *et al*., 1999, Litton, Raich and Ryan 2007) ;
4. une amélioration de l'activité racinaire activity (Fabiao et al. 1995, Persson et al. 1995, Bakker 1998) meme si quelques exceptions existent (Helmisaari et al. 1999, Borken et al. 2007),;
5. une augmentation de la production de fleurs et de fruits (Garbaye et Leroy, Le Tacon et Oswald 1977, Phillipe).
6. la structure de la communauté micorhiziennes et des activités enzymatiques (Rineau 2008)

Ces résultats laissent supposer que l'amendement pourrait engendrer (1) une augmentation de l'allocation à la croissance végétative et reproductive et à la respiration d'entretien et de croissance associée, (2) une augmentation de l'activité racinaire et de la concentration en composés de réserve dans les racines. Cependant, nous n'avons trouvé aucune étude rapportant une estimation complète de l'impact de l'amendement et de l'amélioration de la fertilité minérale sur l'allocation générale du carbone dans l'arbre.

Par ailleurs, les études concernant l'effet du vieillissement ou de la fertilité minérale des sols sur la physiologie de l'arbre concernent en grande majorité des espèces résineuses (Ryan et al. 1997a, Bond et Franklin 2002, Vogt et al. 1996, Helmisaari et al. 1998). Et les résultats obtenus ne sont pas directement transposables à des espèces feuillues, étant données les différences de physiologie, de phénologie et d'anatomie du bois et de sensibilité aux contraintes environnementales entre ces groupes d'espèces. Par ailleurs, si l'âge est un paramètre facile à déterminer dans les plantations de résineux, il en est tout autre dans les peuplements de feuillus souvent régénérés naturellement et les classes d'âges évaluées à partir des dimensions des arbres sont souvent imprécis (Lebourgeois, 1997).
Afin de participer à combler ce manque, notre étude a donc porté sur les espèces feuillues principales du massif forestier français : les chênes sessile (*Quercus petraea* (Matt.) Liebl.) et pédonculé (*Quercus robur* L.) et le hêtre (*Fagus sylvatica* L.). Les espèces feuillues occupent en France 70 % de la superficie forestière et représentent environ 60% du volume du pied. Le hêtre et les deux chênes représentent environ la moitié de la superficie (47%) et du volume (55%) occupé par les espèces feuillues en 2008 (Inventaire Forestier National 2008). Outre leur importance sylvicole, ces espèces présentent des caractéristiques fonctionnelles contrastées.

Le hêtre présente un bois à pores diffus (les vaisseaux de printemps et d'été sont petits et de taille homogène) alors que les chênes étudiés ici sont des espèces à bois à zone initiale poreuse (les vaisseaux formés au printemps sont plus larges et hétérogènes en taille que les vaisseaux formés en été) (Shweingruber 1990). Ces différences anatomiques sont à l'origine des différences de sensibilité à l'embolie hivernale observées entre ces espèces. Entant qu'espèces à zone initiale poreuse, les gros vaisseaux de chênes présentent une forte sensibilité à l'embolie induite par le gel hivernal (Cochard et al. 1992, Bréda et al. 1993). Afin de rétablir un système hydraulique fonctionnel, une partie importante de la croissance radiale (plus de 40%, dont la totalité des gros vaisseaux) est réalisée au printemps, avant le débourrement (Hinckley and Lassoie 1981, Bréda and Granier 1996, Barbaroux and Bréda 2002). Au contraire, les petits vaisseaux xylémiens du hêtre sont modérément atteints pas les dégâts de gel et la conductivité hydraulique est partiellement conservée d'une année à l'autre (Gasson 1987, Anfodillo et al. 1993, Hacke and Sauter 1996). Ainsi, la réactivation cambiale a lieu de manière synchrone au débourrement (Hinckley and Lassoie 1981, Lachaud and Bonnemain 1981, Barbaroux and Bréda 2002).

La plupart des études de comparaison de la phénologie foliaire entre chênes et hêtre suggèrent que le hêtre débourre plus tardivement que les chênes sessile et pédonculé (Comps et al.

1987, Kramer 1995, Differt 2001). Cependant, les observations par télédétection réalisées par Duchemin et al. (1999) tendent à montrer le contraire. L'absence de différence systématique entre les espèces résulte du fait que la phénologie d'un individu est déterminée non seulement par l'espèce à laquelle il appartient, mais également par les conditions environnementales dans lesquelles il se développe, comme le climat ou la fertilité du sol (Kramer 1995, Chuine et al. 1999, 2000). Aucune différence interspécifique de la période de sénescence foliaire n'a été observée entre chênes et hêtre à ce jour (Lebourgeois et al. 2002).

Les chênes et le hêtre sont des *mast seeding species* pour lesquelles la fructification est un évènement occasionnel mais synchrone entre les individus d'un même peuplement, permettant une fructification de masse. Grâce à une méta-analyse des bases données de fructification, Kelly et Sork (2002) suggèrent que cette phénologie particulière de la reproduction résulte d'avantage d'une stratégie d'adaptation aux conditions climatiques favorables pendant la période de floraison/pollinisation que d'une stratégie d'amélioration du succès de la germination en rassasiant les prédateurs par une fructification de masse.
Les données sur la fructification des espèces forestières sont rares. Cependant, la comparaison des études menées en France suggère que la biomasse des fruits produits au cours d'une année de fructification intense est comparable entre chêne et hêtre (Garbaye et Leroy 1974, Oswald 1984). En revanche, la fréquence des fructifications est plus faible chez le chêne que chez le hêtre. Ainsi, Aussenac (1975) estime la période de fructification moyenne du chêne sessile en Lorraine à 5.5 ans alors que Övergaard, Gemmel et Karlsson (2007) détectent une périodicité de 2.5 ans pour le hêtre en Suède. La rythmicité bisannuelle de la fructification du hêtre a également été mise en évidence e Allemagne (Eichhorn et al. 2008).

La croissance radiale des chênes et du hêtre a été largement étudiée par dendrochronologie, notamment dans notre équipe (Badeau 1995, Picard 1995, Becker *et al.* 1994 a et b, Barbaroux, 2002). Les trois espèces présentent une augmentation récente de la croissance radiale amorcée à la fin du XIX^{ème} siècle. L'augmentation de la surface de cerne est comprise entre 65 et 90 % chez le chêne sessile (Becker et al. 1994, Bergès 1998, Dhôte et al. 2000), 40 et 55% chez le chêne pédonculé (Becker et al. 1994, Badeau et al. 1996) et 56 à 115 % chez le hêtre (Badeau 1995, Picard 1995, Bontemps 2006).
Alors que les conditions climatiques régnant avant la saison de végétation sont cruciales pour la détermination de la croissance des chênes (Becker et al. 1994, Garcia-Gonzalez and Eckstein 2003, Van der Werf et al. 2007), la croissance du hêtre est d'avantage sensible aux conditions climatiques régnant au cours de la saison de végétation (Bouriaud et al., 2003, Dittmar et al. 2003, Lebourgeois et al. 2005, Van der Werf et al. 2007). Les différences interspécifiques du déterminisme de la croissance peuvent être en partie expliquées par les

différences interspécifiques de la dynamique de réactivation cambiale vues plus haut mais aussi par la plus grande sensibilité du hêtre aux sécheresses estivales (Leuschner et al. 2001, Bréda et al. 2006).

Récemment, le stockage et la mobilisation des réserves glucidiques ont été étudiés au cours de la saison de végétation, en fonction du contenu en eau du sol et du développement phénologique comparé du chêne sessile et du hêtre (Barbaroux 2002, Barbaroux et Bréda 2002). Cette étude révèle une dynamique saisonnière des réserves glucidiques plus marquées et des concentrations plus élevées chez le chêne que chez le hêtre. Ces résultats sont cohérents avec des besoins en carbone plus important chez chêne en phase hétérotrophe (période pendant laquelle la photosynthèse ne suffit pas à combler les besoins en carbone de la plante). Des expériences de modélisations du bilan de carbone à l'échelle du peuplement suggèrent également que le niveau de réserves ainsi que l'allocation du carbone entre croissance et stockage sont deux éléments déterminants des variations interannuelles de croissance radiale chez le chêne sessile comme chez le hêtre (Barbaroux 2002, Dufrêne et al. 2005).

Enfin, la conductance stomatique comme la photosynthèse maximale sont plus élevées chez les chênes que chez le hêtre. Dès lors, la capacité photosynthétique des chênes est plus importante que celle du hêtre (Aranda et al. 2000, 2005, Backes et al. 2001, Leuschner et al. 2001). Par ailleurs, l'efficience d'utilisation de l'eau semble meilleure chez les chênes que chez le hêtre et la fermeture stomatique en période de déficit hydrique intervient plus précocement chez le hêtre. De plus, même si les valeurs de potentiel hydrique en période favorable sont comparables entre les espèces (Aranda et al. 2000), en période de sécheresse le hêtre présente une diminution plus brutale du potentiel de base que le chêne sessile (Leuschner et al. 2001, Zapater et al., 2008). Enfin, le fonctionnement des racines fines de hêtre est également plus sensible aux évènements de sécheresse que celui du chêne sessile (Leuschner et al. 2001). Ces quatre derniers facteurs mettent donc en évidence la plus forte sensibilité du hêtre à la sécheresse par rapport au chêne sessile. Etant donné la plus forte compétitivité avérée du hêtre par rapport aux chênes, plusieurs auteurs suggèrent que cette forte sensibilité du hêtre à la sécheresse soit une stratégie de protection lui permettant à l'issue d'une sécheresse, de récupérer un fonctionnement physiologique performant plus rapidement que le chêne.

Fort des connaissances acquises sur les facteurs intrinsèques (espèce et vieillissement) et externes (climat et fertilité hydrique et minérale) déterminant le fonctionnement physiologique des arbres, mais aussi conscient (1) du manque criant de données en matière de la gestion des ressources carbonées dans l'arbre et (2) des attentes de la communauté

forestière face aux dépérissements forestiers, nous proposons ici d'étudier l'évolution de l'allocation du carbone chez deux espèces feuillues contrastées (1) au cours d'une révolution forestière et (2) dans des situations contrastées de niveau trophique.

Les effets du vieillissement ont été étudiés à l'échelle de la révolution forestière au travers de deux chronoséquences. Deux dispositifs d'amendement ont permis d'analyser les effets de la fertilité minérale du sol sur l'allocation du carbone dans l'arbre.

Introduction (English)

To avoid confusion between carbon allocation and partitioning (Dickson et al. 1993, Litton et al. 2007), **Allocation,** in the present document, refers, to the fraction of carbon assimilated by photosynthesis that is attributed to a given *function* in the tree (e.g. storage, reproduction, respiration, growth) whereas **Partitioning** refers to the fraction of carbon contained in a given *organ* or *compartment* of the tree (e.g. root, stem and branches or below- and aboveground parts). Carbon allocation can be studied in a given compartment or in the whole plant. Carbon partitioning can be described for a given function (carbon storage, growth, respiration) or for the entire carbon stock of the tree. However, because carbon functioning in plants is not static, allocation and partitioning have to be considered as a picture at a given time of the *changing equilibrium* between sink and source powers.

Age-related decline of forest productivity is a well-known phenomenon in forest management. It was primarily observed in yield tables of managed, non-senescent forests (e.g. Malepeyre 1839, Adrian 1945, Hamilton and Christie 1971, Bouchon 1974, Thill and Palm 1976).

Since then, it has been studied intensively, particularly during the last two decades (Kira and Shidai 1967, see Gower et al. 1996 and Ryan et al. 1997a for reviews). Two types of physiological mechanisms can be mentioned to explain growth decline with age: (1) the mechanisms leading to the reduction of carbon assimilation (*input*) and (2) those leading to the modification of the resource economy, i.e. an increase in the biochemical cost of various metabolic functions, also referred to as a *sink*, and/or a change in the way of distributing assimilates between these sinks, also referred to as carbon allocation (see Insert 1). Yet surprisingly, research at the process level on carbon allocation has fallen far behind research on processes governing carbon assimilation.

Several hypotheses were put forward to explain growth decline with age and are more or less well documented today. Recent advances have made it possible to retain four main causes explaining this decline: (1) the reduction of leaf area, (2) the increase of hydraulic limitation, (3) the decrease of light capture efficiency and (4) the decrease of water and nutrient availability.

The decrease in leaf area results in the reduction in size of the main photosynthetic compartment. It has been assessed at stand (Ryan et al. 1997, Bond-Lamberty et al. 2002, Kashian et al. 2005, Leuschner et al. 2006) and tree scales (Nock et al. 2008).

The age-related increase of hydraulic limitation refers to the reduced capacity of tall trees to convey water from roots (absorption site) to leaves (transpiration/assimilation sites) (Yoda et al. 1965, Ryan and Yoder 1997a, Bond 2000, Magnani et al. 2000, Delzon et al. 2004, Zaehle 2006). With increasing height, the length and the complexity of the path between roots and leaves increase, resulting in a decrease in hydraulic conductivity. The decline of hydraulic conductivity will then increase the tension in the xylem and the risk of cavitation in vessels or tracheïds. The hypothesis first formalised by Ryan and Yoder in 1997 considered that stomatal conductance decreases in response to hydraulic conductivity reduction. The decrease of transpiration and sap flow related to stomatal conductance reduction would increase water potential and thus reduce the risk of cavitation.

Woodruff, Bond and Meinzer (2004) observed that the reduction of water potential in tall Douglas firs induces a decrease in turgor pressure in cells that leads to limitation of cell expansion (Woodruff et al. 2008) and to reduced storage capacity and sap flow.

Niinemets, Sparrow and Cescatti (2005) have shown recently that age-related decline of productivity might also be related to the decrease of the light interception capacity by the canopy. Indeed, they observed that leaves of adult *Agathis australis* (D. Don) Lindl. were more inclined and clumped than those of young trees. This resulted in superior light harvesting in young trees.

Finally, the decrease of water and nutrient availability may contribute to the decrease of carbon assimilation in ageing stands (Ryan et al. 2004, Simard et al. 2007). This reduction could be the result of two independent processes: (1) the reduction of fine root biomass and/or efficiency (Vanninen et al. 1996, Idol et al. 2000, Claus and George 2005) and (2) constant depletion of soil mineral stocks over consecutive forest successions (Vitousek et al. 1989, Simard et al. 2007).

However, the reduction of both assimilation and absorption are not sufficient to explain the observed decline in wood production (Ryan et al. 2004, 2006). Thus, the concept that age-related decline of productivity may not be exclusively related to resource limitation (assimilates) but also to potential modifications in the economy of assimilates, has recently been reinstated (Becker et al. 2000, Ryan et al. 2006). Carbon economy in trees might be determined by (1) the biochemical cost of metabolic functions (sink) and (2) the allocation scheme that determines the amount of assimilates allocated to every sink.

To our knowledge, studies investigating potential changes of trade-off in carbon allocation as a physiological process accompanying tree ageing are scarce (Becker et al. 2000). The increase of respiration was the only carbon sink investigated to explain growth decline in aged stands. It has been largely documented using experimental (Yoda et al. 1965, Ryan et al. 1994, Murty et al. 1996) as well as modelling approaches (Magnani et al. 2000, Makela and Valentine 2001). Living biomass accumulation in adult stands leads to increased amounts of respiration and decreased Net Primary Production (NPP = difference between photosynthesis and maintenance respiration). Even if the importance of respiration in age-related productivity decline is still being debated (Ryan and Waring 1992, Ryan et al. 1997b), its reality is well-established.

Reproduction is often considered as a function defining the adult phase of tree development, so the fact that reproduction represents an increasing cost in older stands is generally assumed. However, to our knowledge, changes in carbon allocation to the reproduction function throughout stand development have not been quantified for forest woody species yet.

Moreover, even if the role of reserves in the maintenance of physiological integrity of trees has been assumed for a long time (Sinnott 1918, Chapin III et al. 1990), carbon allocation to storage has also been considered as a passive buffer, resulting from the excess of assimilation after the satisfaction of growth and respiration needs (Kozlowski et al. 1991, Körner 2003). However, recent studies tend to demonstrate that storage represents a sink that can compete with other sinks like growth (Chapin 1990, Silpi 2007). Moreover, reserves are used by plants to supply carbon needs during periods without photosynthesis (maintenance respiration, growth resumption and foliage building in spring), but also to protect tree physiological integrity against environmental stresses like drought (Bréda et al. 2006), frost (Morin et al. 2006, Poirier 2008), defoliation (Lorio 1986, Wargo 1996, Marcais and Bréda 2006), insect attacks (Rhode et al 1996) and wounds (Bory et al. 1991, Lieutier 2004). Besides, after profiting from their "experience" under development conditions during exposure to disturbance events over time, it has been suggested that adult trees should present higher acclimation levels to their environment than young trees (Reich 2000, Cavender-Bares and Bazzaz 2000, Day et al. 2002, Thomas and Winner 2002). Thus, considering the quantity of carbohydrate reserves as an indicator of the resource pool for tree defence, we suggest that relative allocation to storage function will increase with age.

In addition to this well known productivity decline, ageing of trees is also characterized by an increase of sensitivity to disturbance (Mueller-Dombois 1993). Age is thus considered by many authors as a predisposing factor inducing premature mortality (or dieback) (Manion and Lachance, 1992). Tree to stand dieback has been frequently observed during the last decades (Ogden 1988, Innes 1992, Manion and Lachance 1992, Bréda et al. 2006) and was mainly attributed to recent global changes. However, advances in the understanding of physiological processes related to ageing could make it possible to identify dysfunctions leading to premature decline in trees. Studies assessing this hypothesis by comparing stands at different ages or development stages are scarce: few studies have tried to analyse growth response and sensitivity to climate, of stands from different ages (Penninckx 1999, Rozas 2005, Esper et al. 2008, Yu 2008).

Furthermore, several studies have shown that unbalanced mineral nutrition and poor fertility might be one of the predisposing factors giving rise to forest decline on acidic soil (Zoettl et al. 1989, Huettl et al. 1990, Le Goaster et al. 1990, Kandler, 1993). Soil acidification resulted in the increase of protons inputs from external and internal sources – plant uptake, nitrification or decomposition of organic matter. Atmospheric deposition is one of the main external agents increasing soil acidification and desaturation (Bonneau et al. 1983, Weissen et al. 1990, Dupouey et al. 1998), which may disturb stand nutrition and production (Nys 1989, Landmann and Nageleisen, 2001). Furthermore, previous studies showed alteration of mineral nutrition in ageing trees (Vitousek et al. 1989, Vanninen et al. 1996, Idol et al. 2000, Claus and George 2005, Simard et al. 2007). Concomitancy of these two predisposing factors (ageing and mineral element imbalances) in a large proportion of forests in Europe has led forest managers and scientists to consider liming as a practice to restore soil mineral fertility and to remediate stand decline (Van Praag et Weissen 1986, Mohamed et al. 1993, Bonneau 1995, Misson et al. 2001). In this context, several research programs have been initiated in Europe, like the DEFORPA program (dépérissement des forêts attribué à la pollution atmosphérique, 1983), coordinated by M. Bonneau for France. Results related to the effects of liming on forest ecosystems are not fully convergent and the controversy surrounding large scale liming in European forests is still active (Ven Breemen 1985).

Liming induces a rise in the soil solution pH and base saturation linked to a decrease in acidity (mainly related to a decrease in aluminium) (Mohamed et al. 1993, Misson et al. 2001). In addition, liming reduces nutritional imbalances resulting from plant uptake (Mohamed et al. 1993, Belkacem et al. 1992, Huber 2006). The biological activity of soils is often stimulated by liming. Thus, density of earthworms increases with treatment (Kreutzer 1995, Robinson et al. 1996), improving the degradation of organic matter and in turn humus quality. So liming induces an overall improvement of mineral fertility and reduces risks of mineral imbalance (Lebourgeois 1995, Becker et al. 1996).

Concerning the carbon balance in trees, previous fertilization experiments show:

1. an increase in aboveground tree growth (Larsen et Buch, 1995, Bakker *et al.*, 1999);
2. an increase in root carbohydrate contents (Wargo et al. 2002);
3. an increase in the |Root:Shoot] ratio (Ericsson, 1995, Bakker *et al.*, 1999, Litton, Raich and Ryan 2007);
4. a positive impact on root activity (Fabiao et al. 1995, Persson et al. 1995, Bakker 1998) even if some exceptions occur (Helmisaari et al. 1999, Borken et al. 2007);
5. an increase in flower and seed production (Garbaye et Leroy, Le Tacon et Oswald 1977)

6. changes in the structure of the ectomycorrhyzal comunity and associated enzymatic activities (Rineau 2008).

These results imply that liming may induce an increase in growth, carbohydrate concentrations in roots, roots activity and fruiting. However, no study was found supplying an integrated assessment of the impact of liming and mineral nutrition improvement on the overall carbon allocation in trees.

Studies concerning ageing and soil mineral fertility impacts on tree physiology are mainly related to coniferous species (Ryan et al. 1997a, Bond et Franklin 2002, Vogt et al. 1996, Helmisaari et al. 1999), and the transposition of these results to broadleaved species might be difficult, given the wide differences in physiological functioning, phenology, wood anatomy and sensitivity to environmental conditions between these groups. Moreover, if age determination is easy in evergreen plantation, it is not the case in deciduous naturally regenerated stands and it has been reported that ages estimated from tree size for forest management are often imprecise or wrong (Lebourgeois, 1997).
In order to fill these gaps, the present study concerns ageing, based on reliable estimates, and soil mineral element fertility effects on the most widespread broadleaved species in France: sessile oak (*Quercus petraea* (Matt.) Liebl.), pedunculate oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.). Indeed, 47 % of the forested area covered by broadleaved species (i.e. 70 % of the total forested area) were occupied by sessile and pedunculate oaks and beech in France in 2008 (Inventaire Forestier National 2008). Furthermore, these species also presented contrasting functional characteristics.

While beech is a diffuse porous species (i.e. latewood and earlywood vessels are small and homogeneous in size), sessile and pedunculate oaks are ring porous species (i.e. earlywood vessels are conspicuously larger than latewood vessels) (Schweingruber 1990). These contrasting wood anatomies result in specific differences in vulnerability to frost damage. In the spring, most of large earlywood vessels of ring porous species are embolised by frost events of the previous winter (Cochard et al. 1992, Bréda et al. 1993). Then, radial growth needs to be initiated prior to budburst in order to restore soil to leaf hydraulic conductance (Hinckley and Lassoie 1981, Bréda and Granier 1996, Hacke and Sauter 1996, Barbaroux 2002). In contrast, small vessels of diffuse porous species like beech are less vulnerable to winter embolism (Gasson 1987, Anfodillo et al. 1993, Hacke and Sauter 1996). Hydraulic conductivity is thus partly preserved from year to year. Therefore, early growth, as a key factor for sap flow recovery, is less essential than for oaks (Hacke and Sauter 1996, Lemoine et al. 1999) and cambial reactivation occurs synchronously with bud-burst.

Several phenological comparisons between beech and oaks suggest that bud-burst occurs earlier for oaks (Comps et al. 1987, Kramer 1995, Differt 2001, Lebourgeois et al. 2002). However, Duchemin et al. (1999) observed an inverse trend from remote sensing data. The lack of systematic differences in phenology between oaks and beech resulted from the fact that other factors, in addition to species, may determine individual phenology, like climate or site fertility (Kramer 1995, Chuine et al. 1999, 2000). No significant difference between species has been reported concerning leaf fall date (Lebourgeois et al. 2002).

Oaks and beech are mast seeding species, ie. mass seed production occurs occasionally but synchronously in trees belonging to the same stand or the same region. The meta-analysis conducted by Kelly and Sork (2002) suggests that masting is often an adaptive reproductive trait overlaid on the direct influence of weather rather than a strategy of satiation of seed predators.
Field data concerning fructification are scarce, however a few studies suggest that total fruit biomass produced during a mast year is comparable between beech and oaks (Garbaye et Leroy 1974, Oswald 1984). In contrast, frequency of masting seems to be lower for oaks compared to beech. Övergaard, Gemmel and Karlsson (2007) detected a mast periodicity of 2.5 years for beech in Sweden, whereas significant masting of oak occurred every 5.5 years on average in the Lorraine region, France (Aussenac 1975). A biannual rhythm of mast for beech has been also reported in Germany (Eichhorn et al. 2008).

Radial growth of beech and oaks has been intensively studied using dendrochronological analyses (Badeau 1995, Picard 1995, Becker *et al*. 1994 a et b, Barbaroux, 2002). Recent growth increase initiated in the late 19th century, was reported for the three species: from 65 to 90 % for sessile oak (Becker et al. 1994, Bergès 1998, Dhôte et al. 2000), from 40 to 55% for pedunculate oak (Becker et al. 1994, Badeau et al. 1996) and from 56 to 115 % for beech (Badeau 1995, Picard 1995, Bontemps 2006).
Moreover, substantial differences in climatic determinism of radial growth have been reported: whereas climatic conditions occurring before the growing season are crucial for oak growth (Becker et al. 1994, Garcia-Gonzalez and Eckstein 2003, Van der Werf et al. 2007), beech growth is mostly determined by the climate occurring during the growing season (Bouriaud et al., 2004, Dittmar et al. 2003, Lebourgeois et al. 2005, Van der Werf et al. 2007). These differences may be related to differences in the phenology of cambial reactivation, as described above, and to the greater sensitivity of beech growth to summer drought (Leuschner et al. 2001, Bréda et al. 2006).

Recently, the seasonal dynamics of carbohydrate reserve compounds was studied for sessile oak and beech in relation to soil water content (Barbaroux 2002, Barbaroux and Bréda 2002). It revealed that sessile oak presents wider seasonal dynamics of carbohydrate reserves compared to beech. Indeed, the early growth occurring in oak trees during the heterotrophic period is supported by carbohydrate reserves and induces a sharp depletion in carbon storage that must be refilled during the autotrophic season. Furthermore, modelling experiments suggest that carbohydrate contents and carbon allocation between growth and storage are two decisive factors determining year-to-year variations of radial growth in trees (Barbaroux 2002, Dufrêne et al. 2005).

Finally, oaks present higher stomatal conductance, maximum assimilation rate and resulting photosynthetic capacity than beech (Aranda et al. 2000, 2005, Backes et al. 2000, Leuschner et al. 2001). Oaks and beech have similar water potential during favourable periods (Aranda et al. 2000). Yet, during water stress periods, beech displays a stronger decrease in predawn water potential than oaks (Leuschner et al. 2001, Zapater et al., 2008). Finally, beech fine roots display higher sensitivity to drought compared with oak fine roots (Leuschner et al. 2001). These results reveal that oaks are more drought-tolerant than beech. Considering the higher competition capacity of beech, many authors suggest that its high sensitivity to drought is an efficient strategy to protect its physiological functioning during crises in order to restore an effective functioning more rapidly than oaks.

Despite great advances achieved to understand the influence of intrinsic and external factors on several physiological processes, the determinism of carbon allocation in trees has been largely overlooked. This lack added to the expectations of forest managers facing forest dieback, led us to study the carbon allocation in these two contrasted broadleaves species (1) during a forest succession and (2) in conditions of contrasting soil mineral element fertility. Ageing effects on carbon allocation were studied using a diachronic approach with two monospecific chronosequences. The impact of soil mineral element fertility on carbon functioning in trees was studied using ecosystem modification, i.e. liming experiments.

Age-related variation in carbon allocation at tree and stand scales in beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) using a chronosequence approach

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Age-related variation in carbon allocation at tree and stand scales in beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) using a chronosequence approach

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Summary

Two types of physiological mechanisms can contribute to growth decline with age: (1) the mechanisms leading to the reduction of carbon assimilation (*input*) and (2) those leading to modification of the resource economy. Surprisingly, the processes relating to carbon allocation have been little investigated as compared to research on the processes governing carbon assimilation. The objective of this paper was thus to test the hypothesis that growth decrease related to age is accompanied by changes in carbon allocation to the benefit of storage and reproductive functions in two contrasting broadleaved species: beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.).

Age-related changes in carbon allocation were studied using a chronosequence approach. Chronosequences, each consisting of several even-aged stands ranging from 14 to 175 years old for beech and from 30 to 134 years old for sessile oak, were divided into five or six age classes. In this study, carbon allocations to growth, storage and reproduction were defined as the relative amount of carbon invested in biomass increment, carbohydrate increment and seed production respectively. Tree ring width and allometric relationships were used to assess biomass increment at the tree and stand scales. Below-ground biomass was assessed using a specific allometric relationship between root:shoot ratio and age, established from the literature review. Seasonal variations of carbohydrate concentrations were used to assess carbon allocation to storage. Reproduction effort was quantified for beech stands by collecting seed and cupule production.

Age-related flagging of biomass productivity was assessed at the tree and stand scales and carbohydrate quantities in trees increased with age for both species. Seed and cupule production increased with stand age in beech from 56 gC/m²/year at 30 years old to 129 gC/m²/year at 138 years old. In beech, carbon allocation to storage and reproductive functions increased with age to the detriment of carbon allocation to growth functions. In contrast, the

carbon balance between growth and storage remained constant between age-classes in sessile oak.

The contrasting age-related changes in carbon allocation between beech and sessile oak are discussed with reference to the differences in growing environment, phenology and hydraulic properties of ring-porous and diffuse-porous species.

INTRODUCTION

Age-related decline of forest productivity is a well-known phenomenon in forest management. It was primarily observed on yield tables of managed, non-senescent forests (e.g. Hamilton and Christie 1971, Bouchon 1974, Thill and Palm 1976), and because forest productivity is the key-factor in wood production and carbon storage at the ecosystem level, age-related decline of forest productivity has been intensively studied, particularly during the last 40 years (Kira and Shidai 1967, see Gower et al. 1996 and Ryan et al. 1997 for review). Several hypotheses were put forward to explain growth decline with age and are more or less well documented today. Most of them were described in the well-known review of Ryan et al. (1997). Recent advances since this review have retained three main causes to explain this decline: (1) decreasing leaf area, assessed at stand (Ryan et al. 1997, Bond-Lamberty et al. 2002, Kashian et al. 2005, Leuschner et al. 2006) and tree scales (Nock et al. 2008), (2) decrease in photosynthetic rate due to hydraulic limitation and decrease in stomatal/canopy conductance with tree height (Yoda et al. 1965, Ryan and Yoder 1997, Magnani et al. 2000, Delzon et al. 2004, Zaehle 2006), (3) decrease in nutrient availability (Ryan et al. 2004, Simard et al. 2007). However, reduction of assimilation and absorption are not sufficient to explain the observed decline in wood production (Ryan et al. 2004, 2006). Recently, new hypotheses have emerged concerning physiological processes potentially involved in productivity decline (Ryan et al. 2006): the decrease of light capture efficiency in mature trees (Niinemet et al. 2005) or the decrease of the turgor pressure limiting cell expansion and reducing the carbon sink of growth (Woodruff et al. 2004).

In addition to this well-known productivity decline, ageing of trees is also characterized by an increase in sensitivity to perturbations (Mueller-Dombois 1993). Age is thus considered by many authors as a predisposing factor inducing the premature mortality (or dieback) (Manion and Lachance, 1992) frequently observed over the last decades (Ogden 1988, Innes 1991, Manion and Lachance 1992, Bréda et al. 2006). However, studies assessing this hypothesis by comparing stands at different ages or development stages are scarce and few studies have tried to analyze the growth response of stands of different ages to climate (Penninckx 1999, Rozas 2005, Esper et al. 2008, Yu 2008).

In the light of this increasing sensitivity, carbon allocation to storage and/or reproduction functions might be increased to the detriment of growth function in order to ensure tree

longevity and/or to ensure tree regeneration. If this occurred, the shift in trade-off between these functions might explain, at least partially, the decrease in tree and stand productivity with age, but few studies have investigated potential changes of trade-off in the carbon allocation to growth and related respiration functions, and other main tree functions such as storage reserves and reproduction, as physiological processes accompanying tree ageing (Becker et al. 2000). Reproduction is often considered as a function defining the adult stage of tree development and the fact that reproduction is an increasing function in older stands is generally assumed. However, to our knowledge, changes in carbon allocation to the reproduction function during stand development have not been quantified yet for woody forest species. Moreover, even if the role of reserves in the maintenance of physiological integrity of trees has been assumed for long time (Sinnott 1918, Chapin III et al. 1990), carbon allocation to storage has long been considered as a passive buffer, resulting from the excess of assimilation after the satisfaction of growth and respiration needs (Kozlowski et al. 1991, Körner 2003). However, recent studies tend to demonstrate that storage represents a sink that can compete with other sinks like growth (Chapin 1990, Silpi 2007). Reserves are used in plants for maintenance respiration, growth resumption and foliage building in the spring, but also to protect tree physiological integrity against environmental stresses like drought (Bréda et al. 2006), frost (Morin et al. 2006), defoliation (Marcais and Bréda 2006), insect attacks (Rhode et al 1996) and wounds (Bory et al. 1991). Besides, as a result of profiting from their experience of developmental conditions and exposure to disturbance events over time, it has been suggested that adult trees should present higher acclimation levels to their environment than young trees (Reich 2000, Cavender-Bares and Bazzaz 2000, Day et al. 2002, Thomas and Winner 2002). Thus, considering the levels of carbohydrate reserves as an indicator of a resource pool for tree defense, it is possible that relative allocation to the storage function will increase with age.

The main objective of this paper was to test the hypothesis that age-related growth decrease is accompanied by changes in carbon allocation to the benefit of storage and reproduction functions. Therefore, carbon allocation to growth, storage and reproduction functions was assessed during stand ageing by quantifying the age-related differences in radial growth, carbohydrate levels and seed production respectively. These assessments were made during one growing season (2006) for a ring porous and a diffuse porous species in two chronosequences.

Carbon allocation to a given function was defined as the fraction of the total carbon increment attributed to the associated carbon pool. Finally, carbon production at the stand scale was expressed per leaf area as an indicator of the carbon production efficiency of trees.

MATERIALS AND METHODS

SITE AND STAND DESCRIPTIONS

One chronosequence was established for each of the two species. The chronosequence for common beech (*Fagus sylvatica* L.) was located in the state forest of Fougères (48°23'N, 1°09'W, mean elevation 164 m) in north-western France. Many studies are still being carried out on this site, aiming at biogeochemical cycle analysis and quantification (Huet 2004, Lecointe et al. 2006, Legout et al. 2008, Eglin 2008) including tree biomass calculation (Huet et al. 2004). Ecophysiological studies of beech stand growth, transpiration, canopy interception, seasonal stem increment and water balance measurements have also been performed (Peiffer 2005, Peiffer et al. 2005). Soils are developed in about 1.5 m of non-carbonated Aeolian loess, over granitic bedrock (Legout 2008), and Toutain (1965) pointed out the homogeneity of these forest soils, which are mainly classified as Alocrisol-Neoluvisols. The climate is of oceanic type, mean annual temperature and average annual precipitation, calculated for the past 30 years, were 11.6 °C and 916 mm respectively (Météo France). Annual soil water deficit, computed by daily water balance modeling according to Granier et al. (1999) averaged 22.4 between 1971 and 2006.

The chronosequence for sessile oak (*Quercus petraea* (Matt.) Liebl.) was located in two closed state forests of Amance (48°46'N, 6°19E, mean elevation 245m) and Champenoux (48°43'N, 6°21E, mean elevation 260m), in north-eastern France, where previous ecological studies were carried out (Thimonier et al. 1992) on oak ecophysiology (Bréda et al., 1993a, 1993b), oak transpiration and growth (Bréda and Granier, 1996) and the ecophysiologal impact of thinning on tree growth and water use (Bréda et al., 1995). Soils are Neoluvisols developed in a fairly deep loam, over-lying a carbonated clay horizon (Bréda et al. 1993b). The climate is of semi-continental type. Mean annual temperature and average annual precipitation, calculated for the past 30 years, were 10.3 °C and 776 mm respectively for these two forests (Météo France). Annual soil water deficit, computed by daily water balance modeling according to Granier et al. (1999) averaged 62.3 between 1971 and 2006.
For historical reasons, stand age distribution in the two oak forests was unbalanced (lacking old even-aged stands in Champenoux forest and lacking 65-95-year-old stands in Amance forest). Therefore, the chronosequence for sessile oak overlapped the forests of Amance and Champenoux, which were about 5 km apart. Both forests presented similar soil characteristics and had been submitted to similar silvicultural practices (even aged stands, naturally regenerated).

Special attention was devoted to minimizing between-stand environmental variations in each chronosequence. Stands were selected in accordance with different homogeneity criteria in order to isolate ageing signals and to reduce the other sources of variation. These criteria were related to soil type, topography, stand composition and silvicultural practices. Therefore, the chronosequences were composed of pure even-aged, naturally regenerated stands, located on flat luvisols for the sessile oak chronosequence and on flat alocrisols-neoluvisols for the common beech chronosequence. Soils of the sessile oak chronosequence were slightly richer than those of beech chronosequence (Table 1).

Table 1: Principal soil fertility characteristics averaged for the two chronosequences: mineral characteristics of organic and mineral layer (A horizon) [Carbon / Nitrogen] ratio (C/N), pH, cation exchange capacity (CEC), base saturation (BS) and available soil water content (AWC). Standard errors are indicated in brackets.

Site	C/N	pH	CEC (meq/100g)	BS (%)	AWC (mm)
Oak chronosequence	11.9 (1.25)	3.8 (0.25)	9.7 (2.02)	43 (11)	170 (22.9)
Beech chronosequence	22.2 (2.01)	3.8 (0.16)	7.3 (1.34)	24 (12)	160

EXPERIMENTAL DESIGN

The forest management plan classifies stands according to the silvicultural operations to be carried out depending on stand age, and both chronosequences were chosen in large even-aged subdivisions. The stands composing these chronosequences were thus divided into quite narrow age classes. The Beech chronosequence was composed of 23 stands distributed into six age classes (15, 35, 60, 95, 130, 175 years). The Oak chronosequence was composed of 18 stands distributed into five age classes (30, 50, 70, 120, 135 years). Older ages were excluded for silvicultural reasons as the older oak stands were managed as coppice with standards, and this treatment was excluded from the study. Age classes consisted of four different stands, except for the youngest classes because mixed stands were excluded: thus, only three young stands for beech (15 years-old class) and two young stands for oak (30 years-old class) were selected. Stand age covered by these two chronosequences ranged from 26 to 140 years old for oak and from 12 to 200 years old for beech. Circumference at breast height and height of trees were measured in each plot of the two chronosequences and the main stand characteristics are given in Table 2.

Table 2: Principal forestry characteristics averaged for each age class of the two chronosequences: mean age, mean dominant height (Ho), mean maximum leaf area index (LAI), mean basal area (BA) and mean density (N). Standard errors are indicated in brackets.

Species	Age classes	Number of plots	Mean age (years)	Mean Ho (m)	Mean LAI* (m^2/m^2)	Mean BA (m^2/ha)	Secondary species (%)**	Mean N (/ha)
Quercus petraea	Sapling	2	30 (5.1)	14.1 (1.5)	6.4 (0.31)	24.5 (2.59)	19.0 (12.6)	4362 (1646)
	Pole	4	48 (3.9)	18.2 (0.8)	6.2 (0.64)	28.4 (5.06)	17.7 (11.7)	3609 (1051)
	Young high forest	4	73 (2.0)	24.2 (1.3)	5.4 (0.38)	27.5 (4.76)	33.2 (7.2)	1294 (459)
	Mature high forest	4	116 (0.8)	25.2 (1.2)	6.5 (0.59)	29.5 (2.86)	36.4 (12.3)	836 (274)
	Old high forest	4	134 (4.2)	25.9 (1.8)	5.8 (0.50)	26.6 (1.55)	29.9 (8.1)	869 (393)
Fagus sylvatica	Thicket	3	14 (2.2)	7.1 (1.2)	6.6 (1.19)	18.4 (9.84)	15.6 (9.8)	6258 (1377)
	Sapling	4	30 (3.1)	15.5 (1.8)	5.7 (0.50)	26.5 (9.72)	10.0 (9.7)	1831 (518)
	Pole	4	58 (4.8)	25.6 (1.6)	6.5 (1.37)	20.5 (3.26)	11.7 (3.2)	263 (51)
	Young high forest	4	95 (4.6)	26.6 (2.8)	5.3 (0.13)	25.0 (3.69)	19.5 (3.4)	243 (54)
	Mature high forest	4	138 (6.0)	29.6 (1.8)	5.0 (1.15)	22.5 (5.58)	12.71 (6.0)	160 (78)
	Old high forest	4	175 (15.4)	31.3 (1.9)	5.3 (1.03)	29.9 4.29)	18.6 (5.9)	118 (22)

** Total stand LAI (including hornbeam)*
*** Proportion of the stand basal area*

ESTIMATION OF CARBOHYDRATES ACCUMULATED IN 2006

Previous studies in similar ecosystems showed that sessile oak and beech display similar seasonal carbohydrate dynamics (Barbaroux and Bréda, 2002). Minimum total non-structural carbohydrate (TNC) concentrations occur at the beginning of June, when leaves are fully expanded and maximum concentrations occur in October, before leaf fall. Concentration differentials between the two dates give an estimation of carbohydrate accumulation during the growing season. Barbaroux (2002) demonstrated that a good estimation of carbohydrate contents in adult trees can be obtained from samples of wood from the stem at breast height (1.3m above ground) and from the coarse roots. Indeed, these are the two main organs for carbohydrate storage according to their sizes. This method was applied in the present study on five out of the 15 cored trees per plot. One core from the stem (at 1.3m height above ground) and one core from coarse roots (around 40 cm from the stump) were taken from trees at the end of May (on about day of year (DOY) 145 for oak and DOY 137 for beech) and in October (about DOY 298 for both species), i.e. the expected dates of minimum and maximum concentrations respectively. For the 2006 growing season, budburst occurred on DOY 120 for beech and DOY 125 for oak, while leaf fall was completed on DOY 320 at both sites. Note that the samples of coarse roots were taken from different roots at each date and were partially excavated just before coring. Cores were taken using an increment borer (5 mm in diameter), transported with a freeze-pack in the field and then stored at -20°C in the laboratory.

Reserve compounds are stored in living tissues located in the sapwood (Saranpää and Höll 1989, Höll 1997). Assuming that root biomass is free of heartwood for both species, carbohydrate concentrations in roots were determined on the 5 cm of core under the bark. Concerning the above-ground compartment, the radial distribution of sapwood differs between sessile oak, being a ring porous species, and beech, which is a diffuse porous species. Whereas oak exhibits a clear boundary between sapwood and heartwood, the heartwood of beech remains invisible. However, even if sapwood transformation into heartwood is one of the main processes linked with natural ageing in trees (Wagenführ 1989 *cited in* Gjerdrum 2003), it is commonly accepted that heartwood is negligible or absent in beech in the age range considered in the present study (Lüttenschwager and Remus, 2007, Schäffer et al., 2000). Therefore, in order to facilitate comparison between both species, carbohydrate concentrations in stems were determined on the whole visible sapwood for oak and the 10 most recent tree rings for beech. The decrease in TNC in the outer-most part of beech xylem was quantified on 20 trees (data not shown). Concentrations in the inner part of the stem were assumed to represent 62.5 % of the concentration occurring in the outer 10

rings. The bark was removed from the cores and TNC analysis was restricted to the xylem. Carbohydrate contents were computed from the product of concentrations and tree biomass of tissues containing TNC. For sessile oak, sapwood width was measured on every core according to wood colour transition and the proportion of vessels obstructed with tyloses.

CARBOHYDRATE ANALYSIS

Total non-structural carbohydrates were quantified enzymatically according to Barbaroux and Bréda (2002). Total non-structural carbohydrates (TNC) were calculated as the sum of the main soluble sugars (glucose, fructose, sucrose) and starch and were expressed in glucose equivalents which were converted to carbon mass (gC) by applying a 40% carbon content in glucose.

TREE RING ANALYSIS AND TREE AGE MEASUREMENT

Fifteen trees per plot were cored to the pith at breast height using an increment borer, taking one core per tree. The circumference of each tree at breast height was also measured. Growth coring and circumference measurements were made in February 2007. Tree-ring chronologies were developed from wood cores using standard dendrochronological procedures (Stokes and Smiley, 1996). After surface treatment, air-drying and preliminary visual ring counting, tree-ring widths were measured to the nearest 0.01 mm with a binocular microscope and a digitalizing table. Cross dating was then performed for each tree following the method described by Douglass (1941). Then age was also determined at breast height for each sampled tree.

BIOMASS ESTIMATION AT TREE SCALE

Dry matter biomass (g DM) was estimated for each of the fifteen trees cored per plot. Mean tree biomass was then computed for each plot of the two chronosequences.

Aboveground biomass was computed as the product of volume and wood density. Total aboveground volume was estimated from the allometric equations using both tree circumference and height published by Vallet et al. (2006) for northern France. Wood density of beech was estimated from a relationship depending on tree age (Barbaroux 2002). For sessile oak, wood density was estimated from a model using tree ring width and cambial age

that was fitted to sessile oak in northern France by Le Moguédec and colleagues (2002). Then, the sapwood volume of oak was computed as the difference between total volume and heartwood volume. Heartwood diameter was computed as the difference between stem diameter resulting from the measured circumference and sapwood width measured on the cores. As there were no existing allometric relationships linking root biomass and tree age, a collection of published data sets containing above and belowground biomass estimations was made to estimate belowground biomass of beech and sessile oak. Dry matter biomass was converted to carbon mass (gC) by applying a 48% carbon content (Nys, personal communication).

CARBON INCREMENT IN WOOD AND NON STRUCTURAL CARBOHYDRATES IN 2006

Wood production in 2006 was calculated for each tree as the difference between wood biomass in 2005 and that of 2006. Tree ring measurements were used to estimate diameter increment and diameter at breast height between 2005 and 2006.

Total non-structural carbohydrate increment in 2006 was calculated as the difference between the TNC content at the end and at the beginning of the growing season. TNC contents were calculated as the product of TNC concentration and the related biomass.

Carbon increment in wood and storage production were then scaled-up to stand level by summing the carbon increment in wood and TNC storage for each inventoried tree and were expressed per unit of leaf or ground area.

CARBON ALLOCATED TO SEED PRODUCTION AT THE STAND SCALE

The year 2006 was a significant masting year in the beech chronosequence and a bad to null masting year for the sessile oak chronosequence. Considering the great variability of seed production between individual trees (Gysel 1956), seed production of beech was estimated at stand level from a systematic network of 15 collection points which were each 0.7 m^2, distributed regularly within a 1ha area, and centered in the middle of each plot. Seed production was estimated in 3 randomly selected plots per age class, except in the youngest (thicket) where no seed production was observed. Finally, seed production was estimated from a total of 225 harvest points, distributed in five age classes in the beech chronosequence.

Beechnuts and cupules were collected directly on the ground between DOY 310 and DOY 315. In fact, several studies on beech fructification in the north and centre of France show that more than 95 % of seeds and cupules have fallen from the trees at the end of October (Le Tacon and Oswald 1977, Oswald 1984). To ensure the total harvest of seeds and cupules, all of the litter fall was collected at each sampling point and seeds and cupules were sorted in the laboratory. Moreover, to take into account wildlife predation of beechnuts, we corrected beechnut counts using lignified cupule counts, as they are not consumed by wildlife – each cupule containing two nuts (Le Tacon and Oswald 1997). Seeds and cupules from each sampling point were counted, dried at 105 °C for 48 hours and weighed. The carbon content of seeds and cupules was fixed at 50 % (Lebret 2002).

LEAF AREA INDEX MEASUREMENTS AND THE CONTRIBUTION OF OAK OR BEECH LAI TO TOTAL STAND LAI

To estimate carbon productivity per leaf area and to carry out water balance calculations, Leaf Area Index was estimated at each plot of both chronosequences with a Licor LAI-2000 (LI-COR Inc., Nebraska, USA). At least 21 measurements were made along transects below the canopy on sunny days, at less than 1 h after sunrise or before sunset. Linearly interpolated values of incident light on three zenith angles were used (from 0 to 43°) (Dufrêne and Bréda 1995).

Beech stands were monospecific so that beech represented the main contribution to measured LAI. Conversely, adult oak stands of the Champenoux site contained an understory composed of hornbeam (*Carpinus betulus*) and so Li-Cor LAI measurements included both species. In order to quantify the influence of hornbeam on LAI measurements, litter collection (Bréda, 2003) and forest inventories (Cluzeau et al. 1998), data coming from 11 permanent oak level II plots of the French part of the Forest Monitoring network (RENECOFOR), were used to calibrate the contribution of hornbeam to total stand LAI, according to Eermak (1998). For reasons of coherency, the relationship between the proportion of LAI and the proportion of basal area was forced to contain (0,0) and (1,1) intercepts. Enclosed in parenthesis are the results of the Fisher test of significance (*F*=Fisher value and *P*= significance probability value).

LAI *Quercus* = LAI Stand * [-0.0661 * (1- exp (2.78 * (BA *Quercus* / BA Stand)))]
(*F*= 540.24, *P*<0.0001)

where: LAI *Quercus* is LAI of oak, LAI Stand is LAI measured with Li-Cor canopy analyser, BA *Quercus* is basal area of oak and BA Stand is basal area of oak and hornbeam.

STATISTICAL ANALYSIS

Data were analysed using the SAS statistical package (SAS 9.1, SAS Institute Inc., Cary, NC, USA) (SAS 1988). A Non-linear model (proc nlin) was used to determine the relationship between Root:Shoot ratio and age. Different types of models were tested and the selection of the best model was based on the lowest residual sum of squares. For the carbohydrate concentration analysis, an initial analysis of variance (ANOVA) was carried out to determine factors that significantly influenced concentrations. Effects of species + site, organ, and date were tested and each factor had two levels. Seasonal differences in concentrations were also tested for each combination of species and organ with an ANOVA. For TNC concentration, biomass, carbon increment and allocation variables, two main effects were tested: (1) species effect, with an ANOVA, and (2) stand age effect with linear regressions for each species. To compare species (+ site) properly, species effect and age effect for each species were tested in comparable age ranges, i.e. the youngest and oldest beech classes were excluded from these analyses.

RESULTS

FACTORS INFLUENCING CARBOHYDRATE CONCENTRATIONS

Concentrations determined enzymatically, concerned a total of 328 wood samples. Carbohydrates were analyzed according to site + species (oak or beech), stand age, tree compartment (stem or coarse root) and date of sampling (May or October). Concentrations were higher for oak than for beech (Table 3). However, because the species were located in different forests, species differences may also include some site influence. Stand age had no significant effect for the two species (Table 3).

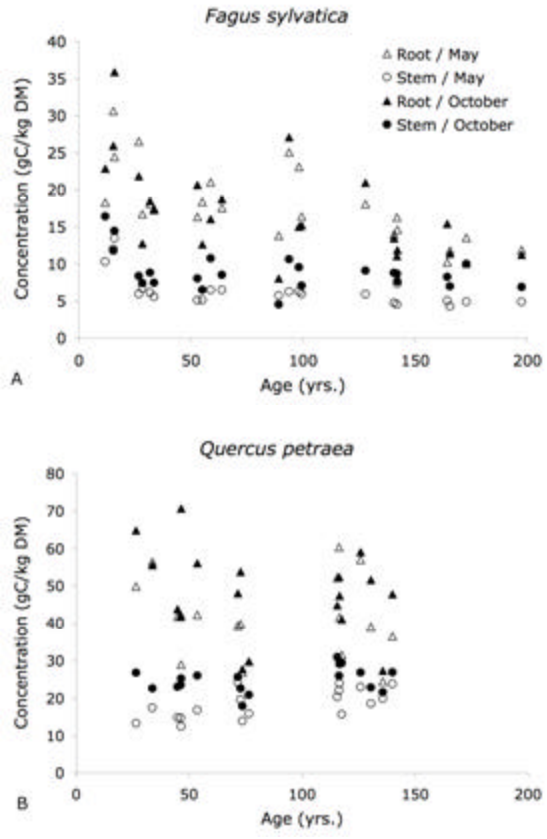

Figure 1: Total non structural carbohydrate concentrations as a function of age class in coarse roots (triangle) and stem (circle) in May (open) and October (solid) for (A) beech and (B) sessile oak.

Depending on stand age, concentrations ranged from 12.5 to 70.7 g/kg of dry matter (DM) for oak and from 4.3 to 37.4 gC/kg DM for beech (Figure 1). Stem concentrations remained stable throughout the age sequence for both species, except for young beech stands (around 15 years old), which exhibited higher concentrations. In coarse roots, concentrations were more variable between the stands. Root concentration decreased sharply up to around 35 years old for beech and around 75 years old for sessile oak. This reduction was followed by stable or slightly rising concentrations for oak up to 145 years old and a slight but constant decrease for beech up to 200 years-old.

Trends of TNC concentrations with stand age were similar for the two dates. Concentrations in October were significantly higher than concentrations in May for both species (F=19.4, P<0.0001 for sessile oak and F=10.5, P<0.0001 for beech), except for coarse beech roots (F=0.01, P=0.9427). No trend with age appeared relative to seasonal differences in concentrations between May and October 2006. As for the raw concentrations, seasonal differences in concentrations were significantly higher for oak than for beech (F=55.9, P < 0.0001). For both species, TNC concentration was higher in coarse roots than in stems (F=19.9, P<0.0001 for sessile oak and F=23.54, P<0.0001 for beech).

Table 3: Effects of species (+ site) and age on biomass and carbon increments. Species comparison was carried out by analysis of variance on similar age ranges, i.e. excluding the youngest and oldest beech stands. Linear regression was used to assess age effect. Age effect was tested for each species. Abbreviations:* F= *Fisher test value,* P=*probability.

