

CHAPTER 2. Environmental control of carbon fluxes in forest ecosystems in France: a comparison between temperate, Mediterranean and tropical forests.

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1. Introduction

Since 1990, the French national forest-wood industry sector has been a fast growing carbon sink, thus contributing to the fulfilment of national commitments of the Kyoto protocol. The French forests carbon sink is mainly due to the unbalance between the harvest and production rates, which in turn, is partly a consequence of a continuous increase in stand productivity (Dupouey et al. Chap 5, this volume). The enhancement in productivity is attributed to the global change effects, e.g. increase in nitrogen deposition rate, temperature, and CO₂ concentration and to the age structure of French forests because, as most European Forests, they are largely in a growing phase (Spiecker, 1999; Nellesmann & Thomsen, 2001; Vries et al.,2006). Hence, the national carbon balance of French forest, typical of European temperate forests, is a result of an interaction between environmental and management, e.g. the age structure, effects. Previous studies aiming at comparing the response of European forests to climate led to the conclusion that they all behave in a comparable way in water and carbon fluxes. The differences among them have been ascribed to latitude (Valentini et al.,2000), air temperature and tree age (Magnani et al.,2007) which are mainly mediated by the difference in leaf area index (Watson, 1947) (Granier et al.,2002a, b). These comparative analyses of the carbon flux measured across a network of forest ecosystem flux sites revealed a powerful tool to understand and quantify the management-environment interaction.

In this part, we analyse and synthesise the main features in the carbon and water fluxes variation with climate and stand age among a range of French and remote forest ecosystems investigated by the national project “Carbofor”. The sites examined in this section cover a range of species, site and climate conditions, which were chosen in order to satisfy the fetch and homogeneity requirements of the eddy covariance methodology. In majority, they are mature sites belonging to the high productivity site class. The sites investigated here are equipped with eddy-covariance towers allowing at measuring energy and mass fluxes exchanges between forest and the atmosphere and the main methods used will be briefly described in section1. The sites are located in forests growing under contrasted climates (see Table 2-1) and soil types. Four of them are located in France, one in the Democratic Republic of Congo. Some additional data, from a recently installed site in a tropical rainforest of French Guiana, are also included in this study.

This sample does not cover the life cycle of forest. The age of trees is however a major factor of the forest carbon cycle in temperate and Mediterranean forests

(Gower et al.,1996; Bond-Lamberty et al.,2004; Magnani et al.,2007). In the final part of this chapter, we completed therefore the comparative analysis of French forest “Flux” site by an analysis of the causes and impacts of the age of forest on its primary productivity of maritime pine forest, the first species for softwood production in France,. The age effect on the soil carbon balance is also covered by the chapter 3 of this volume by Guillet et al.

1.1. Methods of measuring CO₂ fluxes and incertitude

1.1.1. Net Ecosystem Exchange, Ecosystem Gross Primary Productivity, Ecosystem Respiration

In normal windy conditions and when the assumption of horizontal homogeneity of the canopy can be accepted, the CO₂ mass balance equation applied to the terrestrial ecosystem leads to correspondence between the net CO₂ ecosystem exchange (*NEE*) and the CO₂ turbulent vertical flux above the canopy, F_c combined with the CO₂ storage in the canopy air (Aubinet et al.,2000; Finnigan et al.,2003). Following definitions proposed in chapter 1 of this volume, this holds when non CO₂ atmospheric exchange are neglected. The CO₂ turbulent vertical flux, F_c , is equal to the temporal average of the product of the CO₂ concentration and vertical wind velocity temporal variances. The time average is performed on a period during which the micrometeorological conditions can be considered as constant (typically one half-hour). The temporal variances correspond to the difference between the instantaneous value and its average over a period going from few minutes to a complete half-hour. The determination of the net CO₂ flux requires the measurement of the CO₂ concentration (C) and vertical wind velocity (w) at a reference level which may be optimally immediately above the roughness layer and at a frequency of at least 10Hz.

When the wind turbulence is low, essentially during quite nights, the CO₂ stored in the canopy air and the CO₂ transported by other process than vertical turbulence (e.g. horizontal advection) represent a non-neglecting quantities in comparison with the vertical turbulent flux (Aubinet et al., 2005). The storage flux in the air layer below the measurement level can be easily obtained by difference between two successive estimations of the CO₂ content as deduced from repeated CO₂ concentration measurements along a vertical profile between the soil and the measurement levels (Yang et al., 2007). The measurement of the other fluxes is more difficult and the determination of a correct methodology is still under process. Presently, to overcome these difficulties, the eddy covariance data, eventually corrected by the air storage, are selected to represent the net CO₂ ecosystem exchange when the friction velocity (u^* , variable representing the turbulence level) is above a threshold that has to be determined for each site and year (Gu et al., 2005; Papale et al., 2006). The u^* threshold corresponds to the value below which the night flux decreases without any change of the micro-meteorological drivers, e.g. w .