Variable	Species (+Site)			Age					
				Quercus petraea			*Fagus sylvatica*		
	Fag. syl. versus Querc.pet.	*F*	*P*	Estimate	*F*	*P*	Estimate	*F*	*P*
TNC concentrations	Lower	114.20	<0.0001		0.02	0.9002		0.67	0.4157
Biomass		0.03	0.8530		0.00	0.9509		0.97	0.3410
Biomass increment per leaf area	Lower	23.34	<0.0001	-0.60	38.68	<0.0001	-5.65 E-3 *	27.71	<0.0001
TNC increment per leaf area	Lower	16.88	0.0003	-0.16	6.30	0.0232		0.02	0.8939
Seed production per leaf area							0.222	66.65	<0.0001
Biomass increment per soil area		0.06	0.8033	-3.82	30.34	0.0001	-4.44	14.41	0.0020
TNC increment per soil area	Lower	7.37	0.0106	-0.96	6.35	0.0228		0.00	0.9636
Seed production per soil area							1.026	82.64	<0.0001
Carbon allocation to growth	Lower	7.27	0.0111		0.13	0.7255	-4,03 E-3	53.51	<0.0001
Carbon allocation to TNC	Lower	16.63	0.0003		0.13	0.7255	5.52 E-4	1.1411	0.3037
Carbon allocation to reproduction							3.48 E-3	72.18	<0.0001

STAND BIOMASS THROUGHOUT THE CHRONOSEQUENCES

Stand biomasses were estimated (1) from allometric relationships to estimate tree biomass and (2) from stand inventories. Without existing allometric relationships linking root biomass and tree age, an age-related relationship of [Root:Shoot] ratio (RS) was assessed from published data concerning deciduous species belonging to *Quercus* and *Fagus* genera located in temperate forests of different continents. The references are listed in Appendix 1. Indeed, meta-analysis conducted by Cairns and colleagues (1997) revealed that, except for a latitudinal effect distinguishing species distribution, climatic parameters (i.e. temperature and rainfall) had no influence on RS. For the *Quercus* genera, RS described an exponential decrease with stand age before stabilization at about 0.18 after 90 years old (Figure 2). A non-linear model was fitted for RS as a function of stand age (F=32.26, P<0.0001).

$$RS_{Q.p.} = 0.1893 + 0.8295 * \exp(- 0.0496 * age).$$

For *Fagus,* RS presented a more precocious and abrupt decrease than for *Quercus*, stabilizing after 25 years old at about 0.18 (F = 120.55, P<0.0001).

$$RS_{F.s.} = 0.1830 + 1.6259 * \exp(-0.3174 * age).$$

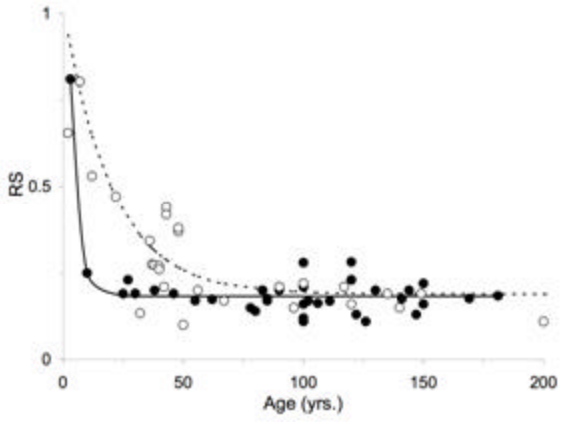

Figure 2: [Root:Shoot] biomass ratio extracted from the literature review, as a function of stand age for* Quercus *(open circle, dotted line) and* Fagus *(solid circle, solid line).

The order of magnitude of stand biomass was similar for beech and sessile oak stands (Figure 3). In beech stands, biomass increased significantly with stand age while it remained constant over time in sessile oak stands (Table 3, Figure 3). However, the proportion of stand basal area occupied by hornbeam increased with stand development from around 9.4 % in the youngest oak stands up to 44 % around 115-year-old (Table 2, insert in Figure 3).

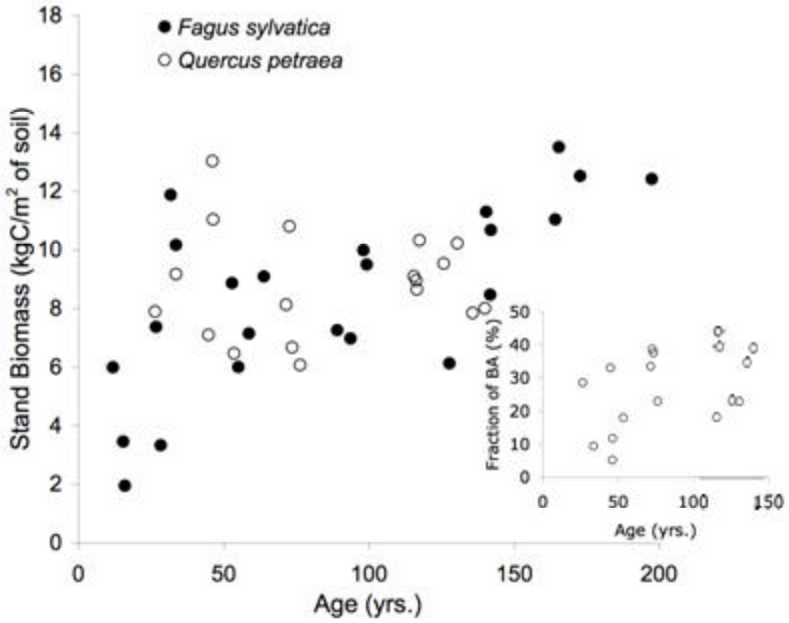

Figure 3: Variation in stand biomass per unit of soil area (aboveground + belowground) with stand age for beech (solid circle) and sessile oak (open circle). The insert is the relationship between the percentage of stand basal area (BA) occupied by hornbeam in the oak chronosequence and stand age.

GROWTH, STORAGE AND REPRODUCTION BALANCE AT THE STAND SCALE FOR YEAR 2006

Upscaling of carbon increments to the stand scale was performed using carbon increments estimated at the tree scale and from forest inventories. Seed production was estimated from fruit collection at the stand scale. Oak and beech LAI was used as a proxy of carbon assimilation at the canopy level. Carbon increment, expressed per leaf area unit, and allocation coefficients were displayed in Figure 4. Carbon invested in seeds, biomass, TNC increment, expressed per ground area unit, was averaged for each age class and is given in Table 4. Carbon increments averages for each age classes are displayed in the following paragraph.

Table 4: Seed production, biomass and TNC increments per unit of soil area, during growing season 2006 averaged by age class for oak and beech chronosequences.

Species (+ Site)	Mean Age (years)	Seeds (gC/m^2)	Biomass ($gC/m^2$of soil/yr)	TNC (gC/m^2 of soil/yr)
Quercus petraea	30	-	513 (47)	118 (18)
	48	-	388 (137)	149 (40)
	73	-	279 (74)	48 (11)
	116	-	185 (20)	55 (25)
	133	-	202 (56)	48 (8)
Fagus sylvatica	14	0	457 (107)	32 (5)
	30	56 (1)	556 (140)	26 (4)
	58	76 (3)	221 (37)	27 (3)
	95	64 (1)	191 (28)	13 (7)
	138	129 (6)	142 (38)	29 (4)
	175	101 (4)	95 (14)	54 (5)

For beech, the annual biomass increment was high in the youngest stands and decreased sharply with stand age from an average of 103 gC/m^2 of leaf/yr at around 30 years old to an average of 39 gC/m^2 of leaf/yr at around 60 years old. It decreased slightly in the oldest stands to 20 $gC/m^2/yr$ at around 175 years old (Figure 4a). Considering the same age range for sessile oak, the TNC annual increment did not change with age (Table 3). However, the age

related increase of TNC annual increment became more significant when the entire age range was considered (F=2.39, P=0.0979). Seeds (Table 3) and TNC annual increment increased slowly and regularly with stand age to 19 and 13 gC/m²/yr respectively at around 175 years old (Figure 4a). For sessile oak, annual biomass increment increased with stand age to a peak average of 161 gC/m² of leaf/yr at around 75 years old and decreased sharply to 74 gC/m²/yr at around 135 years old (Figure 4b). After a short increase, annual TNC increment decreased slowly with stand age from 43 to 12 gC/m² of leaf/yr (Table 3, Figure 4b). For both species, age-related changes in carbon increments expressed per ground area unit were similar to those observed for carbon increments expressed per leaf area unit (Table 3, Table 4)

Comparing the carbon allocation for beech in 2006 (Figure 4b,d), we observed that carbon invested in growth, i.e. biomass increment, decreased significantly with stand age to the benefit of storage, i.e. TNC increment and reproduction (seed and cupule production) (Table 3, Figure 4b). Considering the same age range for sessile oak, carbon allocation to TNC did not change with age (Table 3). However, the age related increase of carbon allocation to TNC became significant when the entire age range was considered (F=12.35, P=0.0021). For sessile oak, carbon allocated to growth and storage remained constant with stand age (Table 3, Figure 4c).

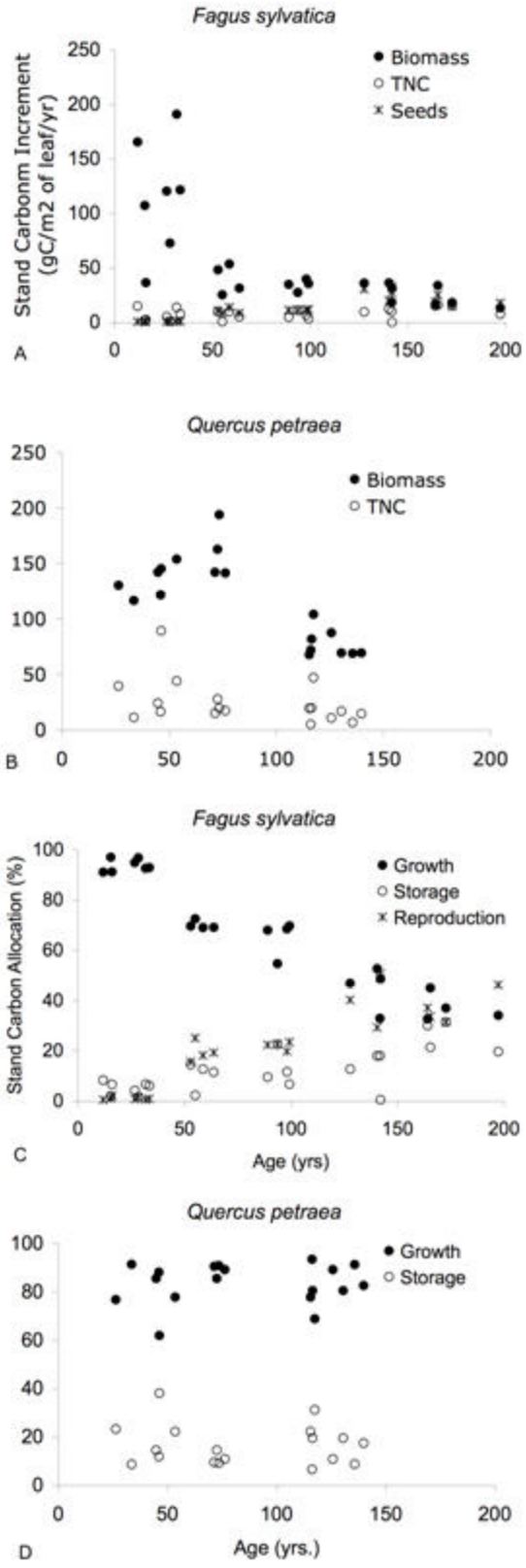

Figure 4: Variation with age at the stand level of: (A&B) absolute carbon increment and (C&D) carbon allocation per unit of leaf area and per year for beech (A&C) and sessile oak (B&D). Biomass increment and growth (solid circle), TNC increment and storage (open circle) and seed production and reproduction (star) are represented for growing season 2006.

DISCUSSION

AGEING EFFECT ON TNC CONCENTRATIONS

The specific and seasonal differences in TNC concentrations observed in our work agree with existing TNC distribution descriptions. As previously reported, TNC concentration was higher for oak than for beech (Barbaroux and Bréda 2002, Barbaroux et al. 2003, Hoch et al. 2003, Valenzuela-Nunez 2006), higher in coarse roots than in stems and higher in October in comparison with May, except in the coarse roots of beech (Jones and Bradlee 1933, Dubroca 1983, Bollmark et al. 1999, Barbaroux and Bréda 2002, Barbaroux et al. 2003, Palacio 2007). This pattern was observed for all age classes. If we consider concentration to be an equilibrium between storage and consumption at a given time, the decrease in root TNC concentrations of beech during the growing season 2006 can be interpreted as a failure in the allocation of carbon to root storage or an intense consumption of carbohydrates during the growing season, exceeding carbohydrate inputs. Indeed, drought did occur in 2005 and 2006 at the beech site inducing a significant soil water deficit as computed by daily water balance calculation (data not shown). Yet, Leuschner et al. (2001) showed clearly that in a mixed stand, drought stress induced a large increase of fine root growth in beech while this was not observed in sessile oak. Thus, droughts coupled with high fine root sensitivity to drought could have induced higher levels of damage to fine roots in beech stands than in sessile oak stands. Therefore, belowground carbohydrates in beech could have been used in order to restore the fine root stock after a severe drought (Leuschner et al. 2001) and to sustain fine root growth allowing water uptake in late summer and early autumn (Idol et al. 2000, Ponti et al. 2004, Satomura et al. 2006).

In contrast to Sala and Hoch (2009), who found an increase of carbohydrates concentrations with tree height, we found that TNC concentrations decreased or remained stable with tree age. This difference might be related to the structure of the stands studied. The sites studied by Sala and Hoch were located in stands with trees of different height. Therefore, the height-related differences in carbohydrate concentration might combine age-related changes and changes related to the status of the tree in the stand.

Age effect on TNC concentrations was restricted to young stands for both species. Both species presented the highest TNC concentrations in the youngest trees, except in sessile oak

stems. This profile reflects distribution changes in the early stage of stand development. Firstly, the concentration decrease between sapling and other ages could be linked to high differences between foliar area and sapwood biomass distribution. Indeed, young stands are characterized by a lower [Sapwood biomass / Leaf Area] ratio (Bartlink 1996, Lebret 2001 and Huet 2004). If we consider the foliar compartment as a mainly "production" site and wood compartment as a mainly "storage" site, young trees are characterized by a high carbohydrate production capacity and a low carbohydrate storage capacity, resulting in a higher concentration of TNC in wood. With increasing age, the [Sapwood biomass / Leaf Area] ratio increased, inducing a possible decrease of TNC concentrations.

In beech stands, despite the constant increase in storage capacity (i.e. sapwood biomass) relative to assimilation capacity (i.e. leaf area), TNC were not diluted and concentrations remained stable over time, after a short depletion in the young stands (30 years old). We have shown that this stabilization resulted from an increase in carbon allocation to the storage function in adult trees. Furthermore, turgor pressure seems to decrease with increasing tree height, as already shown in tall Douglas fir trees (Woodruff et al. 2004). If this hypothesis was verified, lower turgor pressure in tall old trees would limit cell expansion and induce an increase in TNC concentrations (Ryan et al. 2006). In oak stands, the [Sapwood biomass / Leaf Area] ratio increased up to 90 years old and decreased afterwards (data not shown). This decrease has been related to the increasing weight of accompanying species with stand age that induced a decrease in oak LAI and a limited increase in hornbeam biomass. The weakening of storage capacity and constancy of allocation to storage with age resulted in the very slight, non-significant increase of TNC concentrations with age.

Finally, a concentration decrease in coarse roots between the sapling stage and other stages of development could be linked to the early decrease of RS with stand age that we established from the literature review, which was contrary to the previous broader meta-analysis of Cairns and colleagues (1997), but in accordance with Bartelink (1998). Indeed, variations of RS with age reflect variations of belowground growth relative to aboveground growth. Large values of RS can reveal high levels of root growth compared to aerial growth. Then, high belowground concentrations in young trees of both species could be intended to finance a large growth rate of root systems. It is all the more likely that a decrease in concentrations with age followed a decrease in the RS with age for both species.

INCREMENT OF GROWTH, CARBOHYDRATES AND REPRODUCTION DURING THE GROWING SEASON 2006

In young stands, biomass increments of beech were higher than those found by Granier et al. (2008) in a similar aged stand in Hesse forest, France (556 gC/m²/year in the present study *versus* 418 gC/m²/year in the study of Granier et al. 2008). These differences were coherent with other productivity indicators: despite higher stand density, the basal area was lower in the Hesse site compared to the Fougères site. In adult stands, the biomass increments were consistent with results from previous studies (Lemaire et al. 2005, Matinez-Vilalta et al. 2007). For both species, growth efficiency sharply decreased with age from the pole stage to old-growth forests. These observations are in accordance with the widely described age-related decline in forest productivity (e.g. Gower 1996, Ryan et al. 1997, Mencuccini et al. 2005, Zaehle et al. 2006, Martinez-Vilalta et al. 2007). As for RS, productivity decline occurred earlier for beech than for oak. Seed production was significant from 58 years old, in agreement with previous knowledge that sexual maturity for beech is reached at about 60 years old (Oswald 1984). Yet, traces of viable seed production were found from 14 years old. Seed production increased with age to 130 gC/m² in the 138-year-old stand in 2006, revealing a good masting year (Oswald 1984, Le Tacon et al. 1977, Övergaard et al. 2007). For both species, carbohydrate increment (and seed production for beech alone) did not offset growth decline. This result suggests that carbon functioning in old trees might be limited by carbon availability (Ryan et al. 2006).

TWO CONTRASTING CARBON ALLOCATION PATTERNS?

Comparing wood, carbohydrate increment and seed production (for beech only) allowed us to estimate shifts in the carbon allocation between growth, storage and reproduction during stand development. For sessile oak, carbon allocation to growth and storage remained constant over the age range we studied. Carbon allocation to acorn production could not be estimated because of a lack of masting during the observation year. Conversely, for beech the carbon allocation to growth decreased sharply with stand age to the benefit of storage and reproduction: the allocation scheme shifted from a stage which was mainly an "allocation to growth" in young stands, where prospecting the environment was high, to a mainly "allocation to reproduction and storage" stage in older stands, to finally ensure tree regeneration (Oliver and Larson 1990, Becker 2000).

Thus, whereas carbon allocation to growth decreased sharply with ageing for beech, it seems to remain stable for sessile oak (in the age range we sampled). The maintenance of a high carbon allocation to growth in sessile oak trees throughout their lifespan is probably be related to the hydraulic properties of ring-porous species. In the spring, most of the early wood vessels of ring porous species are embolised by frost events of the previous winter and the radial growth prior to budburst is required for soil to leaf hydraulic conductance recovery (Hinckley and Lassoie 1981, Bréda and Granier 1996, Hacke and Sauter 1996). For diffuse porous species like beech, which are less vulnerable to winter embolism, hydraulic conductivity is partly preserved from year to year. Therefore, early growth, as a key factor for sap flow recovery, is less essential than for sessile oak (Hacke and Sauter 1996, Lemoine et al. 1998).

Furthermore, several studies have demonstrated a negative correlation between radial growth and seed production for different species belonging the *Fagus* genera (Piovesan and Adams 2001, Kitamura et al. 2007), for *Nothofagus truncata* (Monks and Kelly 2006) and for other species (Waller 1979, Selas et al. 2002). Therefore, the massive production of seeds observed in adult beech stands may have emphasized the age-related decrease of carbon allocation to growth. The lack of significant seed production in sessile oak stands may not have induced such a decrease. Moreover, silvicultural practices in Europe are characterized by intensive thinning. During masting years, intensive thinning and seeding felling may favour seed production and emphasize the effect of seed production on the age-related decrease of carbon allocation to growth (Perry et al. 2004). In contrast, during non-masting years, intensive silvicultural practices may favour tree growth (Bastien et al. 2005) and sustain a high growth

rate in adult stands. This reason may partly explain the high carbon allocation observed in mature stands of sessile oak.

Carbon allocation to storage was higher for sessile oak than for beech, whatever the age of stands. High levels of carbon allocation to storage observed for sessile oak might be partially related to the necessity to achieve early growth prior to budburst. Before bud-burst, this early growth is dependent on storage compounds (Barbaroux 2002). Thus, for ring porous species like sessile oak, carbohydrate reserves are necessary to sustain early growth and it seems to be a key factor for tree maintenance and survival. These properties result in an equilibrium in the carbon allocation between growth and storage functions and this balance remains stable throughout the lifespan of the tree. Beech, as a diffuse porous species, initiates the growing period after budburst (Barbaroux and Bréda 2002). Therefore, early growth is less dependent on reserve amount and the reserve pool might be lower than for sessile oak.

Furthermore, soil water deficits occurring at the continental site of the sessile oak are around three times more severe than those occurring at the beech site subjected to an oceanic climate type. The intense and repeated drought events to which sessile oak stands are subjected, may not be compensated for by the slightly higher mineral fertility (Table 1). These repeated soil water deficits may have induced a selection pressure favoring trees presenting high storage capability for reserve compounds to combat soil water deficits (Yordanov et al. 2000).

Over the same age range, carbon allocation to storage remained constant for both of the studied species. However, allocation to storage in beech increased significantly with age when younger and older stands were integrated in the analysis. This increase may ensure maintenance respiration of large woody tissues, may improve the defense capacity of ageing trees against environmental perturbation and may help to ensure soil to leaf hydraulic conductivity (Niinemet et al. 2002, Mencuccini et al. 2005, Ryan et al. 2006). Additional work might be conducted on older even-aged oak stands to check whether this trend occurred for this species as well.

Even if reproductive shoots support most of the reproduction (Miyazaki et al. 2002, Hoch et al. 2005), starch concentrations in the non-reproductive shoots seem to decrease during the mast year as well (Gaümann 1935, Hoch et al, 2003, Miyazaki et al. 2002). Furthermore, the mast event may induce a leaf area decrease in beech (Innes 1994). Therefore, the age-related increase of seed production observed in the beech chronosequence may have mitigated the age-related increase of carbon allocation to storage.

Finally, our study was focused on ageing effects on carbon allocation to handle the productivity-decline during a standard forest rotation. However, these results pointed out the need to extend this analysis to trees reaching the limits of longevity, i.e. 150-300 years old for beech and 500-1000 years old for sessile oak (Rameau et al., 1989). Senescing processes could be different from ageing processes.

During masting years, we observed that carbon allocation to seed production increased with stand age for beech, which may have induced a decrease in growth and carbohydrate concentrations. The effects of acorn production on carbon allocation were not assessed for sessile oak but we suppose that the impact on growth and storage pools would be similar to those observed for beech. However, the additional constraints related to the need to complete a minimum growth with a minimum amount of reserves may reduce the amount of carbon available for seed production. This hypothesis may explain the lower frequency of mast years for sessile oak compared to beech. Indeed, Aussenac (1975) reported that the frequency of significant masting events for sessile oak at the site studied was around 5.5 years (an average over 107 years from 1865 to 1971) while beech masting occurred at a biannual rhythm in the site studied (C. Nys pers.comm.).

The additional growth constraint makes the allocation pattern of sessile oak more stable but also less flexible than that of beech. This difference could be linked to the higher variability of radial growth to environmental perturbation observed in beech (Leuschner et al. 2001, Ashoff et al. 2006). Growth in beech could be an "adjustment variable" to a certain extent, allowing trees to increase storage production and mobilization during environmental perturbation. However, these results concerned one year of observations and need to be confirmed by similar studies under different growth conditions, notably concerning drought intensity and masting events.

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APPENDIX 1

Published studies containing Root:Shoot ratio measurements on Quercus and Fagus species at tree or stand level. AGB = Aboveground biomass expressed in kg at tree scale or in t/ha at stand scale. BGB = Belowground biomass expressed in kg at tree scale or in t/ha at stand scale. RS = Root:Shoot ratio.

Species	Country	Age (years)	Height (m)	Density (/ha)	Scale	BGB (kg or t/ha)	AGB (kg or t/ha)	RS	Reference
Quercus petraea	France	2	2		Tree	0.245	0.375	65.4	Van Hees et al. 2003
Quercus petraea	France	7	0.9		Tree	0.013	0.016	81.3	Drexhage 2003
Quercus petraea	France	32	12	8400	Tree	5	35	14.3	Drexhage 1999
Quercus robur	Sweden	149	20		Tree	165	866	19.0	Anderson 1970 *cited in* Santantonio 1975
Quercus robur	USSR	12	5		Stand	23	43	52.8	Rodin and Basilevich 1967 *cited in* Cannell 1981
Quercus sp	USSR	22			Stand	29	62	46.8	Sonn 1960 *cited in* Santantonio 1975
Quercus mongolica	Korea	36	13	3175	Stand	27	79	34.4	Park et al. 2005
Quercus variabilis	Korea	37	10	2450	Stand	19	68	27.5	Park et al. 2005
Quercus variabilis	Korea	38	14	2900	Stand	26	97	27.3	Park et al. 2005
Quercus robur	USSR	40	11		Stand	32	118	26.9	Rodin and Basilevich 1967 *cited in* Cannell 1981
Quercus robur	USSR	40	11		Stand	32	123	26.0	Smirnova and Gorodentseva 1958 *cited in* Santantonio 1975
Quercus sp	USSR	42			Stand	29	141	20.6	Sonn1960 *cited in* Santantonio 1975
Quercus robur	USSR	43	18		Stand	46	105	43.8	Rodin and Basilevich 1967 *cited in* Cannell 1981
Quercus robur	USSR	43	18		Stand	46	109	42.2	Mina 1955 *cited in* Santantonio 1975
Quercus robur	USSR	48	23		Stand	70	187	37.5	Rodin and Basilevich 1967 *cited in* Cannell 1981
Quercus robur	USSR	48	23		Stand	70	191	36.6	Remezov et al.1960 *cited in* Santantonio 1975
Quercus rubra var *borealis*	USA	50	17		Stand	16	165	9.7	Ovington et al. 1963 *cited in* Santantonio 1975
Quercus sp	USSR	56			Stand	38	194	19.6	Sonn1960 *cited in* Santantonio 1975
Quercus robur	Belgium	67	18	310	Stand	25	152	16.8	Yuste 2005
Quercus petraea and *Q. robur*	Belgium	90	20	190	Stand	32	154	20.8	Duvigneaud et al. 1971 *cited in* Santantonio 1975
Quercus petraea and *Q. robur*	Belgium	90	21	180	Stand	35	169	20.7	Duvigneaud et al. 1971 *cited in* Santantonio 1975
Quercus petraea and *Q. robur*	Czecoslovakia	96			Stand	46	315	14.6	Vyskot 1976 *cited in* Röhrig 1991
Quercus petraea and *Q. robur*	Poland	100		297	Stand	50	226	22.1	Medwecka-Kornas et al. 1981 *cited in* Röhrig 1991
Quercus petraea	Belgium	117	24	160	Stand	55	261	21.1	Duvigneaud et al. 1971 *cited in* Santantonio 1975
Quercus robur	Belgium	120	24	110	Stand	52	332	15.7	Duvigneaud et al. 1971 *cited in* Santantonio 1975
Quercus petraea and *Q. robur*	Belgium	135	22	420	Stand	39	204	19.1	Duvigneaud et al. 1971 *cited in* Santantonio 1975
Quercus petraea and *Q. robur*	The Netherlands	140		300	Stand	42	273	15.4	Van der drift 1981 *cited in* Röhrig 1991
Quercus sp	USSR	200			Stand	43	407	10.6	Sonn1960 *cited in* Santantonio 1975
Quercus robur	USSR	220	30		Stand	97	403	24.2	Rodin and Basilevich *cited in* Cannell 1981
Quercus robur	USSR	220	30		Stand	97	406	23.9	Mina 1955 *cited in* Santantonio 1975
Quercus petraea and *Q. robur*	USSR	250		557	Stand	92	300	30.7	Goryshina 1974 *cited in* Röhrig 1991

Species	Country	Age (years)	Height (m)	Density (/ha)	Scale	BGB (kg or t/ha)	AGB (kg or t/ha)	RS	Reference
Fagus sylvatica	Nursery	3	1.8		Tree	0.231	0.285	81.1	Van Hees et al. 2003
Fagus sylvatica	Sweden	78	20		Tree	137	917	14.9	Nihlgard 1972 *cited in* Santantonio, 1975
Fagus sylvatica	USA	106	16		Tree	105	645	16.3	Whittaker,1974 *cited in* Santantonio, 1975
Fagus sylvatica	Belgium	120			Tree	122	433	28.2	Mund 2004
Fagus sylvatica	France	25		5000	Stand	14	75	18.7	Lemée 1978
Fagus sylvatica	France	30		3500	Stand	15	78	19.2	Granier et al. 2000b
Fagus sylvatica	Germany	30	13.1	1664	Stand	6	33	18.9	Mund 2004
Fagus sylvatica	Germany	38	12.4	2048	Stand	9	43	19.9	Mund 2004
Fagus sylvatica	Denmark	46	18	3110	Stand	26	134	19.4	Möller et al. 1954 *cited in* Santantonio, 1975
Fagus sylvatica	Germany	55	24.7	1320	Stand	19	114	17.0	Mund 2004
Fagus sylvatica	Germany	62	28.5	625	Stand	25	145	17.4	Mund 2004
Fagus sylvatica	Germany	80			Stand	22	159	13.9	Mund 2004
Fagus sylvatica	Denmark	85	26	320	Stand	46	265	17.4	Möller et al. 1954 *cited in* Santantonio, 1975
Fagus sylvatica	Germany	85	29.8	560	Stand	23	132	17.6	Mund 2004
Fagus sylvatica	Denmark	90		370	Stand	43	221	19.5	Holm and Jensen, 1981 *cited in* Röhrig, 1991
Fagus crenata	Japan	100		357	Stand	37	173	21.4	Kakubari, 1977 *cited in* Röhrig, 1991
Fagus sylvatica	Bulgaria	100		2500	Stand	38	314	12.1	Garelkov, 1973 *cited in* Santantonio, 1975
Fagus sylvatica	Bulgaria	100	14	2000	Stand	50	441	11.3	Garelkov, 1973 *cited in* Santantonio, 1975
Fagus sylvatica	Bulgaria	100	17	1200	Stand	55	197	27.9	Garelkov, 1973 *cited in* Santantonio, 1975
Fagus crenata	Japan	100	24		Stand	57	276	20.7	Kakubari, 1977 *cited in* Röhrig, 1991
Fagus sylvatica	Germany	102	34.6	84	Stand	33	197	16.9	Mund 2004
Fagus sylvatica	Germany	111	36.9	224	Stand	33	195	16.9	Mund 2004
Fagus sylvatica	Belgium	120	25	199	Stand	62	269	23.0	Devillez et al. 1973 *cited in* Santantonio, 1975
Fagus sylvatica	Belgium	120		199	Stand	62	269	23.0	Devillez et al. 1973 *cited in* Santantonio, 1975
Fagus sylvatica	Germany	122			Stand	37	275	13.5	Mund 2004
Fagus sylvatica	Germany	126		239	Stand	32	293	10.9	Ellenberg et al., 1986 *cited in* Röhrig, 1991
Fagus sylvatica	Belgium	130		190	Stand	68	340	20.0	Duvigneaud et al. 1971 *cited in* Santantonio, 1975
Fagus sylvatica	Germany	141	38.3	100	Stand	25	144	17.5	Mund 2004
Fagus sylvatica	Belgium	144		160	Stand	74	374	19.8	Röhrig, 1991
Fagus sylvatica	France	150		350	Stand	40	246	16.3	Lemée,1978
Fagus crenata	Japan	150		785	Stand	64	292	21.9	Ogino, 1977 *cited in* Röhrig, 1991
Fagus sylvatica	Germany	169	39.8	64	Stand	20	111	17.6	Mund 2004
Fagus sylvatica	Germany	181	34.7	84	Stand	24	130	18.5	Mund 2004

Age-related variations of radial growth and its interactions with climate, from a dendrochronological approach: from long term to year-to-year time scales

INTRODUCTION

Tree-ring analysis may be used either as an indicator of tree growth or as an indicator of internal and environmental conditions occurring during growth. As an indicator of tree growth, tree ring width provides an estimate of the quantity of biomass produced (Bouriaud et al. 2005). Thus, tree rings have been used in the present study to assess past year-to-year variations of biomass and net primary productivity (NPP) at stand level, as already performed in recent studies (e.g. Graumlich et al. 1989, Yanai et al. 2000, Acker et al. 2002, Bond-Lamberty et al. 2002, Mund et al. 2002, Bascietto et al. 2004, Martinez-Vilalta et al. 2008).

Furthermore, the systematic study of annual tree rings is a valuable resource to relate the chronicle of radial growth of trees and stands. Indeed, considering the factors susceptible to determine radial growth, Cook (1987) conceptualized tree ring series as a linear aggregate of the following determinants:

$$Rt = At + Ct + Dt + Et$$

where Rt is the observed ring-width series, At is the growth trend associated with increasing age, Ct is the climatic signal that can vary at low or high frequency (e.g. global warming or annual drought), Dt is the tree disturbance signal divided into local and stand-wide disturbances (e.g. pruning and thinning respectively) and Et is the unexplained variability. In other words, Rt is mainly determined by age on the one hand and by events occurring at a given calendar date or period of growth on the other hand, as illustrated in Figure 5a. These factors affect growth rate at different time scales, commonly described as low, medium and high frequency signals. Low frequency signals group factors that affect growth over decades or centuries, like ageing or global changes. Medium frequency signals gather together factors affecting growth over several years, like thinning or fire. High frequency signals group factors affecting growth over one to two years, like year-to-year climatic variability or moderately defoliating insect attacks.

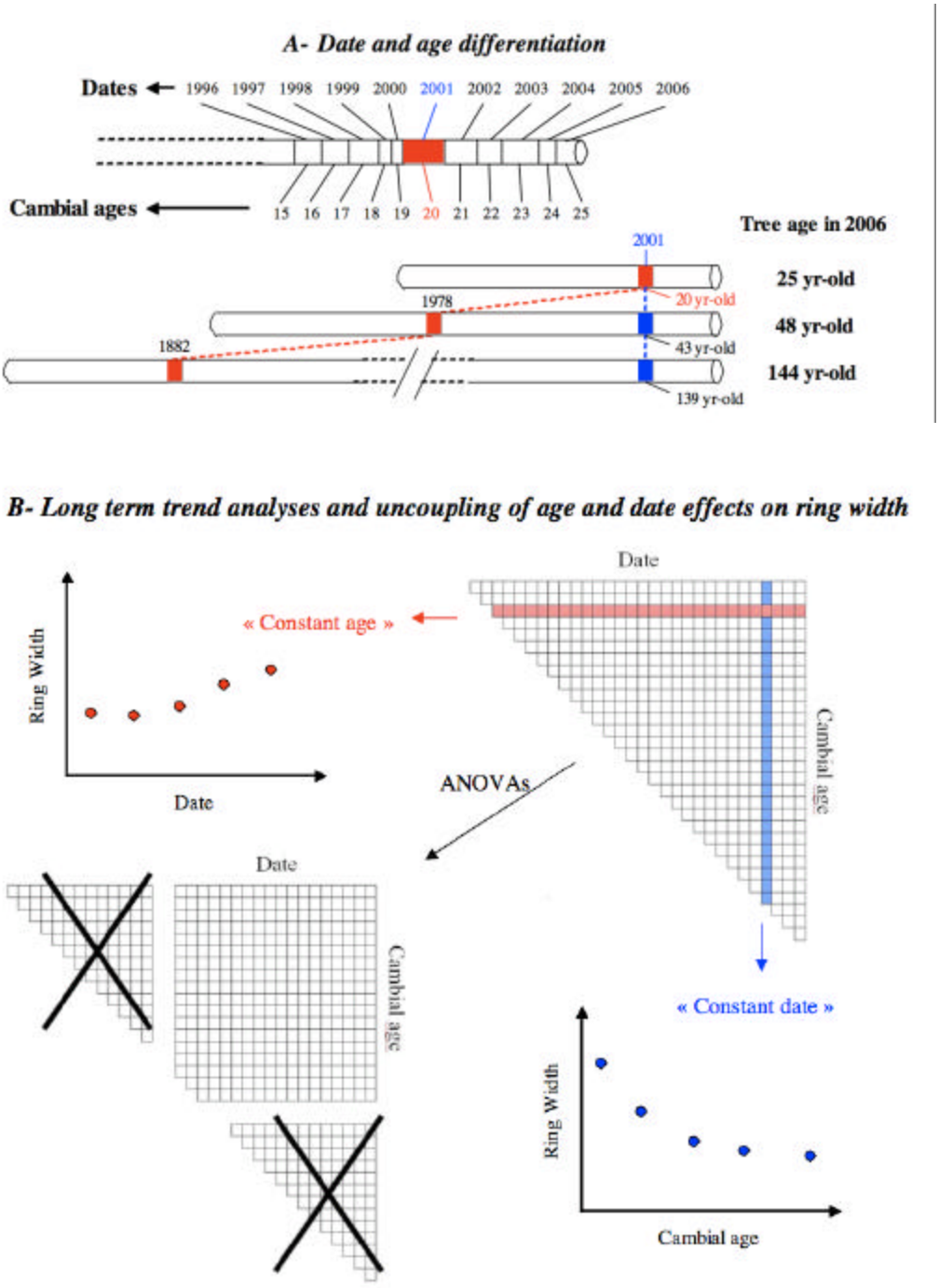


Figure 5: (a) Illustration of age and date differentiation on a core and (b) Illustration of two methods used to separate age and date effects on the long term trend of tree-ring width series: constant age and constant date curves and simultaneous analyses of age and date effects on ring-width series through analyses of variance on a balanced set of date and age combination (From Badeau, 1995).

The long-term effects of age on radial growth have long been considered as a background noise to be removed from a time series in order to study other sources of variations affecting radial growth. To that end, in the early studies of dendrochronology, many authors described the variation of radial growth with age, often consisting of an exponential function (Fritts 1976, Zeide 1993, Cook and Briffa 1990, Bontemps 2006). The removal of the age effect on tree ring series is known as standardization (Fritts 1976).

Except for standardization purposes, the effect of ageing *per se* remains poorly studied in dendrochronology. Yet, whereas a lot of studies underline an increased growth of adult trees over the last century (e.g. Briffa 1992, Jacoby et al. 1996, Becker et al. 1994, 1995, Badeau et al. 1995, 1996, Lebourgeois et al. 2000, 2001), several studies have pointed out premature mortality (or dieback) in many forested regions (Manion and Lachance, 1992) particularly over the last decades (Ogden 1988, Innes 1991, Manion and Lachance 1992, Bréda et al. 2006). This apparent paradox suggests that changes in the ageing process of growth may have occurred over time and the well-known exponential decrease of radial growth with ageing may have changed in shape, in response to the recent global changes. However, to our knowledge, no study concerning the impact of global change on the age/growth relationship has been conducted yet.

Two hypotheses could explain this paradox: (1) the increase of radial growth induced by global change may lead to a depletion of the carbohydrate reserves, resulting in a dramatic increase of the sensitivity of the tree to environmental disturbances, or (2) the growth response to climatic variations may be different, depending on the age of the tree; global changes inducing an increase in radial growth in adult trees but inducing a dramatic growth decline in the older stands. Currently, the lack of long-term inter-annual surveys of growth and storage compounds in forest species means that it is impossible to make a statement about the first hypothesis. Several studies using the dendroclimatological approach document the second hypothesis. However, the impact of ageing on the climate-growth response is still being debated. While significant differences in growth-climate relationships between young and old trees were reported for *Picea glauca* (Szeicz and MacDonald 1994), *Abies lasiocarpa* (Ettl and Peterson 1995) and *Larix decidua* (Carrer and Urbinati 2004). *Quercus robur* (Rozas, 2005), *Sabina przewalskii* (Yu et al. 2008), *Pinus pinaster* (Vieira et al. 2009), there were no signi?cant differences in growth-climate relationships between young and old trees for *Pinus aristata* (Fritts 1976) and *Larix lyalii* (Colenutt and Luckman 1995). *Pinus cembra* (Esper et al. 2008).

Finally, the studies on the impact of ageing on the climate-growth relationship concern almost exclusively coniferous species. Studies concerning ring porous and diffuse porous species are

very scarce. Yet, the differences in wood anatomy (Shweingruber, 1990), in growth phenology (Priestley et al. 1933, Hinckley and Lassoie 1981, Bréda and Granier 1996, Barbaroux and Bréda 2002) and on the sensitivity to climate (Cochard et al. 1992, Bréda et al 1993, Badeau et al. 1996, Oren and Pataki 2001, van der Werf et al. 2007) between ring-porous and diffuse-porous species suggest that the impact of ageing on growth and growth determinism may be different for these two groups.

Therefore, in order to gain a better understanding of the interactions between climate and ageing on radial growth over both the long-term and short-term, the objectives of this chapter were, (1) to assess the impact of recent global change on the long-term age-growth relationships, (2) to test whether the response of tree-ring to climate is age-dependant, and (3) to analyse whether the anatomical differences between ring porous and diffuse porous species induce differences in climate-age interactions on radial growth.

MATERIALS AND METHODS

SITE AND STAND DESCRIPTIONS

One chronosequence was established for each of the two studied species. The chronosequence for common beech (*Fagus sylvatica* L.) was located in the state forest of Fougères (48°23'N, 1°09'W, mean elevation 164 m) in north-western France (Figure 6a,b). Soils are developed in about 1.5 m of non-carbonated Aeolian loess, over granitic bedrock (Legout 2008), and Toutain (1965) pointed out the homogeneity of these forest soils, which are mainly classified as Alocrisol-Neoluvisols. The climate is of oceanic type, mean annual temperature and average annual precipitation, calculated for the past 30 years, were 11.6 °C and 916 mm respectively (Météo France). Annual soil water deficit, computed by daily water balance modeling according to Granier et al. (1999) averaged 22.4 between 1971 and 2006.

The chronosequence for sessile oak (*Quercus petraea* (Matt.) Liebl.) was located in two closed state forests of Amance (48°46'N, 6°19E, mean elevation 245m) and Champenoux (48°43'N, 6°21E, mean elevation 260m), in north-eastern France (Figure 6a,c). Soils are Neoluvisols developed in a fairly deep loam, over-lying a carbonated clay horizon (Bréda et al. 1993b). The climate is of semi-continental type. Mean annual temperature and average annual precipitation, calculated for the past 30 years, were 10.3 °C and 776 mm respectively for these two forests (Météo France). Annual soil water deficit, computed by daily water balance modeling according to Granier et al. (1999) averaged 62.3 between 1971 and 2006.
For historical reasons, stand age distribution in the two oak forests was unbalanced (lacking old even-aged stands in Champenoux forest and lacking 65-95-year-old stands in Amance forest). Therefore, the chronosequence for sessile oak overlapped the forests of Amance and Champenoux, which were about 5 km apart. Both forests presented similar soil characteristics and had been submitted to similar silvicultural practices (even aged stands, naturally regenerated).

Special attention was devoted to minimizing between-stand environmental variations in each chronosequence. Stands were selected in accordance with different homogeneity criteria in order to isolate ageing signals and to reduce the other sources of variation. These criteria were related to soil type, topography, stand composition and silvicultural practices. Therefore, the chronosequences were composed of pure even-aged, naturally regenerated stands, located on

flat luvisols for the sessile oak chronosequence and on flat alocrisols-neoluvisols for the common beech chronosequence.

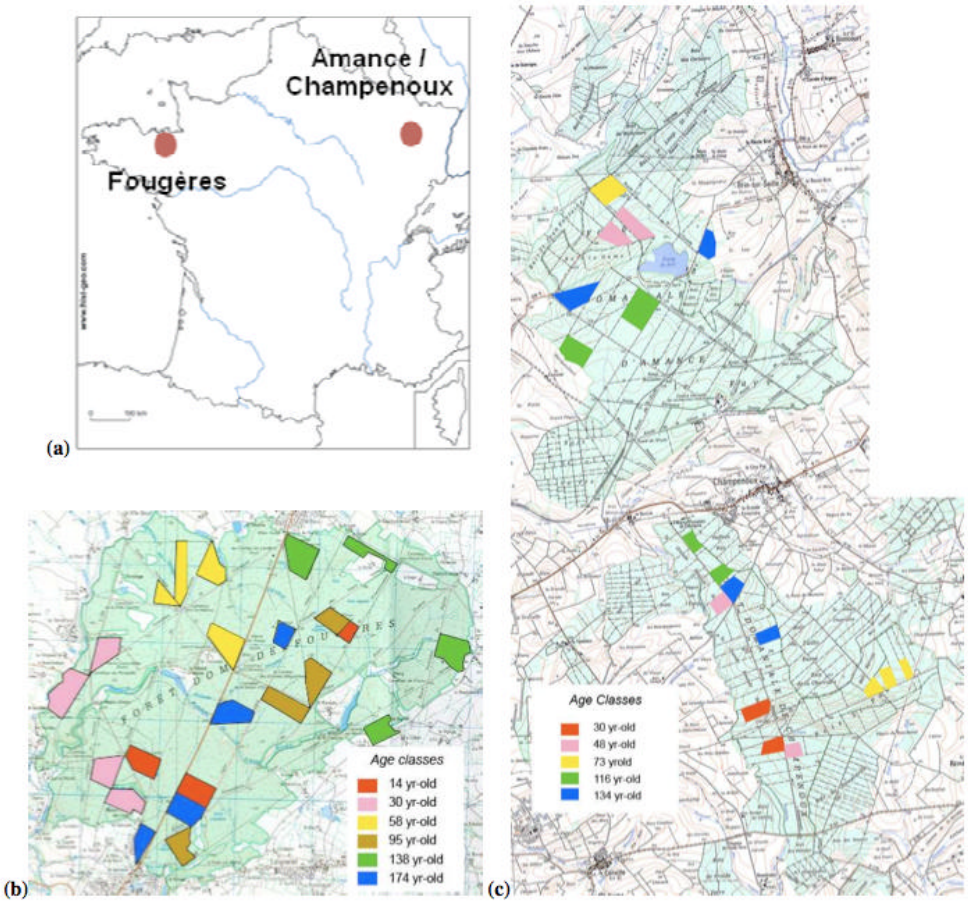


Figure 6: (a) Situation of the two chronosequences. Localization of every stands composing (b) the chronosequence of Fagus sylvatica in the Fougères's forest and (c) the chronosequence of Quercus petraea in the Amance/Champenoux's forests.

SAMPLING FOR TREE RING ANALYSES

Fifteen trees per plot were cored to the pith at breast height using an increment borer, taking one core per tree. To avoid bias on ring width due to competition constraints on crown development, ring-width chronologies were built from dominant and co-dominant trees. Particular attention was paid to avoiding distorted zones and wounds. Circumference at breast height of each tree was also measured.

Coring and circumference measurements were performed in February, 2007. After surfacing, air drying and preliminary visual ring counting, tree-ring widths were measured to the nearest 0.05 mm with a binocular microscope, a digitalizing table connected to a computer and the Leonardo software, designed by Dupouey, J-L. For sessile oak, a ring-porous species, earlywood and latewood were measured separately. For beech, a diffuse porous species, the early-/latewood differentiation was not made because the boundary between the two types of wood was not clear enough.

Tree age was deduced from the number of tree-rings counted from the bark to the pith. When the core did not pass directly through the pith of the stem, the distance between the limit of the youngest ring of the core and the potential pith location of the stem was deduced using a target laid on the core according to the ray direction and the curvature of the ring limits, as illustrated in Figure 7. The number of rings between the potential pith location and the youngest ring limit of the core was estimated by dividing the distance from the youngest ring limit to the pith by the mean width of the 5 youngest rings counted on the core.

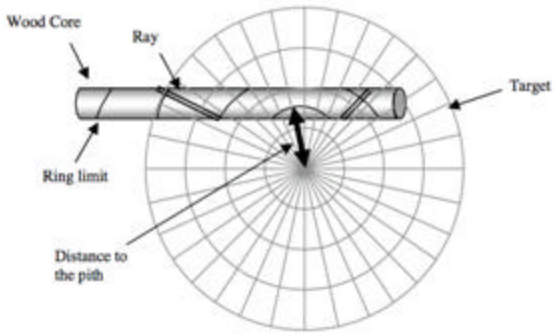


Figure 7: Method to assess the distance from the youngest ring limit to the pith. The target is laid on the core following ray direction and ring limit curvature.

CROSS-DATING

Tree ring series were carefully cross-dated using *pointer years*. A year is defined as a pointer year if conspicuous rings occur in several series (Schweingruber, 1996). Conspicuous rings were detected using the annual variation of relative growth differences (RGD):

$$RGD_n = [RW_n - RW_{(n-1)}] / RW_{(n-1)}$$

where RGD_n is the relative growth difference at year n and RW_n and $RW_{(n-1)}$ are ring, earlywood or latewood width at year n and (n-1) respectively. A given year n was considered as a pointer year if (1) RGD between year n and the previous year (n-1) was greater than 10% and (2) at least 70% of the measured rings presented the same increasing or decreasing trend (Becker et al. 1994). Years containing less than 30 observations were excluded from the computation. At first, pointer years were computed for each site, combining all measured time series.

These sets of pointer years were then compared with available sets assessed in former studies for the same sites. For the Fougères site, a dendroecological study had been conducted on two adult beech stands to assess the impact of fertilization on species composition and tree growth (Marsalle, 1996). 366 trees had been double-cored for ring width analyses in 1993. For the Champenoux site, a great number of sessile and pedunculate oaks and beech stands had been sampled to study short- and long-term changes in stand productivity (Nieminen 1988, Becker et al. 1994). For sessile oak, 121 plots had been settled and 529 trees had been double-cored at 240 cm height for dendrochronological analyses.

Cross-dating was performed using the Interdate software, developed by Dupouey et al., Phytoecology laboratory, INRA – France.

CLIMATIC DATA AND CARBON AND WATER BALANCE CALCULATIONS

We used the dendroclimatologic approach to study the determinism of radial growth. Dendroclimatologic analyses entail the confrontation of growth data with climatic data of the corresponding period of time to built models able to predict at best the radial growth. Two types of models exist:

1. Climatic models: these models are empirical, they are based on simple correlations between growth variables and raw climatic variables;
2. Bioclimatic models: these models are more mechanistic because they take into account the constraints and interactions between growth and the climatic variables.

For example, a climatic model revealing a positive correlation between radial growth and (1) a high temperature in May and (2) a high precipitation in August may suggest a significant effect of the phenology and the summer drought on radial growth. In that case, a bioc limatic model may contain a negative effect of the date of budburst and the soil water deficit on radial growth.

In the present study, climatic data was procured from weather stations located around the two studied sites. The climatic variables used in these analyses concerned the temperature, precipitation, relative humidity, wind speed and global radiation.
The bioclimatic data were computed from simulations using process-based models simulating carbon and water cycles of the ecosystems. The bioclimatic variables used in these analyses concern the drought constraint, the phenology and the carbon assimilation.

Climatic variables

For the sessile oak chronosequence, daily meteorological data used for carbon and water balance simulations (precipitation, maximum and minimum temperature, global radiation, air humidity and wind speed) came from the Tomblaine weather station (# 54526001) owned by Météo France and located 10 km from the site. For the beech chronosequence, temperature, precipitation, air humidity and wind speed data came from a weather station of the French national network of forest monitoring (RENECOFOR), located in Louvigné-du-Désert, 16 km from the site. Daily global radiation data came from the Rennes weather station (# 35281001) owned by Météo France and located 50 km from the site. For both sites, climatic data covered a period of 17 years, from 1970 to 2006.

Bioclimatic variables: simulations of carbon and water balance using process based models

To quantify the drought constraint of current and past years on tree growth, a daily forest/soil water balance model (Granier et al. 1999) was used to calculate water balance at the stand scale. The site-related parameters of the model include stand structure and tree phenology (maximum Leaf Area Index (LAImax) and budburst and leaf fall dates), and soil properties (maximum extractable water and vertical distribution of fine roots in particular). Output data were simulated from daily to annual time steps and concerned throughfall, rainfall interception, stand transpiration, evaporation, total evapotranspiration, soil water content and drainage. Soil water deficit was assumed to occur when the soil water content dropped below 40% of its maximum value (Granier et al. 1999, Granier et al. 2000a, 2000b). The model had already been implemented and validated against soil water content and stand transpiration measurements for *Quercus petraea*, *Fagus sylvatica*, *Pseudostuga mensiezii*, *Pinus sylvestris* and *Picea abies* stands (Granier et al. 1999, Granier et al., 2000a).

To quantify the impact of phenology, carbon assimilation and indicators of water use efficiency of current and past years, on tree growth, a multi-layer process-based model (CASTANEA, Dufrêne et al. 2005) was used. Input parameters included stand structure (above- and belowground stand biomass, stand height and age, LAImax), canopy composition (leaf mass area, leaf nitrogen and chlorophyll contents), and soil properties (maximum extractable water). Output data concerned (1) state variables like the evolution of LAI over time, standing biomass, soil water and carbon content and (2) flux variables like canopy assimilation, soil and stand respiration, stand biomass growth, transpiration and evaporation. The simulations were performed at stand scale and no variability between trees was assumed. The model had already been implemented and validated against carbon fluxes and tree growth measurements for *Fagus sylvatica*, *Quercus petraea*, *Quercus robur*, *Quercus ilex*, *Pinus sylvestris* and *Pinus pinaster* stands (Davi 2004).

For both models, simulations were performed using one set of averaged stand/soil parameters per age class. Indeed, low sensitivity of carbon and water fluxes to the aggregation of spatial parameters (e.g. soil water content, leaf area index, leaf mass area, leaf nitrogen content) had already been shown in an old-growth forest composed of beech and oak stands similar to the stands used in the present study (Davi et al. 2006).

LONG TERM GROWTH TREND ANALYSES

The analysis of the impact of long-term environmental changes on the age/growth relationship required a correct separation of the environmental low-frequency trend and the ageing trend on ring-width series. Two methods, illustrated in Figure 5b, were used in order to perform this discrimination. A simple method consists of considering the tree rings developed at a given date but at various cambial ages (the "constant date curve", denoted CDC later on). This method was used (1) to describe how growth trends vary with age, and (2) to perform graphical analyses of the influence of the period of growth on age-related trends. This method was initially developed by Becker (1987) to study effects of date for a given cambial age (the "constant age curve") on silver fir in the Vosges Mountains. The principal disadvantage of the method is that the number of observations averaged to give constant age or constant date curves is limited. In the present study, the dates were grouped per period of 10 yrs between 1916 and 2006. In each 10 year period, ring widths with the same cambial age were averaged in order to reduce the background noise related to the inter-annual variability. All averages containing less than 5 observations were excluded from the data set.

To make the comparison between CDCs easier, a deterministic growth model was used to estimate ring width as a function of cambial age. Using the same model for every CDC allows a direct comparison of parameters between curves. Several models exist to reproduce growth trend with age (Zeide 1993, Cook and Briffa 1990, Bontemps 2006), but we selected the generalized exponential function (Warren 1980):

$$RW = K * CA^{b} * \exp^{(-c * CA)}$$

where RW is ring width measurement, CA is cambial age of the measured ring and K, b and c are parameters of the model.

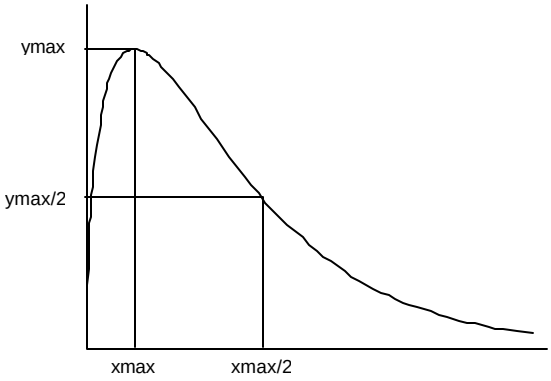


Figure 8: Shape of the generalized exponential model linking cambial age (x axis) to growth (ring width) (y axis). Growth indicators used in the analyses are represented.

This model was used because (1) it is possible to fit the juvenile increase and the subsequent exponential decrease of radial growth with age, (2) it is defined by a limited number of parameters and (3) it was the most explicative model compared to the other models tested, like Michaelis-Menten and Lundqvist Matern. Three parameters were used to compare CDCs (1) the maximum value of each growth curve (ymax indicated in Figure 8) as an indicator of juvenile growth, (2) the cambial age at maximum growth (xmax indicated in Figure 8) as an indicator of the duration of the juvenile phase and (3) the cambial age at half-maximum growth (xmax/2 indicated in Figure 8) as an indicator of the decay velocity of radial growth in adult trees: the lower the xmax/2, the faster the decay.

To complete these analyses by a statistical comparison of cambial age and calendar date effects on radial growth, a method developed by Dupouey and colleagues (1992) was used. This method is based on analysis of variance of ring width using a bilinear model considering additive effects of age (Ai) and date (Cj), a multiplying interaction of age and date (u.Bi.Dj), a non multiplying interaction (Fij) and an error term (Eijk):

$$Rijk = Ai + Cj + u.Bi.Dj + Fij + Eijk$$

where Rijk is the observed ring width at age i, during year j and from tree k. The non multiplying part of the interaction between age and calendar date was not significant in the initial study concerning 1650 silver fir trees from the Vosges Mountains, France. We thus decided to simplify this model and to remove this term from the equation. The original set of ring widths concerned a large range of cambial ages and calendar dates, but for each combination of age and date, a varying number of rings was measured and half of these combinations remained empty because rings from old trees could not be observed in the ancient dates (Figure 5b). This resulted in an unbalanced set of age x date combinations where young age for recent dates and old age for ancient dates were weakly represented. However, to be reliable, analyses of variance needed to be performed on a balanced and sufficiently large number of observations for each combination of age and date. This condition was fulfilled in two steps, as proposed by Dupouey et al. (1992). A "squared" matrix was selected from the original triangular matrix in order to balance the different age/date combinations. Furthermore, in order to increase the number of measured rings per age/date combination, age and date factors were divided into a limited number of classes, each class containing a comparable number of observations. Data structure for the ANOVAs is indicated in Table 5. Prior to the ANOVA, ring widths belonging to the same tree were averaged in each combination of age and date classes in order (1) to reduce the impact of the inter-tree variability in the analysis and (2) to limit the dependence between age and date.

Table 5: Data structure for the ANOVAs on ring widths and sensitivity (top) and autocorrelation (bottom) for* Fagus sylvatica *(left) and* Quercus petraea *(right). Number and percentage of trees analyzed are indicated for each combination of cambial age and date classes and in total. Range of cambial age and date classes are also indicated.

Fagus sylvatica

Cambial age \ Date	[1920-1939]	[1940-1957]	[1958-1974]	[1975-1991]	[1992-2006]	Total
[10-26]	**60** 3.82	**48** 3.06	**63** 4.02	**84** 5.35	**100** 6.37	**355** 22.63
[27-47]	**56** 3.57	**60** 3.82	**58** 3.7	**63** 4.02	**83** 5.29	**320** 20.4
[48-71]	**61** 3.89	**51** 3.25	**62** 3.95	**74** 4.72	**59** 3.76	**307** 19.57
[72-93]	**70** 4.46	**61** 3.89	**34** 2.17	**61** 3.89	**60** 3.82	**286** 18.23
[94-120]	**47** 3	**68** 4.33	**75** 4.78	**53** 3.38	**58** 3.7	**301** 19.18
Total	**294** 18.74	**288** 18.36	**292** 18.61	**335** 21.35	**360** 22.94	**1569** 100

Quercus petraea

Cambial age \ Date	[1940-1953]	[1954-1966]	[1967-1979]	[1980-1992]	[1993-2006]	Total
[10-26]	**53** 3.68	**57** 3.96	**68** 4.72	**83** 5.76	**29** 2.01	**290** 20.12
[27-44]	**32** 2.22	**53** 3.68	**59** 4.09	**64** 4.44	**76** 5.27	**284** 19.71
[45-64]	**76** 5.27	**38** 5.27	**52** 3.61	**60** 4.16	**72** 5.00	**298** 20.68
[65-81]	**77** 5.34	**79** 5.48	**46** 3.19	**23** 1.6	**56** 3.89	**281** 19.5
[82-100]	**31** 2.15	**66** 4.58	**90** 6.25	**66** 4.58	**35** 2.43	**288** 19.99
Total	**269** 18.67	**293** 20.33	**315** 21.86	**296** 20.54	**268** 18.6	**1441** 100

Cambial age \ Date	[1920-1951]	[1952-1980]	[1981-2006]	Total
[10-40]	**120** 11.47	**102** 9.75	**144** 13.77	**366** 34.99
[41-78]	**100** 9.56	**120** 11.47	**108** 10.33	**328** 31.36
[79-120]	**110** 10.52	**128** 12.24	**114** 10.90	**352** 33.65
Total	**330** 31.55	**350** 33.46	**366** 34.99	**1046** 100

Cambial age \ Date	[1940-1962]	[1963-1983]	[1984-2006]	Total
[10-38]	**98** 12.44	**58** 7.36	**130** 16.50	**286** 36.29
[39-69]	**104** 13.20	**58** 7.36	**88** 11.17	**250** 31.73
[70-100]	**90** 11.42	**130** 16.5	**32** 4.06	**252** 31.98
Total	**292** 37.06	**246** 31.22	**250** 31.73	**788** 100

INTER-ANNUAL VARIATIONS OF GROWTH

Inter-annual variations of growth are mainly related to stochastic changes in environmental conditions induced by climate or by other biotic and abiotic factors (defoliating insect attack, masting, fire). The high to medium frequency growth signal was studied in order to test the assumption commonly used in dendrochronology, that climate-growth relationships are age independent once the growth trend has been accounted for. Potential age-related changes in the high frequency signal in tree rings were studied using (1) the sensitivity of radial growth to environmental conditions, (2) the influence of past growth conditions on current growth (autocorrelation) and (3) the identification of climatic variables that determine radial growth. Comparisons were performed between species, and type of wood for sessile oak. However, because the species were located in different forests, species differences may also include some site influence.

Detrending and growth index computation

Analysis of the high to medium frequency signal of radial growth first needs to remove the low frequency signal, considered as noise. The removal of noise was done by (1) estimating the long-term trend of growth and (2) removing this trend through computation of indices. This procedure is known as *standardization* (Fritts 1976). According to Cook and Peters (1981) and Meko (2008), long- and medium-term trends of growth for every sampled tree were fitted to a cubic spline with a 50% frequency response of 50 years, which was flexible enough to considerably reduce trends in growth. Examples of fitted curves are given in Figure 9. The indices for individual time series were then computed as:

$$I_n = RW_n / pRW_n$$

where I_n is the ring index for a given tree and a given calendar date n, RW_n is the measured ring width at date n and pRW_n is the ring width predicted from the fitted curve at date n. Indices computed for every time series were averaged by calendar date to obtain master series for each species and age-class. Dates containing less than 20 observations were removed from the master series.

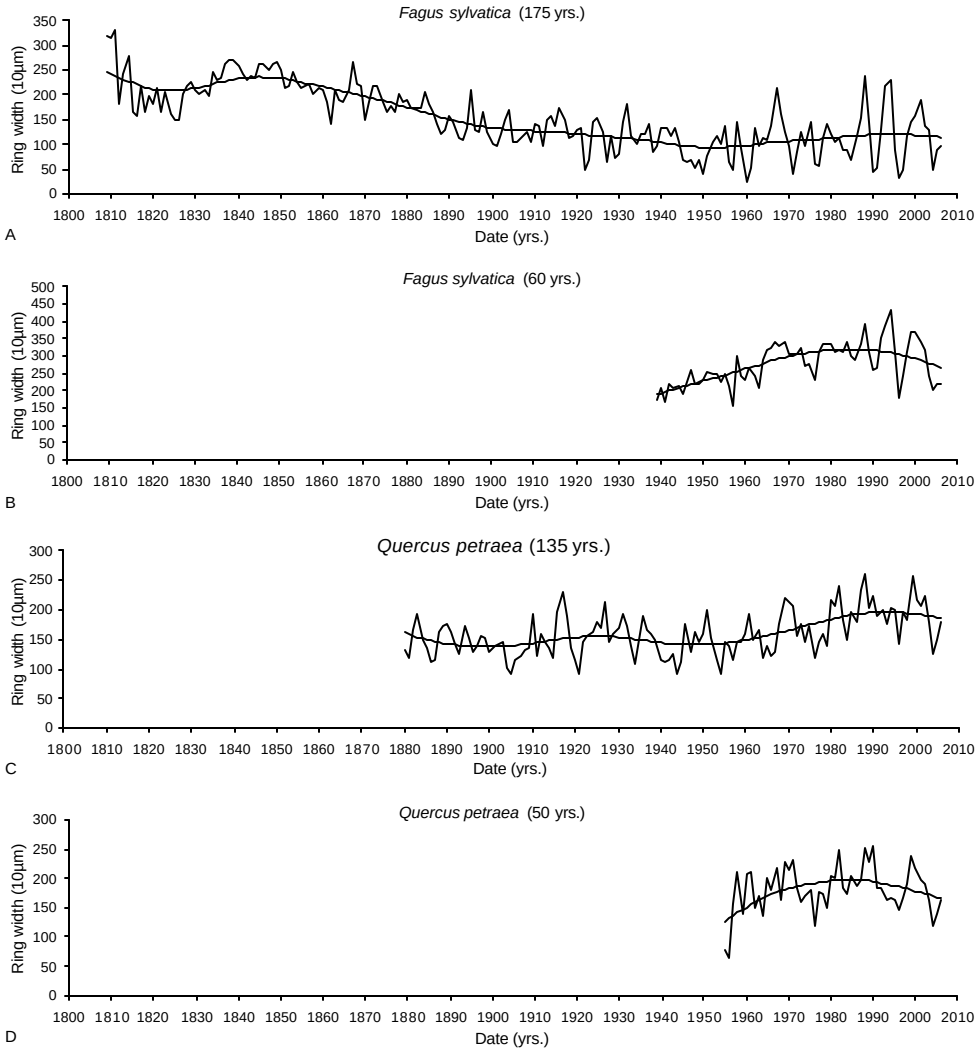


Figure 9: Example of long-term trend fitting for* Fagus sylvatica *and* Quercus petraea *trees belonging to different age-classes.

Sensitivity to climate computation

Sensitivity of radial growth to climate was estimated according to (Schweingrubber 1988), as the difference between two successive values of index, weighted by the mean of these successive values:

$$S_n = 2 \,.\, (I_n - I_{(n-1)}) \,/\, (I_n + I_{(n-1)})$$

where S_n is the sensitivity for a given tree at a given calendar date n, I_n and $I_{(n-1)}$ are the index values at date n and n-1 respectively. In order to remove the bias of the age-related growth trend effect on inter-annual variation of growth, the sensitivity was computed using ring index instead of raw ring width. Because environmental conditions of growth are susceptible to change over time, the relationship between age and sensitivity to environmental conditions was studied as a function of calendar date. Cambial age and calendar date effects on growth sensitivity were studied simultaneously using analyses of variance as described before for the long-term trend study of radial growth (Dupouey et al. 2002). A "squared" matrix was selected from the original triangular matrix in order to balance the different age/date combinations. Age and date factors were divided into a limited number of classes; each class containing almost the same proportion of sensitivity computation. Data structure for the ANOVAs is indicated in Table 5. Prior to the ANOVA, sensitivity values belonging to the same tree were averaged in each combination of age and date classes in order to reduce the impact of the inter-tree variability in the analysis and to limit the dependence between age and date.

Autocorrelation computation

Autocorrelation refers to the correlation of an index value with its own past values. Autocorrelation can be related (1) to a possible direct effect of the climate of the previous year on current year growth (e.g. late summer drought might reduce current year growth and prevent a complete refill of the soil water reservoir during a dry winter, reducing growth during the following year) or more probably, (2) to a lag effect of growth conditions that occurred during the previous year, on the tree physiology during the current year (e.g. favourable years for radial growth may also enhance fine root growth, increasing the water uptake capacity of trees for the next year). A 95% confidence limit was chosen to test the significance of autocorrelation (Meko 2008). Significance of partial autocorrelation at different time lags (0 to 10) was tested on every series sampled and only lag 1 autocorrelation

was significant for more than 20% of the series. Other lags of autocorrelation were thus neglected.

As environmental conditions of growth are susceptible to change over time, autocorrelation might be modified as well. Hence, cambial age and calendar date effects on autocorrelation were studied simultaneously using analyses of variance, as described before for the sensitivity analysis. A "squared" matrix was selected from the original triangular matrix in order to balance the different age/date combinations. To be reliable, autocorrelation has to be estimated on a sufficient number of observations: in order to enlarge the period for which autocorrelation is computed, the number of age and date classes were reduced from five to three, each class containing at least 22 years. Data structure for the ANOVAs is indicated in Table 5 (bottom). Autocorrelation was computed on ring index in order to remove the correlation link to age-related growth trend.

Dendroclimatic analyses

The growth-climate relationships were estimated for the period [1971-2006] for which meteorological data were available at both studied sites. Climatic variables, composed of monthly mean temperatures and total precipitation, were calculated from direct meteorological measurements. Bioclimatic variables were computed from simulations of water and carbon balance models (see *Bioclimatic variables:* simulations of carbon and water balance using process based models section). The climatic year considered in these analyses differed from the calendar year: it began in November of the previous year and ended in October of the current year during which the growth ring was formed. Because earlywood growth occurred at the beginning of the growing season, climatic and bioclimatic variables concerning the period extending beyond May of the current year were excluded from the analysis of the earlywood compartment in oak (Bréda and Granier 1996). Only age-classes covering the entire period [1971-2006] were analysed: youngest age-classes were excluded from the analyses.

The autocorrelation is characteristic of time series of radial growth. Yet, this relationship violates the assumption of independence necessary for most statistical analyses and detrended index I_t may not be an appropriate response variable to be used in multiple regression (Monserud 1986, Visser and Molenaar 1990). Various authors handle the problem of using autocorrelated variables by including lagged variables into the dataset of predictors. However, this method weakens the model by increasing the number of predictors whereas the number of observations is often low, particularly in the present study (36 years). In order to remove autocorrelation in the time series, an autoregressive (AR) model was used for each detrended

index series. AR models of order 1 were used for both species (+site) and type of wood. Dendroclimatic analyses were performed using residuals of the AR models. Individual series were averaged to compute one master series per age class for each species, and type of wood for oak.

Furthermore, climatic variables are often highly intercorrelated (Blasing et al. 1984). In order to take into account multicollinearity between climatic variables, the influence of climate on radial growth was studied using response functions (Fritts, 1986)., The use of ordinary regression procedures, when climatic variables are highly correlated, may induce overestimation of regression coefficients and its standard errors, high fluctuation of coefficients in sign and magnitude and overestimation of the percentage of variance estimated by the model (Dagnélie 1975, Fekedulegn et al. 2003). To handle the problem of multicollinearity, climatic variables were orthogonalized prior to regression by transforming them into principal component eigenvectors. According to Fekedulegn et al. (2003), the following principal components selection rules were applied: (1) selection of the first components whose combined eigenvalue product is greater than unity, then (2) selection of components significant at the 15% level using stepwise selection. 95% confidence intervals were computed for regression coefficients associated with each climatic variable. If the confidence interval included zero, the regression coefficient was not considered to be statistically significant at the 0.05 level.

In order to reduce the number of predictors of radial growth, climatic and bioclimatic parameters were first selected separately. An initial preliminary analysis was performed using all monthly climatic variables alone (mean temperature and sum of precipitation). This analysis allowed the selection of the climatic variables presenting a significant influence on the growth variables. Successive monthly variables with identical response function coefficients (in sign and magnitude) were grouped and averaged. A second preliminary analysis was performed to select bioclimatic predictors alone. Indicators of phenology, photosynthesis, transpiration, evapotranspiration and water deficit were tested. Only parameters with significant response function coefficients were kept for further analyses. Then, a final analysis was conducted using only the climatic and bioclimatic variables selected during the preliminary analyses.

STATISTICAL ANALYSIS

Data were analysed using the SAS statistical package (SAS 9.1, SAS Institute Inc., Cary, NC, USA) (SAS 1988). A non-linear model (proc nlin) was used to determine the relationship between ring width and cambial age on "constant date curves". The comparison of long-term effects of age and date on radial growth, sensitivity and autocorrelation was studied using the analysis of variance performed on the initial data set split into balanced cambial age and date classes. For growth, sensitivity and autocorrelation, three main effects were tested: species (+site), type of wood and tree age in 2006. Species and type of wood effects were handled with analyses of variance. Because early- and latewood were not differentiated for beech, species comparisons only concerned total ring width and wood type comparison only concerned Sessile oak. Tree age was considered as a quantitative variable and regressions were carried out for each species and each type of wood.

As described in Chapter 1, the age range of the beech chronosequence (from 12 to 200 years-old) is larger than that of the sessile oak chronosequence (from 26 to 140 years-old). To compare species (+ site) properly, species effect and age effect for each species were tested in comparable age ranges i.e. the youngest and oldest beech stands were excluded from these analyses. Furthermore, because the species were located in different forests, species differences may also include some site influence.

RESULTS

For clarity in the text and to avoid potential confusion, ring age will be referred as "cambial age" or "cambial age classes" while tree age measured in 2006 will be referred as "2006 age" or "2006 age classes".

LONG TERM TRENDS

"Constant date" curves (CDC)

Constant date curves represent ring width trends with cambial age at a given calendar date or short period of time. In order to increase the number of observations per CDC, dates were grouped by periods of 10 years between 1916 and 2006 (in the text, periods are identified by the midpoint value: 1921, 1931, etc). To reduce the noise related to the inter-annual variability in the analysis, ring widths with the same cambial age were averaged inside each date period. Observed CDCs are presented in Figure 10. To make the comparison between CDCs easier, a deterministic growth model was used to estimate ring width as a function of cambial age. The fitted CDCs are shown in Figure 11. Three parameters were used to compare CDCs: (1) the maximum growth of each curve (ymax indicated in Figure 8) as an indicator of juvenile growth, (2) the cambial age at maximum growth (xmax indicated in Figure 8) as an indicator of juvenile growth duration and (3) the cambial age for which ring width reaches half - maximum growth (xmax/2 indicated in Figure 8) as an indicator of the decay velocity of radial growth in adult trees. Relationships between these indicators and the corresponding growth period are presented in Figure 12.

For both species (+site), ring widths decreased with cambial age (Figure 10a, b) respecting the Pressler law (ring surface increases to a maximum value, then once this value is reached, the corresponding ring width will therefore decrease geometrically), but this decay was more pronounced for beech than for sessile oak.

Furthermore, the short but sharp increase in growth in the young stage of development was more visible for beech than for oak. For sessile oak, the growth trend with cambial age was also different between earlywood and latewood. Earlywood width increased with age up to 50 years old and decreased slowly afterwards, whereas latewood width decreased with cambial age (Figure 10c, d). For both species and all types of wood, growth was higher for recent periods (orange shaded dots) than for ancient periods (blue shaded dots) except in the first stage of development.

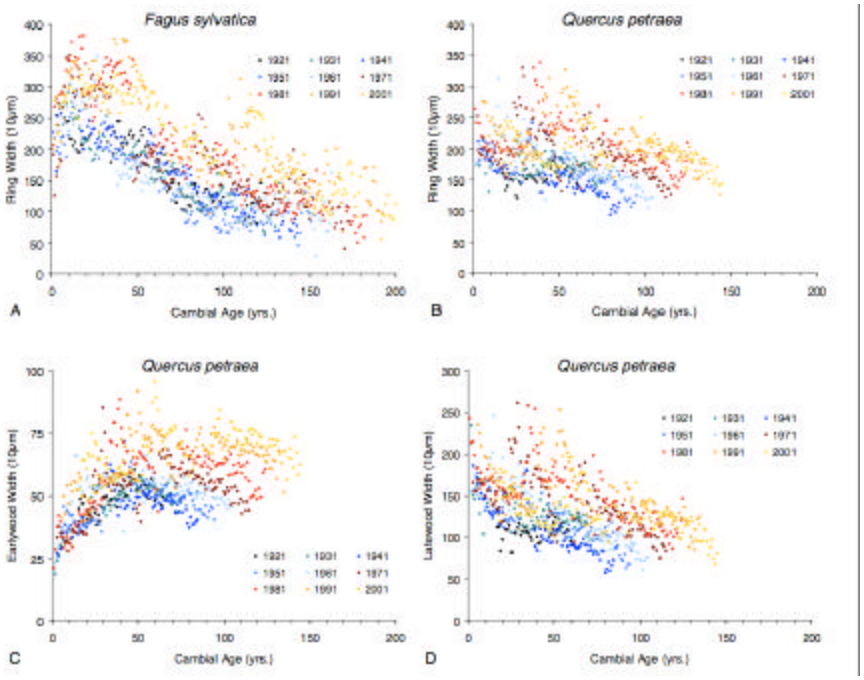


Figure 10: Relationships between cambial age and (a) ring width of* Fagus sylvatica*, (n= 338 beech trees, n = 20 200 tree rings), (b) ring width, (c) earlywood width and (d) latewood width of* Quercus petraea *(n= 264 oak trees, n= 17 500 tree rings) for the period [1916-2006]. Each symbol displays mean ring width of trees with similar cambial age. Each colour represents a sub-period of 10 years. In the legend, midpoints of each sub-period are indicated.

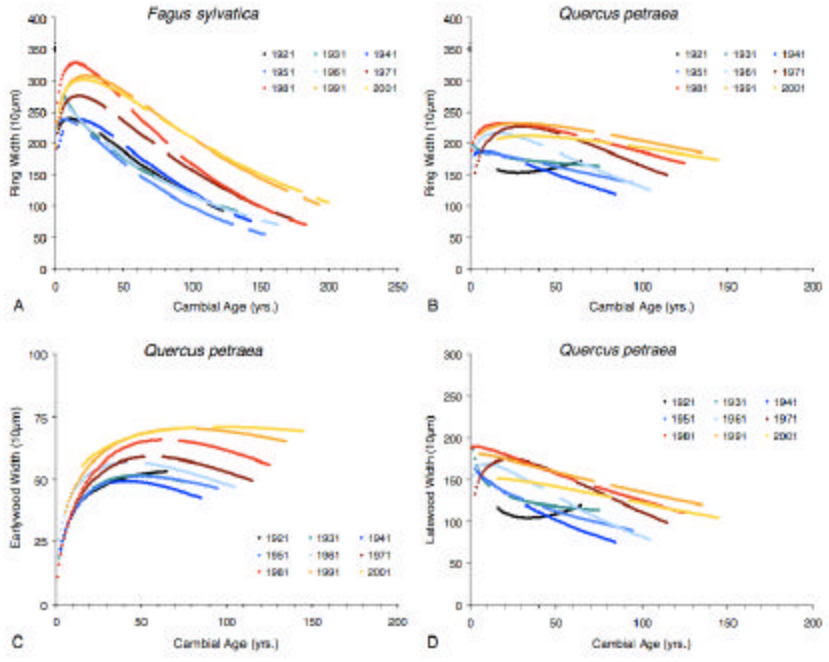


Figure 11: Constant date curves fitted with a generalized exponential model for (a) ring width of* Fagus sylvatica*, (b) ring width, (c) earlywood width and (d) latewood width of* Quercus petraea *for the period [1916-2006]. Each colour represents a sub-period of 10 years. In legend, midpoints of each sub-period are indicated.

The generalized exponential model was successfully fitted for all periods, species and type of wood considered (Figure 11). The increase of growth in the juvenile phase was missing from some CDCs, especially in latewood width and for ancient periods of growth.

For beech (Figure 11a, Figure 12a), juvenile maximum growth (maximum values of CSCs) increased with time from 2.39 mm in 1921 to 3.28 mm in 1981. After the '80s juvenile maximum growth decreased slightly to 3.02 mm in 2001. Cambial age at maximum growth did not change markedly over time. Cambial age at half-maximum growth increased slightly from 97 years old in 1921 to 149 years old in 2001 (crosses in Figure 12a). We saw that this value could be considered as an indicator of decay velocity of radial growth in adult trees: the lower the cambial age at half-maximum growth, the faster the decay. Thus, we could deduce that the velocity of adult growth decline with age decreased slightly with time after 1950.

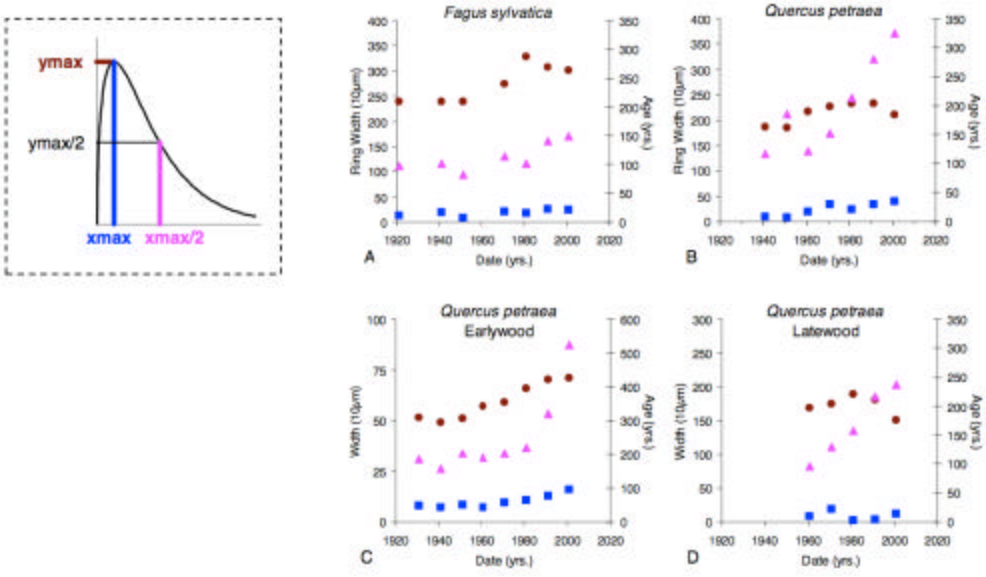


Figure 12: Relationship between maximum value of growth (brown dot), cambial age at maximum growth (blue square) and cambial age at half-maximum growth (pink triangle) and calendar date for (a) ring width of* Fagus sylvatica*, (b) ring width, (c) earlywood width and (d) latewood width of* Quercus petraea *for the period [1916-2006].

For sessile oak (Figure 11b, Figure 12b), juvenile maximum growth increased slightly between 1941 and 1991, from 1.86 to 2.32 mm, and then decreased to 2.11 mm in 2001. Cambial age at maximum juvenile growth also increased slightly from 8 years old in 1941 to 34 years old in 2001 (asterisks in Figure 12b). Cambial age at half-maximum growth increased sharply after 1961, from 122 to 325 years old in 2001. This trend indicated a sharp deceleration of the velocity of the adult growth decline with age.

Maximum juvenile growth of oak earlywood increased regularly over time from 1941, from 51 to 71 mm (Figure 11c, Figure 12c). The cambial age at maximum earlywood growth also increased from 51 years old in 1951 to 71 years old in 2001. Finally, the velocity of the adult earlywood growth decline with age decreased sharply over time, particularly after 1981 as indicated by the increase in cambial age at half-maximum growth from 186 years old in 1931 to 524 years old in 2001.

CDC forms of latewood width were very similar to CDCs of total ring width for sessile oak (Figure 11d, Figure 12d). Maximum juvenile latewood growth increased from 1.69 mm in 1961 to 1.89 mm in 1981 and decrease to 1.51 mm afterwards. Cambial age at maximum latewood growth did not change markedly over time. Cambial age at half-maximum latewood growth increased sharply from 1961, from 96 to 237 years old in 2001. As for total ring width, this trend indicated a sharp deceleration in the velocity of adult growth decline with age.

Analyses of Variance (ANOVAs)

In order to make a direct comparison between cambial age and date effects of total ring, earlywood and latewood width, analyses of variance were performed on the initial data set split into balanced cambial age and date classes.

ANOVAs showed that the model chosen was highly significant, for both species and all types of wood (

Table 6). However, it was twice as explanatory for beech as for sessile oak (R^2 of 0.40 and 0.21 respectively). This difference was mostly related to the contrasting effect of cambial age on radial growth of the two species. Whereas cambial age accounted for 24% of the ring width variability in beech, it explained less than 2% of the total ring width variability and less the 10% of the earlywood and latewood width variability in sessile oak. The most explanatory factor was cambial age for beech (R^2=0.24), while for sessile oak, calendar date explained the largest part of the ring, earlywood and latewood variance (14%, 13% and 13% respectively). The interaction between cambial age and date explained a significant part of the variance for each species and all types of wood, i.e. the responses of growth to climate change and ageing are interdependent. Indeed, the analyses of the "constant date curves" showed that the age/growth relationship changed over time. Likewise, the date/growth relationships displayed in Figure 13, were different depending on the age-class considered. Differences in level between each curve were consistent with the constant age curves described previously for each species and tree ring compartment.

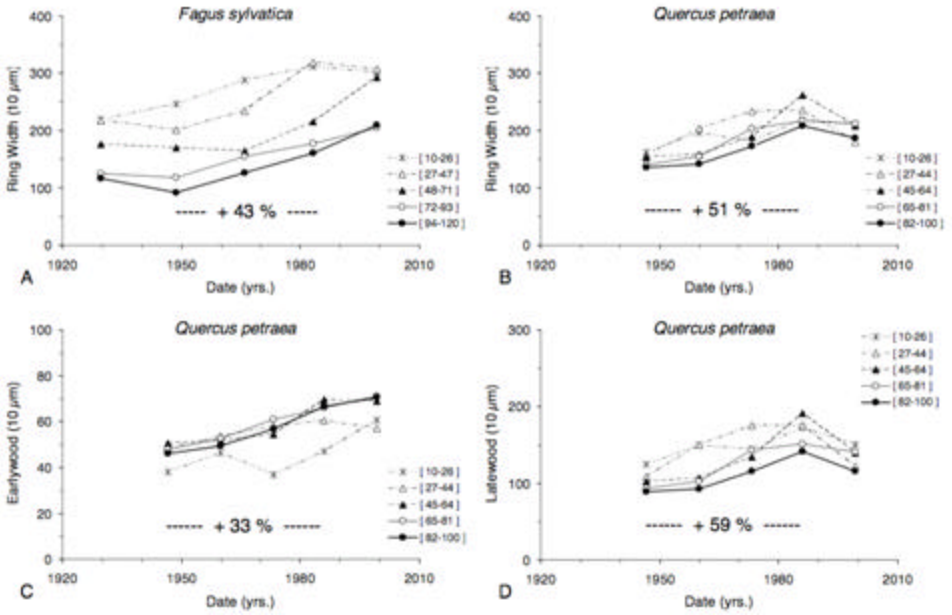


Figure 13: Least square means against calendar date for (a) ring width of* Fagus sylvatica, *(b) ring width, (c) earlywood width and (d) latewood width of* Quercus petraea. *The lines join the different date classes for each cambial age class.

Table 6: Results of analyses of variances carried out to study effects of cambial age class, date period and interaction between the two factors on ring width, latewood and earlywood width for* Fagus sylvatica *and* Quercus petraea*. df = degrees of freedom , MS = mean square, F=Fisher value, p= significance probability value and R^2 = coefficient of determination.

Species	Type of wood	Effects	df	F	p	R^2
Fagus sylvatica	Total ring	Cambial Age classes	4	166.9	<.0001	0.241
		Date period	4	92.8	<.0001	0.134
		Interaction	16	3.8	<.0001	0.022
		Error	1544			
Quercus petraea	Total ring	Cambial Age classes	4	7.3	<.0001	0.016
		Date period	4	66.6	<.0001	0.143
		Interaction	16	6.0	<.0001	0.051
		Error	1416			
	Earlywood	Cambial Age classes	4	43.8	<.0001	0.090
		Date period	4	64.1	<.0001	0.131
		Interaction	16	3.2	<.0001	0.026
		Error	1416			
	Latewood	Cambial Age classes	4	19.6	<.0001	0.041
		Date period	4	62.8	<.0001	0.130
		Interaction	16	6.0	<.0001	0.050
		Error	1416			

Least square means plotted against calendar dates revealed a long-term increase of growth during the twentieth century for both species and both types of wood. This increase was almost regular with time for beech ring width and sessile oak earlywood width (Figure 13a, c) while the growth trend for ring width and latewood width of sessile oak declined after 1985 (Figure 13b, d). The common period of growth increase for both species and all types of wood ranged from the end of the 1940s to the end of the 1980s. During this period, growth increase was slightly higher for sessile oak (51 %) than for beech (43 %) and higher in oak latewood (57 %) than in oak earlywood (33 %). Smaller date-related changes concerned the youngest cambial age classes for both species and types of wood (Table 7). Finally, date related increase in growth rose regularly with cambial age for earlywood growth.

Table 7: Date-related changes of ring width variables for* Fagus sylvatica *(left) and* Quercus petraea *(right). Mean changes, expressed in percent, were computed for each cambial age class.

Cambial age class	*Fagus sylvatica* Ring width
[10-26]	26.7
[27-47]	58.7
[48-71]	26.5
[72-93]	51.5
[94-120]	74.2

Cambial age class	*Quercus petraea*		
	Ring width	Earlywood width	Latewood width
[10-26]	35.2	23.7	38.7
[27-44]	49.7	24.7	60.8
[45-64]	70.5	37.5	86.8
[65-81]	53.9	37.6	62.2
[82-100]	54.0	44.3	59.0

INTER-ANNUAL ANALYSES OF GROWTH

Gross radial increment

Ring width series descriptions

Mean annual variation of radial growth for each 2006 age-class for both species and all types of wood are presented in Figure 14. Differences in level between curves were consistent with the age-related growth trends described previously for each species and type of wood. Furthermore, the regular ring width decrease observed in oldest age-class of beech throughout the nineteenth and the first half of the twentieth century (Figure 14a) may be partly related to the age-related decline of growth. Similarly, the increase of earlywood growth over time for sessile oak (Figure 14c) might be partly explained by the age-related increase of growth described previously (Figure 11c). During the last two decades, beech time series showed three intense growth crises in 1990, 1996 and 2004, following very favourable periods of growth. These crises were particularly marked for older age-classes.

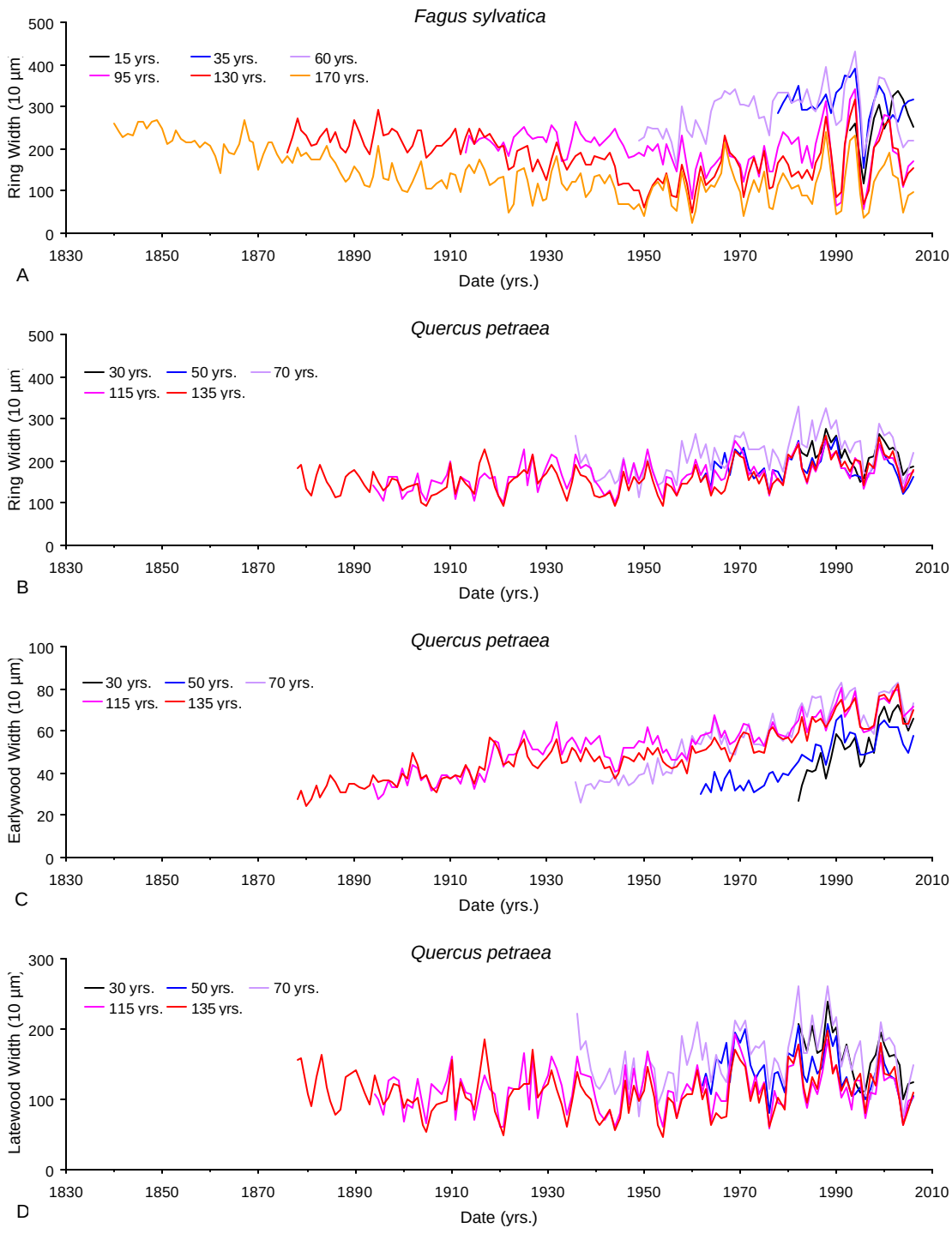


***Figure 14: Growth series of each 2006 age class for (a) ring width of* Fagus sylvatica, *(b) ring width of* Quercus petraea*, (c) earlywood width of* Quercus petraea *and (d) latewood width of* Quercus petraea**

Compared evolution of radial growth and climatic parameters over time: [1971-2006]

Figure 15 shows a comparison between mean annual radial growth and climatic parameters for each species (+site). Climatic parameters were the sum of precipitation, mean temperature and soil water deficit (SWD) for the period [1971-2006]. Climatic parameters were computed for two periods: the "rest" period from November to April and the "growing" period from May to October. For both periods, the mean temperature increased significantly at both sites between 1971 and 2006 (Table 8). Warming was higher at the Champenoux site than at the Fougères site and higher during the growing season than during the rest period. In Fougères, mean temperatures increased by 0.030°C/year and 0.049°C/year during rest and growing periods respectively (Figure 15c). In Champenoux, mean temperatures increased by 0.042°C/year and 0.077°C/year during rest and growing periods respectively (Figure 15g). SWD also increased significantly with time (2.08 mm/year) at the Champenoux site, but not in Fougères

Comparison between mean radial growth and climatic parameters revealed that beech growth crises occurring at the beginning and in the middle of the 1990s coincided with periods of high soil water deficit (SWD) in 1989/1990 and 1996 respectively, as shown in Figure 15 (a, d). The growth depletion occurring at the beginning of the 2000s coincided with drought events in 2003 and 2005 and with successive masting years in 2000, 2002, 2004 and 2006 (brown solid arrows in Figure 15a).

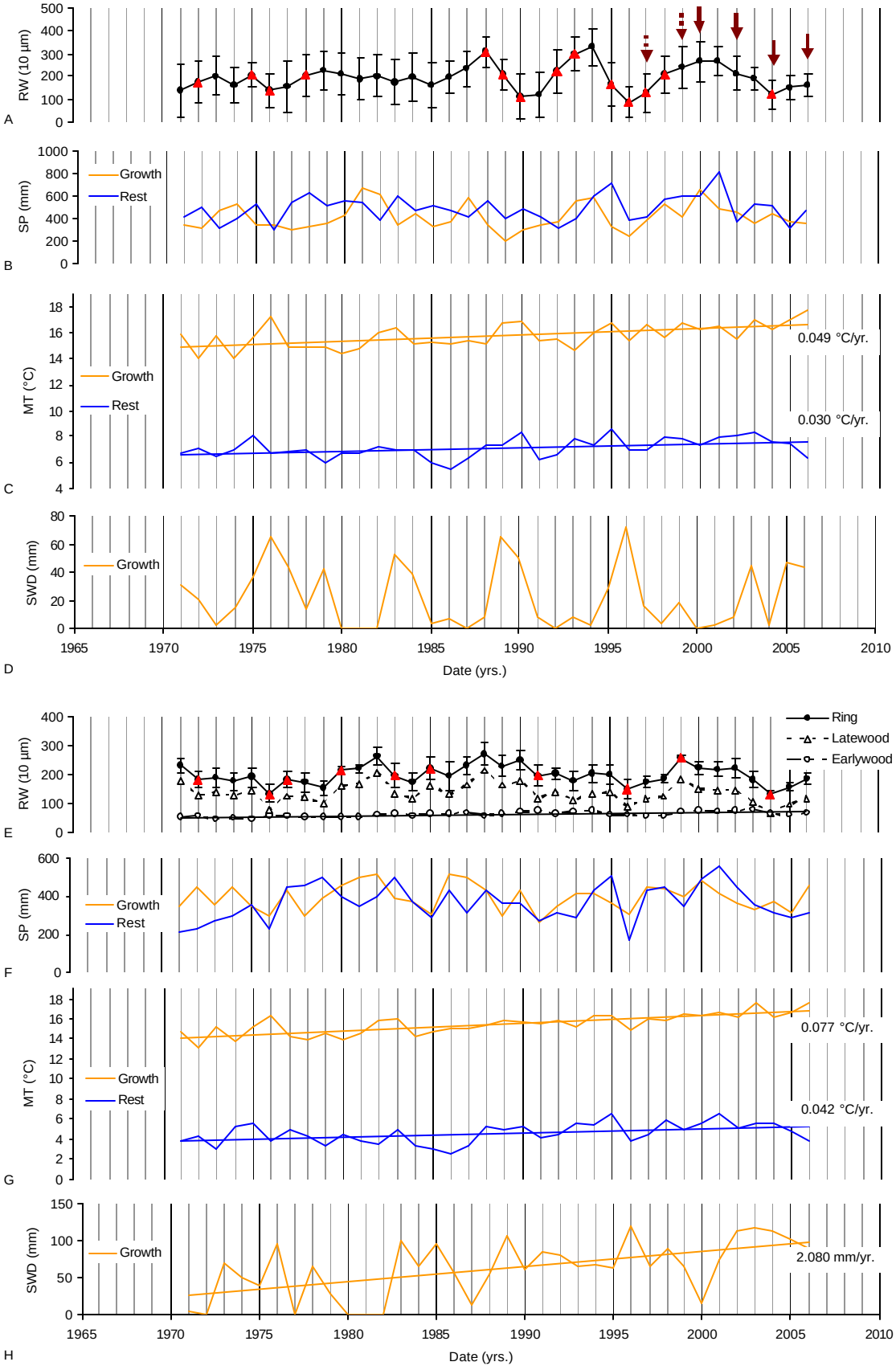
Growth decreases in sessile oak also occurred during periods of high soil water deficit as in 1976, 1984, 1996 and 2004. Finally, medium-term increases in SWD and mean temperature coincided with a significant increase in earlywood growth with time (Table 8). In contrast with early wood, late wood and total ring width did not display a significant time/growth relationship between 1971 and 2006 (Figure 13).

Table 8: Time effect on mean temperature during the growing season (May to October) and the rest season (November to April) and time effect on annual soil water deficit. n = number of observations, F=Fisher value, p= significance probability value and R^2 = coefficient of determination.

Class Variable	*Fagus sylvatica*				*Quercus petraea*			
Parameters	n	F	p	R^2	n	F	p	R^2
Mean Temperature during growing season	36	15.49	0.0004	0.31	36	54.54	<0.0001	0.62
Mean Temperature during rest season	36	7.71	0.0088	0.19	36	8.12	0.0074	0.19
Soil water deficit	36	0.07	0.793		36	17.03	0.0002	0.33
Earlywood width					36	37.61	<0.0001	0.53

Figure 15: Times series of (a) ring width (RW) – red triangles indicate pointer years – recent moderate (dotted arrows) and intense (solid arrows) masting years, (b) Sum of precipitation (SP), (c) mean temperature (MT) and (d) soil water deficit (SWD) for* Fagus sylvatica *in Fougères, from 1971 to 2006. Panels (e, f, g, h) represented the same times series for* Quercus petraea *in Champenoux. Growth period extended from May to October and Rest period extended from the previous November to the current April. Vertical lines are standard errors (for clarity, standard errors of earlywood and latewood growth are not shown).

See figure on following page.


A
RW (10 µm)
500
400
300
200
100
0
B
SP (mm)
1000
800
600
400
200
0
Growth
Rest
C
MT (°C)
18
16
14
12
10
8
6
4
Growth
Rest
0.049 °C/yr.
0.030 °C/yr.
D
SWD (mm)
80
60
40
20
0
Growth
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
Date (yrs.)
E
RW (10 µm)
400
300
200
100
0
Ring
Latewood
Earlywood
F
SP (mm)
600
400
200
0
Growth
Rest
G
MT (°C)
18
16
14
12
10
8
6
4
2
0
Growth
Rest
0.077 °C/yr.
0.042 °C/yr.
H
SWD (mm)
150
100
50
0
Growth
2.080 mm/yr.
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
Date (yrs.)

Pointer years

Comparison with previous studies

Pointer years computed in the present study were compared with a set of pointer years assessed in previous studies for both chronosequences. Comparative data are summarized in Table 9. Considering the different periods covered for comparison, 72% and 81% of the pointers years detected in the present study for the Champenoux and Fougères sites respectively, had been detected in previous studies as well. This comparison allowed us to validate our cross-dating work.

Table 9: Comparison of pointer year sets between the present and previous studies.

		Fougères's site – *Fagus sylvatica*		Champenoux'site – *Quercus petraea*	
		Present study	Marsalle 1996	Present study	Becker et al. 1994
Sampling charact.	Date of coring	2006	1993	2006	1987
	Number of plots	23	2	18	121
	Number of trees	345	366	270	529
	Number of cores per tree	1	2	1	2
Compar.	Positive pointer years	6	16	20	15
	Negative pointer years	10	12	19	16
	Common pointer years	13		28	
	Period covered for comparison	1923-1993		1880-1985	

Thirty-nine pointer years were detected in the present study concerning the oak chronosequence whereas Becker and colleagues (1994) detected only 31 pointer years in the same forest, over the same period of time. This difference might be related to the differences in the respective goal that governing the selection of plots in the two studies. The main goal of Becker's study was to understand the impact of stand and soil characteristics on radial growth. Therefore, the set of 121 plots of this study was selected in order to represent the larger variability in soil (e.g. hydromorphic level, mineral fertility, soil texture, etc.) and stand characteristics (e.g. structure, age, vegetation, etc.) represented in the forest studied. In the present study, concerning the impact of ageing on radial growth, the 18 plots studied were selected in a narrower gradient of stand and soil characteristics, except for stand age naturally. Therefore, the smaller number of plots and the greater homogeneity between the plots of the present study may explain the greater homogeneity in the climate/growth response and the resulting larger number pointer years.

Similarly, whereas the study of Marsalle (1996) concerned two comparable beech stands, the present beech chronosequence concerned 23 stands selected over a large gradient of stand age. Therefore, the larger number of plots and the lower homogeneity between plots of the present study may explain why 16 pointer years were detected in the present study, whereas 28 pointer years were detected in the study of Marsalle (1996).

Species (+site) comparison

Information about pointer years for both species (+site) and all types of wood is presented in Figure 16. During the twentieth century, pointer years occurred more frequently for sessile oak (3.1 years per decade) than for beech (2.3 years per decade). The distribution of pointer years between negative and positive RGD was balanced for both species over the entire period considered. However, we observed a greater proportion of negative pointer years from 1980 to 2006 for sessile oak. Frequency of oak pointer years remained regular over time, whereas frequency of beech pointer years increased, particularly after 1950, with the occurrence of large positive values of RGD (Figure 16a, b). As compared to oak, the magnitude of ring width variation is much larger in beech. Smaller absolute values of RGD for negative pointer years are related to a biological limitation of growth: radial growth for a given year cannot be smaller than nil.

Type of wood comparison for sessile oak

Concerning differences between types of wood, pointer years were missing in earlywood series (0.02 year per decade); pointer years observed on ring width series of sessile oak were essentially related to latewood annual variations (Figure 16c). Moreover, the amplitude of RGD was lower for earlywood width than for latewood width, revealing a lower rate of year-to-year variation for earlywood growth.

Comparison of age-classes in 2006

To compare the frequency of pointer years between the 2006 age-classes, pointer years were computed for the recent period of growth shared by all 2006 age-classes. Pointer years were synchronous between age-classes for both species (Figure 16d,e). The youngest beech age-class presented two times fewer pointer years (2 yrs/decade) than the other age-classes whereas pointer year frequency was identical for every age-class of the sessile oak chronosequence (3.5 years per decade). RGD absolute values were higher for old age-classes than for the young ones in the beech chronosequence, especially during pointer year events, and were similar among age-classes for sessile oak.

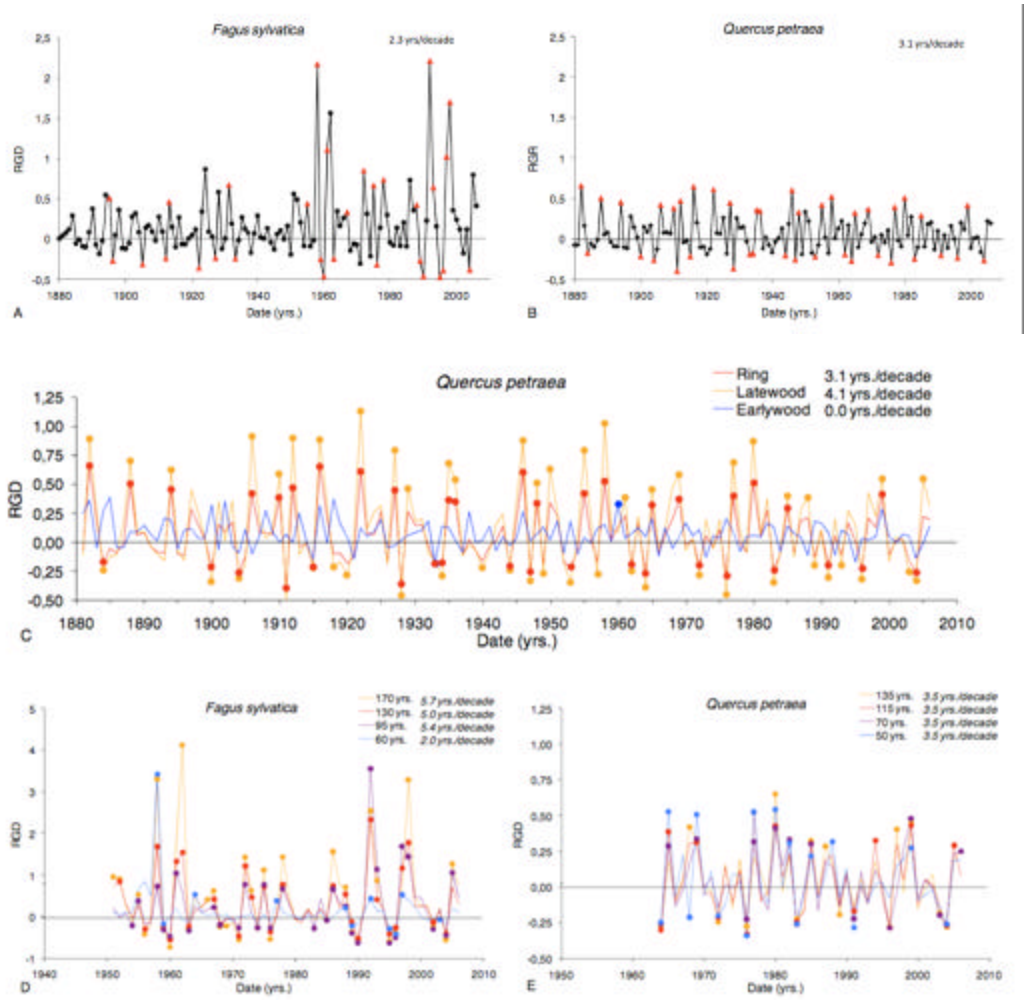


Figure 16: Pointer year information for each species (+ site) and type of wood. Panels A and B present annual variation of relative growth differences (RGD) for (a)* Fagus sylvatica *and (b)* Quercus petraea *between 1880 and 2006, pointer years are indicated by red triangles. Panel C presents annual variation of RGD for all types of wood of* Quercus petraea *from 1880 to 2006. Panels D and E present annual variation of RGD for 2006 age-classes of (d)* Fagus sylatvica *and (e)* Quercus petraea *from 1950 to 2006. For all panels, mean frequency of pointer years per decade are indicated.