The eddy covariance system is composed of one three-dimensional sonic anemometer measuring the three wind velocity components and one infrared gas analyser measuring the CO₂ and water vapour concentration. These two instruments must operate at a frequency of 10 Hz or more. The anemometer is installed above the canopy. If the analyser includes an internal cell for the infrared absorption (closed path analyser), the air sample has to be sucked from the top of the tower (close to the anemometer) by a pump at high rate (few litres min⁻¹). In the case of an open path

analyser use (air is free to circulate between the infrared source and the receptor) then this analyser is simply placed near the anemometer with attention to not perturb the wind flow measured. The air CO₂ vertical profile can be measured with a system combining a pump, an infrared gas analyser and automated vanes that switch the air uptaken to the infrared analyser between different levels.

Some corrections and post processing have to be performed on the raw data coming from the eddy covariance system before to calculate the CO₂ flux. If a closed path is used, there is a time lag between the measurements of w and C respectively due to the time of air transfer from the sampling point to the analyser. The transfer time value corresponds to the time for which the maximum of the w and C covariance is found. The wind data must be delayed from this time lag before to compute the flux with the w and C covariance (Aubinet et al., 2000). The second correction introduced by a closed path analyser comes from the reduction of the C high frequency oscillations due to the air mixing during its transfer to the analyser. The factor correcting this effect can be obtain by comparison of the co-spectra of C with a theoretical co-spectra (Kaimal et al., 1972) or with the sensible heat one which is not affected by the air transfer as it is calculated only from the anemometer data. When an open path analyser is used, the air density variations introduce some errors in the determination of CO₂ concentration from the analyser measurement that gives the number of CO₂ mole by volume unit (Webb et al., 1980). The correction factor can be calculated from values of the air temperature and atmospheric pressure.

Finally, the corrected fluxes have to be selected to keep only the value recorded when the eddy covariance system works correctly. A first step of data screening can be operated on the high frequency data (10 Hz) by statistical analysis to avoid the electronic and other technical failings from the database (Vickers & Mahrt, 1997; Longdoz et al., 2008). The fluxes obtained when u^* is below the threshold (see above) should also be excluded and the measurements performed during rain or frog events should be taken with care. Moreover, the presence of water at the sensor surfaces (open path analyser and anemometer) is able to perturb the sound or infrared transmission and induce some abnormal values. The data rejected by these different tests have to be replaced to estimate the annual carbon sequestration by the ecosystem. Different data gap filling methods could be applied. For gap smaller than two hours, the linear regression is recommended. Otherwise, the look up table, neuronal network and multiple imputations could be used (Falge et al. ,2001; Papale & Valentini 2003; Hui et al. ,2004, Reichstein et al., 2005).

When the non CO₂ flux from the ecosystem can be neglected, F_c can be equated to the net ecosystem exchange (NEE). Under such conditions, it is possible to infer from F_c the estimations of the ecosystem respiration ($Reco$) and gross primary productivity (GPP). The net fluxes obtained during nights and leafless periods (for deciduous forest) correspond to $Reco$. These values can be used to calibrate some $Reco$ response to temperature and soil water content. With the assumption of identical respiration behaviour from the forest components during daylight and night, the response function driven by daylight micro-meteorological data provides a surrogate of the daylight $Reco$. During the daylight, the difference between the NEE measured and $Reco$ gives GPP (Falge et al.,2002a, Reichstein et al. 2005).

1.1.2. Soil CO₂ efflux

The most widely used method for monitoring CO₂ efflux from the soil is based on different kinds of chambers that intercept the flux coming out across the soil surface.

The chambers are directly put on to the soil or laid on collars previously inserted in the soil. Soil respiration chamber systems can be grouped in three categories based on their working principle. In closed chamber system, the CO₂ accumulates (closed system) and flux is determined from the concentration increase during a known period of time. Closed chamber systems can further be divided into two major categories: closed dynamic and closed static.

In closed static chamber system (also known as non-steady-state non-flow-through chambers), the CO₂ is usually trapped with chemicals such as NaOH or soda lime (Raich et al., 1990). Thus, normally, the CO₂ concentration within the chamber remains relatively stable. The CO₂ efflux can be calculated from the amount of CO₂ bound in the trapping solution, exposure time and the cross sectional area of the soil intercepted by the chamber. In some static chambers, successive air samples are extracted with a syringe and analysed separately with a CO₂ analyser, (either infrared analyser or gas chromatograph).