Growth sensitivity to environmental conditions

In order to perform a direct comparison of cambial age and calendar date effects of growth sensitivity to environmental conditions, analyses of variance were performed on the initial data set split into balanced cambial age and date classes.

ANOVA results are summarized in Table 10. Statistics revealed that the chosen model was highly significant, for both species and all types of wood. However, it was more explanatory for beech than for sessile oak (R^2 of 0.34 and 0.10 respectively), and for oak latewood than for oak earlywood (R^2 of 0.11 and 0.05 respectively). The most explanatory factor was cambial age for beech and oak earlywood (R^2 of 0.24 and 0.03 respectively) while calendar date explained most of the oak ring and latewood variance (R^2 of 0.05 and 0.06 respectively). Interaction between cambial age and date explained a small but significant part of the variance for nearly all species and types of wood, except for oak earlywood.

Table 10: Results of analyses of variance carried out to study effects of cambial age class, time period and interaction between the two factors on growth sensitivity to environmental conditions. df = degrees of freedom, MS = mean square, F=Fisher value, p= significance probability value and R^2 = coefficient of determination.

Species	Type of wood	Effects	df	MS	F	p	R^2
Fagus sylvatica	Total ring width	Cambial Age classes	4	2,96955	122,5	<.0001	0,243
		Date period	4	0,69132	28,5	<.0001	0,057
		Interaction	16	0,11485	4,7	<.0001	0,038
		Error	1340	0,02425			
	Total ring width	Cambial Age classes	4	0,03665	4,54	0,0012	0,012
		Date period	4	0,16061	19,88	<.0001	0,054
		Interaction	16	0,02195	2,72	0,0003	0,030
		Error	1323	0,00808			
Quercus petraea	Earlywood width	Cambial Age classes	4	0,0715	8,63	<.0001	0,025
		Date period	4	0,04002	4,83	0,0007	0,014
		Interaction	16	0,00607	0,73	0,762	0,008
		Error	1323	0,00828			
	Latewood width	Cambial Age classes	4	0,12311	6,31	<.0001	0,017
		Date period	4	0,44677	22,90	<.0001	0,061
		Interaction	16	0,05982	3,07	<.0001	0,033
		Error	1323	0,01951			

Growth sensitivities were comparable among species for the young age-classes and different for the older ones (Figure 17a). Globally, beech growth sensitivity was significantly higher than sessile oak growth sensitivity ($F=269.4$, $p<0.0001$). Beech growth sensitivity increased linearly with age up to approximately 80 years old and stabilized at around 0.44 afterwards, whereas sessile oak growth sensitivity decreased very slowly with increasing cambial age, from 0.26 at 18 years old to 0.23 at 91 years old.

For sessile oak, earlywood growth sensitivity was lower than latewood growth sensitivity ($F=515.5$, $p<0.0001$; Figure 17b). Earlywood growth sensitivity decreased from 0.24 at 18 years old to 0.21 at 91 years old whereas latewood growth sensitivity increased weakly from 0.34 at 18 years old to 0.37 at 91 years old.

As observed for the time series (Figure 14a), beech growth sensitivity was amplified around the 1960s and during the last 20 years, whereas sessile oak growth sensitivity decreased regularly with time from 1960 to 1990 and seemed to stabilize afterwards (Figure 17c). Earlywood growth sensitivity decreased regularly over time whereas latewood growth sensitivity decreased with time from 1960 to 1990 and increased afterwards (Figure 17d).

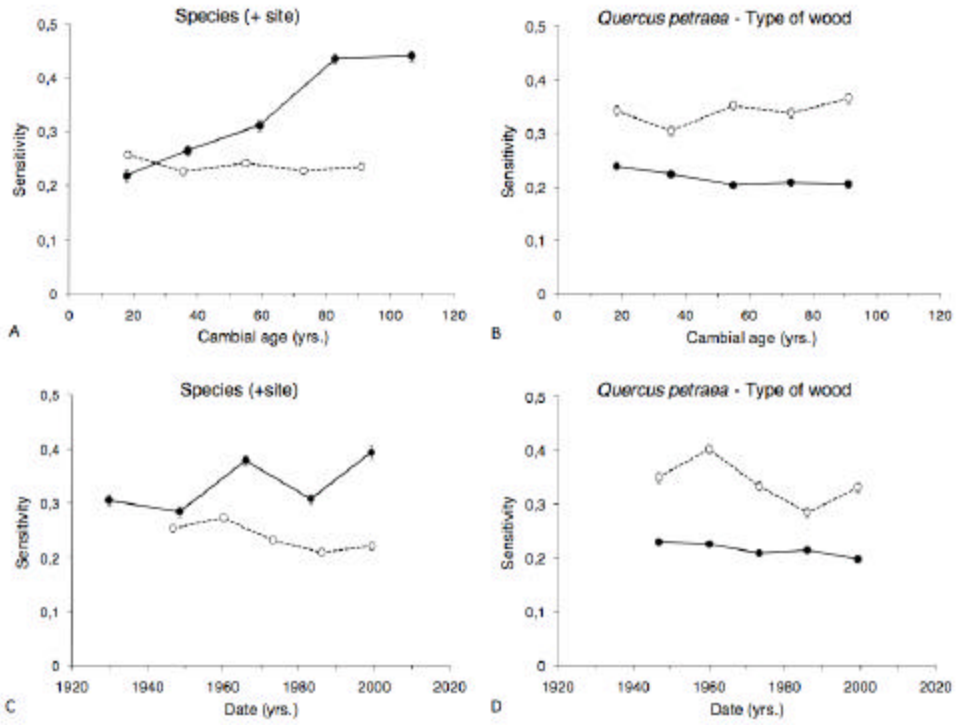


Figure 17: Least square means of sensitivity against cambial age for (a) ring width of* Fagus sylvatica *(dot, solid line) and* Quercus petraea *(circle, dotted line), (b) cambial age for earlywood (dot, solid line) and latewood (circle, dotted line) of* Quercus petraea. *Panels C and D present the least square means of sensitivity against calendar date. Vertical lines represent standard errors.

Autocorrelation

Positive lag1 autocorrelation was detected in 83 % of beech ring index series and in 80%, 42%, 72% of sessile oak ring, earlywood and latewood index series respectively (Figure 18a, b, c and d). Cambial age and calendar date effects of growth autocorrelation were studied using analyses of variance. To be reliable, autocorrelation has to be estimated on a sufficient number of observations: in order to enlarge the period for which autocorrelation was computed, the number of cambial age and calendar date classes was reduced from five to three, each class containing at least 22 years. ANOVA results are summarized in Table 11. The model was more explanatory for beech than for sessile oak. The most explanatory factor of beech autocorrelation was calendar date (R^2 of 0.11). Only interaction between age and date had little significant effect on the autocorrelation of total ring, earlywood and latewood growth of sessile oak.

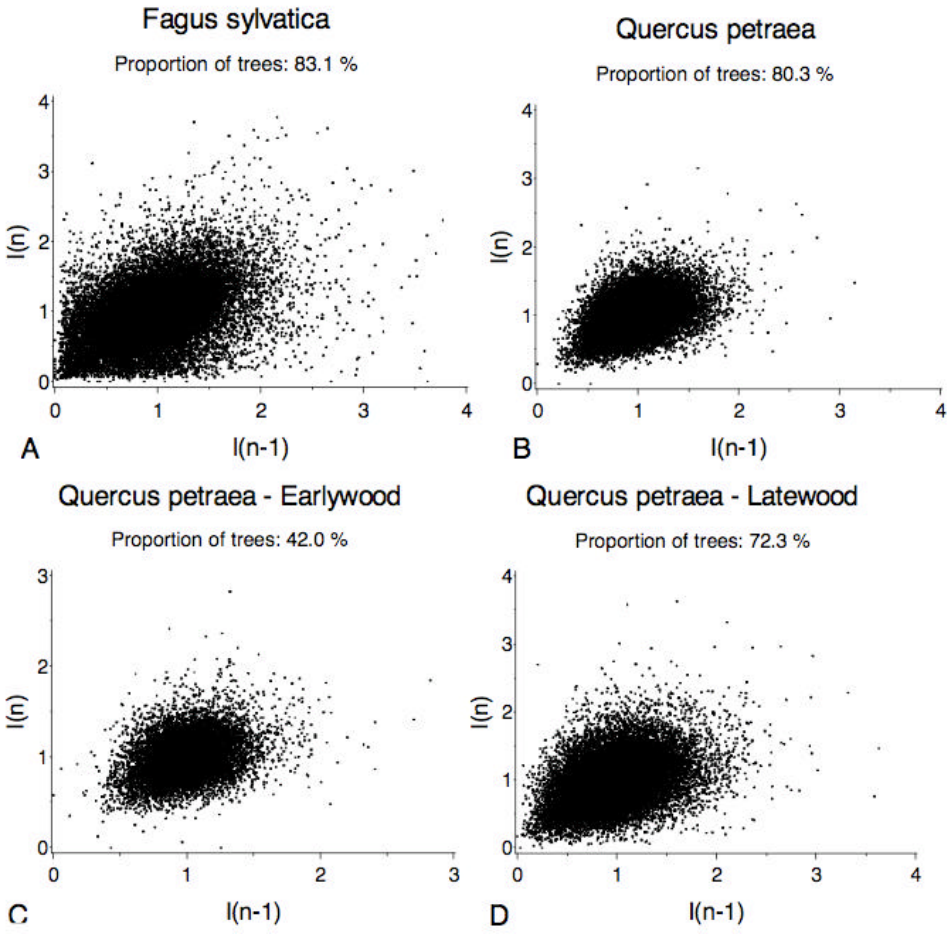


Figure 18: Lag 1 autocorrelation for (a)* Fagus sylvatica *ring index, (b) ring index, (c) earlywood index and (d) latewood index of* Quercus petraea *Only index series significantly autocorrelated are displayed.

Table 11: Results of analyses of variance carried out to study effects of cambial age class, time period and interaction between the two factors on growth autocorrelation. df = degrees of freedom, MS = mean square, F=Fisher value, p= significance probability value and R^2 = coefficient of determination.

Species	Type of wood	Effects	df	MS	F	p	R^2
Fagus sylvatica	Total ring width	Cambial Age classes	2	0,203	6,76	0,0013	0,022
		Date period	2	1,043	34,80	<.0001	0,112
		Interaction	4	0,157	5,22	0,0004	0,034
		Error	514	0,030			
Quercus petraea	Total ring width	Cambial Age classes	2	0,067	1,26	0,285	
		Date period	2	0,045	0,85	0,4287	
		Interaction	4	0,151	2,82	0,025	0,028
		Error	385	0,054			
	Early-wood width	Cambial Age classes	2	0,070	1,30	0,2724	
		Date period	2	0,016	0,30	0,741	
		Interaction	4	0,134	2,49	0,0431	0,025
		Error	385	0,008			
	Late-wood width	Cambial Age classes	2	0,071	1,45	0,2362	
		Date period	2	0,035	0,71	0,493	
		Interaction	4	0,236	4,81	0,0009	0,047
		Error	385	0,049			

Beech autocorrelation decreased with increasing cambial age (Figure 19a) and was not significantly different from sessile oak autocorrelation (F=0.02, p=0.879). For oak, the autocorrelation was significantly higher for latewood than for the earlywood index series (F=7.15, p<0.001; Figure 19b).

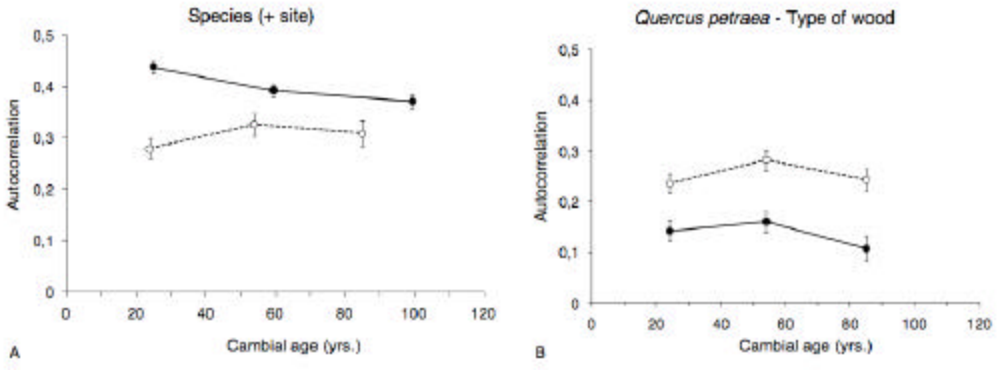


Figure 19: Least square means of autocorrelation against cambial age for (a) ring width of* Fagus sylvatica *(dot, solid line) and* Quercus petraea *(circle, dotted line), (b) for earlywood (dot, solid line) and latewood (circle, dotes line) width of* Quercus petraea. *Vertical lines represent standard errors.

Dendroclimatic analyses

The growth-climate relationships were estimated for each 2006 age-class of each species (+site) and each type of wood for sessile oak. Analyses were performed for the period [1971-2006], by taking the monthly mean temperatures and the sum of precipitation as climatic predictors, and parameters of water and carbon balance as bioclimatic parameters. In order to reduce the number of predictors, pre-analyses were performed using climatic and bioclimatic parameters separately. In the analysis using climatic predictors only, successive monthly variables with identical response function coefficients (in sign and magnitude) were grouped and averaged. In the analysis using bioclimatic predictors only, indicators of phenology, photosynthesis, transpiration, evapotranspiration and water deficit were tested; only parameters with significant response function coefficients were kept for further analyses.
These parameters are listed in Table 12. The final analysis presented below was carried out using these climatic and bioclimatic parameters.

Table 12: Description of parameters used for dendroclimatic analyses.

Variable	Description
WD	Water Deficit during growing season
DWD	Water Deficit duration
BB	Day of bud-burst
p1, mt1	Sum of precipitation (p) and mean temperature (mt) from previous October to November
p2, mt2	Sum of precipitation (p) and mean temperature (mt) from previous December to current February
p3, mt3	Sum of precipitation (p) and mean temperature (mt) of current March
p4, mt4	Sum of precipitation (p) and mean temperature (mt) from current April and May
p5, mt5	Sum of precipitation (p) and mean temperature (mt) from current June to September

In order to remove autocorrelation in ring width indices, dendroclimatic analyses were performed using residuals of autoregressive models, referred to as ARR. Response function coefficients were computed after principal component analyses on climatic and bioclimatic variables. Response function coefficients (RFC), i.e. the value of principal component estimators for the standardised climatic and bioclimatic variables, are presented in Figure 20. The higher the RFC, the higher the influence it has on ring width indices. Total determination coefficients are also displayed for each 2006 age-class.

Part of the variance of ARR explained by the climatic models was higher for sessile oak time series (R^2=0.48 in average) than for beech time series (R^2=0.38 in average) as shown by the values of the coefficients of determination (R^2 on Figure 20a,b). For beech, young age-classes presented lower coefficients of determination than older ones. Finally, homogeneity in response functions between age-classes was similar for sessile oak and for beech: factors influencing radial growth were almost identical between age classes.
For both species, rainfall in summer (P5) presented high positive RFCs. Precipitation during the previous autumn (P1) and current March (P3) substantially increased the radial growth of sessile oak, except for the youngest age class. High temperatures were almost unfavourable for beech growth, especially during late summer and autumn (MT1) and the advanced growing season (MT4, MT5). Mean temperature had a positive effect on sessile oak growth, particularly in the early growing season (MT4). Concerning bioclimatic parameters, water deficit (WD) and duration of water deficit (DWD) were of course unfavourable for radial growth of both species. Finally, precocious budburst had a negative influence on beech radial growth.

The model was not relevant for earlywood annual growth determination, and regression with parameters taken one by one did not reveal any additional correlation. The proportion of latewood growth variance explained by the model was higher than for total ring growth (Figure 20d). Parameters influencing latewood growth were similar to those influencing total ring growth.

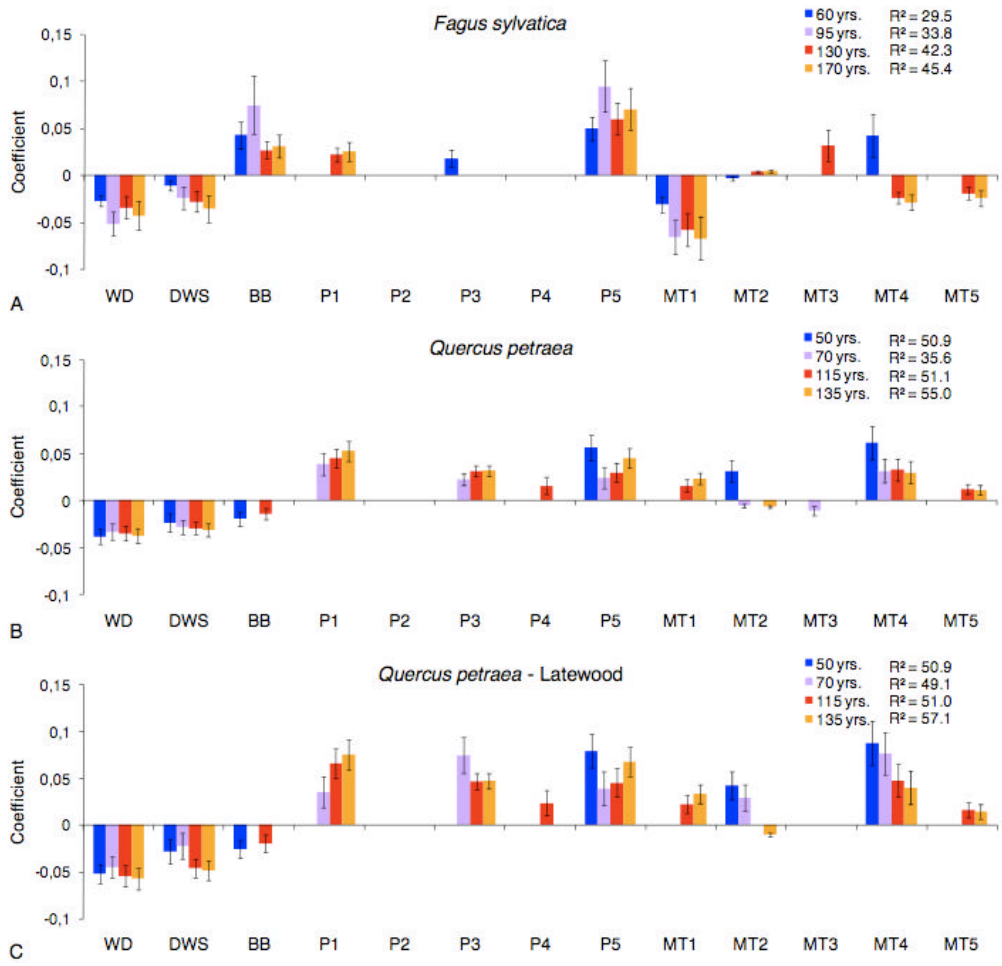


Figure 20: Response function coefficients for corrected indices of (a) ring width of* Fagus sylvatica *(b) ring width and (c) latewood width of* Quercus petraea *for the period [1971–2006]. Colours of bars differentiate age-classes. Vertical lines represent Standard errors. Parameter abbreviations are explained in Table 12.

DISCUSSION

Our sampling procedure, stratified by age classes, allowed us to study age-effect on radial growth separately from calendar date effect, using a balanced data set in which all ages were well represented in the various time periods.

CONTRASTING INFLUENCE OF CAMBIAL AGE ON OAK AND BEECH RADIAL GROWTH

After a short period of increase, ring width decreased with increasing cambial age in both species (+site) (Figure 10a, b). This decrease may be mainly related to geometrical constraints (Fritts 1963, 1976, Cook et al. 1990). However, this decline was more pronounced for beech than for sessile oak: compared to sessile oak, radial growth of beech was higher for young ages and lower for older ages.
Differences in the young stage of development might be related to differences in silvicultural practices at the two sites. Indeed, comparison of stand densities revealed that thinning may be more intensive and/or more frequent in the Fougères beech stands than in the Champenoux oak stands, and may be responsible for the higher radial growth observed for young ages of beech (Becker 1989, Becker et al. 1995). However, without a chronicle of silvicultural practices, this hypothesis cannot be confirmed.

The well-known decrease of radial growth with cambial age was very limited in oak (Figure 11b). The relative stability of earlywood growth with age should be related to the functional role of radial growth in hydraulic spring recovery in oak. Indeed, as a ring porous species, sessile oak exhibits high vulnerability to frost-induced embolism (Cochard et al. 1992, Bréda et al. 1993). Therefore, a large part (more than 40%) of the radial increment takes place during the spring, before leaf expansion (Hinckley and Lassoie 1981, Bréda and Granier 1996, Barbaroux and Bréda 2002) in order to recover a functional hydraulic pathway after winter frost damage. Yet, we demonstrated that earlywood growth was less sensitive to year-to-year environmental variations, presenting no pointer years and a low sensitivity level (previously illustrated by Degron and Nepveu 1996, Bergès 1998, van der Werf et al. 2007). Therefore this early growth seems to be “forced” by internal factors to be stable over time in order to ensure the physiological integrity of tree. This hypothesis is supported by the very

slight age- related decrease of earlywood width (Figure 11c). In contrast, only a few vessels in beech are fully embolized during the winter (Gasson 1987, Anfodillo et al. 1993, Hacke and Sauter 1996) and cambium re-activation and budburst occur simultaneously (Lachaud and Bonnemain 1981, Barbaroux and Bréda 2002), as in other diffuse porous species (Hinckley and Lassoie 1981). Thus, compared to sessile oak, the decrease in hydraulic conductance after winter damage and the subsequent necessity for early growth is less important in beech. Therefore, internal control of radial growth level may be less intense than for sessile oak. This concept is supported by the higher interannual sensitivity to environmental conditions exhibited by beech, compared to sessile oak (Figure 17a and Figure 16a; van der Werf et al. 2007).

Furthermore, the low age-related decline of oak latewood and total ring growth compared to beech might result from differences in carbon allocation strategies, as demonstrated in Chapter 1. Indeed, we have shown that whereas the carbon allocation of beech shifted from a priority to growth in the young stage of development to a priority to storage and reproduction in the older stage of development, the carbon allocation to growth remained high throughout the stand development in sessile oak. In addition, the inter-species differences assessed through the retrospective analysis of radial growth were coherent with the inter-species differences in carbon allocation strategy assessed in Chapter 1.

LONG-TERM TRENDS IN GROWTH

Comparison of curves fitted onto different "constant date curves" made it possible to demonstrate that age curve shape has changed over time during the twentieth century: we observed (1) an increase in the maximum growth value in the juvenile phase until the 1980s and a slight decrease afterwards for both beech and sessile oak rings and latewood rings, (2) an increase in the juvenile phase duration for sessile oak rings and earlywood rings and (3) a deceleration in age-related growth decline in the adult phase of development for both species (Figure 10, Figure 11). This interaction between cambial age and calendar date was confirmed statistically by analyses of variance (Figure 10).

There is clear evidence of a long-term increase in radial growth in both species. Radial growth increase was 43% for beech and 51% for sessile oak between 1940 and 1990 (Figure 13). This trend was consistent with previous studies concerning temperate deciduous and evergreen species (e.g. Becker et al. 1994, 1995, Picard et al. 1995, Badeau 1995, Badeau et al. 1996, Berges 1998, Rathegeber et al. 1999, Lebourgeois et al. 2000, Dhôte and Hervé 2000, Bontemps 2004, Martinez-Vilalta et al. 2008). Considering the positive effect of high temperature in the early growing season on sessile oak growth (Figure 20b, c), radial growth improvement could be partially related to an established increase in average temperature (Figure 15c, g). This argument is not valid for beech, considering the negative effect of the previous autumn temperature on beech growth (Figure 20a). A similar conclusion regarding the negative effect of temperature on radial growth was obtained by Martinez-Vilalta et al. (2008) concerning Scots pine in Spain. Date-related growth increased has also been related to atmospheric CO_2 (Graumlich 1991, Becker 1994, Norby 1996, Martinez-Vilalta et al. 2008), intensification of silvicultural practices (Mund et al. 2002) or increases in N deposition (Kenk and Fisher 1988, Binkley and Högberg 1996, Hättenschwiler et al. 1996, De Vries et al. 2006, Pregitzer et al. 2008). The latter hypothesis could be put forward in our study, as Brittany is subjected to high N depositions due to intensive pig farming.

After the 1980s, sessile oak displayed a decrease in latewood growth (Figure 13d) leading to a decrease in total ring width. This result is consistent with the higher proportion of negative pointer years observed from 1980 (Figure 16a): stresses that resulted in a growth decrease have been more frequent during the last two decades. The significant increase in drought observed from 1980 could explain this growth depletion (Figure 15h). Indeed, dendroclimatic analyses revealed that rainfall, water deficit and water deficit duration during the growing season were the most important factors determining radial growth variation in sessile oak

latewood (Figure 20b). This result constitutes a further confirmation of the well-known sensitivity of sessile oak growth to drought events (e.g. Cochard et al. 1992, Becker et al. 1994, Bréda 1994, Granier et al. 1999, Leuschner et al. 2001, Granier et al. 2007). In contrast, earlywood growth has continued to increase over time since the 1980s. The improvement of earlywood growth was also reported by Lebourgeois et al. 2000 for Corsican pine. The regular increase of earlywood growth may be related to (1) the phenology of earlywood growth and (2) the recent warming observed at the Champenoux site. We saw that earlywood was formed early in the growing season, so it may not be limited by water deficit. Furthermore, even if no correlation between earlywood growth and climatic or bioclimatic parameters has been detected at present, we found that the warm April and May favoured sessile oak radial growth. Furthermore, Bergès (1998) found a small but significant and positive effect of temperature in March on earlywood growth ($R^2 = 0.05$). In addition to a positive effect on growth rate, high temperature may have also hastened the date of cambial activation, as observed for budburst date (Hänninen 1991, Kramer 1994, Menzel and Fabian 1999, Morin 2006). Despite the positive effect of increasing earlywood growth on stand productivity, this change may also weaken the capacity of the trees to resist their environment. Indeed, because earlywood is formed before leaf expansion, earlywood growth improvement may exhaust the carbon storage in trees.

Growth increase over time was found to be lower for the young age-classes than for the older ones. It even rose regularly with cambial age for earlywood growth of sessile oak. A lower impact of global changes on young tree growth compared to older ones is consistent with an age related increase of the climatic determinism of growth detected for both species in dendroclimatic analyses (coefficient of determination of various age classes in Figure 20). However, this result disagreed with previous findings. Studying radial growth of sessile oak in the north of France, Bergès, Dupouey and Franc (2000) found higher changes over time in ring width and ring density belonging to younger age-classes. Badeau (1995) came to the same conclusion for beech in north-eastern France. For both studies, analyses of variance were used to assess cambial age and calendar date effect on growth; a previous "cutting" in an initial data set was also done in order to perform analyses on a balanced subset between cambial ages and calendar dates (see Materials and Methods). However, despite this "cutting", the subset used by Bergès et al. remained fairly unbalanced: 47% of the youngest rings analysed were developed during the most ancient period [1924-1936] while 51% of the oldest rings analysed were developed during the most recent period [1964-1993]. Hence, in the context of growth increase over time, the set of young ring widths was unbalanced towards a less favourable period of growth, resulting in an overestimation of date-related increase in growth, whereas the set of older ring widths was unbalanced towards a more

favourable period of growth, inducing an underestimation of date-related increase in growth. Concerning the analyses of beech growth in north-eastern France carried out by Badeau (1995), ANOVAs were performed on a well balanced data set but the use of ring area, instead of ring width, may have induced the age-related decrease observed in recent growth changes. Indeed, ring area depends on ring width as well as tree size, but recent growth increment will have a greater impact on the size of young trees than that of older ones: e.g. if we consider normal radial growth as constant, an abnormal increase of 5% per year in growth over 10 years will increase the stem ray by 5% in 10-year-old trees whereas it will increase the stem ray by only 0.5% in 100-year-old trees. Hence, the effect of radial growth increment on tree size will result in recent growth changes being overestimated in small young trees and underestimated in older trees. Ring width is less size-dependent and might be a better variable to compare trees of different ages.

INTERANNUAL VARIATION OF RADIAL GROWTH

For both species and all age classes, rainfall in summer (P5) presented high positive RFCs, when summer drought affected growth (Figure 20): not surprisingly, water deficit and water deficit duration were negatively correlated with radial growth of both species. Precipitation during the previous autumn (P1) substantially increased current radial growth of adult and old sessile oak and beech trees. Carbohydrate reserves are mainly accumulated during the second half and end of the growing season (Barbaroux 2002, Skomarkova et al. 2006), and by limiting drought stress in the late growing season, precipitation sustains the carbon assimilation and carbon storage that will be available for growth the following year (Barbaroux 2002, Helle and Schleser 2004, Skomarkova et al. 2006). Positive correlation between rainfall in March (P3) and radial growth of sessile oak has been observed by van der Welt et al. in Netherlands (2007) too. Garcia-Gonzales and Eckstein (2003) reported the strong dependence of early wood vessel lumen area on rainfall between February and April, resulting in wider early wood width. This may be related to the subsequent refilling of the soil water reservoir before a new growing season, which could impact vessel ontogeny. A warm April and May (MT4) favoured radial growth of sessile oak. During a period of elevated growth rate (Béda and Granier 1996, Barbaroux and Bréda 2002, van der Werf 2007) and very scarce soil water, temperature was the main growth stimulator. A negative correlation between beech growth and previous late season temperature (MT1) supported the hypothesis put forward by Skomarkova et al. (2006) that wood density, positively correlated with late summer temperature (Bouriaud et al., 2004), competed with carbon storage in the autumn. In this case, the warm autumn promoted wood density and reduced storage formation available

for growth the following year (Barbaroux and Bréda 2002). High temperature may also increase respiration rate which may contribute to a reduction in storage formation. Finally, early budburst (BB) had a negative influence on beech radial growth. Indeed, precocious budburst may enhance risks of spring frost damage on young leaves (Becker 1994).

Pointer year frequency found in the present study accorded with previous studies performed on the French level II plots network RENECOFOR (Lebourgeois 1997, Lebourgeois et al. 1995, Lebourgeois et al. 2006). We showed that climate signal was maximized in older trees of both species, at low and high frequency, revealing more stressful conditions of growth in ageing trees (Carrer and Ubinati 2004). However, the age effect on radial growth was more pronounced for beech (Penninck 1999) than for sessile oak in terms of sensitivity to environmental conditions (pointer year frequency, mean sensitivity and determination of the bioclimatic model). Moreover, the recent increase of beech growth sensitivity, also reported by Dittmar, Zech and Elling (2003), was not detected for sessile oak. These results reinforce the idea that growth of sessile oak is partially determined by internal factors to fulfill a minimum growth, whereas beech radial growth is more determined by environmental conditions. Furthermore, differences of year-to-year variations of growth between species may be related to frequency of growth reduction caused by masting events (Selas et al. 2002, Monks and Kelly 2006). Indeed, Aussenac (1975) reported that frequency of significant masting events for sessile oak in the site studied were around 5.5 years (an average over 107 years from 1865 to 1971) while beech masting seemed to occur at a biannual rhythm in the site studied (C. Nys pers.comm.), as already reported in Europe (Hilton et al. 2003, Overgaard et al. 2007). Thus, growth variation induced by masting events may be more frequent for beech than for sessile oak.

Age-related variations of carbon assimilation capacity at leaf and canopy levels

INTRODUCTION

With the development of process-based models simulating carbon and water cycles at different scales of time and space, numerous studies have tried to assess the links between different leaf traits and functions (e.g. Reich et al. 1997, Niinemets 2001, Wright et al. 2002) in order to identify the best parameters describing leaf to canopy physiology and their response to the environment.

Many of the studies concerning leaf physiology consist of manipulation experiments on tree seedlings (e.g. Poorter & Bergkotte 1992; Grime et al. 1997), and these results are often used to predict the response of seedlings in their natural environment. However, the conditions of competition for resources that greatly determine individual development in natural conditions are rarely reproduced in experimental manipulations. On another hand, most of the experiments studying seedlings under natural conditions used populations growing under a canopy of mature trees (Cavender-Bares and Bazzaz 2000). Yet in even-aged stands, a widespread forest structure cultivated in temperate forests, seedlings grow in dense stands without an overstorey canopy, experiencing full sunlight (Boudru 1989, Bastien and Wilhelm 2000, Pothier et al. 2003). This configuration of growing conditions (high competition for soil resources and full sunlight) is rarely seen, either in experimental manipulations, or in experiments under natural conditions.

Similarly, results obtained from tree seedlings are often used to predict the response of mature trees for which experimental data are more difficult to collect (Woodward et al. 1991, Ziska et al. 1991, Wullschleger et al. 1995). Several authors have developed experimental designs combining experimental manipulation and observation under natural environments, in order to predict the response of adult trees from seedlings by integrating ontegenetic and environmental changes related to stand and tree ageing (Bazzaz Cavender-Bares and Bazzaz 2000, Cornelissen et al. 2003, Mediavilla and Escudero 2009); but because physiological response to the environment may change with age (Donovan and Ehleringer 1992), the age-related changes in leaf traits might be dependant on the environmental conditions.

For example, many authors have shown that photosynthesis decreases with stand development. This age-related decline has been attributed to (1) the decrease in the size of the assimilation compartment, i.e. decrease in Leaf Area Index (Ryan et al. 1997, Bond-Lamberty et al. 2002, Kashian et al. 2005, Leuschner et al. 2006), (2) the decrease in the photosynthetic capacity, i.e. the decrease of nitrogen and chlorophyll contents (Martinez-Vilalta et al. 2007), leaf mass area (Thomas et al. 2002, Delzon 2004) or maximum photosynthetic rate and (3) the changes in stomatal functioning (Yoder et al. 1994, Ryan et al. 2006, Zaehle et al . 2006, Martinez-Vilalta et al. 2007). However, results are not always concordant and homogenous age-related trends concerning photosynthesis are scarce (see Ryan et al. 1997, Becker et al. 2000, Thomas et al. 2002, Delzon 2004). Furthermore, a large majority of these studies are focused on conifers and few studies concern deciduous broadleaved species like beech and sessile oak. Sessile oak and beech present contrasting levels of tolerance to shade, and whereas beech is a shade-tolerant species, especially in the early stages of development, sessile oak is a light-demanding species (Rameau et al. 1989). Yet many studies have related inter-species differences in leaf and growth traits to differences in level of shade tolerance (e.g. Walter and Reich 1996, Janse-ten Klooster et al. 2007). So, we suspected that there are different ontogenetic pathways in leaf characteristics between beech and sessile oak, based on their contrasting shade tolerance.

Therefore, we examined the changes in leaf traits occurring during two chronosequences of beech and sessile oak at leaf and canopy levels in order to (1) identify and quantify the suspected age-related decline of the assimilation capacity of leaves and the canopy, (2) examine the changes in structural and chemical leaf traits related to this age-related decline, and (3) compare the ontogenetic changes in leaf characteristics between two deciduous species presenting contrasting tolerance to shade.

MATERIALS AND METHODS

SITE AND STAND DESCRIPTIONS

See section entitled *Site and Stand descriptions*, page 63 in Chapter 2.

CANOPY-LEVEL MEASUREMENTS

Maximum Leaf Mass Area (LAI)

Leaf Area Index was estimated for each plot of both chronosequences with a Plant Canopy Analyser Licor LAI-2000 (LI-COR Inc., Nebraska, USA). Above and below canopy measurements were realised alternately. According to the size of the plot, transmitted light was measured at intervals ranging from 5 to 10 m. At least 20 measurements were made below the canopy. All measurements were made during sunny, cloud-free days, at less than 1 h after sunrise or before sunset respectively. Leaf area index was calculated by the Li-Cor program C2000 (Li-Cor 1992) using linearly interpolated values of incident light at three zenith angles (from 0 to 43°). The two most horizontal angles were excluded from the computation to reduce the influence of woody components of aboveground cover (especially trunks) on LAI estimates. A view restrictor of 180° was used to exclude the operator's silhouette from the measurement area. Diffuse and direct radiation from the direction of the sun was blocked from the sensor by the shadow of operator. This operating mode was used in previous studies and results were consistent with direct LAI estimates from litterfall (Dufrêne and Bréda 1995, Bréda et al. 2002, Bréda 2003). In order to estimate maximum LAI, measurements were made after maximum leaf expansion and before leaf yellowing (at the beginning of the autumn).

In Fougères beech forest, LAI measurements were performed between day of year (DOY) 177 and 182, in 2006. To fulfil the requirements of a project concerning the ecological modelling of the carbon balance at the forest scale using field measurements and remote sensing[1], LAI measurements were performed at the forest unit scale instead of the experimental plot scale. These LAI measurements were compared with the standard deviation of the Normalized Difference Vegetation Index (sNDVI) (1) to be able to predict LAI of all stands of the Fougères forest from remotely sensed NDVI acquisition and (2) to compare this relationship with previous ones estimated at different sites (Le Maire et al. 2006) and to assess the inter-site variability. However, because the within stand heterogeneity was frequently high, each stand had first been surveyed by the operators to identify the boundaries of the largest areas with a topography (mostly flat), species composition and canopy structure similar to the initial plot. These limits were then transferred onto a map and transects of measurements were drawn to cover the identified area.

In the oak chronosequence, LAI measurements were performed between DOY 189 and 200, in 2006. This site was not involved in the ORE F-ORE-T project. Measurements were thus restricted to a smaller area than in the Fougères site. Data were taken in eight directions (North, North-East, East, South-East, South, South-West, West, and North-West) from the most central tree of the original plots (constituted by the trees cored for carbohydrate and growth measurements). Thirty-two measurements were made in an 8000 m² circle, following the scheme presented in Figure 21. Homogeneity of topography, species composition and canopy structure was checked systematically.

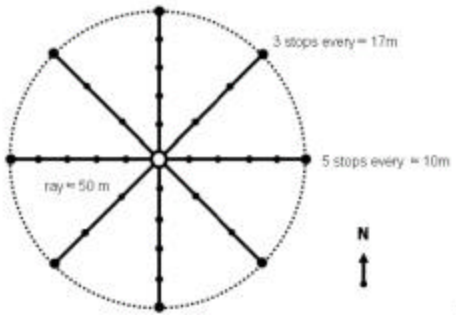


Figure 21: Scheme of sampling for LAI measurements in plots of Champenoux site

[1] Spatial analysis and carbon scaling from stand to forest, coordinated by Dr. E. Dufrêne from the Ecology, Systematic and Evolution Laboratory (ESE), CNRS/University of Paris Sud, Orsay, France, and involving the Phytoecology Team from the Forest Ecology and Ecophysiology Unit, National Institute of Agronomic Research (INRA), 54280 Champenoux, France, financed by the ORE F-ORE-T program of GIP ECOFOR.

Stand inventories

Stand inventories were carried out in all plots of both chronosequences. For the Champenoux chronosequence, inventories were made in February, 2007 by our team. The diameter of the area inventoried ranged from 24 to 80 m, depending on stand age class. Inside these areas, species and stem circumference at a height of 1.3m were recorded for each tree. Circumferences were measured with metallic rules. For the Fougères chronosequence, inventories were made by the National Forest Office during the winter of 2006/2007. The diameter of the area inventoried ranged from 36 to 50 m. Inside these areas, species and the stem diameter of each tree at a height of 1.3m were recorded. Diameters were measured with a compass.

For each plot at both sites, the total heights of 5 dominant trees were measured to assess stand dominant height. Tree heights were measured using a clinometer Vertex IV (Häglof, Sweden) in adult trees and a telescopic pole in the youngest stands.

Influence of understorey in stands of the Champenoux site

As shown by the distribution histograms presented in Figure 22, the structure of the adult stands at the Champenoux site was characterised by an overstorey dominated by oak species and a substantial understorey dominated by hornbeam (*Carpinus betulus*). Conversely, the stands of the Fougères chronosequence were almost pure beech (Figure 23).

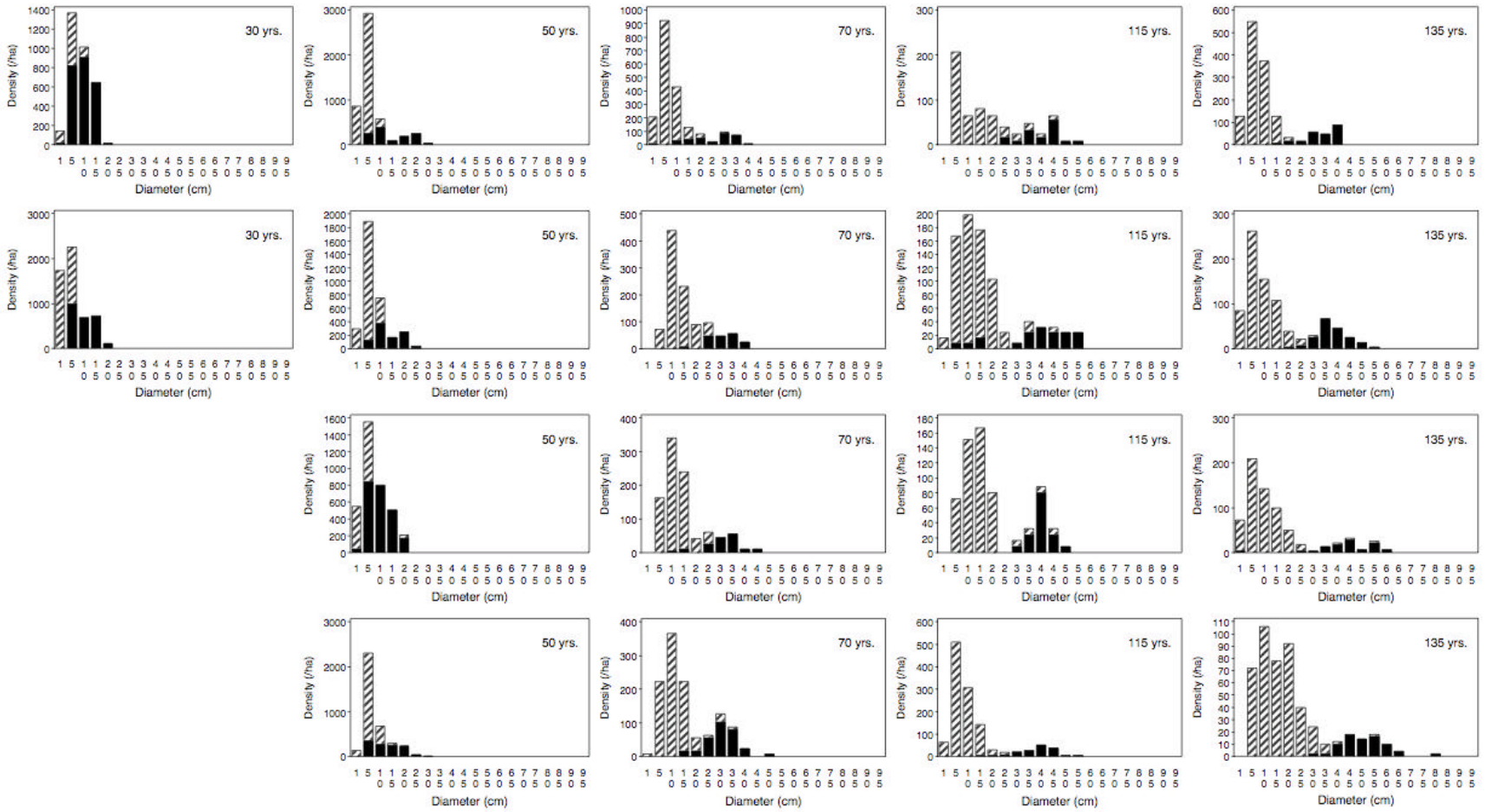


Figure 22: Histograms of tree density distribution by diameter classes for the Champenoux chronosequence. Black bars represent* Quercus petraea *densities and dashed bars represent other species. Age classes are indicated.

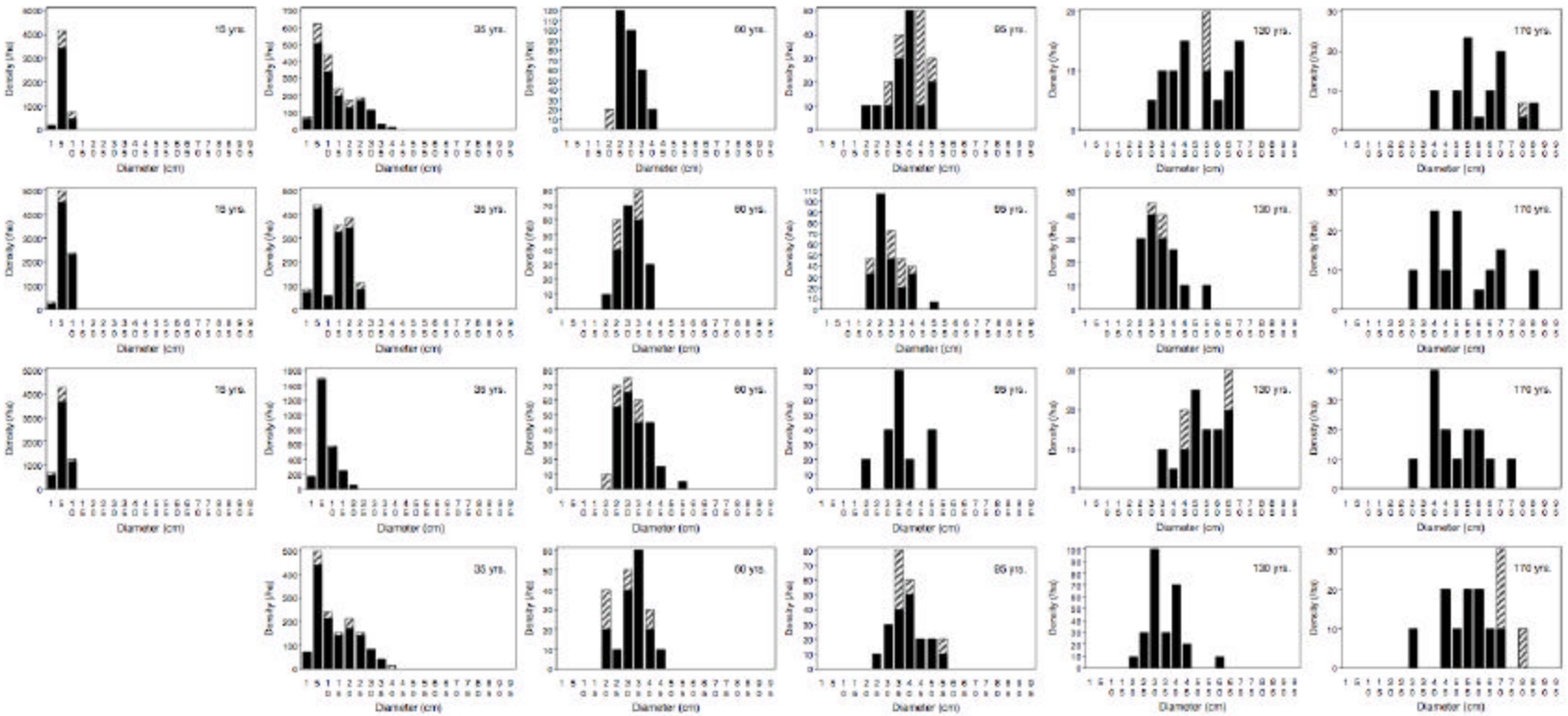


Figure 23: Histograms of tree density distribution by diameter classes for the Fougères chronosequence. Black bars represent* Fagus sylvatica *densities and dashed bars represent other species. Age classes are indicated.

Because LAI measurements were made at breast height, the understorey was included in LAI estimations. In order to quantify the weight of the understorey on LAI estimations, litter collection and forest inventory data from permanent plots of the French network RENECOFOR (*Réseau National de Suivi à Long Terme des Ecosystèmes Forestiers*) were used (Bréda, 2003). Data were collected in 1995. Stands dominated by *Quercus petraea* and/or *Quercus robur* located in north-eastern France and presenting a structure similar to our stands were selected (Cluzeau et al. 1998). The litter collected was sorted by species allowing an estimation of LAI contribution of each species to the total LAI of the selected stands. Partial LAI and basal area of oak were then compared (Figure 24).

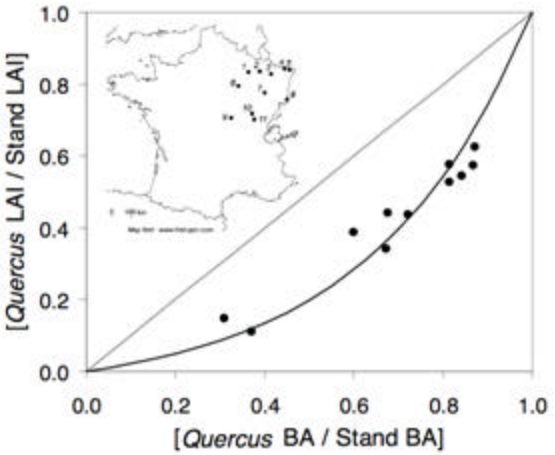


Figure 24: Oak Relative LAI as a function of Oak Relative Basal Area. Measurementss (dot), predicted values (black line) and 1:1 proportion line (grey line) are presented. Location of Level II plots selected is inserted.

The relationship between the proportion of LAI and the proportion of oak basal area was of an exponential type. For a given stand, the proportion of LAI was lower than the proportion of basal area. This distribution has been already seen in deciduous broad-leaved forest (Eermak 1998). For reasons of coherency, the relationship between the proportion of LAI and the proportion of basal area were forced to contain (0,0) and (1,1) intercepts.

LAI *Quercus* = LAI Stand * [-0.0661 * (1- exp (2.78 * (BA Quercus / BA Stand)))]
($F = 540.24$, $p<0.0001$)

Sapwood Area and [Leaf Area: Sapwood Area] Ratio (AL:ASW)

The leaf-to-sapwood area ratio is one of the parameters commonly used as a proxy for the hydraulic conductance in trees. This ratio quantifies the area of transpiring leaves supported by a unit of conducting sapwood area. With increasing age and size, many studies have shown that the hydraulic effects of increased stature can be offset partly by decreasing the $A_L:A_{SW}$ ratio (i.e. Barnard and Ryan 2003).

Without allometric relationships to compute tree leaf area in the studied sites, we estimated [Leaf Area : Sapwood Area] Ratio at the stand scale, as the ratio between overstorey LAI and the sum of sapwood area of each trees composing the overstorey.

Sapwood estimation at tree level

We considered that beech did not develop visible heartwood (see Chapter I, section entitled *Estimation of carbohydrates accumulated in 2006*, page 29). We thus assumed that the whole of the sectional area of the stem constituted sapwood. For sessile oak, the limit between heartwood and sapwood was clearly visible. Sapwood width was measured on cores taken at a height of 1.3 from the stems of 15 dominant trees per plot. The estimation of the heartwood/sapwood limit was based on wood colour transition and the proportion of vessels obstructed by thylosis. Observations were made using a binocular microscope. .

Sapwood area at tree and stand level

For sessile oak, the diameter at breast height for each inventoried tree was obtained from circumference measurements. Sapwood area was measured directly for only 15 trees per stand. For the other trees, sapwood area was estimated using an allometric relationship linking sapwood proportion – as the ratio between sapwood diameter and stem diameter – and stem diameter (Figure 25). This relationship was assessed for the studied site using the 438 sapwood width and diameter measurements described above. The negative exponential obtained was the following:

$$Ratio = 2.7994 * dbh^{-0.4806} \qquad (F = 3482.21, p<0.0001)$$

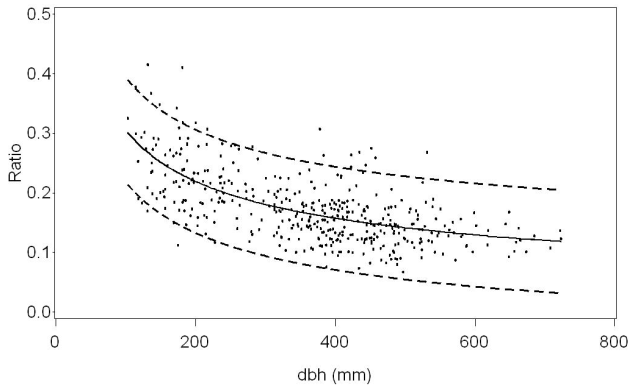


Figure 25: Unit-less* Quercus petraea *[Sapwood diameter: Stem diameter] ratio as a function of stem diameter. Observations are plotted by age classes.

This statistical relation allowed the estimation of sapwood width for each tree. Sapwood area was then calculated as the total wood area minus the heartwood area at a height of 1.3 m. Sapwood areas of the recorded trees were finally summed to deduce sapwood area at the stand scale.

For beech, section area at breast height was estimated from the diameter measurements for every recorded tree. Section areas of recorded trees were summed to the deduce basal area at stand scale.

LEAF-LEVEL MEASUREMENTS

Sampling

Leaf parameters were measured on 3 samples of 10 sun leaves per tree, for 10 dominant trees per plot (Bonneau 1995), in every plot of the two chronosequences i.e. 1230 samples from 410 trees.

Ten dominant trees were chosen in the vicinity of the trees selected for carbohydrate measurements, while paying attention to site homogeneity regarding soil, vegetation and structure. For each of the selected trees, one branch from the upper third of the canopy was shot, using a rifle, in the adult stands; and an averruncator was used in the youngest, smallest stands. Thirty leaves were randomly selected from the branches and divided between 3 plastic bags, each containing 10 leaves. In the field, bags were then stored in a cold atmosphere (icebox containing freezer-packs) to prevent respiration by the foliar tissues that might reduce leaf weight and thus induce an underestimation of leaf mass area. In the laboratory, the plastic bags were stored in a cold chamber (4°C) until measurements and drying could be carried out. Leaf area was measured within 48 hours following harvesting.

Total chlorophyll content (CHL)

One of the batches of 10 leaves was taken to measure the chlorophyll content using a chlorophyll meter (SPAD 502, Konica Minolta Sensing Inc., Osaka, Japan). SPAD measurements were made in the field immediately after leaf collection. For each of these ten leaves, at least 10 SPAD measurements were made at different locations on the leaf (avoiding the principal nerve, holes and coloured or faded spots). The average value per leaf was calculated and converted into chlorophyll content (g/m^2) using the following relationships calibrated for each species:

$CHL = 0.02063253 * SPAD - 0.1479003$ for oak

$CHL = 0.06856534 + 0.0005764338 * SPAD + 0.0003370486 * SPAD^2$ for beech

Relationships between SPAD values and chlorophyll content were calibrated from 20 leaf samples for each species. After SPAD measurements, chlorophyll contents were estimated using spectrophotometric measurements after dissolution in DiMethylSulfOxyde. Calibrations

were carried out by Dr. B. Caquet (Forest Ecology and Ecophysiology Unit, Bioclimatology Team, Institut National de la Recherche Agronomique (INRA)).

Leaf Mass Area (LMA)

Three bags per tree, each containing ten leaves, were used for LMA estimation. The cumulative area of the ten leaves per bag was measured with a planimeter LI-3000A with a transparent belt conveyer LI-3050A (LI-COR Inc., Nebraska, USA). Leaves were then oven-dried for 72 hours at 60°C before being weighed. The LMA was the ratio of cumulated leaf dry weight to leaf area (g/m^2). The three values were then averaged by tree.

Carbon and Nitrogen contents

After drying and LMA measurement, the 30 leaves per tree were ground using a rotary grinder with rings (SODEMI, Cergy Pontoise, France). Before analyses, samples were dried again for 4 hours at 60°C. 1.5 to 1.7 mg of powder were weighed with Sartorius MC5 microscales (Data Weighing Systems, Inc., Chicago, Illinois, USA), stored in a tin capsule and analysed by dynamic flash combustion with an elemental analyser (Flash 2000 NC, Thermo Fisher Scientific Inc., Miami, Florida, USA).

STATISTICAL ANALYSIS

Data were analysed using the SAS statistical package (SAS 9.1, SAS Institute Inc., Cary, NC, USA) (SAS 1988). . Two main effects were tested: (1) species effect, with an analysis of variance (ANOVA), and (2) stand age effect with linear regressions for each species. However, because the species were located in different forests, species differences may also include some site influence. To compare species (+ site) properly, species effect and age effect for each species were tested in comparable age ranges, i.e. the youngest and oldest beech classes were excluded from these analyses.

RESULTS

Results concerning ANOVAs testing species (+site) differences, and linear regressions testing age effect by species on a similar age range, are given in Table 13 for each leaf parameter studied.

LEAF PARAMETERS AT LEAF LEVEL

Leaf Mass Area

The leaf mass area (LMA) was estimated on 30 sun leaves per tree, for 10 dominant trees per plot. LMA is the ratio between leaf mass and leaf area. As the inverse of Specific Leaf Area (SLA), it is a widely used indicator of leaf morphology.

Sessile oak trees presented significantly higher LMA (Table 13), leaf mass and leaf area than beech leaves. Moreover, LMA trends with age were significantly different between the two species (+site) (Figure 26A, D). After a slight increase in the youngest stands, LMA of beech trees decreased significantly with age, especially in adult stands, from 97 to 77 g/m². The LMA decrease resulted from a log-decrease of leaf mass (from 0.25 to 0.10 g per leaf), which was steeper than the inverse-decrease of leaf area in adult stands (from 29 to 12 cm² per leaf) (Figure 26B, C). As opposed to beech, LMA of sessile oak trees increased regularly with age from 88 to 114 g/m². Linear increase of LMA was mainly linked to a linear decrease of leaf area, from about 35 to 23 cm² per leaf, whereas leaf mass remained almost constant with age, around 0.29 g per leaf (Figure 26E, F).

Table 13: Effects of species (+ site) and age on Leaf traits. Analyses were carried out on a similar age range, e.g. excluding youngest and oldest beech stands. Analysis of variance was used to assess the differences between species. Linear regression was used to assess age effect. Age effect was tested for each species. n = number of observations, F=Fisher value, p= significance probability value and R^2 = coefficient of determination.

Variable	Species (+ Site)				Stand Age									
					Fagus sylvatica					*Quercus petraea*				
	n	F	p	R^2	Transf.	n	F	p	R^2	Transf.	n	F	p	R^2
LMA	340	57.0	<0.0001	0.144	square	160	4.6	0.0112	0.056		180	27.3	<0.0001	0.134
Leaf mass	340	378.7	<0.0001	0.528	log	160	85.8	<0.0001	0.352		180	0.2	0.6597	0.001
Leaf area	340	307.8	<0.0001	0.477	inv	160	81.8	<0.0001	0.341		180	7.4	0.0072	0.040
Carbon content per mass unit	340	276.8	<0.0001	0.452		160	1.5	0.2236	0.009		180	3.4	0.0669	0.019
Nitrogen content per mass unit	340	0.6	0.4299	0.002		160	5.4	0.2130	0.033		180	4.6	0.0338	0.025
[C/N] ratio	340	10.0	0.0017	0.029		160	4.4	0.3666	0.027		180	5.9	0.0159	0.033
Chlorophyll content per mass unit	340	414.0	<0.0001	0.552		160	2.3	0.1335	0.014		180	26.8	<0.0001	0.132
Carbon content per area unit	340	23.4	<0.0001	0.066	square	160	3.9	0.0217	0.048		180	28.1	<0.0001	0.139
Nitrogen content per area unit	340	52.7	<0.0001	0.136	square	160	1.1	0.3169	0.014		180	5.1	0.0247	0.029
Chlorophyll content per area unit	340	1131.9	<0.0001	0.770		160	0.0	0.8252	0.000		180	1.1	0.3067	0.006
Stand LAI	34	2.0	0.1689	0.058		16	2.5	0.1341	0.153		18	0.1	0.7379	0.001
Corrected LAI	34	48.1	<0.0001	0.600						inverse	18	11.3	0.0039	0.415
[AL : ASW]	34	3.1	0.0872	0.088	log	16	0.8	0.3748	0.057		18	4.05	0.0613	0.202
Leaf biomass	34	47.3	<0.0001	0.596		16	4.9	0.0449	0.257	inverse	18	9.2	0.0078	0.366
Nitrogen quantity	34	37.2	<0.0001	0.538		16	3.4	0.0847	0.197	inverse	18	11.0	0.0044	0.407
Chlorophyll quantity	34	3.0	0.0952	0.085		16	2.1	0.1674	0.131	inverse	18	11.9	0.0033	0.426

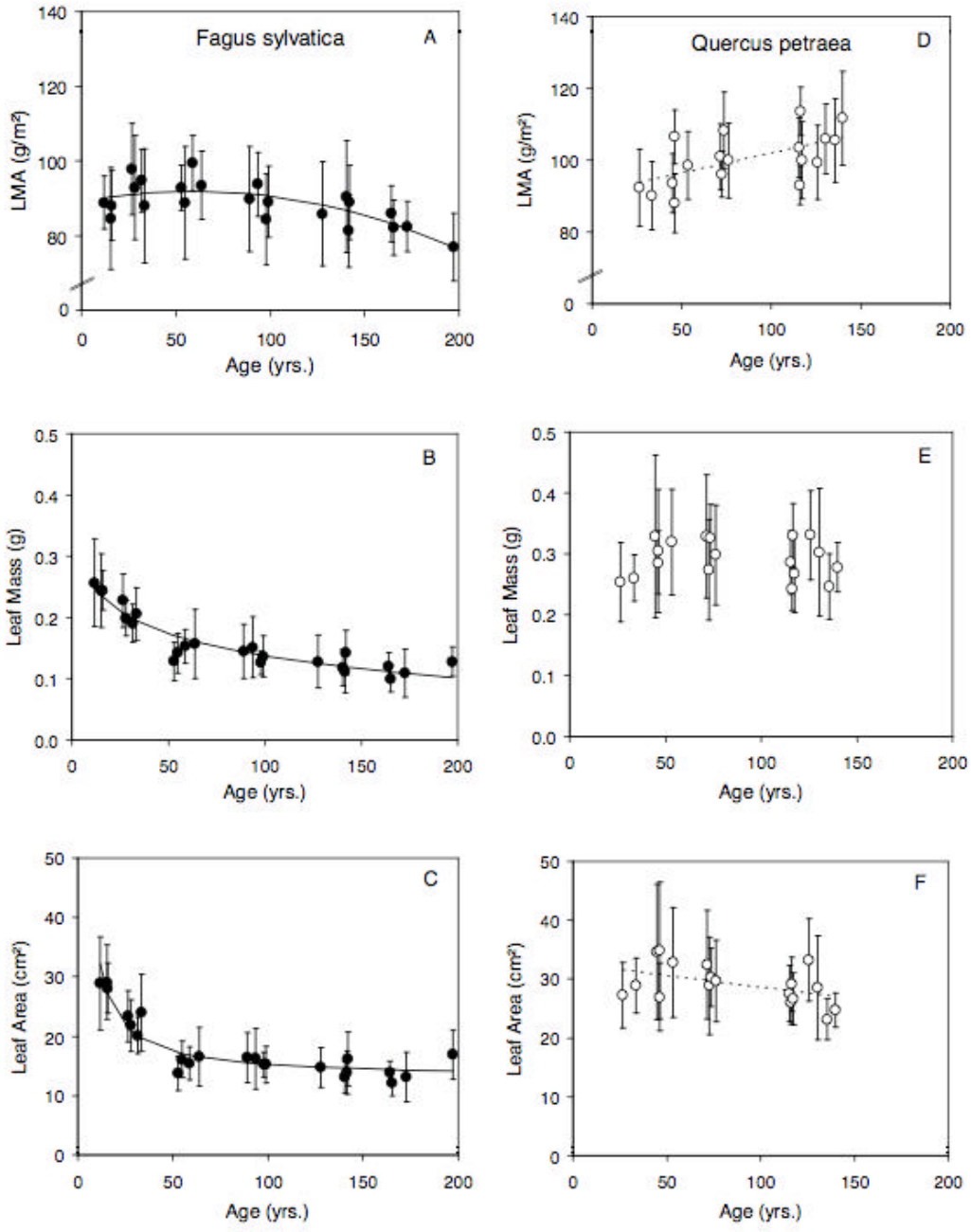


Figure 26: Relationship between stand age and (A) Leaf Mass Area (LMA), (B) Leaf Mass and (C) Leaf Area for* Fagus sylvatica *(Fougères site). Panels (D), (E) and (F) represent relationships for* Quercus petraea *(Champenoux site). Vertical bars present standard errors at the plot scale (n = 300 leaves per plot).

Leaf Composition: Carbon, Nitrogen and Chlorophyll Contents

Leaf composition was estimated on 30 sun leaves per tree, for 10 dominant trees per plot. Carbon, Nitrogen and total chlorophyll contents were given by both leaf mass and leaf area units.

A higher [Carbon / Nitrogen] ratio ([C/N]) in beech leaves compared to sessile oak was essentially related to higher carbon content (Table 13). Moreover, we observed that carbon, nitrogen and chlorophyll content per unit area and chlorophyll content per unit mass were significantly higher for sessile oak than for beech.

For beech, carbon, nitrogen and chlorophyll contents per unit mass were not significantly influenced by age (Figure 27A, B, D), ranging from 480 to 507 g/kg for carbon, from 19.1 to 22.2 g/kg for nitrogen and from 3.7 to 5.7 g/kg for chlorophyll. Carbon content per unit area (Figure 28A) followed a quadratic decrease with age ranging from 41.0 to 53.6 g/m². Over an age range similar to oak, nitrogen and chlorophyll contents per unit area did not change with age (Table 13), but when younger and older stands were integrated into the analysis, nitrogen and chlorophyll contents followed a linear and quadratic decrease with age ($n=230$, $F=15.3$, $p<0.0001$ and $n=230$, $F=5.5$, $p=0.0204$ respectively), ranging from 1.9 to 2.6 g/m² for nitrogen and from 0.58 to 0.74 g/m² for chlorophyll (Figure 28B,C). [C/N] remained stable with age, around 24 (g/g).

For sessile oak, carbon content per mass unit increased slightly with age while nitrogen and chlorophyll contents decreased slightly with age (Figure 27E, F, H). This resulted in a linear increase of [C/N] ratio, ranging from 20 to 26 (Figure 27G). Carbon, nitrogen and chlorophyll contents per mass unit ranged from 464 to 483 g/kg, 18.5 to 23.0 g/kg and 7.60 to 5.51 respectively. Carbon content per unit area increased linearly with age, ranging from 40.9 to 53.6 g/m² (Figure 28D). Likewise, nitrogen content per unit area increased slightly with age, from 2.6 to 5.51 g/m² (Figure 28E). Chlorophyll content per unit area was not influenced by age and fluctuated around 0.65 g/m² (Figure 28F).

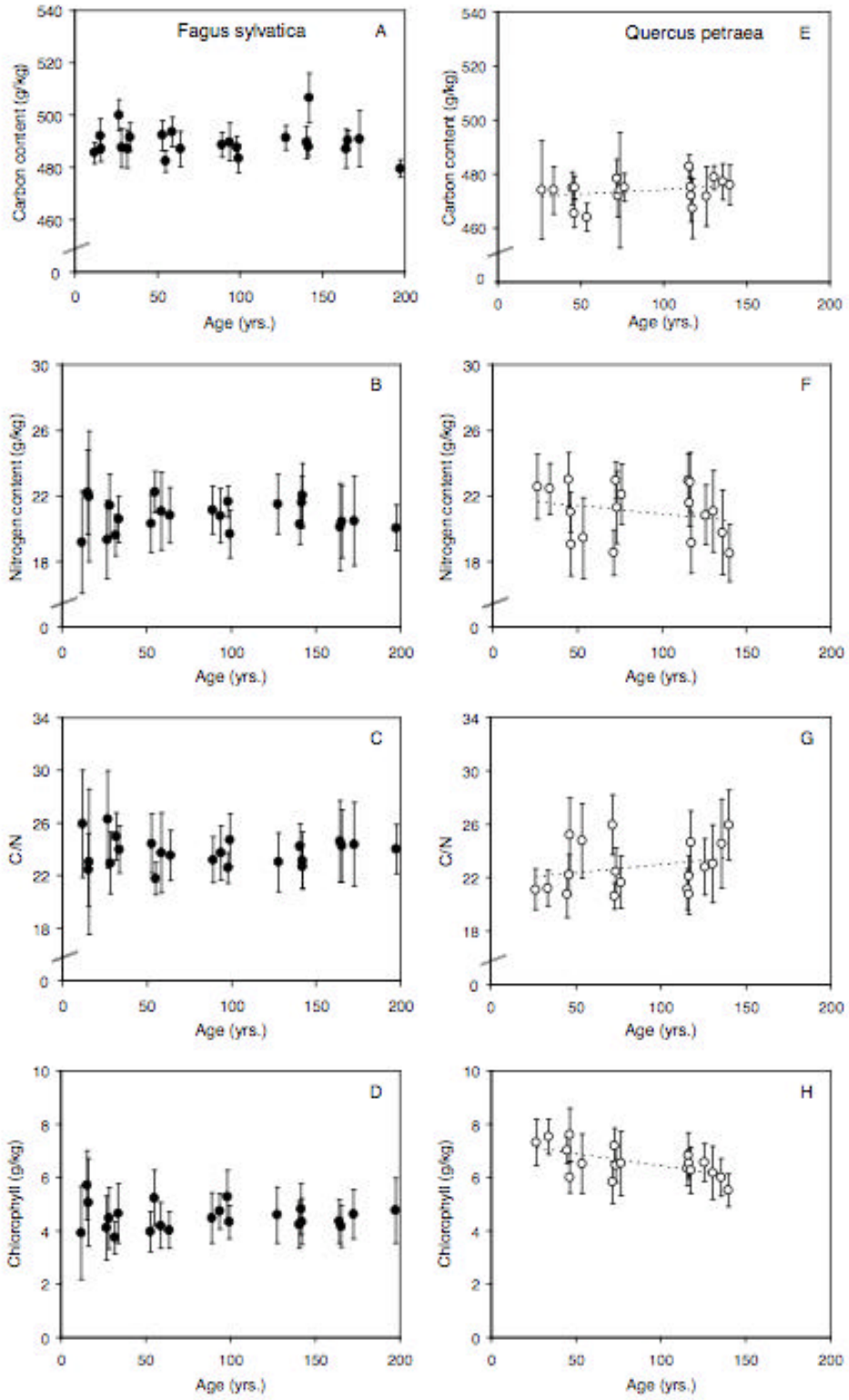


Figure 27: Relationship between stand age and (A) Carbon content, (B) Nitrogen content, (C) [Carbon/Nitrogen] ratio and (D) Chlorophyll content per leaf mass unit for* Fagus sylvatica *(Fougères site). Panels (E), (F), (G) and (H) represent relationships for* Quercus petraea *(Champenoux site). Vertical bars present standard errors at the plot scale (n = 100 leaves per plot).

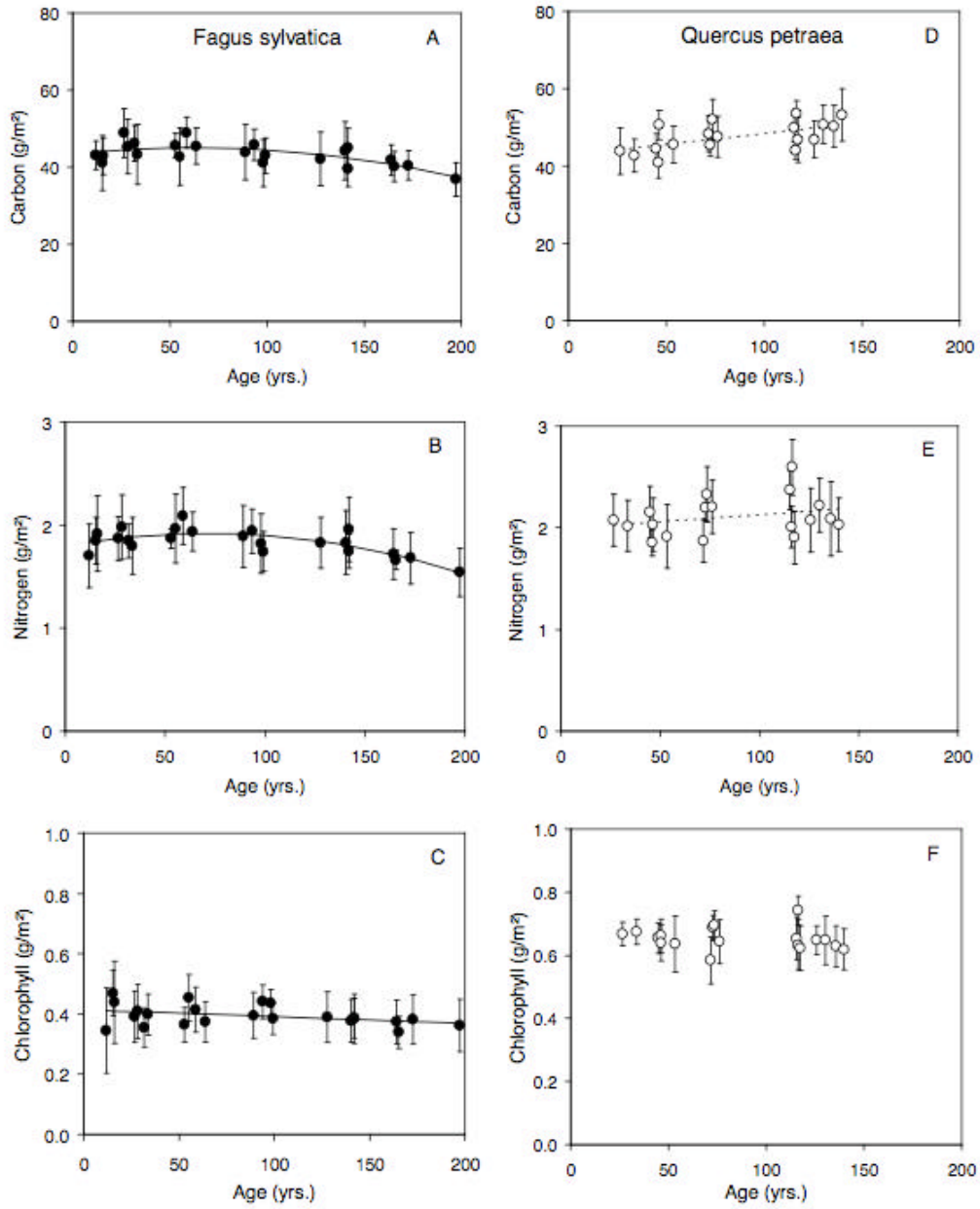


Figure 28: Relationship between stand age and (A) Carbon content, (B) Nitrogen content and (C) Chlorophyll content per leaf area unit for* Fagus sylvatica *(Fougères site). Panels (D), (E) and (F) represent relationships for* Quercus petraea *(Champenoux site). Vertical bars present standard errors at the plot scale (n = 100 leaves per plot).

LEAF PARAMETER AT STAND SCALE

Leaf Area Index

Leaf area index (LAI, leaf area per unit of soil area) was measured indirectly for each plot of both chronosequences using a Plant Canopy Analyzer.

In a common range of stand ages, total LAI was not significantly different between the two species (+site) (Table 13), ranging from 4 to 8 m^2/m^2 (Figure 29a). LAI measured in sessile oak stands were corrected in order to exclude the understorey (mainly hornbeam). This correction induced a large decrease of LAI, from about 6.5 m^2/m^2 to about 2.5 m^2/m^2 in adult stands (Figure 29b). As a result, LAI in adult stands was significantly lower in sessile oak stands than in beech stands.

Since secondary species extended with stand age (Figure 22), LAI of sessile oak stands decreased sharply with age, following an inverse slope. For beech, the linear decrease of LAI with age (Figure 29b) was not significant when a similar age range to oak was considered (Table 13) but became significant when younger and older stands were integrated (n=23; F=4.2; p=0.0536).

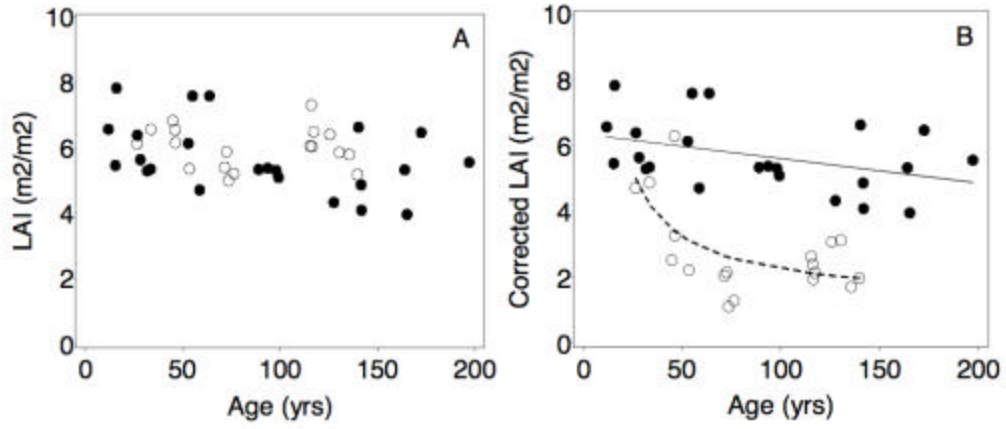


Figure 29: Leaf Area Index (LAI) as a function of stand age for* Quercus petraea *(circle, dotted line) and* Fagus sylvatica *(dot, solid line). Panel (A) presents LAI estimated for the entire canopy. Panel (B) presents LAI of the overstorey.

[Leaf Area: Sapwood Area] Ratio

Without allometric relationships to compute tree leaf area in the sites studied, we estimated [Leaf Area: Sapwood Area] Ratio (A_L:A_{SW}) at the stand scale, as the ratio between LAI and the sum of sapwood area of all trees composing the overstorey. For beech, we assumed that sapwood represented 100% of stem section area.

In a common range of stand ages, A_L:A_{SW} were not significantly different between beech and sessile oak (Table 13). For beech, the ratio followed a log decrease with age (Figure 30a) that was not significant for an age range comparable to oak (Table 13), but became significant when younger and older stands were integrated (n=23; F=5.9; p=0.0243). A significant but linear decrease of A_L:A_{SW} with age was observed for oak (Table 13).

For both species, A_L:A_{SW} followed a logarithmic decrease with stand height, from 0.56 to 0.2 (Figure 30b). The coefficient of determination revealed that stand height was a slightly better estimator of A_L:A_{SW} than stand age.

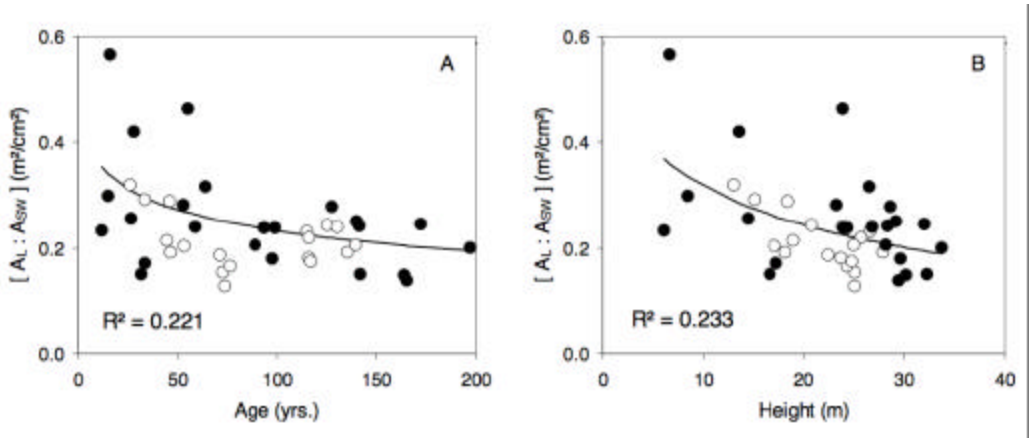


Figure 30: [Leaf Area : Sapwood Area] ratio (A_L:A_{SW}) computed at the stand scale, as a function of (A) stand age and (B) dominant stand height for* Fagus sylvatica *(dot) and* Quercus petraea *(circle). Solid line represents logarithmic function A_L:A_{SW} linking and age.

Leaf biomass, nitrogen and chlorophyll quantities

Total biomass, nitrogen and chlorophyll quantities in the canopy were deduced from stand LAI measurements, the leaf mass area, and carbon, nitrogen and chlorophyll contents measured in sun leaves. For oak stands, only LAI of the overstorey was considered.

Leaf biomass and nitrogen contents in the canopy were significantly higher in beech than in oak stands (Table 13) and these differences increased with age (Figure 31a,b). Considering the results previously described, this difference resulted mainly from inter-species differences in LAI. Even if no significant differences were detected between the average chlorophyll content of the canopy of beech and oak stands (Table 13), Figure 31c reveals that the chlorophyll content was higher in young oak stands than in young beech stands and this difference was reversed in adult stands where beech stands presented higher chlorophyll contents.

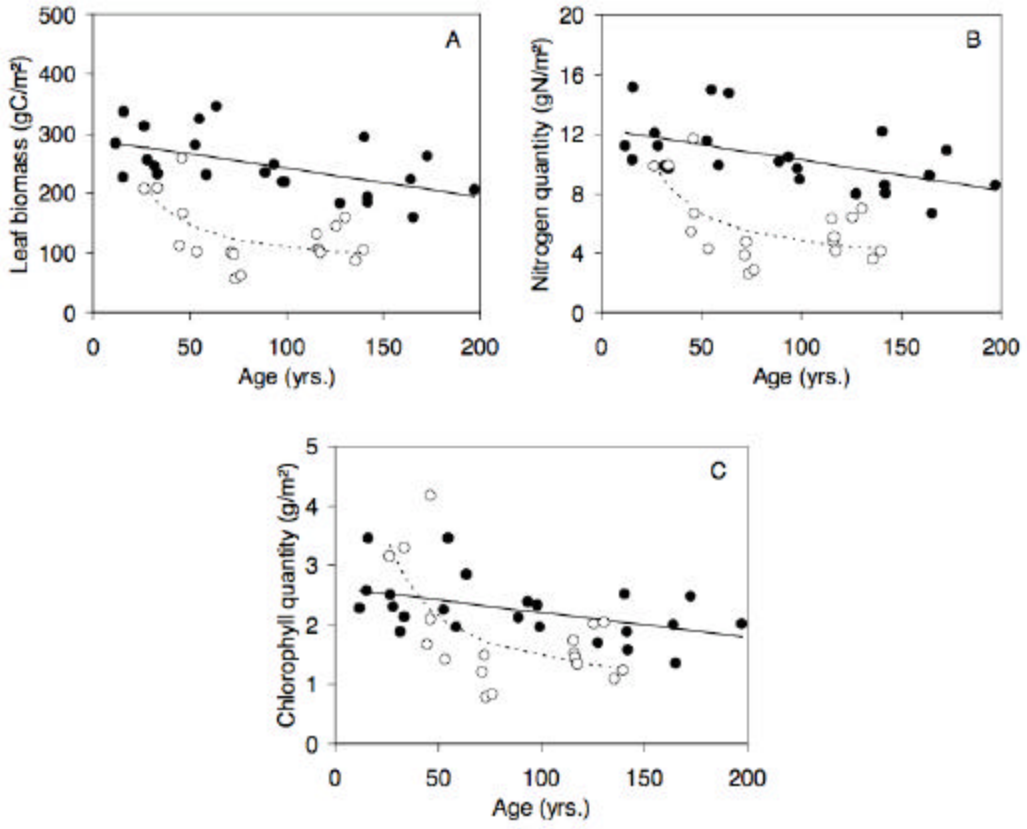


Figure 31: Relationship between stand age and (A) Leaf biomass (gC/m²), (B) Nitrogen quantity (gN/m²), (C) Chlorophyll quantity (g/m²) for* Fagus sylvatica *(dot, solid line) and* Quercus petraea *(circle, dotted line).

Leaf biomass, nitrogen and chlorophyll contents of beech stands ranged from 158.5 to 345.9 gC/m^2, 6.7 to 15.2 gN/m^2 and 1.3 to 3.5 g/m^2 respectively. These three variables decreased linearly with age. This decrease was not significant for the chlorophyll content when an age range similar to the oak chronosequence was considered, but became significant when the younger and older stands were integrated into the analyses (n=23, F=6.1, p=0.0218). In oak stands, leaf biomass, nitrogen and chlorophyll contents ranged from 57.4 to 258.4 gC/m^2, 2.6 to 11,7 gN/m^2 and 0.7 to 4.2 g/m^2 respectively. These three variables decreased inversely with age. These decreases were largely related to the inverse decrease of the LAI observed in Figure 29b.

DISCUSSION

Despite similar silviculture practices (the stands at both sites are even-aged stands), the structures of beech and oak stands were different. During ageing, an understorey mainly composed of secondary species (hornbeam) developed in oak stands, whereas beech stands remained pure and devoid of an understorey. Differences in tolerance to shade between beech and sessile oak could explain the differences of stand structures. Beech trees, with a high tolerance to shade (Rameau et al. 1989), develop and maintain a dense canopy all throughout the lifespan of the stand, preventing any consistent understorey from developing. In contrast, sessile oak needs a higher light supply to achieve its development (Rameau et al. 1989), resulting in a more heterogeneous canopy which transmits enough light to the ground for understorey development.

For both species, we observed a decrease in overstorey LAI with increasing age. This occurrence adds to numerous observations of age related decline of LAI at stand (Ryan et al. 1997, Bond-Lamberty et al. 2002, Kashian et al. 2005, Leuschner et al. 2006) and tree levels (Nock et al. 2008). This decrease was steeper for sessile oak, especially between 30 and 50 years old, because of the development of the understorey with stand age. In this experiment, it was thus impossible to separate the influence of stand structure and the effect of ageing of the individual tree leaf area itself on the age-related decline of stand LAI.

Without allometric relationships to compute tree leaf area, we calculated the $A_L:A_{SW}$ ratio at stand level. However, the order of magnitude and trends of $A_L:A_{SW}$ ratio with age (and size) were similar to results from previous studies obtained at the tree-level. For beech, Schäfer and colleagues (2000) found $A_L:A_{SW}$ ranging from 0.36 m²/cm² for trees 11m high to 0.17 m²/cm² for trees 39m high. Comparing the relationships between $A_L:A_{SW}$ and tree height for different species, McDowell and colleagues (2002) recorded $A_L:A_{SW}$ ranging from 0.09 to 0.71. The decrease in $A_L:A_{SW}$ with age for beech and sessile oak revealed a decrease in transpiring area versus sap conducting area. This trend has been widely described in previous studies (Schäfer et al. 2000, McDowell et al. 2002, Delzon et al. 2004, Martinez-Vilalta 2007). Many authors (Sperry et al. 1993, Cochard et al. 1997, Hubbard et al. 1999, Becker et al. 2000, Thomas and Winner 2002, Delzon et al. 2004) describe this decrease as one of the mechanisms in plants to compensate for the increase in water transport resistance with tree height and to maintain minimum leaf water potential above the threshold that induces embolism (Loustau et al. 1990, 1996, Cochard et al. 1997, Delzon et al. 2004).

Because LMA was estimated for leaves sampled from the ground with a rifle, the risk of taking shade-leaves increased with the height and age of the stands. In this case, age effect on leaf parameters would be confused with the well-known light effect on leaf traits. A direct way to assess this risk is to make a direct comparison between sampled leaves and established sun-leaves from same trees. For the Fougères site, such comparisons were performed by Peiffer (2005) by taking leaves directly from the tree crown after felling. LMA estimated in 2006 was more than 20 % higher than LMA estimated on established sun-leaves in 2002 and 2003 (Table 14).

Table 14: Comparison of Leaf Mass Area (LMA) estimations in Fougères forest.

Date	Sampling	LMA (g/m^2)	Sampling Method	Author
2002	3 plots – 900 leaves	73.55	Directly in the canopy	Peiffer, 2005
2003	3 plots – 300 leaves	71.37	Directly in the canopy	Peiffer, 2005
2006	23 plots – 6 900 leaves	88.65	From the soil	Present study

An indirect method to check that age and light effects on leaf parameters were not confused was to compare age effect assessed in this study, with the light effect widely described in the literature (e.g. Hanson 1917, Evans 1989, Thompson and Wheeler 1992, Ellsworth and Reich 1993, Niinemets 1995, Hättenschwiller 2001, Poorter et al. 2006, Davi 2008). Table 15 summarises this comparison. A large proportion of the effects of light regimes on leaf morphology and chemistry are highly constant between species. The shade effect induced a decrease in leaf mass area, leaf mass and nitrogen content per unit area and induced an increase in leaf area and chlorophyll content per unit area. For both species, the pattern of leaf traits attributed to age differs from the pattern related to a strictly shade effect. Indeed, whereas all leaf parameters decreased with age in beech stands, including LMA and chlorophyll content, no trend related to shade effect was observed for oak. Since measured age-effect was different from expected shade effect, we conclude that the trends of leaf parameters observed on the two chronosequences were mainly related to age, without excluding any mitigating effect related to the potentially increasing proportion of shade-leave in samples from older stands.

Table 15: Evolution of leaf traits with age in stands of both species (+sites) compared to results from the literature concerning shade-effect on leaf traits.

Leaf parameters	Age effect		Shade effect
	Fagus sylvatica	*Quercus petraea*	
Leaf mass area	?	?	?
Leaf mass	?	~	?
Leaf area	?	?	?
Nitrogen content per mass unit	~	?	~
Nitrogen content per area unit	?	?	?
Chlorophyll content per area unit	?	~	?

The trend of LMA with stand ageing in 2006 was different for the two species. For beech, LMA decreased significantly with stand age, along with a decrease in leaf mass and leaf area. While LMA of sessile oak increased with age and this increase was mainly due to a reduction in leaf area.

In a meta-analysis of existing data concerning the different photosynthetic traits of adult and sapling trees, Thomas and Winner (2002) showed that LMA increase with age is the characteristic which is most widely shared by tropical, temperate deciduous and coniferous species. Indeed, all studies reviewed reported an increase of LMA with age. Results obtained for sessile oak confirm this evidence. Furthermore, the fact that the young stands grew up in open areas and not under an overstorey canopy like most of the previous studies, reinforces the evidence that age-related change in LMA is related to ontogenetic processes rather than to environmental changes in light regimes (England and Attiwill 2006, Juarez-Lopez et al. 2008, Holdaway et al. 2008). Also, the observed age-related decreases in leaf area might contribute to a reduction in the hydraulic constraint related to the greater height of aged trees, by reducing transpiration capacity per photosynthetic unit mass (Niinemets 1995, Thomas and Winner 2002).

Regarding previous results, the significant decrease of LMA with age observed for beech seems to be driven by a mechanism other than ageing. Indeed, increase of LMA with age has already been reported for beech in Germany (Wieser et al. 2003) and in The Netherlands (Bartelink 1997). After eliminating the sampling problem (see above), we suppose that this decrease of LMA in older stands resulted from the increase of seed production, inducing the formation of smaller and thinner leaves. However, few studies exist to support this

hypothesis. Innes (1994) showed that beech masting increases crown transparency during the current year, and to a lesser extent, during the following year. Innes and Boswell (1991) also demonstrated a light negative correlation between seed abundance and leaf size of beech during masting year 1990. Finally, Han et al. (2008) showed that more nitrogen and carbohydrates are expended in producing buds containing both leaf and flower primordia than in producing buds containing leaves only. Thus we suppose there is a greater competition for resources between flower and foliar primordials during development, resulting in a reduction of leaf size.

The decrease in foliar C/N ratio with age observed for sessile oak resulted both from an increase in carbon content and a decrease in nitrogen content per mass area. The increase in carbon content per unit leaf mass of aged trees may be related to an increase in the lignin content (Apple et al. 2000). It was unlikely that this increase in carbon content was caused by an increase in carbohydrate content resulting from an enhanced photosynthetic rate, since the photosynthesis-related compounds, nitrogen and chlorophyll, decreased with tree age. These variations in carbon and nitrogen contents per unit mass and C/N ratio with tree age were not consistent with the changes in carbon and nitrogen contents observed in the soil. Despite a significant increase in soil nitrogen and carbon contents per unit mass with age, the C/N ratio remained constant (n=16, F=2,21, p=0.1593), as shown in Figure 32. In addition, potential shrinkage in nutrient uptake with age cannot be explained by a decrease in nutrient resources from the soil, but the observed nutrient uptake limitation in adult oak could result from the growing competition for soil resources, due to the extended understorey.

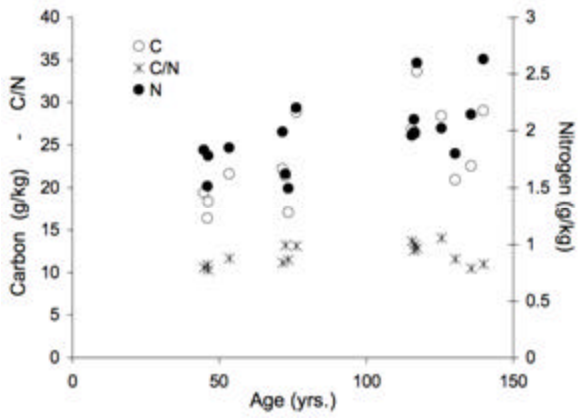


Figure 32: Carbon content (circle), nitrogen content (dot) and C/N ratio (star) in the organo-mineral soil layer as a function of stand age in the sessile oak chronosequence.

In the beech chronosequence, carbon and nitrogen contents per unit mass and C/N ratio in leaves did not change significantly with tree age. Similarly, Duquesnay (1998) did not find any relationship between mean foliar nutrient composition and stand age of 85 beech stands covering north-eastern France. However, Legout, Walter and Nys (2008) found significant decreases in K, Ca and Mg concentrations in humus with increasing age at the Fougères site. The absence of an age-related decrease in nitrogen concentrations per unit mass in leaves, despite the observed nutrient concentration decrease in humus, may be related to an increase in internal nutrient translocation from senescing leaves to storage organs (Niambar et Bowen 1986) with stand age. Indeed, Colin-Belgrand, Ranger and Bouchon (1996) showed that translocation of N, P and K in stem wood increased with stand age during a crop rotation in *Castaneae sativa* stands. Moreover, previous studies on nutrient uptake in spruce indicated that the ratio between internal translocation and soil uptake increased with stand age (Dambrine et al. 1991). Regarding these results, the importance of internal nutrient translocation could increase in ageing stands to improve their autonomy in nutrient supply and thus reduce the effect of the decrease in soil nutrient availability observed at the Fougères site.

The leaf area, with stomatal characteristics, largely determines the amount of water transpired and the potential for carbon assimilation through photosynthesis. Therefore, nitrogen and chlorophyll contents expressed per unit leaf area are better expressions of leaf composition in relation to their role in carbon assimilation than these contents expressed per unit leaf mass. It should be noted that we observed age-related decreases in nitrogen and chlorophyll contents per unit area in the beech chronosequence, indicating a decrease of photosynthetic capacity with age. However, seed production may also contribute substantially to such a decrease. Indeed, flowering and fruiting are nitrogen-limited processes, as shown long ago (Ross and Pharis 1985). The distinction between age and mast effects on leaf composition is thus difficult. For sessile oak, nitrogen and chlorophyll contents per unit area remained unchanged or slightly increased with age suggesting no loss of photosynthetic capacity with age.

At the ecosystem level, we observed an age-related decline in the quantities of carbon, nitrogen and chlorophyll contained in the canopy. This decrease was steeper for the oak chronosequence because of the increasing development of the understorey and its negative impact on the overstorey leaf area. However, these decreases were also observed in the beech chronosequence devoid of a substantial understorey. In this case, the age-related decline of carbon and nitrogen stocks in the canopy may be directly attributed to the internal ageing processes of beech trees. The impact of increased fruiting effort with age, on leaf morphology

and nitrogen content may contribute to these age-related declines and further studies are needed to separate the effects of ageing and fruiting on canopy decline in adult stands.

Effect of soil mineral fertility on carbon allocation at tree scale in beech (*Fagus sylvatica* L.) and pedunculate oak (*Quercus robur* L.) from liming experiments

INTRODUCTION

Several studies have shown that unbalanced mineral nutrition and low fertility might be important predisposing factors leading to forest decline on acidic soils (Zoettl et al. 1989, Huettl et al. 1990, LeGoaster et al. 1990, Kandler, 1993).
Soil acidification results in the increase of proton inputs from external and internal processes – plant uptake, and nitrification or decomposition of organic matter. Atmospheric deposition is one of the main external agents increasing soil acidification and desaturation (Bonneau et al. 1983, Weissen et al. 1990, Dupouey et al. 1998) which may disturb stand nutrition and production (Nys 1989, Landmann and Nageleisen, 2001). The effect of atmospheric deposits on soil acidification might be exacerbated in old stands by the impact of ageing on the alteration of mineral element nutrition (Vitousek et al. 1989, Vanninen et al. 1996, Idol et al. 2000, Claus and George 2005, Simard et al. 2007).

The concomitancy of these two predisposing factors (ageing and mineral elements imbalance) in a large proportion of forests in Europe led forest managers and scientists to consider liming as a practice to recover soil mineral fertility and as a remedy for stand decline (Van Praag et Weissen 1986, Mohamed et al. 1993, Bonneau 1995, Misson et al. 2001). In this context, several research programs were initiated in Europe, like the DEFORPA program (dépérissement des forêts attribué à la pollution atmosphérique, 1983), coordinated by M. Bonneau in France.

Liming induces a joint increase in soil solution pH and base saturation leading to a decrease in acidity (mainly related to the decrease in aluminium) (Mohamed et al. 1993, Misson et al. 2001). In addition, liming reduces nutritional imbalances resulting from plant uptake (Mohamed et al. 1993, Belkacem et al. 1992, Huber 2006) and often stimulates the biological activity of the soil. For example, density of earthworms increases with treatment (Kreutzer 1995, Robinson et al. 1996), improving the degradation of organic matter and in turn, humus quality. However, long-term experiments of ecosystem modification often lead to conclusions that would never be expected from the short-term responses observed (Linkens 1989, Magnusson 1990, Shaver et al. 2001).

Concerning carbon balance in trees, previous fertilization experiments have shown:

1. an increase of aboveground tree growth (Larsen et Buch, 1995, Bakker *et al.*, 1999);
2. an increase in root carbohydrate content (Wargo et al. 2002);
3. an increase in |Root:Shoot] ratio (Ericsson, 1995, Bakker *et al.*, 1999, Litton, Raich and Ryan 2007);
4. a positive impact on root activity (Fabiao et al. 1995, Persson et al. 1995, Bakker 1998), even if some exceptions occur (Hemisaari et al. 1999, Borken et al. 2007);
5. an increase in flower and seed production (Garbaye et Leroy, Le Tacon et Oswald 1977)
6. changes in the structure of the ectomycorrhyzal community and associated enzymatic activities (Rineau 2008).

These results imply that liming may induce an increase in growth, carbohydrate concentrations in roots, root activity and fruit production. However, no study was found which supplied an integrated assessment of the impact of liming and mineral nutrition improvement on the overall carbon allocation in trees. Therefore, the objectives of this study were to quantify the long-term response of trees to liming treatment in terms of (1) total non structural carbohydrate (TNC) concentrations and (2) the carbon balance between growth and storage for beech and pedunculate oak (no mast occurred during the field campaigns, for either species). Growth and storage functions were quantified during one growing season (2007) by carbon increment of biomass and TNC carbon pools respectively

Furthermore, despite the widespread assumption of a positive effect of liming on fine root development, published observations are not always in agreement (Haynes et al. 1995, Albaugh et al. 1998, Phillips and Fahley 2007, Rineau 2008). Root descriptions were thus conducted in order to assess the impact of liming on root density of the two species studied.

Finally, crown decay has been observed recently in the control stand whereas the limed stand was not affected (Reuter 2005, Tourette 2006). This decay has been attributed to recent climatic events like late frost events in 2005 and severe droughts from 2003 to 2006. Therefore, in order to test whether changes in carbon allocation induced by liming could be related to better health conditions after climatic constraints, declining trees were also sampled. The objectives were (1) to identify the changes in carbon allocation occurring in declining trees and (2) to compare the carbon allocation with healthy untreated and limed trees.

MATERIALS AND METHODS

Even though the methods of computing carbon allocation and measuring leaf parameters applied here were fairly similar to those used in the chronosequence experiments, they are detailed again in the following paragraphs with regular references to Chapter I. Hopefully this will make it easier to read the following chapter.

SITE AND STAND DESCRIPTIONS

Humont site

The experimental site was located in the state forest of Humont (48°59'52"N, 06°29'37"E, alt. 580 m) in north-eastern France. The region where the site was located, called La Vôge, is included in the lower part of the Vosges Mountains (Figure 33a). In order to reduce soil acidification and tree decline, a liming treatment was carried out in 1991, in a declining plantation of Norway spruce (*Picea abies* (L.) H. Karst, 35 years old), containing patches of naturally regenerated beech (*Fagus sylvatica* L, 75 years old). The beech trees were 58 years old when they were limed. The project was founded by the EU and coordinated by the Biogeochemistry of Forest Ecosystems lab (INRA, M. Bonneau) and the "Office National des Forêts". Treatment was applied by helicopter and consisted of 757 kg/ha of CaO and 380 kg/ha of MgO (Renaud et al. 2001).

The soil was an alocrisol developed on intermediate Triassic sandstone. The climate was semi-continental. Mean annual temperature and average annual precipitation, calculated for the past 15 years, were 10.2 °C and 1365 mm respectively (Météo France data, Station # 88029001).

Les Potées site

The experimental site was located in the state forest of Les Potées (49°51'33"N, 04°29'34"E, alt. 380 m) in the north of France (Ardennes, 08) (Figure 33b). The liming treatment was carried out in winter 1995/1996, in two monospecific plantations of beech (*Fagus sylvatica* L.) and pedunculate oak (*Quercus robur* L.). Both stands were 23 years old in 2007 and healthy, in contrast to the Humont site. The trees were 12 years old when lime was applied in order to study effects of lime on soil and tree growth. Treatment was applied by hand and consisted of 760 kg/ha of CaO and 200 kg/ha of MgO. The project was coordinated by the

Biogeochemistry of Forest Ecosystems lab (INRA, Dr. C. Nys) and the "Office National des Forêts"

The soil was an alocrisol developed on s late. The climate was semi-continental. Mean annual temperature and average annual precipitation, calculated for the past 15 years, were 9.0 C and 951 mm respectively (Météo France data, Station # 08367002).

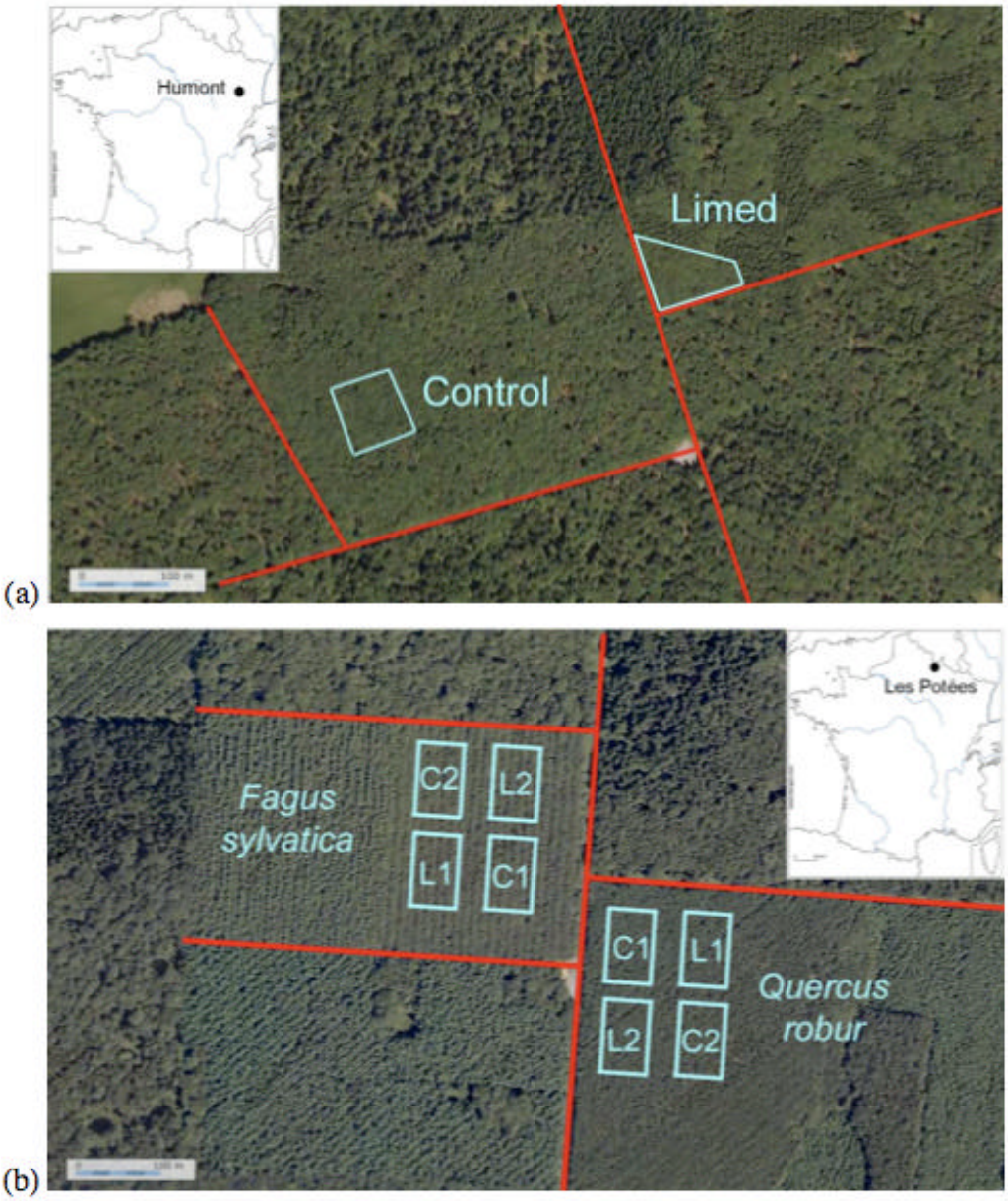


Figure 33: Location and situation of the experimental sites of (a) Humont and (b) Les Potées. Red lines represent stand limits and blue lines represent plot limits. [Source: Géoportail 2007/2009]

EXPERIMENTAL DESIGN

Humont site

The trial consisted of a treated plot of 0.32 ha located in the limed stand and a control plot of 0.25 ha located in a nearby stand (Figure 33a). Both plots were situated in even-aged pure beech stands. Stand characteristics are presented in Table 16. Soil characteristics, topography and elevation were similar for both plots.

The circumference of every tree inside the two plots was measured at breast height. In order to assess the crown condition, the proportion of dead branches in the canopy of every tree was estimated in October 2006 using an index with 4 levels: 1 = 0%, 2 = less than 50%, 3 = more than 50 %, 4 = 100 % of dead branches, according to "Département de la Santé des Forêts" manual (Nageleisen, 1995). Dominant stand height was computed as the averaged total height of the five tallest trees in each plot. Tree height measurements were achieved by staff of the "Office National des Forêts" in each plot with a clinometer Vertex IV (Häglof, Sweden).

In both control and limed plots, 10 dominant healthy trees were selected for age, radial growth and carbohydrate content determination. Selection was based on a standardised index of dominance computed for every tree, i.e. individual circumference corrected by plot area. In the control, 10 dominant but declining trees were selected in addition. No declining trees were found in the limed plot. Selected trees were cored to the pith at 1.3 m height. Tree and stand ages were estimated from ring counting on these cores.