Another major category of closed chambers is closed dynamic chamber system (also known as non-steady-state flow-through chambers). In these systems, the air is pumped from the chamber through a CO₂ analyser before to return to the chamber and so on (Norman et al., 1992). At each passage in the chamber the soil efflux add some CO₂ in the air and the CO₂ concentration measured increased regularly. The CO₂ efflux is calculated from the slope of the concentration change within the chamber's headspace versus time, the system volume and the soil surface intercepted by the chamber. As for static system, this procedure is valid until CO₂ concentration increases linearly in the system. When CO₂ concentration in the chamber's headspace becomes high enough to reduce significantly the vertical gradient, the saturation effect reduces the flux. The measurement must account for this saturation e.g. by using a non-linear equation in the flux calculation. The value obtained with this kind of system is very sensitive to the difference of pressure between inside of the chamber and the atmosphere. An overpressure/depression of few tenth of Pascal in the chamber is able to block/suck important quantity of CO₂ from the soil and then divide/multiple the soil CO₂ efflux by a factor higher than two.

In open chamber system (also known as steady-state flow-through chambers), airflow passes through the chamber (owing to pump system). The CO₂ efflux is determined from the difference between CO₂ concentration at the inlet and outlet of the chamber, the airflow rate and the soil surface intercepted by the chamber (Rayment and Jarvis, 1997). The determination of the CO₂ efflux is very sensitive to accurate concentration of compensation air (the air fed into the chamber). If not measured accurately and synchronized in time, the results can be misleading. Before to perform the measurement, the CO₂ concentration within the chamber must reach steady state (equilibrium) after a time that depends on the airflow rate and the CO₂ efflux from the soil.

1.1.3. CO₂ flux from stem and leafy branches

Similarly, the CO₂ flux from stem section and branches can be measured using either closed or open chambers (Dufrêne et al., 1993; Bosc et al., 2002, Ceschia et al., 2002; Damesin et al., 2003). These techniques were automated and used in the field during international program such as the Boreas and CARBOEUROPE programmes (Rayment et al., 2002).

1.2. Main characteristics of the studied sites

The methods described were applied since 1996 for the oldest in a range of sites located in the French metropolitan area and outside (Tables 2-1 & 2-2). Mean annual temperature is ranging between 8.5 and 15°C for the French sites; it reaches 24°C at Hinda in Congo (Figure 2-1) and 28.3°C at Paracou in French Guiana. A quite large variation in the annual radiation (PAR) is observed among sites, between 8000 and 10000 mol m⁻² y⁻¹ and 13000 mol m⁻² y⁻¹ at Paracou. In France, the lower annual values were recorded at Hesse, the highest at Puéchabon, linked to latitude and to cloudiness.

Table 2- 1. Sites and years selected for the analysis (black cells). Years with significant missing data that (grey cells) could not be used to establish annual balances but were used to fit the response functions.

Table 2- 2. Main characteristics of the 6 studied stands

Figure 2-1 Top : Annual mean of air temperature and cumulated radiation (PAR) in the investigated sites. Bottom : annual mean of vapour pressure deficit (vpd).

2. Comparison of the carbon and water annual balances among ecosystems

2.1. Water and carbon balances

2.1.1. Evapotranspiration vs. available energy

The annual sums of net radiation were comparable from site to site, except at Bilos where re-growing vegetation after clear-cut was still low and sparse (Kowalski et al, 2003) and at Paracou. As an example, time-courses of latent heat flux (λE) and of net radiation (R_n) are presented in Figure 2-2 in three sites. At Puéchabon, we can observe that λE remained low during all the year as compared to R_n . Furthermore, latent flux showed a large decrease on the end of summer during periods when precipitation was very low (DOY 200 to 230 and DOY 237 to 262). At Le Bray, the ratio between λE and R_n was quite constant along the year except, as in Puéchabon, a decrease during a drought period (around DOY 240). At Hesse, λE increased sharply in spring after budburst took place (DOY 120).

Figure 2-2 annual courses of net radiation (R_n) and of latent heat flux (λE) in Puéchabon, La Bray and Hesse (daily data).

The ratio $\lambda E/R_n$, i.e. the proportion of available energy that is transformed into evapotranspiration flux, equalled on average 0.5. Nevertheless, this ratio was variable according to sites and years, from 0.31 (Puéchabon, 2001) to 0.83 (Bilos, 2000 and 2001). Very close values were calculated at Le Bray and Hesse during the leafy period from May to October (cf. Figure 2-3). The low $\lambda E/R_n$ ratio at Puéchabon is probably linked to both the low LAI of this Mediterranean stand (2.9) and to the strong water stress and hence to stomatal closure. The impact of water stress on the ratio $\lambda E/R_n$ is also shown in Figure 2-3a at Hesse for 7 successive years of measurements: more the water deficit is important, less available energy is transformed in latent flux (thus, the sensible flux increases). The Eucalypt stand, despite its low LAI (3.0) exhibits high transpiration rates. This species shows particularly low water use efficiency (see below).

Figure 2- 3 Between-site and years variation in the ratio of latent heat flux to net radiation ($\lambda E/R_n$). Calculation was performed on complete years, except at Hesse where it was restricted to the leafy period (May to October). Right-hand graphs: a) effect of water stress on the ratio $\lambda E/R_n$ at Hesse, expressed as the number of days (NDstr) during which the relative extractable water in the soil is below 0.4; b) relationship between $\lambda E/R_n$ and the leaf area index (LAI) for the same sites and years.

2.1.2. Fluxes of carbon: Net ecosystem exchange, gross assimilation and ecosystem respiration.

Neglecting the non CO₂ flux, the annual net carbon balance (*NEE*) was calculated in all the investigated sites as the sum of half-hourly CO₂ flux measurements corrected for the CO₂ variation in the air between soil surface and the eddy-covariance systems. Gaps due to missing data were filled on a daily time-step, using simple statistical models.

Annual *NEE* variation among sites and years is presented in Figure 2-4. Negative values indicate flux entering the ecosystem, positive a carbon release to the atmosphere. A huge variability is observed: *NEE* varied between -582 and $+229$ gC m⁻² y⁻¹. The Bilos site, a recent clear cut, is a large carbon source. However, there was a tendency for *NEE* at Bilos to decrease during the second year of measurement (i.e. two years after clear-cut), due to vegetation re-growth.

At Le Bray, annual *NEE* showed a low interannual variability (in the range of -450 to -550 gC m⁻² y⁻¹), while at Hesse the variability was much higher (from -68 to -582 gC m⁻² y⁻¹).

Figure 2-4 Variation of the annual net carbon balance (*NEE*) of 6 forest ecosystems. At Le Bray and Hesse, 3 and 7 years of measurement are presented, respectively. Negative values indicate a carbon uptake, and positive values a carbon release from the ecosystem to the atmosphere.

The gross primary production (*GPP*) is calculated as *NEE* minus the ecosystem respiration flux (*Reco*). *Reco* is estimated during the periods when photosynthesis does not occur, during night and, in the deciduous stands, the leafless period. Nevertheless, even when corrected from CO₂ storage variation in the air *Reco* estimate remains still problematic, especially under low turbulence condition (i.e. low wind speed). Therefore, the quite important incertitude in *Reco* estimates propagates directly into the values of *GPP*.

Besides at Bilos where the photosynthetic rates were very low due to reduced plant cover, *GPP* varied in a large range, between -1000 and -2100 g C m⁻² y⁻¹ (Figure 2-5). At Hesse, the between-year variation was much higher. Moreover, a regular increase in *GPP* was observed from 1996 to 2001 and a stabilisation in 2002. A multivariate analysis showed that inter-annual variation in *GPP* at Hesse was explained (at ca. 70%) by both LAI and water stress duration and intensity during the leafy period.

Figure 2- 5 Annual gross assimilation (*GPP*) among sites and years.

The variation in *GPP* among investigated ecosystems is also explained by the LAI values. Another source of variation is the annual incident photosynthetically active radiation (PAR). Therefore, the *GPP*/PAR ratio is correlated to LAI (see Figure 2-6, $r^2=0.73$). At Hinda and Le Bray, the ratio *GPP*/PAR (absolute value) is relatively higher than in other sites, indicating a higher light-use efficiency. A probable explanation lies in the canopy structure of both stands: the eucalypt trees at Hinda

have narrow and elongated canopies, while Le Bray and to a lower extent Hesse in 1999 (just after thinning), the stands were open allowing a high light interception. Anyway, photosynthetic capacity at leaf level probably plays also an important role in the light use efficiency. At Paracou, the value of GPP/PAR is strongly different from all the other sites, reaching $-23.9 \text{ mmol mol}^{-1}$, indicating very contrasted photosynthetic response to the intercepted radiation of the tropical rainforest. The relationship of Figure 2-6 is slightly curvilinear: light-use efficiency does not saturate at the highest LAI values.

Figure 2- 6 Relationship between the gross assimilation to photosynthetically active radiation ratio (GPP/PAR , annual values) and the leaf area index (LAI). Data of Paracou are not included here.

When considering all sites and years, there is a strong positive relationship between absolute values of GPP and $Reco$ (Figure 2-7). Indeed, on an annual time basis, more carbon is fixed by photosynthesis, more growth rates are high and more living tissues respire, leading therefore to large autotrophic respiration fluxes. Nevertheless, the heterotrophic component included in $Reco$ (originating from leaf and root litter, woody debris and soil organic matter decomposition) can dampen this relationship and introduce some lag effects in respiration. This was probably what happened in 1998 at Hesse where an important activity of decomposers organisms was observed in August and September on woody debris remaining on the ground from a previous thinning, with abnormally high respiration rates.

Figure 2-7 Relationship between ecosystem respiration ($Reco$) and gross assimilation (GPP) (annual sums). The regression line does not take into account the data of Bilos.