Table 16: Humont - Stand description of the two plots. Leaf Area Index (LAI) was measured in August 2007.

Treatment	Surface (ha)	Tree density (/ ha)	Basal Area (m^2 / ha)	LAI (m^2/m^2)	Dominant height (m)	Mean age (yrs) (min-max)
Control	0.25	904	38.9	4.4	27.2	72 (58-95)
Limed	0.32	719	34.1	5.4	26.9	72 (55-85)

Les Potées site

The experimental design consisted of two replicates of a limed and a control plot for each species (Figure 33b). Individual plot area was 0.5 ha (100 * 50 m). Stand characteristics of each plot are given in Table 17. Soil characteristics, topography and elevation were similar for all plots, blocks and stands.

Circumference of every tree inside the two plots was measured at breast height in spring 2007 by the laboratory team of "Biogeochemistry of Forest Ecosystems" – INRA. In each plot, 15 dominant trees were selected for age, radial growth and carbohydrate content estimations. The selection was based on a standardised index of dominance computed for every tree, i.e. individual circumference corrected by plot basal area. Selected trees were cored to the pith at 1.3 m height. Tree and stand age were estimated from ring counting on these cores.

Table 17: Les Potées - Stand description of each plot of the experiment. Leaf Area Index (LAI) was measured in August 2007. Rep. = replicate.

Species	Treat.	Rep.	Surface (ha)	Tree density (/ ha)	Basal Area (m^2 / ha)	LAI (m^2/m^2)	Dominant height (m)	Mean age (yrs) (min-max)
Fagus sylvatica	Control	1	0.5	560	20.7	7.8	15.8	25.7 (24-28)
		2	0.5	609	20.9	8	14.2	25.2 (22-29)
	Limed	1	0.5	601	23.1	7.7	16.1	25.6 (21-28)
		2	0.5	510	22.2	8.6	15.3	25.1 (22-28)
Quercus robur	Control	1	0.5	515	14.1	4.6	13.4	22.5 (21-24)
		2	0.5	613	13.0	4.66	12.8	22.5 (21-24)
	Limed	1	0.5	583	14.4	4.77	12.4	22.1 (21-23)
		2	0.5	546	14.5	4.91	13	23.2 (22-25)

SOIL AND ROOT DESCRIPTIONS

Soil descriptions were made (1) to test the homogeneity of soils between limed and control stands and (2) to assess the soil fertility level before treatment. This homogeneity was of particular importance for the experimental site of Humont, devoid of repetitions. Root descriptions were conducted in order to assess the impact of liming on root density.

Trench excavation

In order to describe soil and root profiles, three trenches per plot were dug in October 2007 at Humont and in June 2007 at Les Potées. In Humont, trenches were opened in both treatments. In Les Potées, trenches were dug in one pair of limed/control plots for both species: 12 trenches in total were excavated.

In each plot, trenches were distributed throughout the plots in order to assess soil variability. Each trench was located in the vicinity of a dominant and healthy tree in such a way that the observation wall was positioned at 50 cm from the tree collar. Trenches were excavated to the bedrock and were 1.8 to 2 m deep. Soil descriptions were made by Y. Lefèvre.

Soil analyses

In Humont, soil samples were taken from trenches in each identified soil layer of the whole soil profile. Soil was sampled in October 2007. In Les Potées, soil sampling was performed in 2004 by the Biogeochemistry of Forest Ecosystems lab, INRA. Soil samples were taken from 0 to 45 cm deep with a root corer (Ø 8 cm). Each sampled profile was stratified into 5 systematic layers corresponding to soil depths: 0-5 cm, 5-15 cm, 15-30 cm, 30-45 cm

Samples were air dried for several days and sieved to remove the fraction superior to 2mm. Particle size distribution and exchangeable cations were analyzed by the laboratory of soil analyses – INRA. Exchangeable cations were determined by ICP-AES (Inductively Coupled Plasma-Atomic Emission Spectrometry) following extraction with cobaltihexamin chloride (Legout et al. 2008). Carbon and nitrogen were determined with a carbon nitrogen elemental analyzer in the Analytical pole, INRA.

Soil water content (Humont only)

Slight differences in meso-topography were detected between the two plots: the limed plot was located in a micro-talweg whereas the control plot was not. This difference may increase lateral water supply in the limed plot, compared to the control. Therefore, in order to check whether the soil water contents in both plots were similar outside the drought periods, gravimetric soil water content (GWC) was determined in October 2008 for the entire root profile in one trench per plot. Two volumetric samples (cylinder of 250 cm^3) were taken in each soil layer and particular attention was paid to avoid soil compaction during sampling. Using Baize's method (1988), the cylinders of soil were weighed after sampling to estimate their fresh weight (FW). After oven-drying at 105 °C for 36 hours, the cylinders of soil were weighed again to estimate dry weight (DW). Gravimetric water content was estimated as follow s:

$$GWC = [\ FW - DW\ ] /\ DW$$

Bulk density was also computed as follows:

$$D = DW / WW$$

where WW is the weight of water contained in a cylinder.

Extractable soil water

Extractable soil water (EW) to the maximum root depth was computed using thickness (THN) and bulk density (BD) (related to the texture) of each soil layer according to the following relationship (Baize 1988):

$$EW = \sum_{i=1}^{n} THNi * BDi * (FCi - WPi)$$

where total EW is the sum of EWi computed for every soil layer i ? [1;n], FC(i) and WP(i) are soil moistures at field capacity and wilting point for the texture of the soil layer i respectively. Soil moisture at field capacity and wilting point used in this study were estimated by Jamagne et al. (1977 *in* Baize, 1988) on agricultural soils for each textural class.

Root distribution

In order (1) to test whether liming had an impact on vertical root distribution and density and (2) to estimate extractable soil water, root observations were made as follows (Bréda et al. 1995, Noordwijk et al. 2000). In each trench, the wall closest to the tree was used for root observation. The superficial layer of soil was removed gently from the observation plane in order to reveal roots (considering the compactness of soil, a dagger was used). Roots were counted using a 10*10 cm grid fixed on the trench wall. After Bréda et al. (1995), the root system was divided into five diameter classes: <3mm, 3 to 5 mm; 5 to 10 mm and > 20 mm. Root diameter was measured using a caliper square. Root density was expressed as number of root impacts/m².

At both sites, roots were counted in every trench (6 trenches in Humont and 12 trenches in Les Potées). The sampled area extending to 120 cm wide was centred on the tree stem, as illustrated in Figure 34. At Humont, depth of counting was limited to the upper 30 cm whereas at Les Potées, root density was measured on the whole root profile.
At the Humont site, the aim of fine root counting was to assess the effect of treatment on fine root density. Thus, counting was restricted to shallow soil layers containing the highest fine root density (Lucot and Bruckert 1992, Bréda et al. 1994, Peiffer 2004). In Les Potées site, in addition to the study of the lime effect, the experimental design made it possible to make a valuable comparison between the root profile of pure beech and pure pedunculate oak stands, growing in the same soil. Therefore, the root profile was described for the whole soil depth under both species.

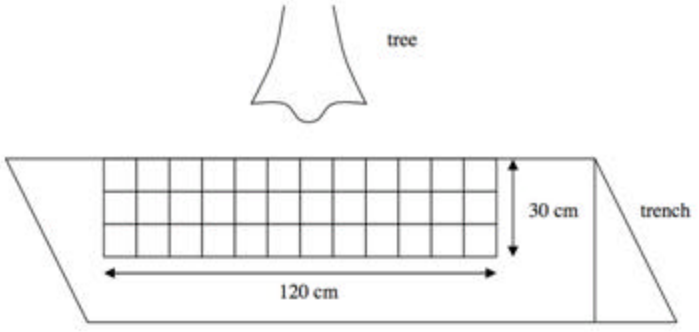


Figure 34: Vertical plan design for root observation in Humont site. For Les Potées, the plan design was similar but deeper, reaching the bottom of the trench.

ANALYSIS OF PAST GROWTH

Inter-annual variations of radial growth were studied in healthy trees in limed plots, and health and declining trees in control plots in order to (1) compare the growth history of the two stands studied and test potential differences, (2) test the impact of liming on year-to-year variations of radial growth in comparison with untreated healthy trees since treatment (1991), (3) date and identify potential causes inducing the crown decline observed in 2007 by comparing untreated healthy and declining trees.

Tree ring analyses

Ten trees per plot were cored to the pith at breast height using an increment borer, taking one core per tree. Circumference at breast height of every tree was also measured. Growth coring and circumference measurements were carried out in February 2007. That means that the last ring of the series grew in 2006. Tree-ring chronologies were developed from wood cores using standard dendrochronological procedures. After surfacing, air-drying and preliminary visual ring counting, every tree-ring width was measured to the nearest 0.01 mm with a binocular microscope and a digitalizing table. After measurements, the individual ring-width series were cross-dated to ensure absolute dating accuracy after progressive detection of so-called "pointer years" (Becker 1989).

Detrending and growth index computation

Removal of the long-term trend on growth was done by (1) estimating the long-term trend and (2) removing this trend by index computation. This procedure is known as *standardisation* (Fritts 1976). According to Cook and Peters (1981) and Meko (2007), long and medium term trend of growth was fitted for every sampled tree to a cubic spline with a 50% frequency response of 50 years, which was flexible enough to considerably reduce trends in growth. Examples of fitted curves are given in Chapter II; page 41. The indexes for individual time series were then computed as:

$$I_n = RW_n / pRW_n$$

where I_n is the ring index for a given tree and a given calendar date n, RW_n is the measured ring width at date n and pRW_n is the ring width predicted from the fitted curve at date n.

Sensitivity to year-to-year growth conditions

Sensitivity of radial growth to growth conditions was estimated after (Schweingrubber 1988) as the difference between two successive values of index weighted by the mean of these successive values:

$$S_n = 2 \cdot (I_n - I_{(n-1)}) / (I_n + I_{(n-1)})$$

where S_n is the sensitivity for a given tree at a given calendar date n. I_n and $I_{(n-1)}$ are the index values at date n and n-1 respectively. Sensitivity was computed on ring index in order to remove long-term growth trend effect on inter-annual variation. Thus, whereas measured tree-rings quantify the growth level of a given year, sensitivity assesses the year-to-year variations of radial growth, free from any contribution of long-term trend.

CARBON ALLOCATION ESTIMATION

In order to quantify between-treatment differences of carbon balance in trees, biomass and carbon increments were estimated during the 2007 growing season.

Tree sampling

In the chronosequence experiments, the variability of carbohydrate concentrations between trees inside the same plot was higher than in the experiments of Barbaroux (2002). This variability was attenuated by replication of stands studied for each age class. For the present liming experiments, only one or two plots were studied for each treatment. Thus, to achieve a reliable estimation of carbohydrates in trees at the stand level, the number of trees sampled was increased.

In Humont, 10 dominant healthy trees were selected in each plot for age, radial growth and carbohydrate content estimations. In the control, 10 dominant but declining trees were selected in addition. No declining trees were found in the limed plot. In Les Potées, 15 dominant trees were selected for age, radial growth and carbohydrate content estimations.

Selected trees were cored to the pith at 1.3 m height. Tree and stand age were estimated from ring counting on these cores.

Estimation of carbon allocated to growth function

Growth in 2006 was calculated as the difference between wood biomass at the end of 2006 and wood biomass at the end of 2005. Tree ring measurements were used to estimate diameter at breast height in 2005 and diameter increment during the 2006growing season.

Tree ring analyses

Ten trees per plot were cored to the pith at breast height using an increment borer, taking one core per tree. Circumference at breast height of every tree was also measured. Growth coring and circumference measurements were carried out in February 2007. That means that last ring of the series grew in 2006. Tree-ring chronologies were established as previously described

Estimation of biomass and biomass increment at the tree scale

Biomass (g DM) was estimated for each of the sampled trees per plot. Mean tree biomass was then calculated for each plot.

Aboveground biomass was computed as the product of volume and wood density. Volume was estimated from total aboveground volume equations using both tree height and circumference at breast height published by Vallet et al. (2006) for northern France. At Humont, tree height was estimated from statistical relationship between tree height and circumference at breast height. For the same circumference, the height of dominant trees measured in Humont (for stand dominant height estimation) was similar to the height of the dominant beeches measured in the Fougères chronosequence, as illustrated in Figure 35. Thus, the statistical relationship used to compute tree height in Humont was the same as the one fitted to the Fougères chronosequence.

$Ht_{F.s.} = 32.309 * (1 - \exp(-0.0156 * CBH))$ (F= 10757; p<0.0001)

where $Ht_{F.s.}$ is total height in m and CBH is the circumference at breast height in cm.

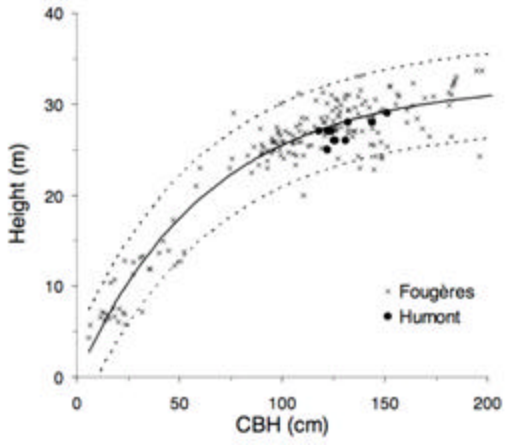


Figure 35: Humont: Relationship between tree height and circumference at breast height (CBH) for Fagus sylvatica in Fougères (crosses) and Humont (dots). Relationship (solid black line) and 95% confidence limits (dotted lines) fitted from the Fougères data are represented.

For Les Potées site, height measurements were made in 2006 by the Biogeochemistry of Forest Ecosystems lab, INRA. In each plot, seven trees covering the circumference range of the stand were selected for biomass estimation. Individual tree height was measured on logged trees. The relationship between tree height and circumference at breast height was significantly different between beech and pedunculate oak ($F=24.13$, $p<0.0001$) (Figure 36). No effect of treatment was detected for either species ($F=0.05$, $p=0.8221$ for pedunculate oak and $F<0.01$, $p=0.9469$ for beech).

$$Ht_{Q.r.} = 13.1286 * (1 - \exp(-0.0682 * CBH)) \qquad (F= 4974;\ p<0.0001)$$

$$Ht_{F.s.} = 16.1993 * (1 - \exp(-0.0458 * CBH)) \qquad (F= 1953;\ p<0.0001)$$

where $Ht_{Q.r.}$ and $Ht_{F.s.}$ are total height in m of pedunculate oak and beech respectively and CBH is the circumference at breast height in cm.

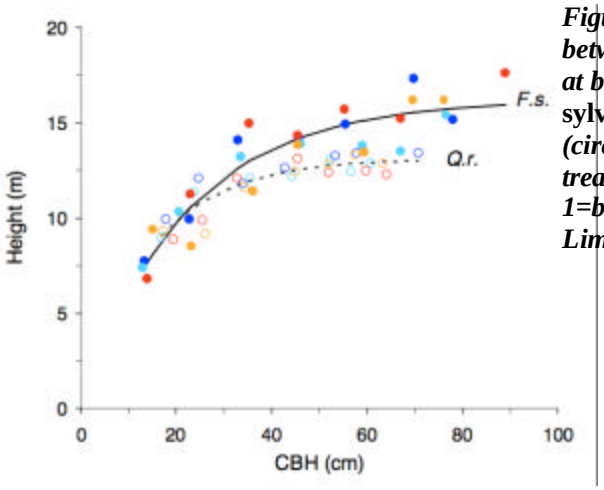


Figure 36: Les Potées: Relationship between tree height and circumference at breast height (CBH) for* Fagus sylvatica *(dots) and* Quercus robur *(circles) in Les Potées. Colours identify treatments and replicates (Control 1=blue; Control 2=cyan; Limed 1=red; Limed 2=orange).

For both sites, wood density of beech was estimated from a model fitted by Barbaroux (2002) on 30 trees from north-eastern France (Badeau 1995). This model estimated tree-ring density from cambial age only. Indeed, tree-ring width of beech had no effect on tree-ring density (Barbaroux 2002, Bouriaud et al. 2004). For pedunculate oak, wood density was estimated from a model using tree ring width and cambial age and fitted for sessile oak in northern France by Le Moguédec et al. (2002). Thus, sapwood volume was computed as the difference between total volume and heartwood volume. Heartwood diameter was computed as the difference between stem diameter resulting from the circumference measured in winter 2007 and sapwood width measured on cores.

Root biomass was computed from aboveground biomass using the relationship linking Root:Shoot ratio and tree age presented in Chapter I (section entitled *Stand biomass throughout the chronosequences*, page 37). Dry matter biomass was converted to carbon mass (gC) by applying a 48% carbon content for both species.

Estimation of carbon allocated to storage function

Carbon allocation to the storage function was assessed by the total non structural carbohydrate (TNC) increment in 2007. TNC increment was calculated as the difference between TNC content at the end and at the beginning of the 2007growing season. TNC contents were calculated as the product of TNC concentration and sapwood biomass.

Estimation of carbohydrate increment in 2006

Previous studies conducted in similar ecosystems described the seasonal dynamics of carbohydrates in beech (Barbaroux and Bréda, 2002). Minimum total non structural carbohydrate (TNC) concentrations occur at the beginning of June, immediately after bud burst and total leaf expansion. Maximum concentrations occur in October, before leaf fall. The concentration differential between the two dates gives an estimation of carbohydrate accumulation during the season. In order to estimate the carbon storage pool accumulated during the season in the whole tree, an estimation of TNC quantities are needed. Barbaroux (2002) demonstrated that good estimations of carbohydrate content in adult trees can be obtained from wood samples of the stem at breast height (1.3m above the ground) and from coarse roots, the main tree storage compartment depending on their sizes. This method was applied at both sites. One core in the stem (at a height of 1.3m above the ground) and one core in coarse roots (about 40 cm from the stump) were taken from trees at the end of May, around day of year (DOY) 135, and in October, around DOY 288, the expected dates of minimum and maximum concentrations respectively. The sampling date in spring was advanced compare to the experiment conducted in 2006 to take into account the precocious budburst (and probably cambial reactivation) observed in 2007 – budburst occurred on DOY 112 in Les Potées forest and on DOY 115 in Humont forest. A precocious budburst was also observed in spruce in Switzerland (Forster et al. 2007) and oaks in France (Caroulle 2008). It may be partially related to the warm winter 2006/2007 and exceptionally high temperatures and low rainfall occurring in April 2007 (Figure 37a, b). An exceptionally warm spring in 2007 was observed throughout European forests (Delpierre et al. 2009). Leaf fall was completed on DOY 300. Note that the coarse roots selected were different at each date and were partially excavated just before coring. Cores were taken using an increment borer (5 mm in diameter), stored with freeze-pack in the field and placed at -20°C after returning to the laboratory.

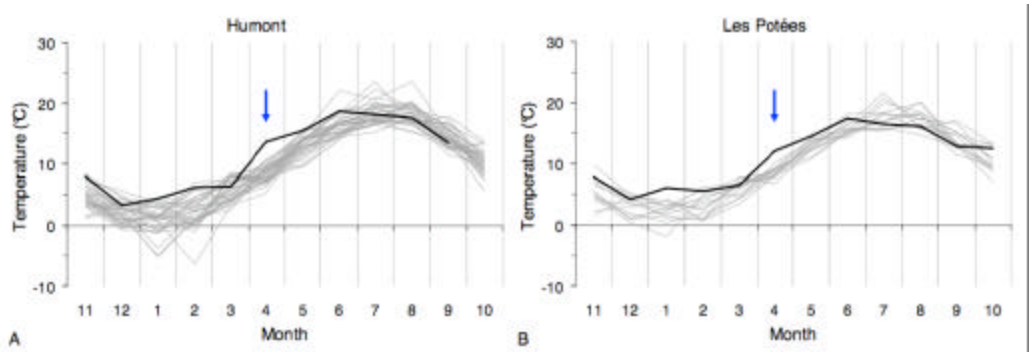


Figure 37: Monthly mean temperatures for (a) Humont from 1973 to 2007 and (b) Les Potées from 1994 to 2007. Each curve represents a year (from November (11) to October (10)). Grey curves concern the period until 2006. The black curve concerns 2007, the year studied. Temperature data for Humont came from the meteorological station of Bains-les-Bains (Météo France # 88029001). Temperature data for Les Potées came from the meteorological station of Charleville (Météo France #8105005).

Heartwood of beech was considered to be negligible (see Chapter I for details). Moreover, after a decrease in the outer rings of beech stems, TNC concentrations remained stable in the inner rings (Barbaroux and Bréda 2002) as observed for the radial distribution of several mineral element concentrations (Penninckx 2001). Therefore, in order to facilitate comparison between different beech experiments and between beech and oak, carbohydrate concentrations in stems were determined on the 10 most recent tree rings, as for the chronosequence experiment. However, in order to estimate TNC concentrations in the inner part of the stem from concentrations measured in the outermost 10 rings, xylem from the pith to the 11th outermost ring was also measured on the 30 samples of trees at the Humont site. The ratio between inner and outer concentrations was computed for each tree. Results illustrated in Figure 38 do not display any differences between treatments and health conditions. Concentration in the inner part of the stem was assumed to represent 62.5 % of the concentration occurring in the outer 10 rings.

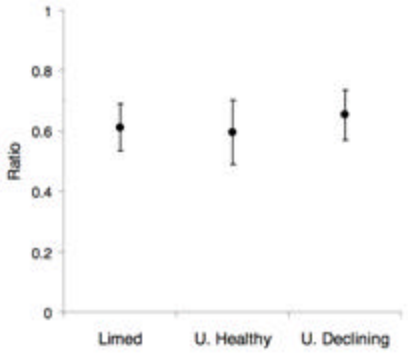


Figure 38: Humont: Ratio between inner and outer TNC concentrations for* Fagus sylvatica *for the different treatments and tree health conditions: limed = limed trees, U. healthy = untreated healthy trees and U. declining = untreated declining trees. Vertical bars are standard errors N=30 trees.

In roots, carbohydrate concentrations were determined on the 5 cm of core under the bark. Bark was removed from cores and TNC analysis was restricted to xylem. Carbohydrate contents were computed from the product of concentrations and sapwood biomass. We assumed that all root biomass was sapwood.

Carbohydrate concentrations

Total non structural carbohydrates were quantified enzymatically after Barbaroux and Bréda (2002). Cores were freeze-dried in a bulk tray dryer (Dura-Top™ and Dura-Dry™, FTS, USA). Dried cores were then ground with a ball mill (Retsch® MM301, Germany). Soluble sugars were extracted three times from 5–10 mg of powder with 80% boiling ethanol (1 ml), for 30 min. The extracts were centrifuged for 10 min at 12 620 ***g***, and then combined and dried overnight with a vacuum-evaporator (Maxi-Dry Plus; Hetomodel DW1, 0-110, Heto-Holten A/S Allerod, Denmark) to eliminate the ethanol. The dried extracts were rehydrated in 0.5 ml of 0.02 N NaOH solution and soluble sugars (glucose, fructose and sucrose) were measured using a colorimetric technique at 340 nm (spectrophotometer model DU640B, Beckman Coulter™, USA) (Boehringer, 1984). Starch was extracted from the remaining dried matter in a boiling solution of 0.02N NaOH for 1 h. Starch was hydrolysed to glucose with α-amyloglucosidase (EC 3.2.1.3, Boehringer Mannheim Biochemicals, Mannheim, Germany) in a 0.32M citrate buffer soluion (pH 4.2) at 50 °C for 30 min. The resulting glucose was assessed as described above (Boehringer, 1984). Starch was quantified as glucose equivalents. Total non-structural carbohydrates (TNC) were calculated as the sum of total soluble sugars and starch. Total non-structural carbohydrate concentrations were expressed in glucose equivalents and converted to carbon mass (gC) by applying a 40% carbon content in glucose.

CANOPY PARAMETER MEASUREMENTS

Maximum Leaf Area Index (LAI): Canopy level measurement

Leaf Area Index was estimated for each plot with two inter-calibrated Plant Canopy Analysers Licor LAI-2000 (LI-COR Inc., Nebraska, USA). Above and below canopy measurements were carried out synchronously. Reference measurements were performed in a nearby clear-cut; the two operators were in radio contact for the synchronisation. Measurements were made during sunny, cloud-free days, at less than 1 h after or before sunrise or sunset respectively. Computation of leaf area index was made by the Li-Cor program C2000 (Li-Cor 1992) using linearly interpolated values of incident light at three zenith angles (from 0 to 43°). The two most horizontal angles were excluded from the computation to reduce the influence of woody components of aboveground cover (especially trunks) on LAI estimates. A view restrictor of 270° was used to exclude the operator's silhouette and the canopy outside the plot, from the measurement area. Diffuse and direct radiation from the direction of the sun was blocked from the sensor by a shadow made by the operator.

This operating mode was used in previous studies and results were consistent with direct LAI estimates from litter fall (Dufrêne and Bréda 1995, Bréda et al. 2002, Bréda 2003). In order to estimate maximum LAI, measurements were made after maximum leaf expansion and before leaf yellowing and the start of leaf fall. Measurements were performed in 2007 at DOY 227 in Humont site and DOY 228 in Les Potées site. In both sites, transmitted light was measured at every corner and in the centre of the plots. At the central point, transmitted light was measured in four orthogonal directions (Figure 39a, b).

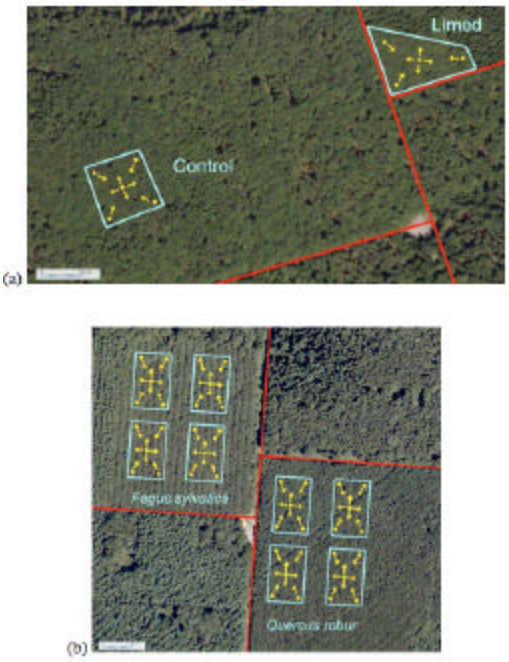


***Figure 39:** Arrangement of points for LAI measurement (yellow dots) and direction of measurement (yellow arrow) in each plot (blue limits) of (a) Humont and (b) Les Potées sites respectively. Limits of forest unit area displayed (red lines). Source: Geoportail 2007/2009.*

LEAF-LEVEL MEASUREMENTS

Sampling

Leaf parameters were measured on 3 samples of 10 sun leaves per tree, for the 10 selected trees per plot (Bonneau 1995).

For each of the selected trees, one branch of the upper third of canopy was sampled, using a rifle in adult stands and an averruncator in the youngest, smallest stands. Thirty leaves were selected randomly from branches and divided between 3 plastic bags containing 10 leaves each. In the field, bags were stored in a cold atmosphere (an icebox containing freezer-packs) to avoid respiration of foliar tissues that could reduce leaf weight and induce an underestimation of leaf mass area. Back in the laboratory, plastic bags were stored in a cold chamber (4°C) until they were measured and dried. Leaf area was measured within 48 hours following harvesting.

Total chlorophyll content (CHL)

One of the batches of 10 leaves was taken to measure the chlorophyll content using a chlorophyll meter (SPAD 502, Konica Minolta Sensing Inc., Osaka, Japan). Chlorophyll contents were measured in the field immediately after leaf collection. For each of these ten leaves, at least 10 SPAD measurements were made at different locations on the leaves (avoiding principal nerve, holes and coloured or faded spots), 1 to 2 cm apart. The average value of these measurements was calculated for each leaf. SPAD values per leaf were then converted to chlorophyll content (g/m^2) using the calibrated relationships for beech and oak (see Chapter 3, section entitled *Total chlorophyll content* (CHL), page 118).

Leaf Mass Area (LMA)

The three bags per tree, each containing ten leaves, were used for LMA estimation. The cumulative area of the ten leaves per bag was measured with a planimeter LI-3000A with transparent belt conveyer LI-3050A (LI-COR Inc., Nebraska, USA). Leaves were then oven-dried for 72 hours at 60°C before being weighed using a digital balance (PB 303 S type, Mettler-Toledo Ltd., Leicester, United Kingdom). The LMA was the ratio of cumulated leaf area to dry weight (g/m^2). The three values per tree were then averaged to give an estimation of tree LMA.

Carbon and Nitrogen contents

After drying and LMA measurement, the 30 leaves per tree were ground using a rotary grinder with rings (SODEMI, Cergy Pontoise, France). Before analyses, the samples were dried again for 4 hours at 60°C. 1.5 to 1.7 mg of powder were weighed with Sartorius MC5 microscales (Data Weighing Systems, Inc., Chicago, Illinois, USA), stored in a tin capsule and analysed by dynamic flash combustion with an element analyzer (Flash 2000 NC, Thermo Fisher Scientific Inc., Miami, Florida, USA) in the Analytical Laboratory INRA.

CLIMATIC DATA AND WATER BALANCE CALCULATION

To quantify the drought constraint of current and past years on tree physiology, a daily soil water balance model BILJOU (Granier et *al.* 1999) was used to estimate soil water deficit. Site-related parameters of the model include stand structure and tree phenology (maximum Leaf Area Index (LAI), budburst and leaf fall dates) and soil properties (maximum extractable soil water, soil bulk density and vertical distribution of fine roots in particular). Soil water deficit is assumed to occur when the available soil water content falls below 40% of its maximum value (Granier et al. 1999, Granier et al. 2000a, 2000b).

For the Humont site, daily precipitation, maximum and minimum temperature were bought from the Météo-France station of Val d'Ajol (# 88487002, alt. 370 m) located 8 km from the site. Air humidity and wind speed were obtained from the Météo-France station of Luxeuil (# 70473001, alt. 270 m) located 20 km from the site. Global radiation was bought from the Météo-France station of Giromagny (# 90052002, alt. 472 m) located 40 km from the site. Climatic data were available from 1/1/1991 to 31/12/2007.

For the Les Potées site, daily precipitation, maximum and minimum temperatures, air humidity and wind speed were bought from the Météo-France station of Charleville (# 8105005, alt. 149 m) located 20 km from the site. Global radiation was bought from the Météo-France station of Reims (# 51183001, alt. 472 m) located 90 km from the site. Climatic data were available from 1/1/1993 to 31/12/2007.

Because of the long distance between the experimental sites and the meteorological stations measuring daily global radiation, data supplied by Météo-France were compared with decadal global radiation computed from remote sensing observations and supplied by SATMOS (Service d'Archivage et de Traitement Météorologique des Observations Spatiales – CNRS, INSU, Météo-France). SATMOS data were available from 1996 to 2006. For the period considered, neither significant difference nor bias were detected between the two data sources for both sites (Figure 40a, b)

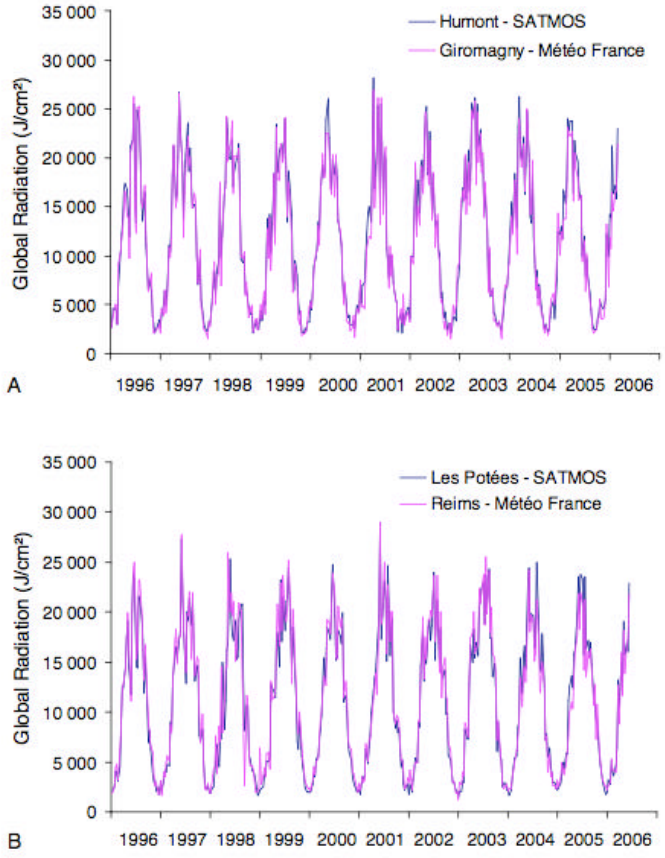


Figure 40: Comparison of decadal mean of global radiation between SATMOS measurements (blue solid line) and Météo France measurements (magenta solid line). (a) comparison between SATMOS measurements in Humont and Météo-France data from the Giromagny station (# 90052002) and (b) comparison between SATMOS measurements in Les Potées and Météo-France data from the Reims station (# 51183001).

RESULTS

EFFECT OF LIMING ON ADULT AND DECLINING BEECH STANDS

Soil characteristics

In each treatment, three trenches were dug to the bedrock in order to describe the soil and vertical root distribution.

Soil description

Precise soil description in both plots was decisive for the experiment at Humont, considering the experiment was devoid of repetition. To attribute differences between stands to treatment effects, the soils had to be similar.

In the treated stand, liming induced an increase in the kinetics of litter decomposition. This was characterized by:

- the shift from a moder (in the control stand) to an oligomull type of humus (Table 18);
- a very high density of worm casts (> 25 / m²);
- an improvement in the structure of the A horizon of the soil (the organo-mineral soil horizon): see Table 19.

In contrast, humus of the control stand presented a lower decomposition rate (moder type) and the A horizon was less well structured (Table 18).

These differences in humus type and upper soil structure between treatments may be related to liming (Bonneau, 1995). Despite these differences, the soil profiles of both stands were similar in soil horizon succession and depth, soil structure (Table 18) and soil texture (Table 19). Both stands were growing on an alocrisol. Soil texture, consisting of a loamy-clay, was fairly constant down to a depth of one metre but below this depth, in the weathered horizon, the proportion of sand (produced from the weathering sandstone) increased, resulting in a sandy texture (50 % sand). The organo-mineral horizon (A1), 8 to 10 cm thick, had an aggregated structure. Below 8-10 cm, the mineral horizons presented a polyedric structure and a more or less developed crumbly sub-structure. A stone line, composed of angular weathered sandstone and a few rounded stones appeared between the mineral horizons and

the weathered horizon (from 80 to 100 cm). The weathered layer consisted of a compact material with a variable percentage of weathered blocks

Furthermore, living fine roots (according to Vogt and Persson (1991) criteria: light coloured, elastic and resistant) were found down to depths of 90 cm and 100 cm in the limed and the control treatments respectively.

Table 18: Humont - Soil description of the limed (left table) and the control (right table) plots.

Limed plot				
Deep (cm)	**Layer**	**Structure**	**Coarse elements**	**Charge & Nature**
+5 – 0	Atur	Wormcasts		
0 – 8	A	Crumb structure	5%	
8 – 45	S1	Sub-angular blocky structure (2-3 cm) with crumb sub-structure	5%	Angular weathered sandstone
45 – 75	S2	Coarse sub-angular blocky structure	5%	A few rounded stones
75 – 90	SC		40-50%	
90 – 160	C	Compact to blocky	10%	
> 160	C		40-50%	Grey blocks of weathered sandstone

Untreated plot				
Deep (cm)	**Layer**	**Structure**	**Coarse elements**	**Charge & Nature**
0 – 8	A	Crumb structure less developed	5%	
8 – 50	S1	Sub-angular blocky structure (2-3 cm) with crumb sub-structure	5%	Angular weathered sandstone
50 – 80	S2	Coarse sub-angular blocky structure	5%	
80 – 100	SC		40-50%	A few rounded stones
100 – 170	2S	Compact to blocky	10%	
> 170	C		40-50%	Grey blocks of weathered sandstone

Table 19: Humont - Results of the particle size analyses for every identified soil layer.

Limed plot					
Deep (cm)	**Clay (g/kg)**	**Fine Silt (g/kg)**	**Coarse Silt (g/kg)**	**Fine Sand (g/kg)**	**Coarse Sand (g/kg)**
0 – 8	338	213	103	225	121
8 – 45	364	217	111	212	96
45 – 75	321	207	122	229	121
75 – 90	322	226	116	214	122
90 – 160	227	189	114	266	204

Untreated plot					
Deep (cm)	**Clay (g/kg)**	**Fine Silt (g/kg)**	**Coarse Silt (g/kg)**	**Fine Sand (g/kg)**	**Coarse Sand (g/kg)**
0 – 8	351	243	126	183	97
8 – 50	338	246	127	193	96
50 – 80	335	252	133	188	92
80 – 100	328	236	133	198	105
100 – 170	215	164	109	310	202

Gravimetric water content and bulk density

Gravimetric water content (GWC) and bulk density (BD) were estimated from volumetric samples after Baize (1988). The stone line made soil sampling impossible between 75 and 100 cm. High GWC values (21.9 % and 22.5 % in the limed and untreated soils respectively) and low BD values (1.23 g/g and 1.19 g/g in the limed and untreated soils respectively) revealed a moist aerated soil. Profiles of decreasing GWC and increasing BD were similar for the two stands studied (Figure 41). The moisture content of untreated soil was higher than that of the limed soil (10 % on average).

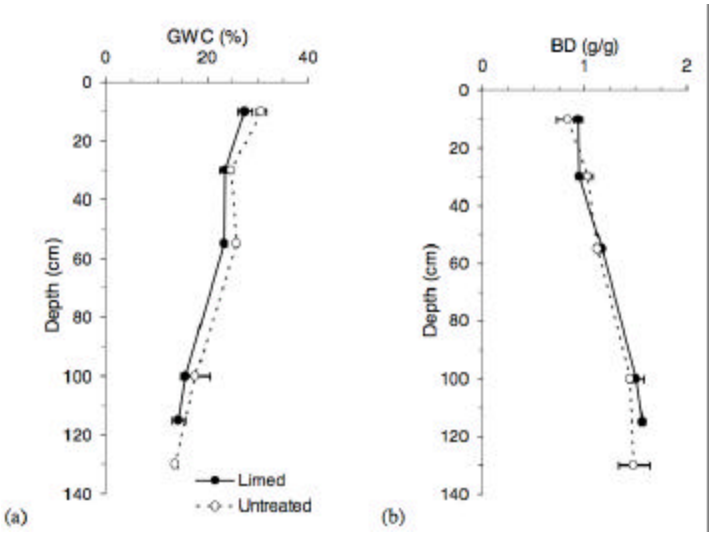


Figure 41: Humont - Profile of (a) gravimetric water content (GWC) measured in October 2008 and (b) bulk density (BD) in the limed (dot, solid line) and untreated (circle, dotted line) stands, at Humont.

Extractable soil water (EW)

Extractable soil water (EW) to the maximum root depth was computed using the thickness (THN), texture (TX) and bulk density of each soil layer (Baize 1988).

Bulk density and maximum root depth were slightly different between treatments (Table 20), resulting in a higher extractable soil water content in the untreated soil (159 mm) compared with the limed soil (115 mm).

Table 20: Maximum root depth and related extractable soil water for both plots of the Humont site.

Treatment	Limed	Untreated
Maximum root depth (cm)	90	100
Soil extractable water (mm)	115	159

Exchangeable elements, carbon and nitrogen in the soil

Exchangeable element analyses were made for each soil layer of both treatments. Results are displayed in Figure 42. The untreated stand revealed an acidic soil (pH KCl = 4.02) which was strongly de-saturated (BS<10%). Comparison between treatments revealed that the impact of liming was still concentrated in the uppermost soil horizon (organo-mineral horizon A1) 16 years after treatment. Overall, liming induced a reduction of acidity (pH increased) and an increase in base saturation (BS). In detail, treatment induced an increase in calcium, magnesium and manganese contents and a decrease in carbon, nitrogen, potassium, phosphorus, sodium and aluminium contents. The increase in calcium and magnesium contents might be related to the direct supply of calcium and magnesium in the soils.

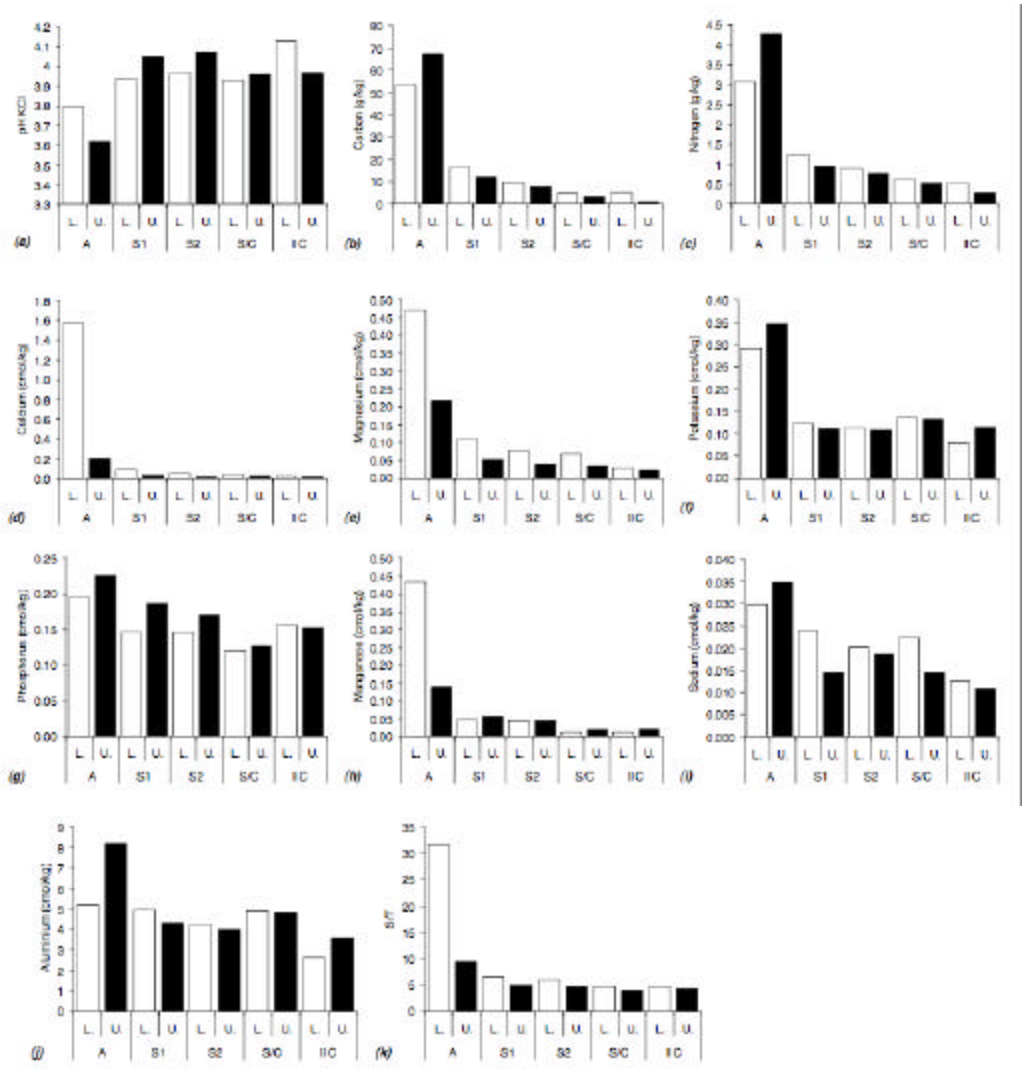


Figure 42: ***Humont - Exchangeable element composition of the limed (L, open bars) and untreated (U, black bars) soils. Variations between soil horizons (cf. Table 18) of (a) the pH, the content of (b) carbon (g/kg), (c) nitrogen (g/kg), (d) calcium (molc/kg), (e) magnesium (molc/kg), (f) potassium (molc/kg), (g) phosphorus (P_2O_5 g/kg), (h) manganese (molc/kg), (i) sodium (molc/kg), (j) aluminium (molc/kg), and (k) base saturation (%).***

Root densities

No effect of distance from the stem was detected (Figure 43): the horizontal colonization by roots was homogeneous. Similarly, no difference in fine root density was detected between trenches.

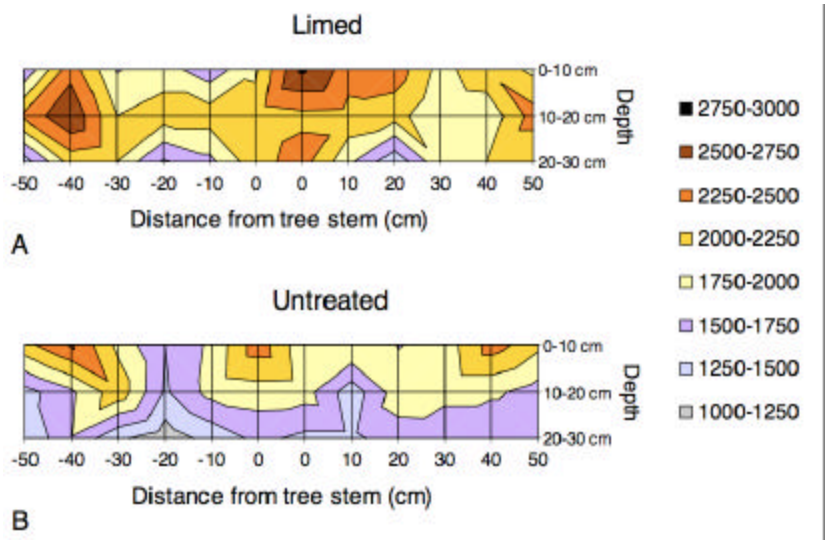


Figure 43: Humont - Fine root densities (Ø<3 mm) expressed as the number of root intercepts per square metre for the upper soil layer (0-30 cm). Root densities were averaged for the three trenches for (a) the limed stand and (b) the untreated stand.

Therefore, the effect of liming on root density was tested considering each square of the grid as an independent observation (Table 21). Between depths of 10 and 30 cm (S1 – Mineral horizon), fine root densities were significantly higher in the limed stand compared to the control. No effect of treatment was detected in the upper horizon of the soil (0-10 cm – mineral and organic horizon).

Table 21: Humont - Effect of treatment on fine root densities (Ø<3 mm) for the upper soil layer (0-30 cm) with Fisher test of significance (F=Fisher value and p= significance probability value).

Depth (cm)	Mean root density (/m²)		Effect of liming		
	Limed	Untreated	Df	F	p
0-10 cm	1958	1992	71	0.008	0.7829
10-20 cm	2061	1675	71	10.31	0.0020
20-30 cm	1769	1433	71	10.31	0.0020

Water Balance Simulation

To quantify the drought constraint of current and past years on tree physiology, a daily soil water balance model (Granier et al. 1999) was used to estimate soil water deficit.

Considering the physiological threshold of water deficit, fixed at 40 % of maximum extractable water (Bréda et al. 1994, Granier et al. 1999, Granier et al. 2000a, 2000b), beech suffered a more intense and longer drought in the limed stand than in the control between 1991 and 2007 (Figure 44). This is consistent with measurements commented on previously at the soil and canopy levels. Indeed, we showed that the limed stand presented lower water content (water supply), slightly higher fine root densities (uptake capacity) and higher LAI (water requirement) than the untreated stand.

The strongest drought of the period [1991-2007] occurred in 2003. 1991 and 1998 were also stressful for both stands. Limed trees suffered during the droughts in 1992, 1996 and 2005 as well.

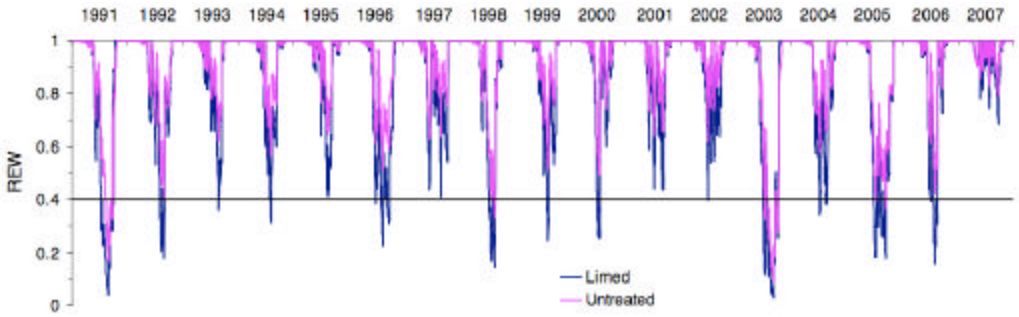


Figure 44: Humont - Year to year variation of relative extractable water (REW) for the limed (solid blue line) and the untreated (solid magenta line) soils at Humont, taking into account differences in extractable soil water, rooting depth and stand LAI.

Canopy parameters

Assessment of tree decline and consequence on LAI

In order to assess crown condition in 2007, the proportion of dead branches in the canopy of every tree inside plots was assessed visually and was quantified by using an index with 4 levels: 1 = 0%, 2 = less than 50%, 3 = more than 50 %, 4 = 100 % of dead branches.
In the limed stand, 97 % of trees did not displayed visual symptoms of decline and only 2 % of trees presented moderate crown damage (Figure 45a). In contrast, in the control plots, only 17 % of the untreated trees were healthy, 51% had moderate and 38 % had severe crown conditions (Figure 45b). Dominated trees were the most concerned by decline. This may be the logical consequence of harsh limitation occurring in dominated trees. More worrying is the high proportion of declining trees belonging to larger size classes (Figure 45c). Despite a high relative growth rate, revealing a good resource supply, around 20 % of trees with a CBH between 50 and 120 cm presented a severe proportion of dead branches. The largest beeches (CBH > 140cm) did not present severe symptoms of crown condition decay.

The high proportion of declining trees in the untreated stand may be the cause of the 1.0 m^2/m^2 lower LAI, despite high stand density (Table 16).

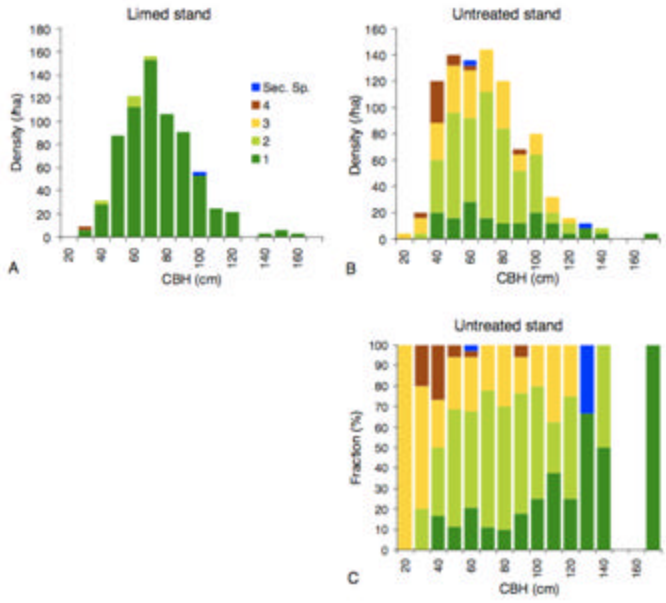


Figure 45: Humont - Histograms of distribution of stand density in the circumference classes (CBH) for (A) the limed stand and (B) the untreated stand. Panel C displays stand fraction per index of dead branches for each circumference class. Colours identify the index of decline.

Leaf characteristics

Leaf mass area and elemental analyses were performed for all selected leaves of both treatments. Results are displayed in Figure 46.

Limed trees presented wider and, to a lesser extent, thicker light leaves than untreated trees. Even if mean LMA was lower in the treated stand, the impact of lime was not significant.

After 16 years, the effect of liming on the element composition of leaves was still significant. Treatment induced an increase of calcium and magnesium content per mass unit. These increases might be related to the direct supply of calcium and magnesium in the soils. Limed trees also presented lower potassium, manganese, sulphur and aluminium contents in leaves compared to untreated trees. Finally, leaves of declining trees presented the highest concentrations in alum inium (Figure 46n).