2.1.2.1. Water and carbon coupling: the water use efficiency

The water use efficiency (WUE) is calculated as the ratio between the annual biomass production and water consumption by vegetation. Unfortunately, the wood increment is not measured in all the investigated sites. We found values of WUE ranging between 0.8 and $2.4 \text{ mmolC mol H}_2\text{O}^{-1}$ (see Figure 2-8). WUE is higher at Hesse, but at Le Bray, the water consumption of the vegetation includes evapotranspiration of the abundant herbaceous vegetation, while the annual biomass increment was measured only for the pines. Former measurements at Le Bray showed that understorey vegetation transpiration was on average 1/4 to 1/3 of the total evapotranspiration. When calculating WUE for pines only, we obtain on average (years 1997, 1998, 2000 and 2001) a value of $2.08 \text{ mmolC molH}_2\text{O}^{-1}$, very close to that of Hesse ($2.05 \text{ mmolC molH}_2\text{O}^{-1}$). At Hinda biomass increment is rather low while the stand evapotranspiration is high, leading to a low WUE as compared to the two other stands.

Figure 2-8. Water use efficiency (annual values) in 3 Carbofor sites over several years of measurements. At Le Bray, WUE is calculated either: 1) with the total evapotranspiration (see text) : right bars, or 2) with an estimate of the pines transpiration, only (left bars).

Canopy water use efficiency ($WUEc$, see Figure 2-8) is calculated as the ratio of GPP to evapotranspiration (GPP/E). Contrastd $WUEc$ are observed among sites: a high $WUEc$ at Hesse, between -5 and $-7 \text{ mmol C mol H}_2\text{O}^{-1}$, with a significant inter-annual variation, the higher value being observed for the dry year 2003. At Puéchabon, Le Bray and Hinda, $WUEc$ ranges between -3 and $-4 \text{ mmolC molH}_2\text{O}^{-1}$. At Le Bray, when calculating $WUEc$ for the pines alone (see above), higher values

are obtained, close to Hesse WUEc (Figure 2-9). At Bilos, WUEc is very low, around $-1 \text{ mmolC molH}_2\text{O}^{-1}$.

Intrinsic water use (WUEi) represents the ratio between *GPP* and canopy conductance for water vapour (*gc*). We calculated *gc* from the Penman-Monteith equation, assuming the big-leaf hypothesis. Similar ranking of the sites for WUEi than for WUEc was obtained (data not shown).

Figure 2-9 Canopy water use efficiency WUEc, calculated as *GPP/E* in 5 Carbofor sites. At Le Bray, WUEc was calculated in two ways (see Figure 2-7).

2.1.2.2. Carbon balances and carbon stocks

When comparing annual *NEE* and biomass increment, some discrepancies are found (see Figure 2-10). The annual biomass increment can be higher or lower than the annual carbon balance. At Le Bray, a good linear relationship, close to the 1:1 line, was observed for the 1996-2000 period. However, in 2002 (a very dry year in this site) this relationship did not match no more: while *NEE* was close to 0, biomass increment was ca. 300 gCm^{-2} . At least two different reasons could explain the discrepancies between both annual carbon balance estimates. First, the carbon flux measurements are performed in the footprint area which extension and direction varies to a large extent according to the aerodynamic condition. Ground measurements at the tree level are never performed in the same area, the sampled trees being at the same locations in the stands. Second, other compartments (aerial and belowground) than the measured standing trees can experience significant variation in carbon stocks: soil organic matter, non-living biomass that are still difficult to estimate on the annual time-step.

Figure 2-10 Relationship between the annual net carbon balance (*NEE*) and biomass increment of the stands.

In order to try to match closer the two estimates of carbon balance, we calculated the sum $\text{NEP} = \Delta W + D - R_h$, where ΔW is the annual stand increment in biomass and *D* is the leaf plus fine root production. The relationship obtained for the 3 sites where the data were available is shown in Figure 2-11. A better agreement between *NEE* and *NEP* than between *NEE* and ΔW (Figure 2-10) is observed. However the most important problem is the fine root production that is poorly known in most forest ecosystems.

Figure 2-11 Relationship between the sum of biomass increment plus fine root and leaf production less the heterotrophic respiration ($\Delta W + D - R_h$) and the annual carbon balance (*NEE*).

3. Response functions of the canopies

3.1. Canopy conductance for water vapour

The canopy conductance was calculated half-hourly from water flux measurements above stands and from climate measurements by inverting the Penman-Monteith equation (Granier and Loustau, 1994 ; Granier and Bréda, 1996). Non-linear fittings were performed for each investigated site using the following model:

$$gc = g_{c_{\max}} [Rg/(Rg+Rg_0)]^* [1/(1+k \text{ vpd})] \quad [1]$$

where R_g is the global radiation, vpd the air vapour pressure saturation deficit and $g_{c_{max}}$, R_{g0} , k are the fitted parameters.

Under high vpd condition ($> 1kPa$), the canopy conductance is close for Hesse, Le Bray and Hinda, while it is much lower at Puéchabon (Figure 2-12). At Hinda, the response of g_c to radiation differs from that of the other sites: saturation is reached at lower radiation level, may be due to the particular architecture of the eucalypts. The models of g_c variation can be included in stand transpiration models to estimate day-to-day variation in soil water content (Granier et al., 2000c).

Figure 2-12 Variation of canopy conductance to water vapour (g_c) for 4 Carbofor sites, fitted according to the equation [1]. Effects of air vapour pressure deficit at $R_g=900 \text{ Wm}^{-2}$ (a) and of global radiation (b) at $vpd=1kPa$.

3.2. Diurnal net carbon flux

The relationship between net carbon flux and radiation (PAR) was fitted according to the following hyperbolic model:

$$NEE = Reco + a \text{ PAR} / [1 - (\text{PAR}/2000) + (a \text{ PAR}/F_{c_opt})] \quad [2]$$

Where $Reco$, a and F_{c_opt} are the fitted parameters; $Reco$ is the ecosystem respiration, a is the slope of NEE at the intercept and F_{c_opt} is the value of NEE when $\text{PAR} = 2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$. The fitted parameters are given in Table 2-3. Figure 2-13 shows the temporal variation of this relationship obtained at Hesse; it is stable for most of the growing season. A decrease was only observed since September, when leaf yellowing took place.

Figure 2-13 Variation of NEE as a function of PAR at Hesse for the June to September period in 2002 (wet year), from the model [2]. The coefficients of regression range between 0.6 and 0.7.

Table 2-3 Fitted parameters of equation [2] for the different sites and years.

The variation of $NEE(\text{PAR})$ relationships are large among the sites (Figure 2-14). The lower values of NEE (absolute values) are observed at Puéchabon and Bilos, below $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$. At Le Bray, a large interannual variation was found. The larger NEE values were observed at Hesse, greater than $-20 \mu\text{mol m}^{-2} \text{ s}^{-1}$ under saturating PAR.

Figure 2-14 Variation of net ecosystem exchange (NEE) as a function of PAR during June in several sites and years. Curves are the best fits of equation [2], obtained for the June measurements. The coefficients of regression range between 0.6 and 0.7.

3.3. Night carbon fluxes

This analysis only took into account the temperature effects on ecosystem respiration. We fitted the same exponential model using the air temperature, because soil temperature was not measured at the same depth in all the sites.

Figure 2-15 Relationship between ecosystem respiration ($Reco$, night measurements) and air temperature in 5 Carbofor sites, during 2001. Data points are bin averages of 10 measurements.

The fitted relationships are shown in Figure 2-15, and the parameters are given in Table 2-4. Besides the relationships are very variable from site to site, the maximum

values are similar. Therefore, the temperature does not explain the variation of *Reco* among sites. At Puéchabon, the negative effect of soil drought can be observed at the highest temperatures. At Hinda, there is a strong increase in *Reco* with temperature that varies in a limited range (less than 10°C).

Table 2-4 Estimated parameters of the relationship $Reco = a \exp(b T_{air})$, and correlation coefficients in 5 sites (year 2001). The column « maxi » corresponds to the estimated ecosystem respiration at the highest observed temperature in each site.

4. The comparative response to climate of carbon and water fluxes among French forest sites: discussion.

This work consisted in a cross-analysis of the flux variation to environmental factors among a contrasted range of forest ecosystems (climate, species, stand structure).

Finally, we showed that energy, water and carbon variation in fluxes mainly depended on climate and canopy structure, and to a lesser extent on the tree species. For instance, the transformation of radiation to latent heat flux was well related to: i) leaf area index as clearly seen in Figure 2-2 for the seasonal variation (Granier et al., 2000a) and in Figure 2-3b for the inter-annual variation; ii) water stress (Figure 2-3a) that reduces the ratio $\lambda E/R_n$, especially at Puéchabon under Mediterranean climate.

There is still some uncertainty in the estimation of gross assimilation and ecosystem respiration from the net carbon fluxes as measured using eddy-covariance. The low turbulence during nights in most sites is the most important methodological problem. Future algorithms would probably change the above presented data.

Nevertheless, gross assimilation among the investigated sites seems to be in the range of 1000 to 2000 g C m⁻² y⁻¹, i.e. 10 to 20 t C ha⁻¹ y⁻¹. In the French Guiana site (Paracou), the annual value is much larger, close to 35 t C ha⁻¹ y⁻¹. Determinism of the inter-annual variation in *GPP* and *Reco* fluxes, and therefore in *NEE*, is still poorly known. At Hesse, the progressive increase of *GPP* from 1996 to 2001 seems to be mostly driven by interaction between drought during the growing season and the intercepted radiation. The eucalypt plantation at Hinda showed a higher light conversion efficiency than the other stands that could be related to both a higher physiological performance and also in its structure, more efficient in terms of radiation interception.

Understorey vegetation is an important component of energy, water and carbon cycles in some forest ecosystems, especially in the open stands like at Le Bray, where a large leaf area index of grasses (*Molinia*) develops as a consequence of the high proportion of radiation transmitted to it (Misson et al., 2007; Jarosz et al., 2008). Such understorey is characterized by a very active water extraction from the soil and high photosynthetic rates, especially during the dry periods, and therefore plays a determinant role in the water and carbon balances.