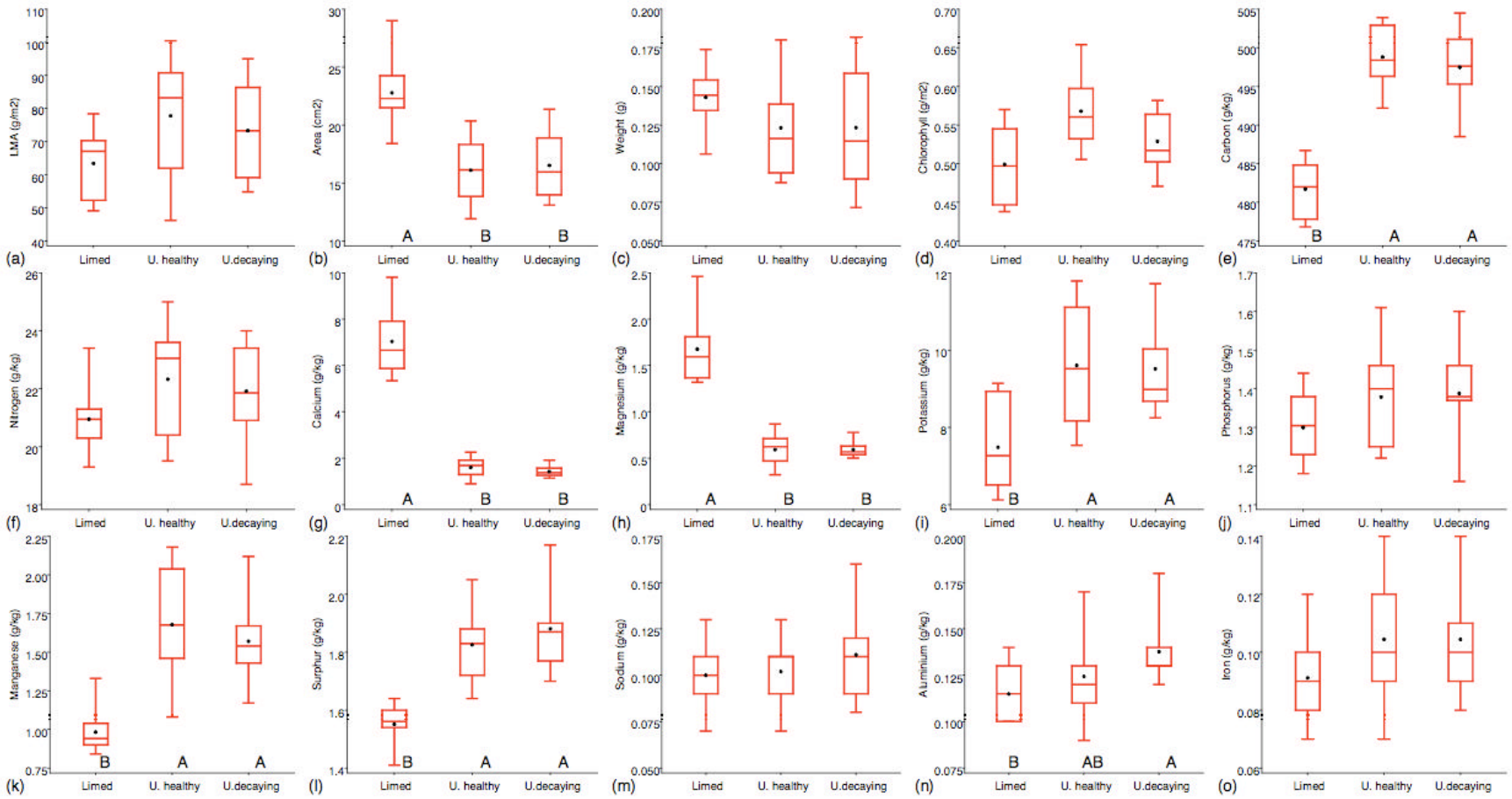


Figure 46: ***Humont - Leaf characteristics of limed (left), untreated healthy (centre) and untreated declining (right) trees. (a) Leaf Mass Area, (b) leaf area, (c) leaf mass, (d) chlorophyll, content per unit area and (e) carbon, (f) nitrogen, (g) calcium, (h) magnesium, (i) potassium, (j) phosphorus, (k) manganese, (l) sulphur, (m) sodium, (n) aluminium, (o) iron content per mass unit. Letters indicate significant differences between tree groups ($P < 0.05$, $n = 10$, Student t-test). The length of boxes represents the interquartile range; the dot represents the mean; the horizontal line in the boxes represents the median; the vertical lines issuing from the boxes extend to the minimum and maximum values of the analysis variables.***

Radial growth history

Comparison of radial growth history between limed, untreated but healthy and untreated declining trees was performed statistically by a year-to-year significance test of comparison of ring width (Figure 47a) and the detrended growth index (Figure 47b). Measured tree-rings quantify the growth level of a given year whereas growth index quantifies the year-to-year variations of radial growth, free from any contribution of long-term trend.

The number of counted tree rings made it possible to confirm that both studied stands were even aged (Table 16, around 72 years old). Significant differences between the three groups of trees were scarce during the period extending from the younger stage to the lime treatment in1991. This testifies that both stands had similar growth levels, i.e. ring width value, and similar growth histories or year-to-year variations, revealed by sensitivity of time series. Yet, smaller ring width was observed in the treated stand from 1972 to 1991. This insignificant reduction in radial growth might be related to delays in stand thinning, as revealed by higher stand density in 2007, compared to the untreated stand (Table 16).

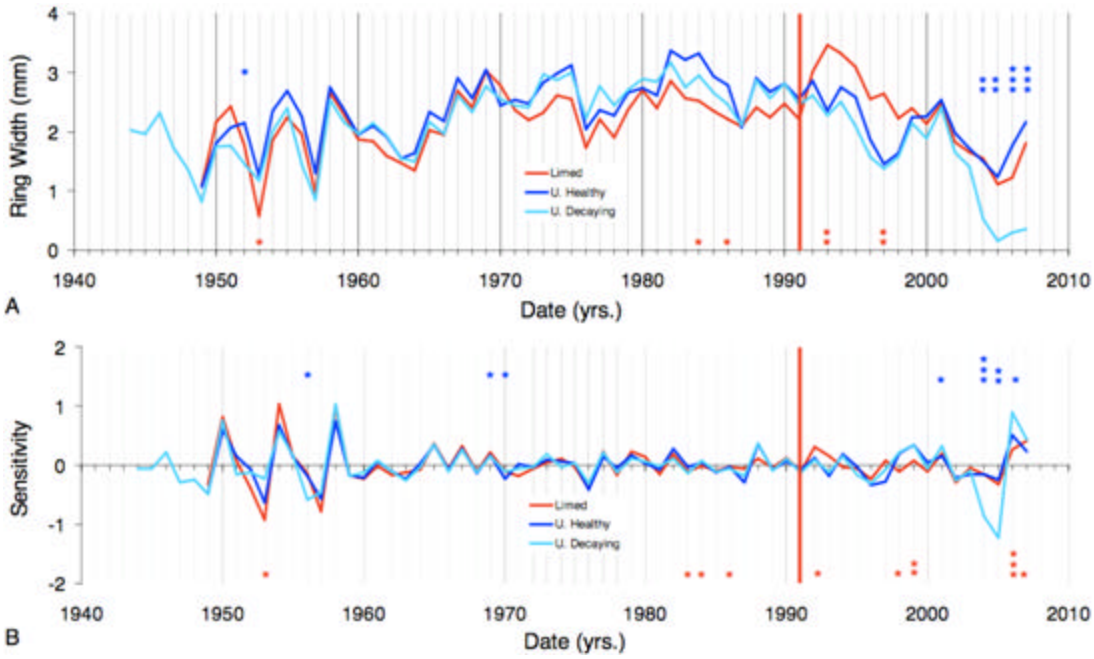


Figure 47: Humont - Time series of (a) ring width and (b) growth sensitivity of limed (red line), untreated healthy (blue line) and untreated declining (cyan line) trees. Red stars indicate significant differences in growth between limed and untreated healthy trees, blue stars indicate significant differences in growth between untreated healthy and declining trees. (Student t-test: * for p<0.05, ** for p<0.01 and *** for p<0.001) N=10 trees per group. For clarity, standard errors are not displayed. Red vertical line indicates the date of lime treatment.

After 1991, liming induced an increase in the radial growth of treated trees compared to untreated healthy trees (red stars, Figure 47a) from 1991 to 1998. However, this increase was only significant in 1993 and 1997. Afterwards, radial growth of limed trees was similar to those of untreated healthy trees, except in 2006: growth recovery after the moderate drought occurring in 2005 (Figure 48d) was lower for limed trees.

Retrospective analyses of growth made it possible to date the beginning of the fall in growth of declining trees. The recent significant decrease in growth of declining trees started in 2004 (blue stars, Figure 47a). However, two previous periods of growth decline could be identified: from 1983 to 1986 and from 1994 to 1996. Both periods were characterized by growth reduction, extending over several years. As the climate at the Champenoux and Humont sites is assumed to be similar, (both sites are located in north eastern France), year-to-year variations of soil water deficit simulated for Champenoux forest revealed that these two periods were also characterized by severe droughts (see Chapter 2, Figure 15) Similarly, growth depletion started in 2004 following a severe drought occurring in 2003, as revealed by the retrospective calculation of soil water deficit displayed in Figure 48d.

Overall, radial growth of limed and control stands has decreased regularly since the beginning of the 90s. Considering the age of both stands, this decrease may not be related to the long-term age-related decline of growth (see Chapter 2 for details). Comparison of radial growth with climatic parameters was no more conclusive: except for the 2003 summer drought, when water supply was quite good during this period (Figure 48b, d). No information about previous stand LAI was available but it should have been higher than that measured during 2007.

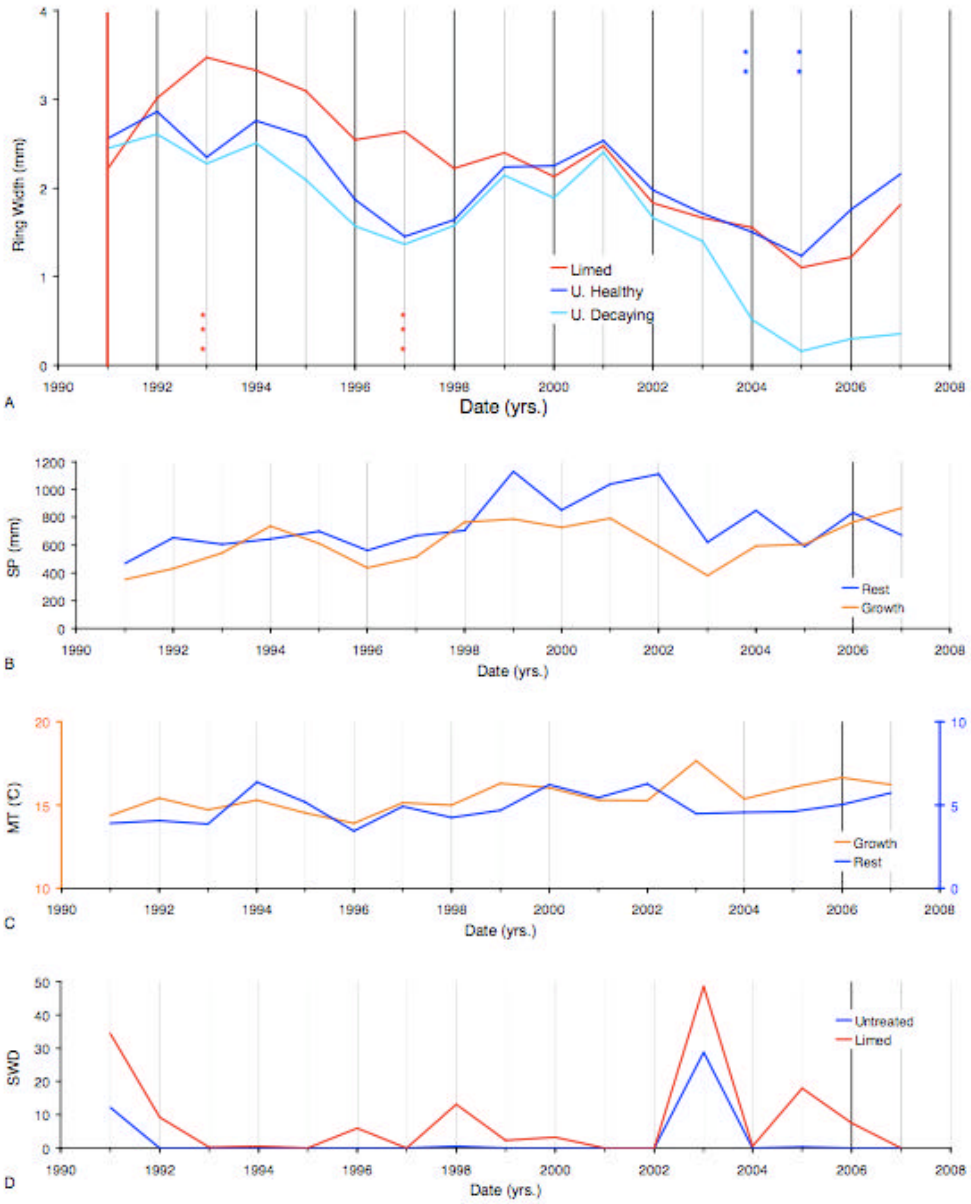


Figure 48: Humont - Times series of (a) growth index – red stars indicate significant differences in growth between limed and untreated healthy trees, blue stars indicate significant differences in growth between untreated healthy and declining trees – (b) Sum of precipitation (SP), (c) Mean temperature (MT) calculated both for the growing period (from May to October) and for the rest period (from previous November to current April) and (d) Soil water deficit (SWD) for Fagus sylvatica in Humont, from 1991 to 2007.

Carbon Balance in the trees

Carbohydrate Concentrations

Total non structural carbohydrate (TNC) concentrations were determined enzymatically for a total of 120 wood samples (30 trees, 2 organs per tree and 2 sample dates).

Regardless of the treatment and decline, concentrations in the stem were significantly higher than concentrations in coarse roots (Table 22). Furthermore, concentrations occurring in October (the date for maximum concentrations) were significantly higher than concentrations in May (the date for minimum concentrations). However, the balance between storage accumulation and storage consumption during the 2007 growing season did not induce a significant increase of TNC concentrations in coarse roots.

Table 22: Humont - Analysis of variance of TNC concentrations as a function of coring dates and tree organs. Abbreviations: df=Degree of Freedom, F= Fisher test value, p=probability.

Effect	Variable	*df*	*F*	*p*
Organ	TNC in May	60	45.68	<.0001
	TNC in October	60	36.70	<.0001
Date	TNC in stem	60	16.60	<.0001
	TNC in roots	60	0.05	0.8255

Comparisons of TNC concentrations between limed, untreated but healthy and untreated declining trees are displayed in Figure 49 for every combination of organ and sampling date. Differences between groups of trees were the same for every combination of sampling date and organ: (1) TNC concentrations were significantly higher in limed trees compared to untreated trees and (2) concentrations between healthy and declining untreated trees were not significantly different.

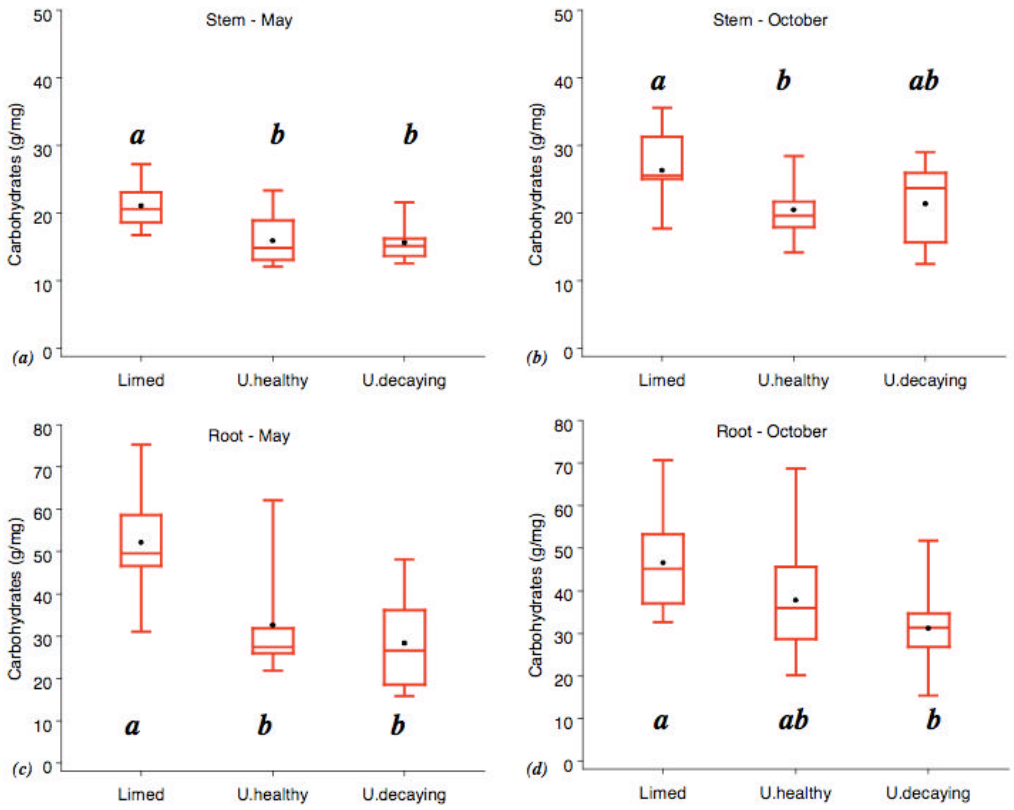


Figure 49: Humont - Total non structural carbohydrate concentrations for limed (left), untreated healthy (centre) and untreated declining (right) trees in stem (panels (a) and (b) and coarse roots (panels (c) and (d), in May (panels (a) and (c) and October (panels (b) and (d). Letters indicate significant differences between tree groups (P < 0.05, n = 10, Student t-test). The length of boxes represents the interquartile range; the dot represents the mean value; the horizontal line in the boxes represents the median; the vertical lines issuing from the boxes extend to the minimum and maximum values of the analysis variables.

Biomass and storage increment during the 2007growing season

Biomass increments were estimated from circumference and tree ring measurements of each of the 30 selected trees. Storage increments were deduced from seasonal differences between measured TNC concentrations, estimated biomass and biomass increment.

The mean tree biomass of around 360 kgC/tree in the autumn, 2007 was not significantly different between groups of trees, (Figure 50a). Indeed, retrospective radial growth analyses did not reveal long term effects of liming or decline on tree growth (Figure 47a).

The biomass increment in 2007 was 9.1, 11.2, 1.6 kgC/tree for limed, untreated but healthy and untreated but declining trees respectively. The, biomass increment was significantly lower in declining trees than in healthy trees in 2007 (Figure 47b). The increment of TNC was around 1.5 kgC/tree in 2007 and no significant differences occurred between trees overall. However, a significant difference in carbon storage in coarse roots was detected between limed and untreated trees. Indeed, TNC storage in coarse roots was negative in limed trees and positive in untreated trees in 2007: the carbon allocation to TNC storage in roots of limed trees was not sufficient to compensate TNC use.

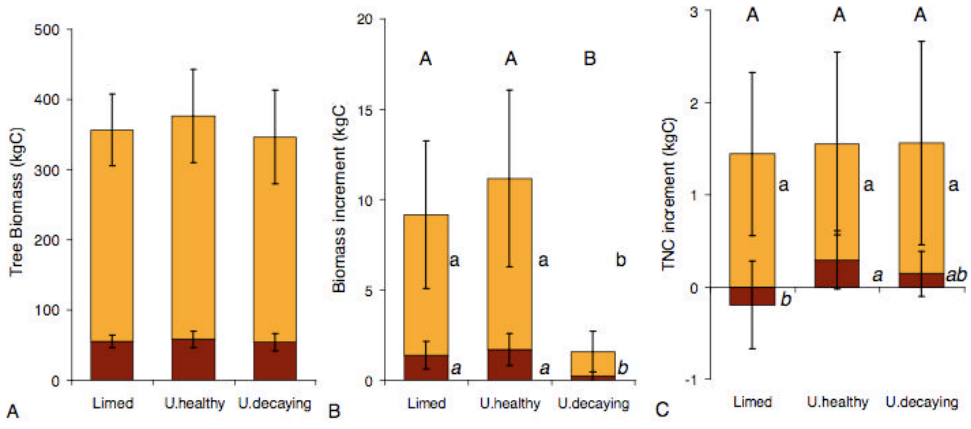


Figure 50: Humont - A) tree biomass, B) tree storage increment and C) tree biomass increment for limed (left), untreated healthy (centre) and untreated declining (right)* Fagus sylvatica *(N=10 trees per group). Carbon increments were computed for the 2007growing season. Letters indicate significant differences between tree groups (P < 0.05, n = 10, Student t-test). Vertical bars represent standard errors.

EFFECT OF LIMING ON YOUNG PLANTATIONS OF BEECH AND PEDUNCULATE OAK

Soil characteristics

In Les Potées, trenches were dug in each treatment of a pair of limed/control plots for both species: 12 trenches were excavated in total. For beech, trenches were opened in control plot C1 and limed plot L2 (Table 23, Table 24). For pedunculate oak, trenches were opened in control plot C1 and limed plot L1 (Table 25, Table 26). Soil descriptions were made for these particular plots. The homogeneity of the soil in the other plots of the experiment had been checked previously by doing brief soil descriptions using a regular soil corer down to depths of 120 cm.

Soil description

In contrast to the experiment at Humont, no effects of liming were detected on humus quality in beech stands. The humus was an oligomull regardless of the treatment. In oak stands, the humus was an oligomull in untreated stands and a mesomull in treated stands. In contrast to the oligomull, the mesomull was devoid of old litter, revealing better litter degradation dynamics. For both species, the structure of the upper soil layer was better developed in limed plots than in the control (Table 23 for beech and Table 25 for pedunculate oak). These differences in humus type and upper soil structure between treatments may be related to liming (Bonneau, 1995).

For beech, despite these differences, the soil profiles below the humus in all plots were similar in soil layer succession and depth, soil structure (Table 23) and soil texture (Table 24). The beech was growing on a deep neoluvisol and soil texture, consisting of a silty loam, was fairly constant to a depth of 85 cm. The mineral and organic horizon presented a blocky structure, with a granular well developed structure in the uppermost layer on the limed soils. The mineral horizon appeared at a depth of 6-8 cm and presented a prismatic structure and a more or less well developed sub-angular structure. A clay enriched horizon (BT) was found at the junction between the upper layers and the C horizon from 85 to 145 cm. In this horizon, the clay content increased by 25 % in the limed plot and 31 % in the untreated plot. In the weathered horizon (below 145 cm), the proportion of clay increased, resulting in a clay loam to clay texture with variable proportions of platy weathered parent material.

The soil profile and structure of pedunculate oak stand (Table 25, Table 26 respectively) were similar to that of the beech stand. However, the Bt horizons in the limed plot presented higher proportions of clay than all the other plots described: whereas the clay content was around 302 g/kg in horizons A and E of the oak limed plot, it was only 206, 197 and 227 g/kg in the untreated oak, untreated beech and limed beech plots respectively.

Finally, maximum root depth was 110 and 150 cm for limed and untreated oak plots respectively and 190 and 200 cm in the limed and untreated beech plots.

Table 23: Les Potées* - Fagus sylvatica*: Soil description of the limed (left table) and the control (right table) plots.

Limed plot : oligomull lying on neoluvisol				
Deep (cm)	**Layer**	**Structure**	**Coarse elements**	**Charge & Nature**
0 – 2	A1	Well developed crumb structure		
2 – 8	A2	Massive structure		
8 – 48	E1	Crumb to blocky structure (3 mm)		
48 – 86	E2	Subangular blocky structure (2 cm)		
86 – 140	BT	Well developed blocky structure (2-3 cm)	5%	Stones (slate)
>140	C	Coarse blocky structure	20%	Platy blocks of slate

Untreated plot : oligomull lying on neoluvisol				
Deep (cm)	**Layer**	**Structure**	**Coarse elements**	**Charge & Nature**
0 – 6	A	Massive structure		
6 – 45	E1	Crumb to blocky structure (5 mm)		
45 – 85	E2	Subangular blocky structure (2-3 cm)	5%	Stones (slate)
85 – 145	BT	Less developed blocky (3 cm)	20-30%	Stones (slate)
> 145	C	Coarse blocky structure	30%	Stones (slate)

Table 24: Les Potées* - Fagus sylvatica*: Results of the particle size analyses for every identified soil layer.

Limed plot					
Deep (cm)	**Clay (g/kg)**	**Fine Silt (g/kg)**	**Coarse Silt (g/kg)**	**Fine Sand (g/kg)**	**Coarse Sand (g/kg)**
0 – 2	254	340	340	40	26
2 – 8	222	361	349	47	21
8 – 48	189	361	350	52	48
48 – 86	245	344	344	43	24
86 – 140	286	325	295	58	36
140 – 200	329	318	227	65	61

Untreated plot					
Deep (cm)	**Clay (g/kg)**	**Fine Silt (g/kg)**	**Coarse Silt (g/kg)**	**Fine Sand (g/kg)**	**Coarse Sand (g/kg)**
0 – 6	200	340	341	55	64
4 – 45	196	341	351	50	62
45 – 85	196	333	357	50	64
85 – 145	310	288	244	67	91
> 145	536	167	129	120	48

Table 25: Les Potées site* - Quercus robur*: Soil description of the limed (left table) and the control (right table) plots.

Limed plot : mesomull lying on neoluvisol				
Deep (cm)	**Layer**	**Structure**	**Coarse elements**	**Charge & Nature**
0-6	A	Well developed crumb structure (5 mm)		
6-33	E1	Crumb structure		
33-66	E2	Subangular blocky structure (3-4 cm)		
66-98	BT			
98-132	BT/C	Blocky structure weakly developed	10%	Grit and stones (slate)
>132	C	Platy	55%	Slabs of slate

Untreated plot: oligomull lying on neoluvisol				
Deep (cm)	**Layer**	**Structure**	**Coarse elements**	**Charge & Nature**
0-6	A	Massive structure		
6-27	E1	Crumb to blocky structure (5 mm)		
27-56	E2	Subangular blocky structure (2-3 cm)		
56-85	E3			
85-128	BT	Blocky structure	10%	stones (slate)
>128	C	Platy	55%	Grit and stones (slate)

Table 26: Les Potées site* - Quercus robur*: Results of the particle size analyses for every identified soil layer.

Limed plot					
Deep (cm)	**Clay (g/kg)**	**Fine Silt (g/kg)**	**Coarse Silt (g/kg)**	**Fine Sand (g/kg)**	**Coarse Sand (g/kg)**
0-6	220	345	354	54	27
6-33	227	342	343	53	35
33-66	311	295	268	54	72
66-98	452	241	166	60	81
98-132	484	201	125	111	79
132 – 200	343	310	137	117	93

Untreated plot					
Deep (cm)	**Clay (g/kg)**	**Fine Silt (g/kg)**	**Coarse Silt (g/kg)**	**Fine Sand (g/kg)**	**Coarse Sand (g/kg)**
0-6	229	349	343	45	34
6-27	184	341	383	53	39
27-56	175	365	385	46	29
56-85	239	344	351	40	26
85-128	350	273	259	58	60
128-200	567	169	93	65	106

Extractable soil water (EW)

Extractable soil water (EW) to the maximum root depth was computed using the thickness (THN), texture (TX) and bulk density of each soil layer (Baize 1988). The high clay fraction and the deep root systems resulted in high values of extractable soil water in both stands (Table 27), ranging from 233 mm in the oak stand to 267 mm in the beech stand.

Table 27: Maximum root depth and extractable soil water for both plots of Les Potées site.

Species	*Fagus sylvatica*		*Quercus robur*	
Treatment	Limed	Untreated	Limed	Untreated
Maximum root depth (cm)	140	145	132	128
Extractable soil water (mm)	267	248	233	234

Exchangeable elements, carbon and nitrogen in the soil

Exchangeable element analyses were made for all soil layers of both treatments. Results are displayed in Figure 51 for the beech stand and Figure 52 for pedunculate oak stands. Compared to Humont, soils presented similar levels of acidity (pH of 3.5 for both stands in the mineral and organic horizon (A)) and similar levels of de-saturation (BS of 14.5% for both stands in the A horizon).

As at Humont, comparison between treatments revealed that liming still had an impact on soil properties 12 years after treatment, but it remained concentrated in the uppermost soil layer (A horizon). Common to both species, limed soils presented lower values of aluminium and higher values of calcium, magnesium and sodium resulting in lower levels of acidity (increased pH) and higher rates of total base saturation (BS) compared to untreated soils. In beech, carbon and nitrogen contents were higher in limed plots than in untreated plots, whereas in oak, carbon and nitrogen contents remained unchanged between both described plots. Finally, the manganese content in the uppermost soil was higher in the limed oak plot than in the untreated one, whereas it did not change in the beech plots described.

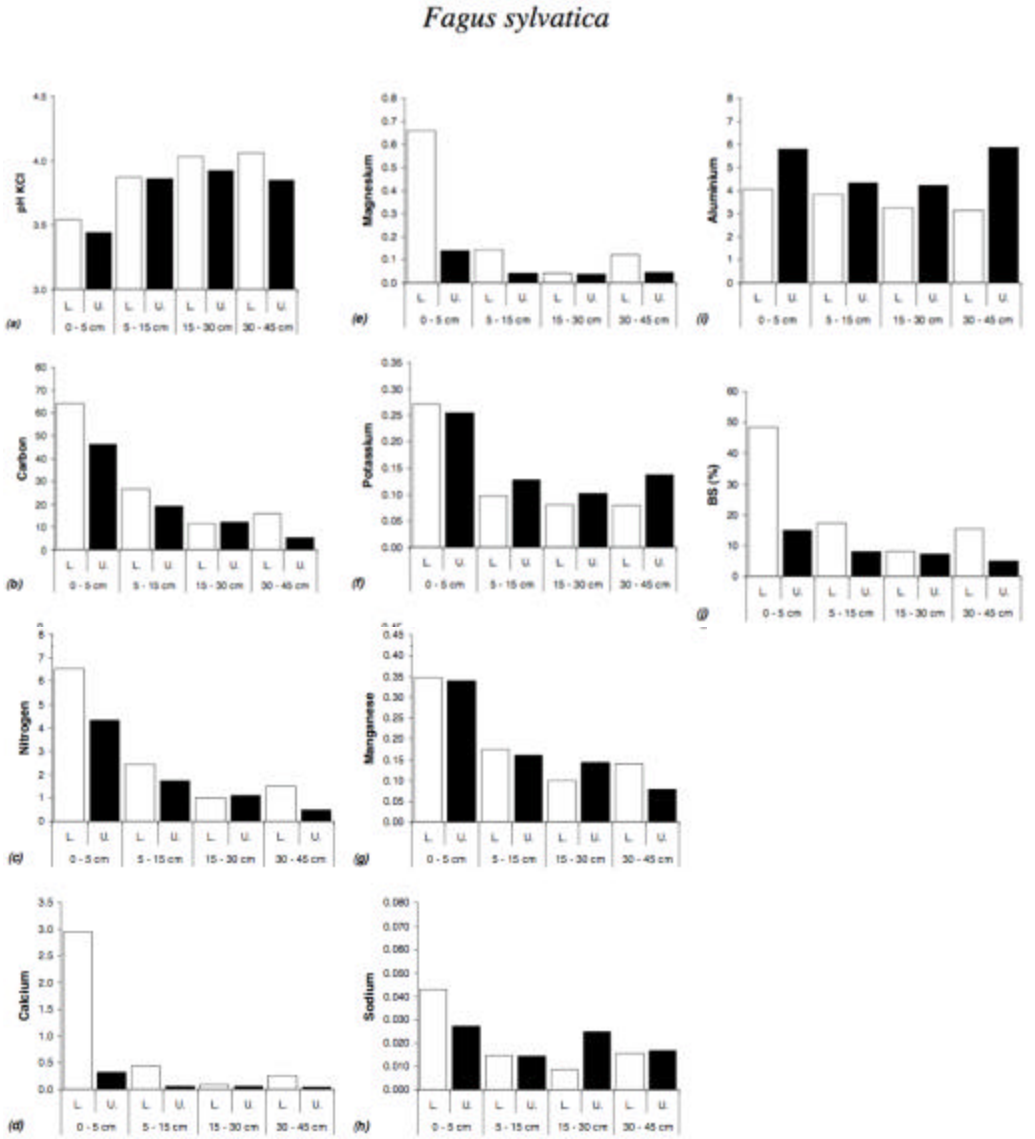


Figure 51: Les Potées site - Mineral composition of the limed (L, open bars) and untreated (U, black bars) soils in* Fagus sylvatica *plots. Variations with depth of (a) the pH, the content of (b) carbon (g/kg), (c) nitrogen (g/kg), (d) calcium (molc/kg), (e) magnesium (molc/kg), (f) potassium (molc/kg), (g) manganese (molc/kg), (h) sodium (molc/kg), (i) aluminum (molc/kg), and (j) base saturation (%). Values are averaged for the two blocks of the two treatments.

Quercus robur

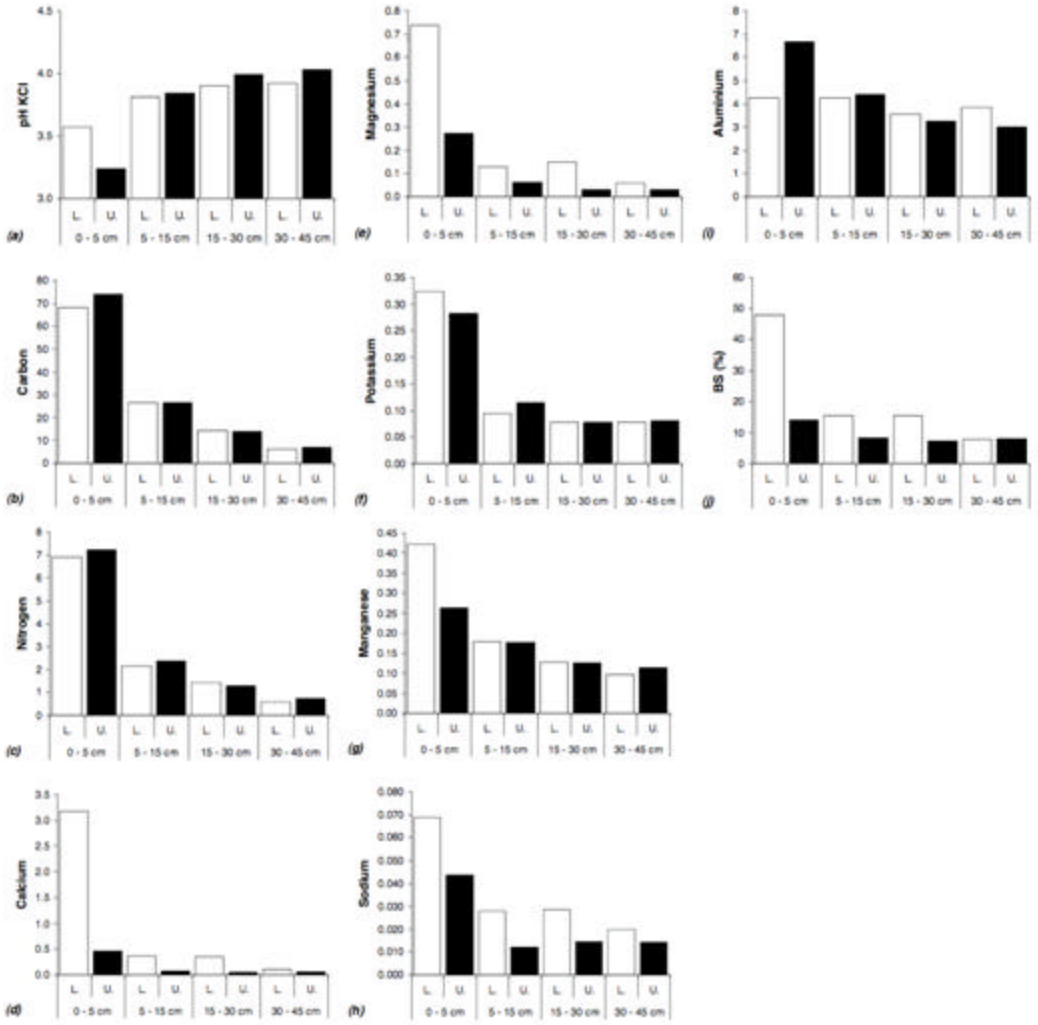


Figure 52: Les Potées site - Mineral composition of the limed (L, open bars) and untreated (U, black bars) soils in* Quercus robur *plots. Variations with depth of (a) the pH, the content of (b) carbon (g/kg), (c) nitrogen (g/kg), (d) calcium (molc/kg), (e) magnesium (molc/kg), (f) potassium (molc/kg), (g) manganese (molc/kg), (h) sodium (molc/kg), (i) aluminum (molc/kg), and (j) base saturation (%). Values are averaged for the two blocks of the two treatments

Fine root densities

As for the Humont site, distance from the stem had no impact on root density in either plot: the horizontal colonization by roots was homogeneous. Similarly, no difference of fine root density (FRD) was detected between trenches. Therefore, the effect of liming on root density was tested considering every square of the grid as an independent observation (red stars in Figure 53). Significant differences between limed and control plots were scarce for both species. Fine root densities were significantly higher in the limed stand than in the control in the 0-10 cm and 30-40 cm layers in the beech stand and in the 40-50 cm layer in oak stand.

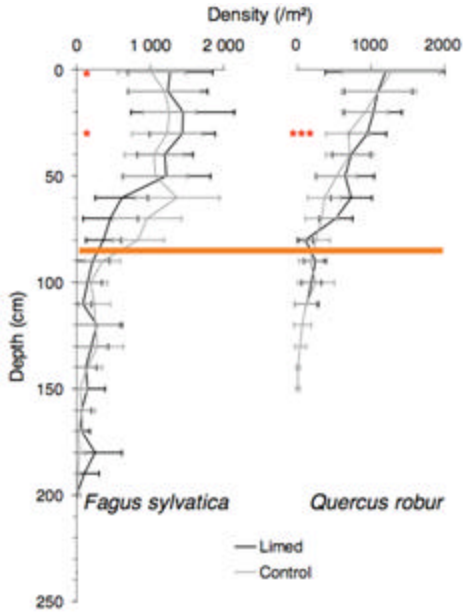


Figure 53: Les Potées site - Fine root densities (Ø<3 mm) expressed as the number of root intercepts per square metre in the soil profile (0-200 cm) of* Fagus sylvatica *(left) and* Quercus robur *(right). Root densities were averaged for the three trenches for the limed stand (black solid line) and the untreated stand (grey solid line). Red stars indicate significant differences in fine root densities between limed and untreated plots. (Student t-test: * for p<0.05, ** for p<0.01 and *** for p<0.001) N=360 per level of description per plot. Horizontal lines represented standard errors. Red horizontal line indicates the uppermost limit of the clay enriched layer.

Fine root densities were at a maximum in the uppermost layer of the soil (0-10cm). Ranging around 1200 impacts/m², maximum densities were similar for both species. Limitation of FRD by the clay enriched horizon (appearing around 85 cm) was also observed for both beech and oak.

Despite these similarities, the FRD decrease with increasing depth was different between beech and pedunculate oak. In beech, FRD remained constant in the upper 50 cm and 60 cm of the soil in limed and untreated plots respectively. In these layers, FRD was higher in the limed plot (1300 impacts/m²), compared to the untreated plot (1170 impacts/m²). It decreased sharply in deeper soil layers until the appearance of the clay enriched horizon (BT). In contrast, FRD of oak decreased regularly with increasing depth down to the BT horizon. Despite the lower clay content and related lower bulk density, this depletion was higher in the untreated plot than in the limed plot. Below the BT horizon, rooting extended deeper in the beech stand (to 200 cm) than in the oak stand (to 150 cm).

Water Balance Simulation

To quantify the drought constraint of current and past years on tree physiology, a daily soil water balance model (Granier et al 1999) was used to estimate soil water deficit retrospectively.

Considering the physiological threshold of water deficit to be fixed at 40 % of maximum extractable water (Bréda et al. 1994, Granier et al. 1999, Granier et al. 2000a, 2000b), the beech stand suffered more intense and longer drought than the oak stand (Figure 54). These differences might be related to higher LAI (water requirement) in beech (LAI=8.0, Table 17: Les Potées - Stand description of each plot of the experiment. Leaf Area Index (LAI) was measured in August 2007. Rep. = replicate.) compared to oak (LAI=4.7).

The strongest droughts of the period [1993-2007] occurred in 1994, 1995, 1996, 2003 and 2006. The 2007 season of our measurements was particularly wet and free from soil water deficit, in contrast to the previous dry year. A lag effect of the 2006 drought should have affected our measurements of both growth (stem, fine root, LAI) and storage (especially spring concentrations).

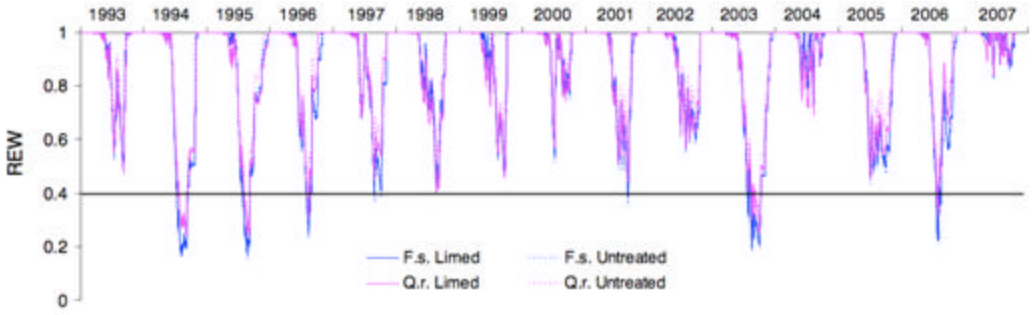


Figure 54: Les Potées site - Year to year variation of relative extractable water (REW) for the limed (solid lines) and the untreated (dotted lines) stands of* Fagus sylvatica *(blue) and* Quercus robur *(magenta) in Les Potées, taking into account differences in LAI, fine root distribution and EW.

Canopy parameters

Leaf mass area and element analyses were carried out for every selected tree of both treatments. Results are displayed in Figure 55 for beech and Figure 56 for pedunculate oak. While treatment had no impact on leaf morphology in oak, limed beeches presented significantly higher leaf mass area than untreated ones.

After 16 years, the effect of liming on element composition of leaves was still significant. For both species, treatment induced an increase in calcium and magnesium content per mass unit. As for Humont, these increases might be related to the direct supply of calcium and magnesium in the soils. Both species also presented significantly lower manganese contents in leaves of limed trees, whereas manganese in the soil of limed oak increased and remained stable in beech. This contrast was also reported at Humont .

For beech alone, liming also induced a significant increase in nitrogen, potassium, phosphorus, sulphur and aluminium contents and a significant decrease in carbon in the leaves.

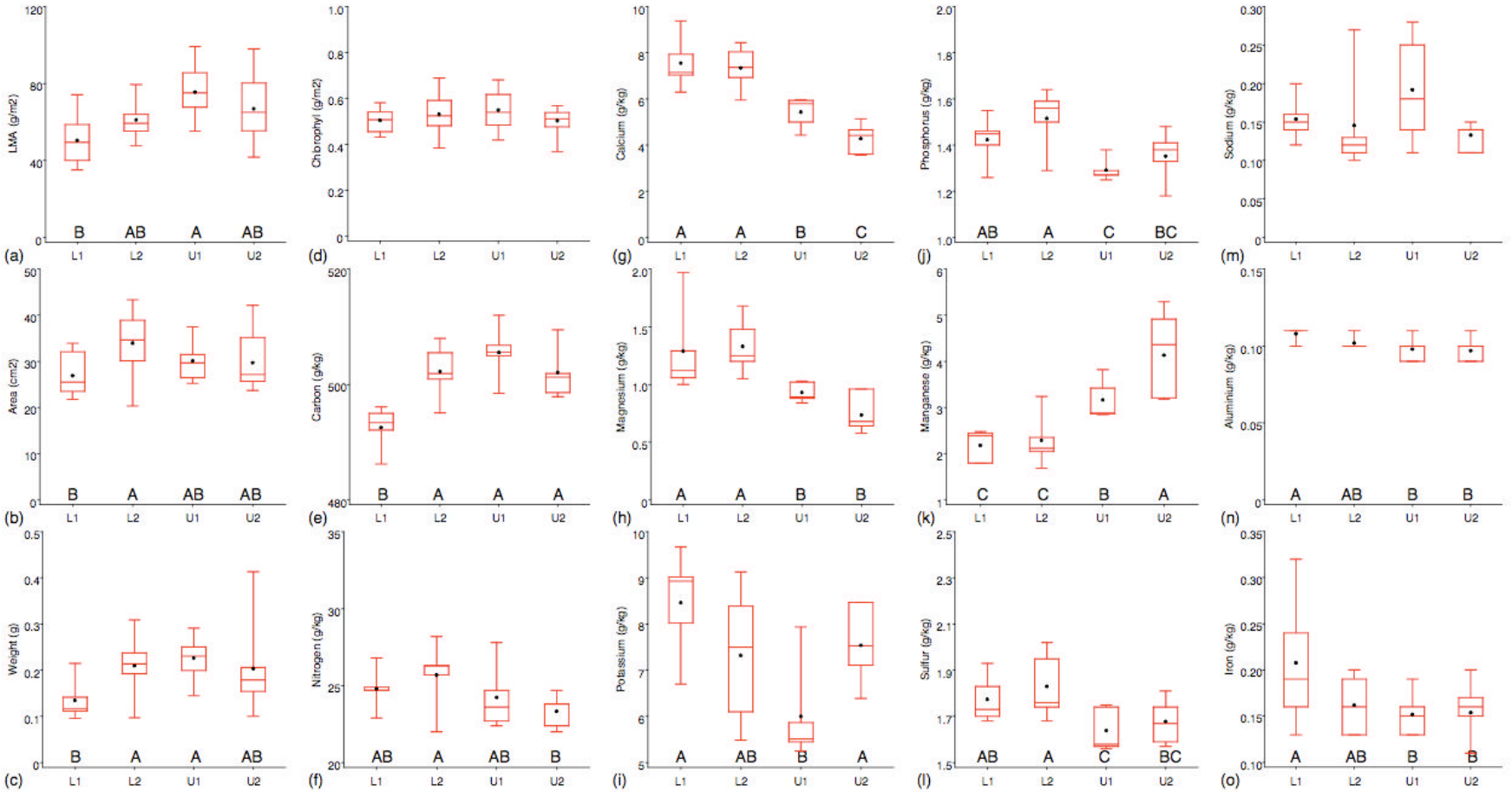


Figure 55: Les Potées – Fagus sylvatica: Leaf characteristics of limed (left – L1, L2) and untreated (right – U1, U2) trees. (a) Leaf Mass Area, (b) leaf area, (c) leaf mass, (d) chlorophyll, content per unit area and (e) carbon, (f) nitrogen, (g) calcium, (h) magnesium, (i) potassium, (j) phosphorus, (k) manganese, (l) sulphur, (m) sodium, (n) aluminium, (o) iron content per mass unit. Letters indicate significant differences between tree groups (P < 0.05, n = 10, Student t-test). The length of boxes represents the interquartile range; the dot represents the mean; the horizontal line in the boxes represents the median; the vertical lines issuing from the boxes extend to the minimum and maximum values of the analysis variables.

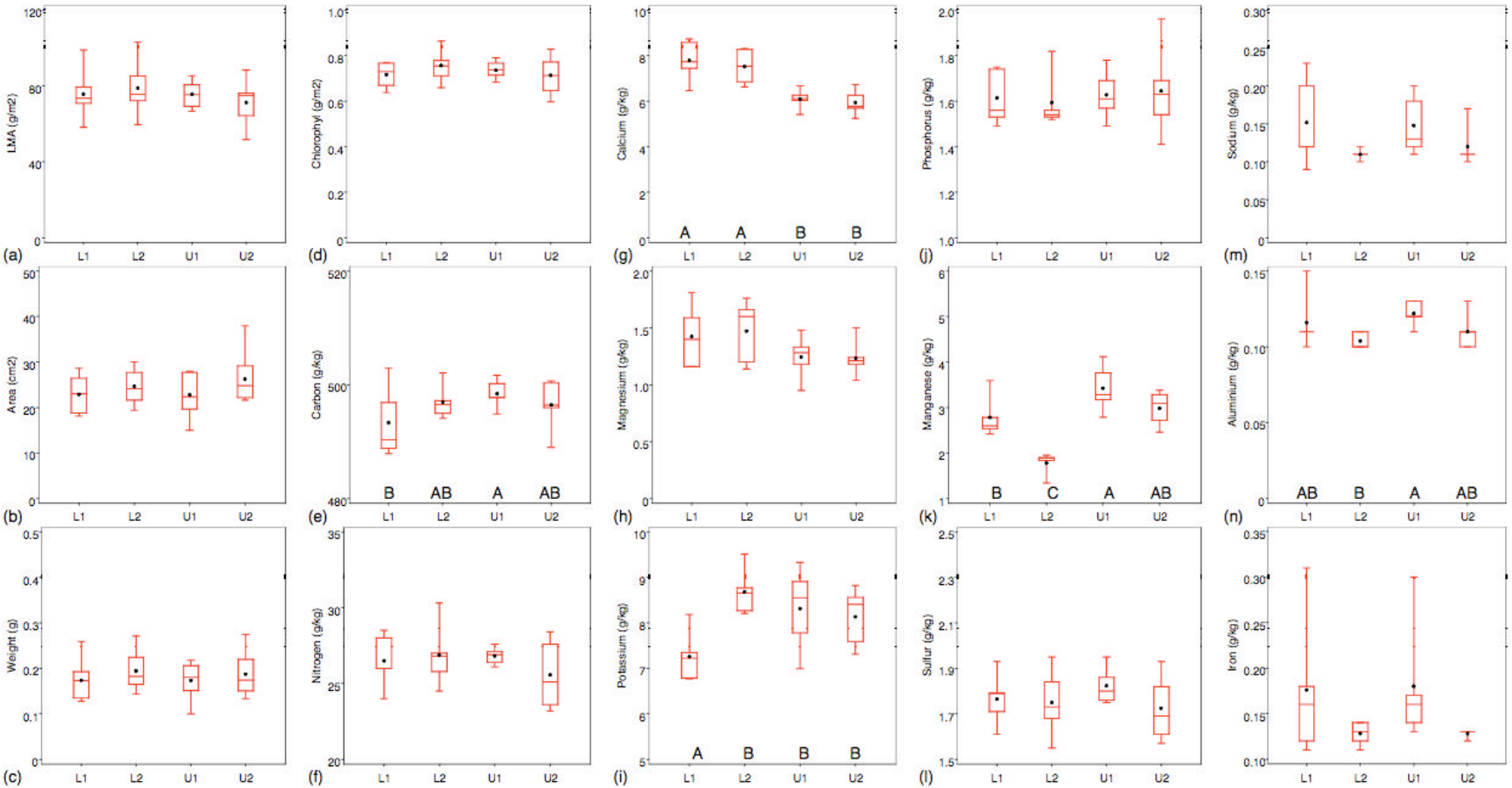


Figure 56: Les Potées - Quercus robur: Leaf characteristics of limed (left – L1, L2) and untreated (right – U1, U2) trees. (a) Leaf Mass Area, (b) leaf area, (c) leaf mass, (d) chlorophyll, content per unit area and (e) carbon, (f) nitrogen, (g) calcium, (h) magnesium, (i) potassium, (j) phosphorus, (k) manganese, (l) sulphur, (m) sodium, (n) aluminium, (o) iron content per mass unit. Letters indicate significant differences between tree groups ($P < 0.05$, $n = 10$, Student t-test). The length of boxes represents the interquartile range; the dot represents the mean; the horizontal line in the boxes represents the median; the vertical lines issuing from the boxes extend to the minimum and maximum values of the analysis variables.

Radial Growth history

A comparison of radial growth history between species and treatment was performed by a year-to-year statistical test of comparison of ring width (Figure 57a) and sensitivity indices (Figure 57b). Measured tree-rings quantify the growth level of a given year whereas sensitivity indices quantify the year-to-year variations of radial growth, free from any contribution of long-term trend.

From 1985 to 1992, ring width of beech was doubled (from 2.8 mm to 5 mm) whereas growth rate of pedunculate oak fluctuated around a mean value of 4.0 mm. This contrasting growth-trend between species might be related to age-related changes in growth rate described on Chapter 2.

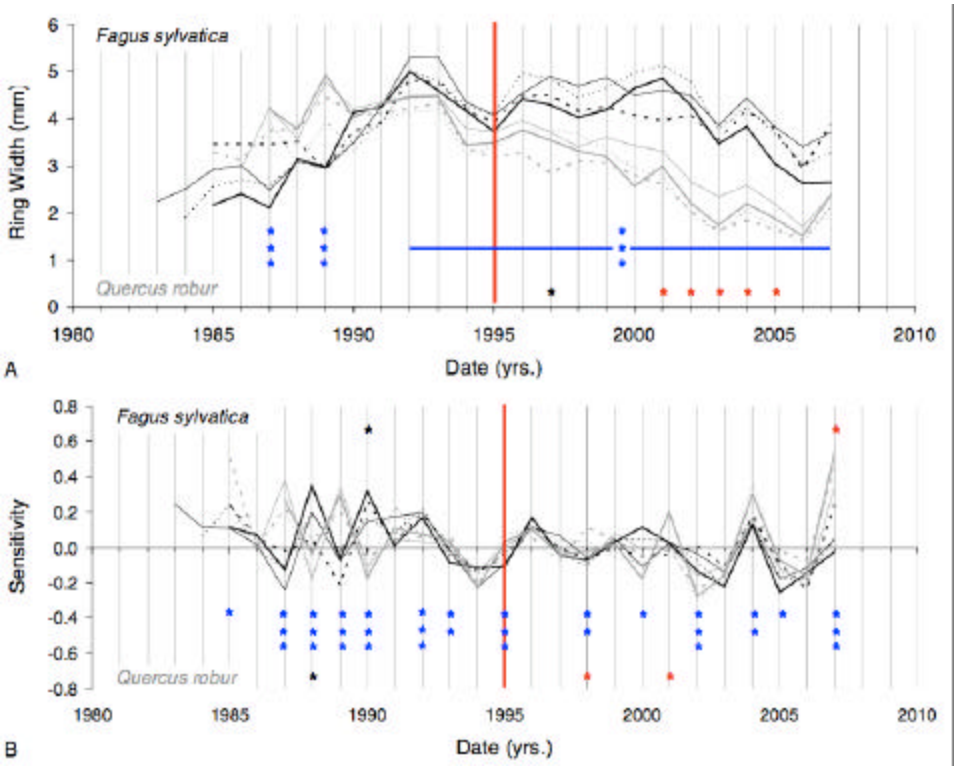


Figure 57: Time series of (a) ring width and (b) growth sensitivity of Fagus sylvatica (black lines) and Quercus robur (grey lines). Solid lines represent limed plots, dotted lines represent untreated plots. Thick lines represent repetition 1 and thin lines represent repetition 2. Red stars indicate significant differences in growth between limed and untreated plots. Blue stars indicate significant differences in growth between Fagus sylvatica and Quercus robur. Black stars indicate significant differences in growth between repetition 1 and repetition 2. (Student t-test: * for p<0.05, ** for p<0.01 and *** for p<0.001) N=15 trees per group. For clarity, standard errors are not displayed. Red vertical line indicates date of lime treatment.