Inter-annual variation in carbon balance is tightly dependent on the variation of ecosystem respiration (Valentini et al., 2000, but see also Janssens et al., 2001): low *NEE* values are observed when *Reco* is high. Its determinism is much less known than for *GPP*, because more complex, involving numerous above and below-ground compartments and different processes, each of them responding to a specific set of environmental variables (see Falge et al., 2002a, b). *Reco* results from: i) the respiratory fluxes linked to the growth and maintenance of all the living tissues in the ecosystem, ii) carbon fluxes resulting from the organic matter decomposition, such as

litter, roots and coarse debris. In forest ecosystems, soil respiration represents more than 50% of *Reco* (Epron et al., 2001). The woody debris can result from the natural mortality of the management practices (thinning, clear-cut). At Hesse, coarse debris resulting from thinning amount to 400 to 500 g C m⁻², every 5-6 years. In the same site, the natural coarse litter (mainly branches) is between 50 and 70 g C m⁻².

Forest management also drives inter-annual variability in carbon balance. Reaction of forests to thinning can be rapid, especially in young fast-growing stands, where light-use efficiency (i.e. ratio *GPP*/*PAR*) temporarily increase the year after thinning.

5. Carbon balance course along the life cycle of forests

The main source of variability in carbon cycling among managed forest stands in Europe is the stand age. Immediately after disturbance, the carbon balance of a forest ecosystem is negative, *GPP* and *NPP* are lowered down to zero and increase subsequently as the canopy develops. They reach a maximum near canopy closure, and finally decrease in older stands (Ryan et al., 1997). This decline in aboveground wood production after canopy closure, known for long by foresters, is a common pattern in even-aged forest stands around the world (Gower et al., 1996; Ryan et al., 1997; Ryan et al., 2004). One compelling need is to explain why *NPP* is reduced in ageing forest stands: the growth patterns are pronounced and predictable but the underlying mechanisms remain unclear. Moreover, recent investigations have confirmed that natural (fire and storm) or anthropogenic (harvest, thinning) disturbances convert mature forest sinks into carbon sources, requiring years to decades to recover their sink status depending of their growth rate (Bond-Lamberty et al., 2004; Kowalski et al., 2004). The importance of these disturbances on the maritime pine forest carbon balance was evidenced in the Landes de Gascogne forest using eddy covariance measurements simultaneously over a clear cut site and a neighbouring mature forest site in 2001 (Kowalski et al., 2003). Data in Table 2-5 show that both components of *NEE*, gross primary production (*GPP*) and total ecosystem respiration (*Reco*), were lower in the clear-cut in comparison to the mature stand.

Table 2-5 Comparison of annual ecosystem fluxes between a clear-cut in 2001 and a mature pine stand at age 28 in 1997-1998 and at age 31 in 2001 (Kowalski et al., 2003).

The clear-cut, covered with remaining understorey woody and herbaceous species, maintained about one-third the *GPP* of the mature stand. Due to past accumulated carbon stocks in soil and canopy (representing harvest residues), total respiration by the clear-cut reached about the two-thirds that of the mature stand, suggesting a dependence of the soil decomposer community on recently assimilated carbon in the maritime pine forest. This is consistent with results from other studies in pine forests (Hogberg et al., 2001), but may not be general for all species of trees (Kowalski et al., 2004). The greater relative reduction in *GPP* (versus *Reco*) positioned the clear-cut to be a significant annual carbon source. It is clear from these data that intensively managed forests loose carbon towards the atmosphere after disturbances. These studies showed this importance of taking into account the initial phase of stand settlement and the resulting carbon loss to estimate accurately forest carbon sink over its full management cycle. The role of old-growth forests in the global carbon cycle is also a matter of interest because the old concept that their biogeocycles are close from equilibrium was recently challenged (Luyssaert et al., 2008)

In the following sections, we summarise the mechanisms that can explain changes in stand productivity and carbon balance over the full management cycle in a temperate forest. First, we enhance the results regarding decline in forest productivity with increasing stand age, pointing out the mechanisms responsible for this decline. Then, we present some preliminary researches investigating the impact of a disturbance occurring at early development stages on the carbon balance of a maritime pine ecosystem.

6. Evidence of growth decline with age in the maritime pine forest

In the “Landes de Gascogne” Forest (south-western France), constituted of even-aged stands of maritime pine trees, empirical evidence for the decline of forest production rates is well documented by inventories operated by the National Forest Inventory. The decrease in wood production was about 70% between 24 and 54 year-old stands, whatever the fertility class, showing that age is one of the main factors inducing variability in forest productivity. Recent studies on growth, based on a chronosequence of even-aged stands of maritime pine, corroborated this trend and further investigated the physiological and structural causes of this decline. A rather clear picture of maritime pine stand dynamics emerges from a chronosequence ranging between 10 and 91-year-old (Figure 2-16, Delzon et al. 2004; Delzon and Loustau, 2005).