Whereas ring widths of oak were significantly higher than those of beech in the earlier stage of development, this trend reversed after 1992 to the benefit of beech growth (blue stars, Figure 57a). Assuming that the age-related trend of radial growth is similar for sessile and pedunculate oak, this decrease in growth of trees younger than 25 years old cannot be explained by ageing (see chapter II) Besides, this growth decrease was followed by an increase in mean sensitivity (average of absolute values of sensitivity index): whereas mean sensitivities of beech and oak were comparable between 1985 and 2000 (0.111 and 0.114 for beech and oak respectively), mean sensitivity of oak increased to 0.197 after 2000 whereas mean sensitivity of beech was only 0.122 after 2000 (Figure 57b). Yet, sensitivity did not change with tree age in oak. So, the growth decline observed for pedunculate oak after 1992 might be related to climatic causes or silvicultural dynamics (canopy closure) rather than ontogenic causes.

Comparison of radial growth with climatic parameters (Figure 58) made it possible to identify potential causes of the growth decline observed in oak. Indeed, two consecutive severe droughts occurred in 1994 and 1995 (as revealed by high values of soil water deficit in Figure 58d) and might have induced the phase of decline observed in oak. After 1995, the year of liming treatment, growth of oak continued to decrease with time. This decline was significantly attenuated in limed plots, but only from 2001 to 2005 (red stars at the bottom of Figure 57a).

Despite the two severe droughts in 1994/1995, radial growth of beech was maintained at a high rate until 2002 (Figure 57a). After 2002, a period of growth decline began with a severe drought occurring in 2003 and was emphasized by a second drought occurring in 2006 (see Figure 58d). In contrast to oak, liming did not reduce growth decline in beech.

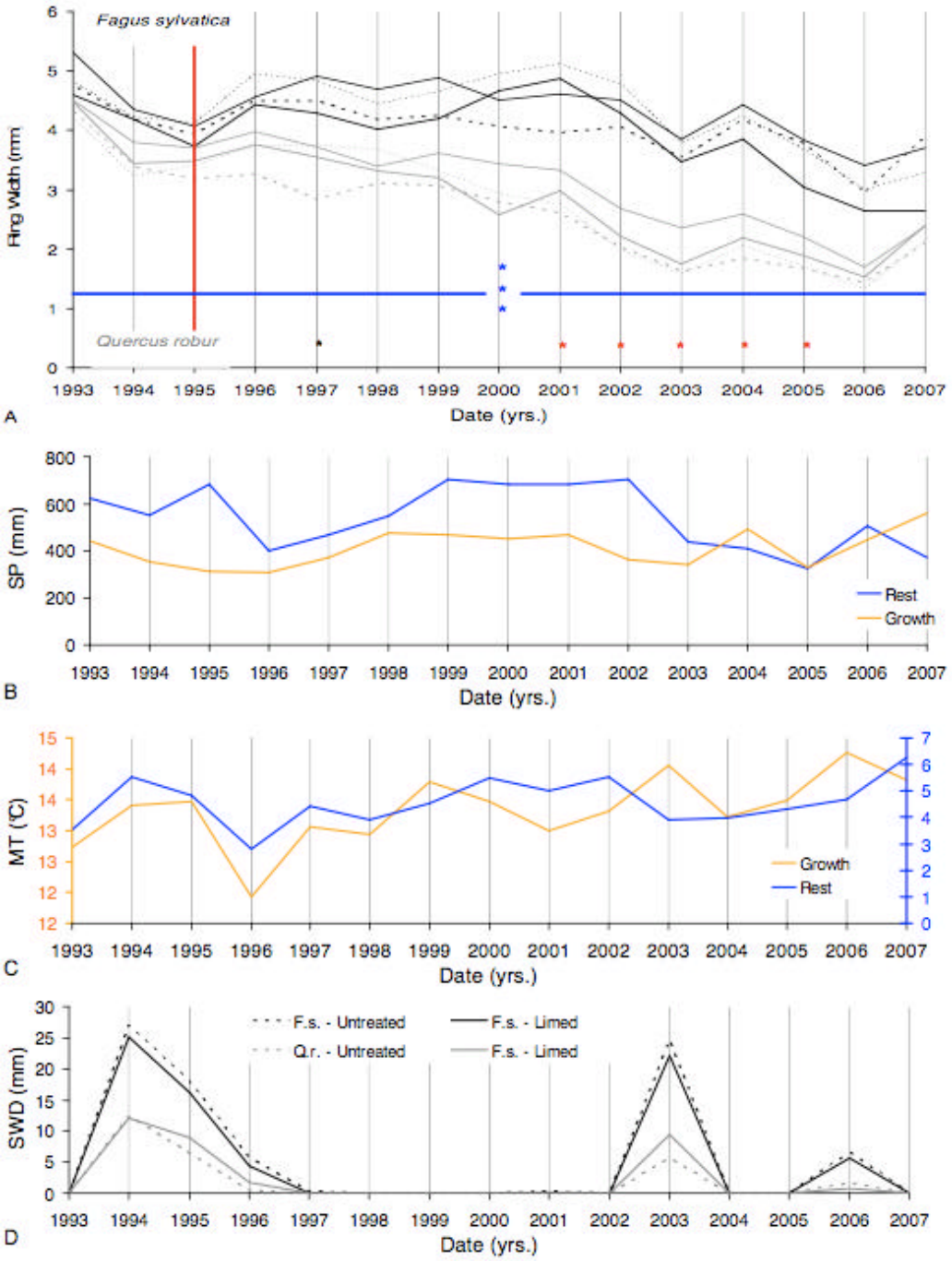


Figure 58: Times series of (A) growth index of Fagus sylvatica (black lines) and Quercus robur (grey lines). – red stars indicate significant differences in growth between limed and untreated trees, blue stars indicate significant differences in growth between Fagus sylvatica and Quercus robur– (B) Sum of precipitation (SP) (C) and mean temperature (MT) calculated both for the growing period (from May to October) and for the rest period (from previous November to current April) and (D) soil water deficit (SWD) for Fagus sylvatica* and Querus robur *in Les Potées, from 1993 to 2007.

Carbon Balance in the trees

Carbohydrate Concentrations

Total non structural carbohydrate (TNC) concentrations were determined enzymatically and concerned a total of 720 wood samples (15 trees per plot, 8 plots, 3 organs per tree and 2 sample dates). TNC concentrations averaged for each plot are displayed in Figure 59 for beech and Figure 60 for sessile oak.

Regardless of treatment, concentrations were classically highest in shoots and lowest in stems for both species. Concentrations in coarse roots were intermediate between shoot and stem concentrations (Table 28 for statistics and Figure 59 and Figure 60 for trends). Differences in TNC concentrations between dates were contrasted between organs and species. From May to October, TNC concentrations in beech shoots did not change significantly, whereas it increased significantly in stems and decreased significantly in coarse roots. For pedunculate oak, concentration increased significantly from May to October whatever the organ considered.

Table 28: Analysis of variance of TNC concentrations as a function of sampling dates and tree organs for Fagus sylvatica and Quercus robur. Abbreviations: df=Degree of Freedom, F= Fisher test value, p=probability.

Species		*Fagus sylvatica*			*Quercus robur*		
Effect	Variable	*df*	*F*	*p*	*df*	*F*	*p*
Organ	TNC in May	39	292.07	<0.0001	39	64.88	<0.0001
	TNC in October	59	484.23	<0.0001	39	273.28	<0.0001
Date	TNC in shoot	39	2.05	0.1605	39	961.93	<0.0001
	TNC in stem	39	6.21	0.0171	39	283.48	<0.0001
	TNC in roots	39	14.23	0.0007	39	37.85	<0.0001

For both species, liming did not have any significant effect on carbohydrate concentrations for any combination of date and organ (see Figure 59 for beech and Figure 60 for oak). Besides, TNC concentrations of oak were significantly higher in trees belonging to block 1 than those belonging to block 2 for shoots ($F=292.07$, $p<0.0001$) and coarse roots ($F=6.27$, $p=0.0221$).

Fagus sylvatica

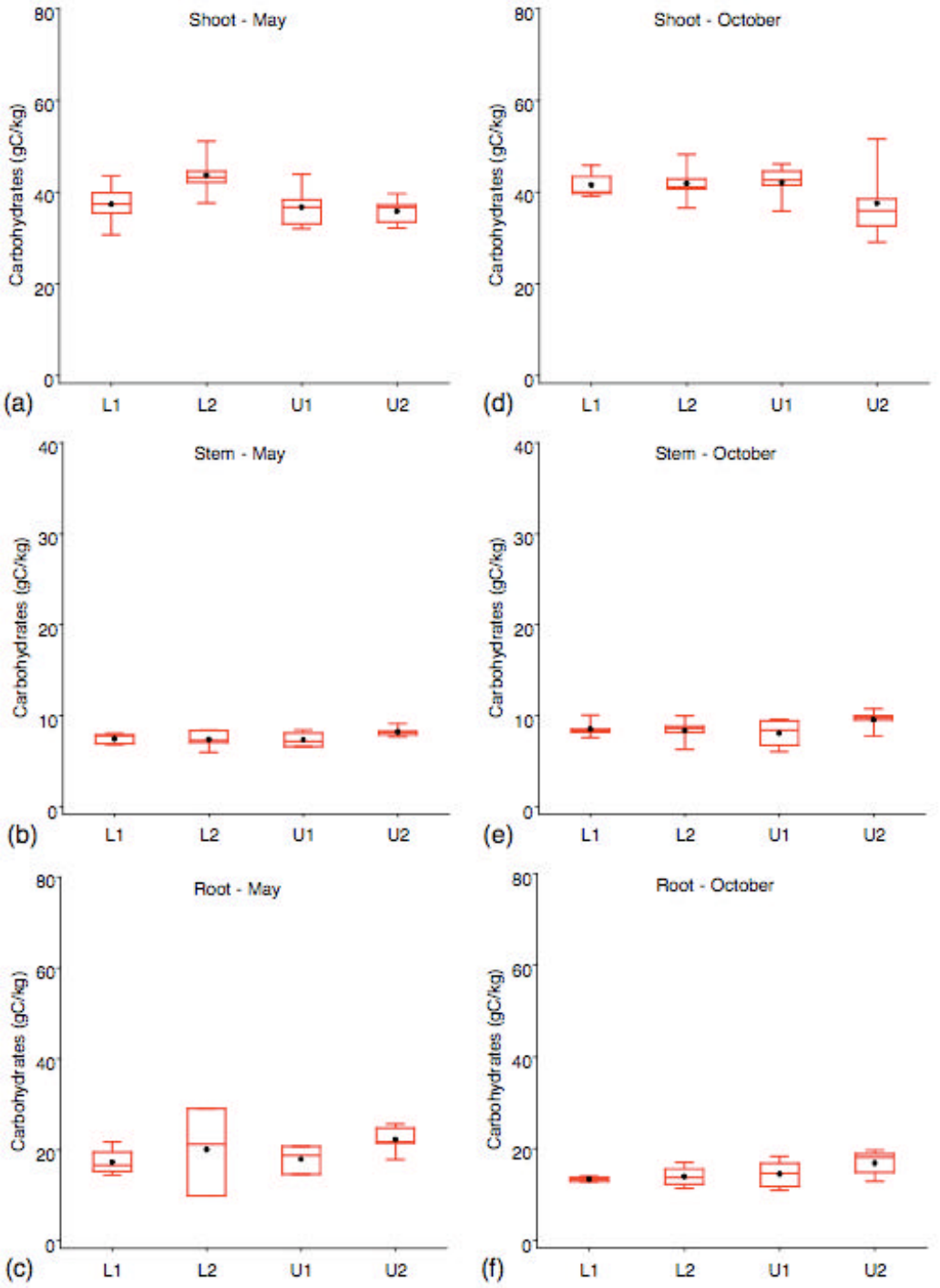


Figure 59: Les Potées - Fagus sylvatica: Total non structural carbohydrate concentrations for limed (left) and untreated (right) trees in shoot (panels a and d), in stem (panels b and e) and coarse roots (panels c and f), in May (panels a, b and c) and October (panels d, e, and f).. Letters indicate significant differences between tree groups (P < 0.05, n = 10, Student t-test). The length of boxes represents the interquartile range; the dot represents the mean; the horizontal line in the boxes represents the median; the vertical lines issuing from the boxes extend to the minimum and maximum values of the analysis variables.

Quercus robur

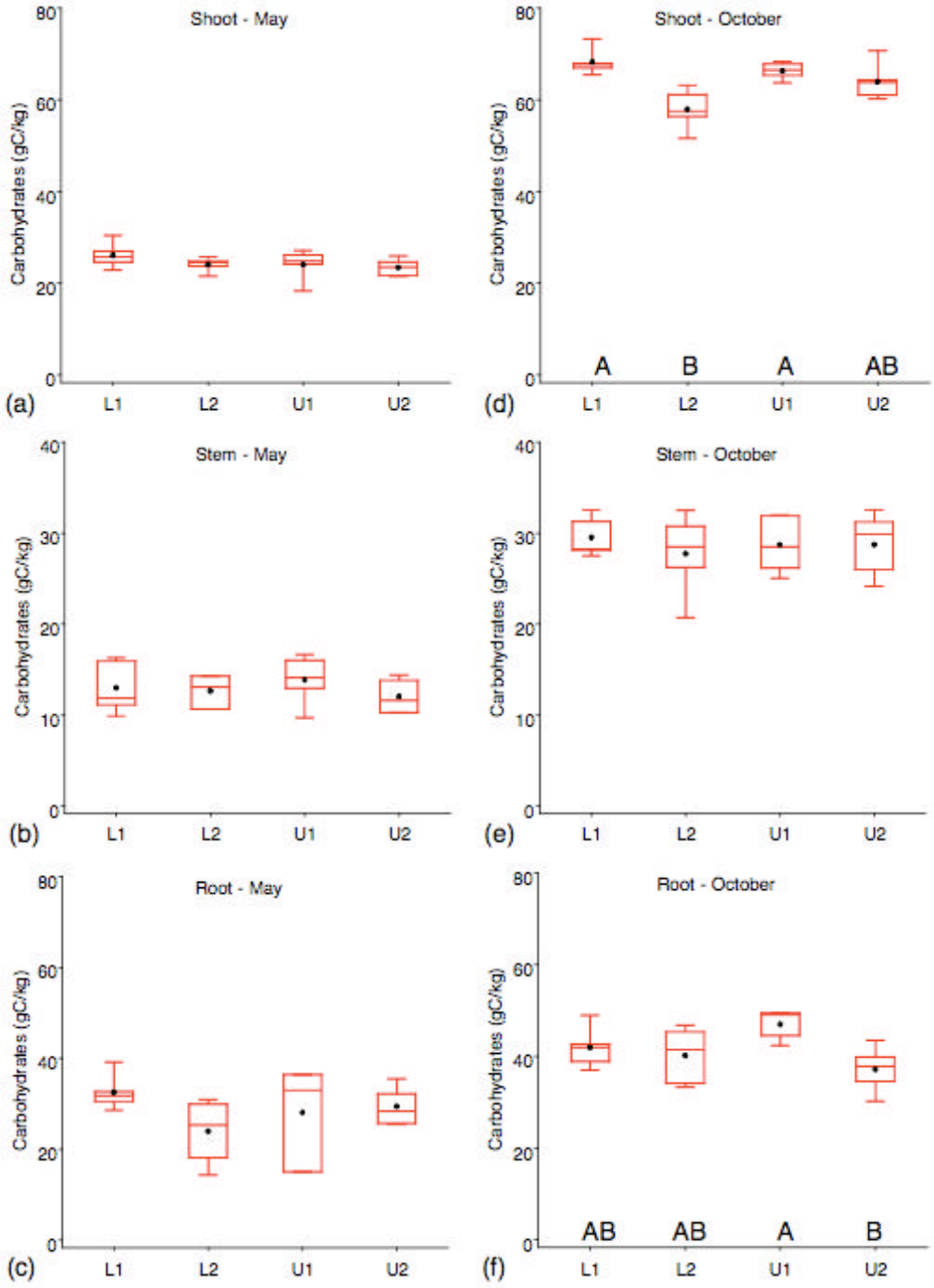


Figure 60: Les Potées – Quercus robur: Total non structural carbohydrate concentrations for limed (L1 and L2) and untreated (U1 and U2) trees in shoot (panels A and D), in stem (panels B and E) and coarse roots (panels C and F), in May (panels A, B and C) and October (panels D, E, and F). Letters indicate significant differences between tree groups (P < 0.05, n = 10, Student t-test). The length of boxes represents the interquartile range; the dot represents the mean; the horizontal line in the boxes represents the median; the vertical lines issuing from the boxes extend to the minimum and maximum values of the analysis variables.

Biomass and storage increment during the 2007growing season

Biomass increments were estimated from circumference and tree ring measurements of each of the 120 selected trees (15 trees/plot and 8 plots). Storage increments were deduced from seasonal differences between measured TNC concentrations, estimated biomass and biomass increment.

Treatment had no impact on tree biomass (Figure 61a, Figure 62a), biomass increment (Figure 61b, Figure 62b) and storage increment (Figure 61c, Figure 62c) during the 2007growing season, except for carbon storage increment in beech ($F=13.37$, $p=0.0006$). As at Humont, the increment of TNC compounds during the 2007 season was lower in limed trees than in untreated trees for beech. Furthermore, the storage balance in beech coarse roots was negative in both limed and untreated trees (Figure 61c).

As a result of a more precocious decline in growth (Figure 57a), tree biomass of oak (51.0 kgC) was significantly lower than that of beech (74.8 kgC) ($F=3597$, $p<0.0001$). Similarly, biomass increment of oak trees was twice (2.9 kgC/yr.) that of beech trees (5.4 kgC/yr.) ($F=37.74$, $p<0.0001$). However, storage increment was higher in oak (1.7 kgC/yr.) than in beech (0.06 kgC/yr.) ($F=477.02$, $p<0.0001$).

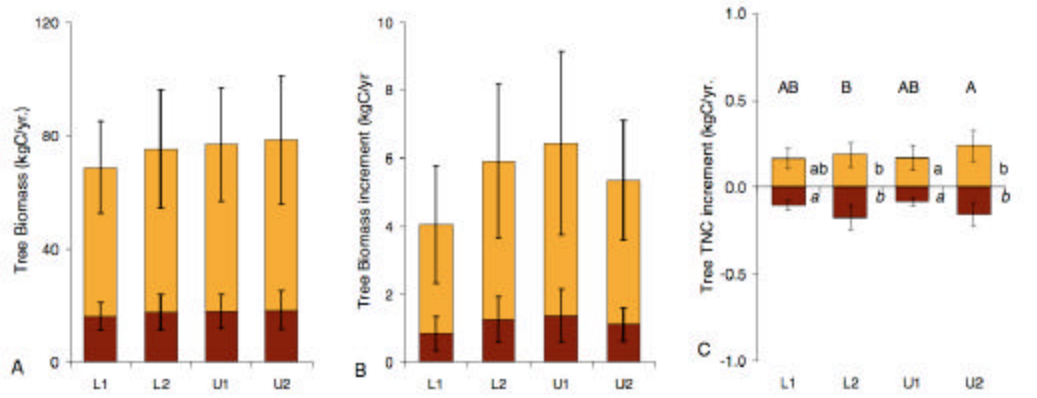


Figure 61: Les Potées* – Fagus sylvatica.** ***(a) tree biomass, (b) tree biomass increment, and (c) tree storage increment and for limed (L1 and L2) and untreated (U1 and U2) beeches (N=15 trees per group). Carbon increments were computed for the 2007 growing season. Letters indicate significant differences between tree groups (P < 0.05, n = 10, Student t-test). Vertical bars represent standard errors.

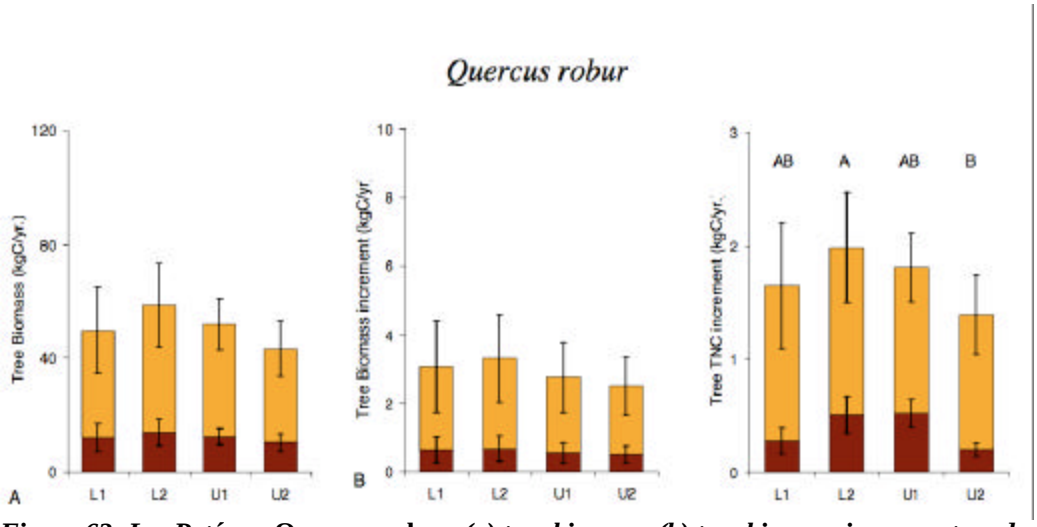


Figure 62: Les Potées* – Quercus robur.** ***(a) tree biomass, (b) tree biomass increment, and (c) tree storage increment and for limed (L1 and L2) and untreated (U1 and U2) pedunculate oaks (N=15 trees per group). Carbon increments were computed for the 2007 growing season. Letters indicate significant differences between tree groups (P < 0.05, n = 10, Student t-test). Vertical bars represent standard errors.

DISCUSSION

The discussion will begin with a brief reiteration of the key points of the two liming experiments presently studied.

After prospecting and visiting the existing network of liming experiments on oak and beech in France, Les Potées (Les Ardennes) and Humont (Vosges Mountains) were selected. Humont site was set up to demonstrate the effects of liming as a potential forestry practice aiming to recover forest decline in the Vosges Mountains. In contrast, Les Potées site was set up to conduct scientific research on the effects of liming on the forest ecosystems functions. Furthermore, both sites presented the same level of mineral fertility. Soil depth and extractable water content were lower in the Humont site compared to Les Potées site. Finally, beech stands in Humont were adult (72 years old) and naturally regenerated whereas stands in Les Potées were young (23 years old) and planted. The liming treatment had been applied 12 years before in Les Potées and 15 years before in Humont.

LIMING EFFECTS ON SOIL AND FOLIAR COMPOSITION

More than ten years after treatment, liming effects on soil structure, litter degradation, soil and foliar composition were still visible in both studied sites. These effects are summarized in Table 29: Summary of the effects of the liming on humus, soil structure, soil exchangeable element composition, foliar mineral composition and foliar morphology for both of the experimental sites studied (Humont and Les Potées). Green arrows reveal positive effects for qualitative variables (eg. humus) and increases in quantitative variables (eg. concentrations). Red arrows reveal negative effects for qualitative variables and decreases in quantitative variables. Na=not assessed. Significance thresholds are presented for foliar composition and morphology: $p<0.05$,* - $p<0.01$, ** - $p<0.001$, ***.. In both sites, liming improved litter decomposition and soil structure, reduced soil acidity and improved base saturation rate in the uppermost soil layers. In Humont, improvement of beech litter decomposition was stimulated by increasing earthworm abundance (Kreutzer 1995). Increased base saturation rate was mainly linked to the increase of calcium and magnesium contents whereas effects of liming on phosphorus, potassium and manganese were more variable between sites. Decreased soil acidity was also related to a decrease in aluminium content. Element composition of leaves was also modified after liming with an increase in calcium and magnesium and a decrease in carbon and manganese. These effects of liming on soil and leaves are widely documented by past studies (e.g. Ranger et al. 1994, Bonneau 1995, Belkacem and Nys, 1997, Bakker et al.

2000). These results, will not be further detailed here, but enabled us to testify that the effect of liming was still obvious in the sites studied.

Table 29: Summary of the effects of the liming on humus, soil structure, soil exchangeable element composition, foliar mineral composition and foliar morphology for both of the experimental sites studied (Humont and Les Potées). Green arrows reveal positive effects for qualitative variables (eg. humus) and increases in quantitative variables (eg. concentrations). Red arrows reveal negative effects for qualitative variables and decreases in quantitative variables. Na=not assessed. Significance thresholds are presented for foliar composition and morphology: p<0.05,* - p<0.01, ** - p<0.001, ***.

Analyses	**Soil analyses**			**Leaf analyses**					
Site	**Humont**	**Les Potées**		**Humont**		**Les Potées**			
Species	***Fagus sylvatica***	***Fagus sylvatica***	***Quercus robur***	***Fagus sylvatica***		***Fagus sylvatica***		***Quercus robur***	
Parameters				***p***	**trend**	***p***	**trend**	***p***	**trend**
Humus	?		?						
Soil structure	?	?	?						
BS	?	?	?						
pH	?	?	?						
Carbon	?	?		***	?	***	?		
Nitrogen	?	?				*	?		
Calcium	?	?	?	***	?	***	?	***	?
Magnesium	?	?	?	***	?	***	?	**	?
Phosphorus	?	na	na			***	?		
Potassium	?		?	***	?	**	?		
Manganese	?		?	***	?	***	?	***	?
Aluminium	?		?	*	?	***	?		
Chlorophyll									
LMA				*	?	**	?		
Leaf mass						*	?		
Leaf area				***	?				

LIMING EFFECTS ON CARBON ALLOCATION AND ABOVE- AND BELOW- GROUND DISTRIBUTION

The order of magnitude of fine root densities (FRD) measured in the present study was similar to those measured in previous studies concerning beech and pedunculate oak (Bréda et al. 1995, Peiffer 2005). For both sites and both species, FRD was found to be slightly higher in the uppermost soil layers of the limed plots compared to those measured in control plots. In both experiments, we saw that this increase in FRD was not related to differences in stand densities. Considering the soil homogeneity between treated and control plots within both sites, it was thus possible to attribute these differences in fine root densities to liming. The positive effect of liming on fine root density was not observed systematically in previous studies. Independently, Hemisaari et al. (1999) and Borken et al. (2007) observed a decrease in fine-root biomass and density in the richest soils of Norway spruce. In contrast, Bakker et al. (1998) observed a stimulation of fine root production in sessile oak. From the carbon balance point of view, we then had to consider an increase of carbon distribution to the belowground compartment in the liming treatment.

Furthermore, retrospective analysis of radial growth revealed that liming had stimulated radial growth of adult beech (Humont) and young pedunculate oak (Les Potées) over several years. For both species, the response of radial growth to liming lagged several years behind the treatment (three years for adult beech trees and six years for young oaks). This lag may be attributed to the time needed for soil incorporation and mineralization improvement. However, effects of liming on radial growth were not strong enough to induce an increase of overall tree biomass in 2007: in both sites and for both species, tree biomass was not significantly different between the limed and control plots. Similarly, no effect of treatment was detected on tree biomass increment performed during the 2007 growing season which was a favourable season for growth, being warm and free from drought. Liming had no effect on radial growth of young beech trees (Les Potées).

LIMING EFFECTS ON CARBON ALLOCATION TO STORAGE

Carbohydrate concentration in 2007 increased in limed adult beeches compared to the control (Humont) whereas it remained unchanged in young beeches and pedunculate oaks (Les Potées).

Finally, liming induced a stimulation of carbohydrate consumption and/or a decrease in carbon storage in roots of adult beeches (Humont), resulting in a decrease in carbohydrate amounts in roots during the 2007 growing season.

Les Potées site provided the opportunity to compare beech and pedunculate oak in pure stands, under identical growing conditions (soil and climate). Comparison of vertical root distribution revealed that pedunculate oak developed a more superficial and less dense root system than beech. For both species, root development was limited by a clay-enriched horizon. However, in contrast to pedunculate oak, roots of beech seemed to penetrate this physical barrier to develop a root system deeper in the profile. The capacity of beech to develop a deep root system has already been described by Curt et al. (2003) in a mixed stand. So, beech presented a higher capacity to develop a deep and dense root system than pedunculate oak in the studied soil which had good vertical drainage. A contrasting rooting pattern was reported where temporary excesses of water occurred (Zapater et al., 2008). This result is in accordance with observations made by Büttner et al. (1994) and Leuschner et al. (2001) comparing root systems of beech and sessile oak in mixed and pure stands.

CONTRASTING RESPONSES OF OAK AND BEECH TO LIMING

Retrospective growth analysis revealed that both species presented growth decline. We also demonstrated that these declines cannot be explained by age-related growth trends. Growth decline of beech began with the severe drought occurring in 2003, whereas growth decline of oak began ten years earlier, with two successive severe droughts in 1994 and 1995. Despite obvious growth decline, young beeches and oaks did not developed crown decay, like the declining adult beech trees at Humont. The lowest LAI we measured in 2007 in oak stands, as compared to beech, could be associated with its low growth rate. It may result from an adjustment of the oak canopy to the recent severe drought. It has been reported that the reduction of LAI due to drought in oak stands lasts for longer (frequently 4 years for pedunculate oak) than in beech stands, which recover within 2 years. Furthermore, the low LAI in oak was associated with a significant cover of *Rubus fruticosus* L., while in beech the understorey vegetation was limited to monocotyledon species receiving low radiation and having a lower water uptake. Assuming this hypothesis to be correct, higher growth decline observed in oak, compared to beech in Les Potées, might be related to the higher below-ground competition (especially during drought) with the deep rooted and high water consuming bramble (Vincke et al., 2005).

Finally, the high investment of beech to root development might partially explain the decrease in root storage compounds in coarse roots observed in Humont and in Les Potées during the 2007growing season. Indeed, Leuschner et al. (2001) observed that drought stimulated fine root growth of beech, probably to compensate for the fine root biomass losses induced by increased fine root mortality. In contrast, drought did not have a significant impact on sessile oak fine roots stock. Thus, drought occurring in 2006 in both studied sites may have damaged fine roots stock of beech and induced an increase of carbohydrate consumption during the 2007growth season in order to recover a sustainable fine roots biomass. If the requirements of carbohydrates for fine roots pool recovery were higher than the amount of carbohydrates allocated to roots for storage, this might have cause the observed decrease in carbohydrate amounts in roots.

SHOULD BEECH DECLINE BE ATTRIBUTED TO CARBON STORAGE LIMITATION?

A comparison of carbon functioning in healthy and declining beech was conducted in the Humont site. This part of our study is original since few cases of beech decline have been investigated from the carbon allocation point of view. The results concerning the mineral composition of leaves imply that decline was not related to mineral nutrition deficiency. Furthermore, retrospective analyse of radial growth demonstrates that crown decline was accompanied by an obvious reduction of radial growth. It also enabled the identification of the drought occurring in 2003 as the starting point of growth decline, visually assessed by crown condition damage in 2006/2007. Finally, we observed that TNC concentrations in declining trees were not significantly different from those of healthy trees. So decline in beeches induces a sharp reduction of radial growth but no modification in TNC concentration and TNC quantities. In conclusion, (1) beech decline was drought induced and (2) beech behaviour to face water shortage was to reduce growth in order to maintain enough carbon storage compounds and maintain its physiological integrity. Indeed, we have seen in Chapter I that compared with oak, the recovery of total hydraulic conductance after winter damage is less dependent on radial growth in beech. Thus, to a certain extent, growth in beech could be an "adjustment variable" allowing trees to increase storage production and mobilisation during climatic constraints.

However, considering the experimental design of the Humont site and the lack of replicates, an unequivocal conclusion cannot be drawn about the impact of liming on declining trees. Furthermore, forthcoming results in dendrochemistry conducted on the trees studied in Humont would enable us to improve our understanding concerning the mineral elements involved in the better physiological functioning of limed trees.

Conclusion (Français)

Dans le but de progresser dans la compréhension des déterminismes de l'allocation du carbone chez les feuillus, le travail exposé ici a consisté à étudier les effets du vieillissement et de la fertilité minérale du sol sur la répartition du carbone assimilé par la photosynthèse entre croissance, stockage et reproduction chez trois espèces contrastées : *Quercus petraea*, *Quercus robur* and *Fagus sylvatica.*

Les effets du vieillissement ont été étudiés à l'échelle de la révolution forestière au travers de deux chronoséquences monospécifiques. Deux dispositifs d'amendements ont été utilisés pour étudier les effets de la fertilité minérale du sol sur l'allocation du carbone dans l'arbre dans des situations contrastées.

Comme Barbaroux (2002) l'a montré à l'échelle de la saison de végétation, nous avons mis en évidence des différences importantes d'allocation du carbone à l'échelle de la révolution forestière chez le chêne et le hêtre.

Au cours du vieillissement du hêtre, l'allocation de carbone à la croissance végétative, majoritaire pendant la phase juvénile de développement, diminue progressivement au profit du stockage de composés de réserve et de la croissance reproductive. En revanche, l'allocation entre croissance végétative, stockage et respiration demeure constante au cours du développement du chêne sessile. Par ailleurs, l'étude croisée des enseignements de la littérature et des résultats expérimentaux présentés dans ce travail suggèrent que l'importance de l'allocation à la reproduction est plus faible chez le chêne que chez le hêtre (Garbaye et Leroy 1974, Aussenac 1975, Oswald 1984, Overgaard et al. 2007).

Nous avons vu que ces différences fondamentales de gestion de la ressource en carbone entre chêne et hêtre résultent notamment des différences interspécifiques du rôle fonctionnel de la croissance radiale dans la survie de l'arbre. Chez le chêne, la sensibilité à l'embolie hivernale, inhérentes aux caractéristiques anatomiques du bois (dimension des gros vaisseaux de printemps), nécessitent la réalisation d'une croissance printanière hétérotrophe pour le carbone. Dès lors, la survie de l'arbre repose à la fois sur la réalisation d'une croissance minimum et sur la présence d'une quantité minimum de réserves carbonées nécessaires au financement de cette croissance. La sensibilité du hêtre à l'embolie hivernale est plus faible que celle du chêne sessile en raison de son anatomie de bois à pore diffus et à vaisseaux de petit diamètre (Cochard et al., 1992, Lemoine et al., 2002). Par conséquent, le rôle de la croissance radiale dans la restauration de la conductance hydraulique de l'arbre au printemps est moins primordiale que pour le chêne.

En revanche, les résultats de la littérature et de notre analyse dendroclimatique de la croissance radiale s'accordent à montrer une forte sensibilité du hêtre aux sécheresses estivales, au niveau du fonctionnement racinaire (Leuschner et al. 2001), de la croissance radiale (Lebourgeois et al., 2005, ICP Forest, 2006), du fonctionnement hydraulique (Backes et al. 2000, Zapater et al. *in prep*) et de la photosynthèse et des réserves (Backes et al. 2000, Leuschner et al. 2001, Bréda et al. 2006). Or, le rétablissement d'un fonctionnement physiologique performant après un évènement de sécheresse dépend notamment des ressources disponibles (réserves) dans l'arbre. De plus, l'analyse de la croissance radiale a également permis de montrer que contrairement au chêne sessile, la sensibilité de la croissance du hêtre aux contraintes environnementales augmente au cours du vieillissement. On peut dès lors interpréter l'augmentation de l'allocation aux réserves observée chez les hêtres vieillissant, comme une adaptation du fonctionnement carboné visant à garantir l'intégrité physiologique de l'arbre malgré l'augmentation des contraintes climatiques.
Par ailleurs, en période de fructification massive, une partie importante des réserves azotées peut être allouée aux organes reproductifs chez le hêtre (Kawada and Maruyama 1986, Yasumura et al. 2006). Ainsi, au cours du vieillissement et avec l'augmentation subséquente de l'intensité des fructifications, les ressources en azotes peuvent devenir limitantes pour d'autres processus comme la photosynthèse (Evans 1989) et le débourrement (Millard et al. 2006, Han et al. 2008). Par ailleurs, des travaux antérieurs ont montré que le ratio entre protéines et acides aminés, deux constituants important des réserves azotées, changeait avec l'âge (Valenzuela Nunes 2008).
Il semble donc que de nouveaux équilibres entre fonctionnements carboné, hydrique et azoté soient établis au cours du vieillissement : les contraintes du transport de la sève augmente avec l'augmentation de la hauteur de l'arbre, l'allocation du carbone change avec la diminution de la productivité et la demande en ressource azotée augmente afin de satisfaire la production de graines.

L'hypothèse du rôle dominant des réserves par rapport à la croissance dans le fonctionnement physiologique du hêtre est renforcée par les résultats issus de la comparaison de l'allocation de carbone des hêtres sains et dépérissants (dispositif de Humont). En condition de dépérissement, l'allocation du carbone à la croissance chute drastiquement au profit de l'allocation aux réserves, permettant aux arbres dépérissants de maintenir des concentrations en composés de réserves glucidiques identiques à celles des arbres sains. Par ailleurs, l'amélioration du niveau de fertilité de la station (amendement) engendre une augmentation de la croissance et des concentrations en composés de réserves. Cependant, alors que l'effet bénéfique de l'amendement sur la croissance disparaît après quelques années, l'augmentation des concentrations en composés de réserves carbonées est observée 15 ans après

l'amendement. Ces deux résultats confirment l'importance du niveau de réserve dans le maintien de l'intégrité physiologique des hêtres adultes. Ainsi, la croissance chez le hêtre peut être considérée comme une variable d'ajustement permettant aux arbres d'augmenter la production de composés de réserves en période de perturbation.
Cependant, le dispositif expérimental du site de Humont et le manque de répétition du traitement ne permet pas de tracer des conclusions univoques sur l'effet de l'amendement dans les peuplements dépérissant. Ces résultats devront être confirmé par des investigations supplémentaires.

L'amendement réalisé sur des jeunes peuplements (dispositif des Potées) n'a en revanche révélé aucun effet sur l'allocation du carbone entre croissance et réserves chez le chêne pédonculé comme chez le hêtre. On peut supposer que dans des stations de fertilité modérée,et de bonne alimentation en eau, le niveau de performance du fonctionnement physiologique des arbres au début de leur développement est relativement indépendant des conditions extérieures de croissance. En effet, en comparaison des arbres adultes, nous avons pu montrer que les arbres jeunes présentent à la fois des niveaux des réserves et de croissance plus élevées.

En résumé, nous avons confirmé que le hêtre présente des concentrations en composé de réserve plus faible que les chênes, quelque soit l'organe ou la date considéré. Cependant, notre étude de la réponse de l'allocation du carbone aux perturbations externes et intrinsèques a révélé que pour malgré cette différence, le stock de composés de réserves carbonées chez le hêtre apparaît comme le paramètre principal du maintien physiologique de l'arbre et garantit la restauration rapide de l'intégrité physiologique de l'arbres après perturbation (Badeau and Bréda, 1997, Le Dantec et al., 2000). Cette stratégie pourrait être impliquée dans le bon état sanitaire de la hêtraie en France et en Europe (ICP Forest, 2007, Favre et Renaud, 2007).

Pour les chênes sessile et pédonculé en revanche, la croissance semble avoir un rôle aussi important que le stockage des réserves dans la survie de l'arbre. Cette contrainte supplémentaire a des répercutions importantes dans la capacité d'adaptation des chênes aux variations intrinsèques et externes des conditions de développement. Lors des crises de croissance, le système d'allocation des chênes semble donc moins flexible que celui du hêtre. Ceci se traduit par une plus forte vulnérabilité aux dépérissements pluriannuels, aboutissant souvent à des mortalités chez les individus les plus âgés (Bréda et Badeau, 2008).

Les cas de dépérissement plus répandu chez les chênes que chez le hêtre peuvent également être liés à la plus large communauté d'insectes ravageurs associée aux chênes. Selon le

Département de Santé des Forêts 97 espèces d'insecte sont associées aux chênes et 11 d'entres elles ont été observées fréquemment entre 1989 et 2002, (voir Nageleisen 2005 pour les détails concernant l'évaluation de la taille des populations) alors que seulement 43 espèces d'insectes sont associées au hêtre et seules quatre d'entres elles ont été observées fréquemment entre 1989 et 2002.

Nous n'avons pas eu l'opportunité dans cette étude de tester l'effet de la fertilité minérale des sols sur l'allocation du carbone chez les chênes adultes. Quelques essais d'amendement ont cependant déjà été réalisés dans des peuplements adultes dépérissant comme à Chimay, Belgique (Anonymous 1996). Cet essai avait pour objectif de tester l'effet croisé de l'éclaircie et de l'amendement sur l'état des houppiers dans un peuplement dépérissant de chênes pédonculés âgés de 100 ans. Les résultats du suivi de l'état des houppiers a permis de montrer que l'éclaircie accompagnée ou non de l'amendement permettant la restauration efficace des houppiers. En revanche l'amendement n'avait pas d'effet significatif sur l'état des houppiers. Dans ce cas, l'alimentation en eau s'est avérée un facteur plus déterminant de l'état de santé des arbres que la nutrition minérale. Cependant, cette étude mériterait d'être élargie à d'autres sites de dépérissement présentant des caractéristiques pédoclimatiques différentes. Ainsi, il serait intéressant d'étudier l'effet de l'amendement sur l'équilibre croissance/stockage dans des chênaies concernées par le récent amendement à large échelle pratiqué dans le massif vosgiens par l'INRA et l'ONF et sur des sites anciens d'amendement.

Les résultats de cette étude originale des facteurs intrinsèques (âge) et externes (fertilité minérale) de variation de l'allocation du carbone chez le chêne et le hêtre, enrichie des enseignements de la littérature, ont permis de confirmer deux modèles de fonctionnement carboné contrastés. Cependant, rappelons que les résultats analytiques d'allocation exposés ici ne concernent que deux saisons de végétation. Or l'impact des variations interannuelles (climatiques, biotiques ou sylvicoles) sur l'allocation du carbone sont aujourd'hui très peu documenté. Entre autres, le rôle potentiel des réserves dans les arrières effets de perturbations environnementales sur la croissance reste encore à être documenté (Rochas et al. 2006). De même, l'importance de la respiration dans la diminution de la productivité des peuplements liée à l'âge fait encore l'objet de débats. En effet, les mesures de respiration sont rares et concernent essentiellement des arbres jeunes (Ceschia 2001). De plus la proportion de cellules vivantes dans l'aubier, déterminante de l'importance de la respiration, au cours du vieillissement reste également méconnue (Ryan and Waring 1992, Ryan et al. 1994).

Enfin, cette étude a permis également de montrer l'importance des racines dans la détermination de l'allocation du carbone dans l'arbre. Or les processus gouvernant l'activité

physiologique des racines reste très mal connue à ce jour. Pour les chênes comme pour le hêtre, le suivi par endoscopie de la croissance, la phénologie et le turnover racinaire a été récemment initié en France. Ces observations devraient permettre d'avancer sur le découplage des facteurs environnementaux et intrinsèques contrôlant l'allocation du carbone dans les racines. Cependant, plusieurs années d'observations seront nécessaires pour différencier les effets directs et les arrières effets de ces contraintes.

Enfin, parce que l'origine et la vocation de ce travail étaient d'apporter des éléments de réponse à des questions sylvicoles, l'étude du vieillissement a été limitée à la durée de la révolution forestière. Cependant, il serait intéressant d'étendre cette étude à l'analyse des peuplements à la limite de longévité de chacune des deux espèces : 150-300 ans hêtre, 500-100 chênes (Rameau et al. 1989). En effet, les processus de sénescence peuvent être en partie différents de ceux observés dans cette étude (Prescott et al. 1989).

Conclusion (English)

In order to increase our understanding of carbon allocation in broadleaved species, our research consisted of studying the effects of ageing and soil mineral fertility on the carbon allocation between growth, storage and reproduction. This work, involving ecology, wood anatomy and growth pattern, was carried out on three contrasting tree species: *Quercus petraea*, *Quercus robur* and *Fagus sylvatica*. Ageing was studied over a forest succession using a chronosequences approach. Two liming experiments were investigated in order to study the variation of carbon allocation with soil mineral fertility in contrasting situations.

For both species, the well-known productivity decline with age was obvious. The productivity decline in beech was followed by substantial changes in carbon allocation, with a continuous decrease of carbon allocation to growth, to the benefit of reproduction and storage functions. Conversely, carbon allocation in oak remained stable for the different age classes. Furthermore, the experimental data presented here, coupled with the literature review suggest that carbon allocation to the reproduction function remains lower for oak, compared with beech (Garbaye et Leroy 1974, Aussenac 1975, Oswald 1984, Overgaard et al. 2007).

These fundamental differences in carbon allocation between oak and beech are discussed with reference to differences in the functional role of radial growth in tree survival.
Oaks, as ring porous species, present high vulnerability to freeze-induced embolism, inherent in their wood anatomy (large earlywood vessels). Consequently, the achievement of heterotrophic early-spring growth is crucial to restore hydraulic conductance from the roots to foliar buds. Thus, tree survival relies on the achievement of a minimum amount of precocious growth and a minimum quantity of storage compounds to support this heterotrophic growth. The allocation scheme in oak is thus determined by overcoming these two constraints.
In contrast, as a diffuse porous species with smaller xylem vessels, beech presents lower vulnerability to freeze-induced embolism (Cochard et al. 1992, Lemoine et al. 1999). Consequently, the role of radial growth in the recovery of hydraulic conductance in spring is less primordial than for oaks. Besides, the results of dendroclimatic analysis presented here and recent advances found in the literature review revealed that beech is highly vulnerable to summer drought. This vulnerability concerns fine root functioning (Leuschner et al. 2001), radial growth (this study, Lebourgeois et al., 2005, ICP Forest, 2006), hydraulic functioning (Backes et al. 2000, Zapater et al. *in prep*), photosynthesis and amount of storage (Backes et al. 2000, Leuschner et al. 2001, Bréda et al. 2006). Furthermore, we observed that the sensitivity of beech radial growth to environmental constraints increases with age. Therefore, assuming that physiological recovery after crises depends on the amount of available resources in the tree (i.e. storage compounds), the age-related increase of carbon allocation to the storage function could be understood as a physiological response of trees facing an

increase in environmental constraints.

Furthermore, large proportions of the nitrogen in beech trees can be allocated to reproductive organs in masting events (Kawada and Maruyama 1986, Yasumura et al. 2006). Therefore, with increasing age and mast intensity, the nitrogen resources may become more limiting for other important processes, notably photosynthesis (Evans 1989) and budburst (Millard et al. 2006, Han et al. 2008). Furthermore, previous results have demonstrated that the ratio between protein and amino acid, two important storage compounds of nitrogen resources, may change with age (Valenzuela Nunes et al. 2008.).
This suggests that a new equilibrium between water, carbon and nitrogen processes is necessary with ageing: water transport constraints increase with increasing tree height, the carbon balance changes with productivity decline, and nitrogen requirements change to satisfy increasing seed production.

The observations made in the liming experiment in declining beech stands further illustrate the decisive role of carbon storage in the physiological functioning of trees. In spite of unfavourable climatic conditions inducing a slump in growth, declining beeches maintained a level of storage compounds comparable to healthy trees. In another hand, we showed that the increase of mineral soil fertility with liming induced an increase of growth and storage compounds. Furthermore, even if the positive impact of liming on radial growth disappeared after a few years, carbohydrate contents in wood were higher than the control when we measured them 15 years after treatment.
Thus, to a certain extent, growth in beech could be an "adjustment variable" allowing trees to increase storage production and mobilisation during perturbations.
Nevertheless, considering the experimental design of the Humont site and the lack of replicates, unequivocal conclusions cannot be made about the impact of liming on declining trees and further investigations are needed.

In the liming experiment carried out in young stands at Les Potées site, measurements made during the 2007 growing season, did not reveal any variations of carbon allocation, eleven years after treatment. Furthermore, retrospective analyses of radial growth did not reveal any variations of growth in the years following the treatment. Therefore, it is assumed that under moderate conditions of mineral fertility and good water supply, the physiological efficiency of young trees is less sensitive to environmental conditions than that of older trees.

In conclusion, we confirm that beech trees exhibit lower total non structural carbohydrate concentrations and content compared with oak, whatever the date and tree compartment

considered. However, our study of the response of carbon allocation to intrinsic and environmental perturbation revealed that the amount of reserve compounds in trees seems to be the key parameter that determines physiological efficiency in beech. The strategy to promote storage before growth may ensure the supply of carbon resources during environment perturbation for a rapid recovery (Badeau and Bréda, 1997, Le Dantec et al., 2000). This mechanism could be involved in the low rate of decline observed in beech in France and Europe (ICP Forest 2002, Favre and Renaud, 2007).

In contrast, the growth function may be as crucial as the storage function in oak survival. This additional constraint could have important consequences on the capacity of oak to adapt to variations in intrinsic and external developmental conditions. Compared with beech, the allocation system of oak appears to be less flexible to face of growth crises. This lack of flexibility, may explain the higher vulnerability of oak to long decline, extending over several years, and leading to dieback in the oldest trees (Bréda and Badeau, 2008).

The higher frequency of reported decline in oak stands compare to beech may be also related to the larger community of hurtful insects and pathogens associated with oak species. For instance, according to Health Forest Department, 43 species of hurtful insects associated with beech have been mentioned from 1989 to 2002, and only four of them have been observed with more than 50 occurrences (Nageleisen 2005). In contrast, 97 hurtful insect species were associated with oaks and 11 of them have been observed with more than 50 occurrences.

We did not have the opportunity to test whether site fertility would have an impact on carbon allocation to the storage function in mature oaks. Few liming had already been applied to declining oak stands with the aim of recovering a healthy status. As an example, Chimay's experimental design should be mentioned (Anonymous, 1996). The objectives were to test whether thinning, liming or both could improve crown condition of declining 100-year-old pedunculate oaks. The conclusions of the tree health monitoring were that (1) thinning was the most effective treatment to improve crown condition, (2) thinning + liming was efficient too, and (3) liming alone did not improve crown condition. Water supply was a more important stress factor than mineral fertility. Nevertheless, it would be worth looking at the liming impact on carbohydrate storage in mature oak stands in France, by sampling old existing experimental designs or by monitoring oak trees in the ongoing forest wide soil restoration in the Vosges Mountains, led by the INRA and the ONF.

The present study concerning intrinsic (ageing) and external (climate and mineral soil fertility) factors influencing carbon allocation for beech and oaks, enriched with findings

described in the literature, allowed us to define two contrasting models of carbon functioning. However, the present work concerns only two growing seasons and year-to-year variations (climatic, biotic or related to silviculture) in carbon allocation between growth, storage and reproduction remains insufficiently investigated. For instance, the role of storage pool in the feedback effects of environmental perturbations on radial growth remains to be documented (Rochas et al. 2006). Similarly, respiration might be an important factor influencing age-related productivity decline and variations in carbon allocation. However, data concerning tree respiration are scarce and concern young individuals (Ceschia, 2001). The age related trend in respiration rate, notably the fraction of living cells occurring in perennial organs of the tree (coarse roots and stem) remains little documented (Ryan and Waring 1992, Ryan et al. 1994). Future research in this field would be very helpful.

Another useful line of research would be to complete the experimental approach we used by investigating the below ground compartment. For both oak and beech, endoscopic monitoring of root growth, phenology and turnover has recently been initiated in France and will help to depict climatic and intrinsic controls on the carbon allocation to this compartment. Unfortunately, several years will be necessary to integrate direct and time-lagged responses to thinning or to climatic events like drought, water logging, or soil temperature.

Because this work was initiated in response to forest managers' questions about age-related decline of forest productivity and the increase of forest dieback, the study of ageing was limited to the duration of a forest succession. However, it would be interesting to extend this analysis to trees reaching limits of longevity, i.e. 150-300 years old for beech and 500-100 years old for sessile oak (Rameau et al., 1989). Senescing processes may or may not be comparable to those of ageing (Prescott et al.1989).

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Résumé

Dans le but de progresser dans la compréhension des déterminismes de l'allocation du carbone chez les feuillus, ce travail de recherche a consisté à étudier les effets de l'espèce (chênes, hêtre), du vieillissement, du climat et de la fertilité minérale sur la répartition du carbone assimilé par la photosynthèse entre croissance, stockage de composés de réserves carbonées et reproduction.

Les effets du vieillissement ont été étudiés à l'échelle de la révolution forestière au travers de deux chronoséquences. Deux dispositifs d'amendement ont permis d'analyser les effets de la fertilité minérale du sol sur l'allocation du carbone dans l'arbre.

Au cours du vieillissement du hêtre, l'allocation de carbone à la croissance, majoritaire pendant la phase juvénile, diminue progressivement au profit du stockage de composés de réserves, de la reproduction et de la respiration. En revanche, cette allocation demeure constante au cours du développement du chêne sessile.
L'étude dendroclimatique des variations interannuelles de la croissance radiale montre également que les deux espèces répondent de façon contrastée aux variations climatiques. L'augmentation de la productivité à long terme a été mise en évidence pour les deux espèces. Au contraire du chêne, cette augmentation du niveau de croissance s'accompagne d'une forte variabilité interannuelle de la croissance radiale chez le hêtre.
En condition de dépérissement chez le hêtre, l'allocation du carbone à la croissance chute drastiquement au profit de l'allocation aux réserves, permettant aux arbres dépérissants de maintenir des concentrations en composés de réserves glucidiques identiques à celles des arbres sains. Par ailleurs, l'amélioration du niveau de fertilité minérale de la station (par amendement) engendre une augmentation transitoire de la croissance radiale. Des concentrations en composés de réserves carbonées plus élevées chez les hêtres amendés ont été observées 15 ans après le traitement. Ces deux résultats suggèrent l'importance du niveau de réserves dans le maintien de l'intégrité physiologique des arbres adultes.

Les résultats de cette étude des facteurs intrinsèques (âge,) et externes (fertilité minérale, climat) de variation de l'allocation du carbone chez le chêne et le hêtre, enrichie des enseignements de la littérature, ont permis de confirmer deux modèles de fonctionnement carboné contrastés.

Mots-clés : *Quercus* sp., *Fagus sylvatica*, bilan de carbone, réserves glucidiques, croissance radiale, climat, fructification, allocation, âge, amendement.