Figure 2-16. Changes in productivity as function of stand age in a maritime pine chronosequence in the Landes de Gascogne of south-western France, by various measures: (a) *aNPP* ($\text{gC m}^{-2} \text{yr}^{-1}$) represents above-ground Net Primary Production estimated using biomass increments and litterfall measurements per stand; (b) Growth Efficiency ($\text{gC m}^{-2} \text{yr}^{-1}$) corresponds to the above-ground annual tree biomass increment expressed per unit leaf area, (c) stand leaf area (LAI: Leaf Area Index and PAI: Plant Area Index; $\text{m}^2 \text{m}^{-2}$) and (d) Tree Number (ha^{-1}).

The aboveground part of *NPP*, *aNPP*, decreased markedly with increasing stand age. This decline corresponded to 60 % comparing the 10 and 91 yr-old stands. It was explained by a 40 % decrease in stand leaf area (i.e. leaf area index (LAI) and plant area index (PAI)) along the chronosequence (due to tree density decline by thinning and crown abrasion). However, forest growth decline was only partly explained by the observed decline in leaf area index and light interception: productivity per unit of leaf area was also reduced (Growth Efficiency Fig. 2-16 b). This result revealed that an altered photosynthesis may contribute to this decline and therefore decreasing carbon fluxes and gains. In conclusion, these studies showed a significant decline in forest growth with age that can likely be explained by decreases both in leaf area at the stand level and in CO_2 assimilation rate at the leaf level.

7. The photosynthesis decline with stand age

Most studies on photosynthesis in woody plants of different ages were not designed to isolate age-induced variation from all other sources of variation (e.g. that owing to size or environment). However, data from experimental studies generally indicated that both photosynthesis (Kolb et al., 2000; Kull et al., 1987; Yoder et al., 1994) and stomatal conductance are reduced as trees get older (Ryan et al., 2000; Schafer et al., 2000). Recent results suggest that the hypothesis of cellular or molecular ageing is not convincing for trees (Mencuccini et al., 2005; Penuelas, 2005): meristematic cellular senescence (age-related control) did not explain forest growth decline with age. Instead, extrinsic factors mediated by size, rather than irreversible senescence, have been proposed to drive decline in growth rates in old/tall trees.

Results from intensive measurements of biomass allocation, leaf water potential, photosynthetic capacity, sapflow and carbon discrimination across a maritime pine chronosequence in southwestern France showed that the dramatic decline in growth with age was explained by increasingly negative hydraulic impacts as trees grew taller (Delzon et al., 2004; Delzon et al., 2005). This conclusion was consistent with the hydric homeostasis hypothesis (Magnani et al., 2000). We demonstrated further that growth decline result from structural compensatory adjustments to height-related hydraulic constraints and stomatal closure. Trees compensate for hydraulic limitation by reducing the amount of photosynthetic area relative to water-conductive area (the leaf to sapwood area ratio, where sapwood is the hydraulically active part of the stem) (Delzon et al., 2004). This structural compensation is however not sufficient to counteract the height effect on hydraulic conductance so that a decline in stomatal conductance with tree height reducing CO₂ diffusion into the leaf (Figure 2-17),.

Figure 2-17. Mean values of canopy (a; g_c) and stomatal (b; g_s) conductance versus air vapour pressure saturation deficit (VPD) for four maritime pine stands of different age. g_c was determined from sap flow measured on six to seven trees per stand and g_s was measured on 1-year-old needles using a steady-state null balance porometer.

This conclusion was also confirmed by the comparison of leaf photosynthetic capacity across the same chronosequence (Delzon et al., 2005). These results are consistent with (Mencuccini et al., 2005), showing that photosynthetic capacity does not decline with tree age and indicating that senescence of the photosynthetic apparatus does not explain reduced forest growth.

8. References

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Table 2- 1. Sites and years selected for the analysis (black cells). Years with significant missing data that (grey cells) could not be used to establish annual balances but were used to fit the response functions.

	location	1996	1997	1998	1999	2000	2001	2002	2004
Puéchabon	S France				grey	grey	black		
Le Bray	SW France	grey	black	black	grey	grey	black		
Bilos	SW France					grey	black		
Hesse	E France	grey	black	black	black	grey	black	black	
Paracou	French Guiana								black
Hinda	Congo						black		

Table 2- 2. Main characteristics of the 6 studied stands

site	species	age in 2002	mean temp. °C	rain mm.y ⁻¹	LAI m ² .m ⁻²	density ha ⁻¹	height m
Puéchabon	Mediterran. oak	60	13.5	883	2.9	8500	6
Le Bray	maritime pine	32	12.5	950	4.2	425	20
Bilos	maritime pine	0	12.5	950	1.5	-	1.5
Hesse	beech	36	9.2	820	7.3	3800	13
Hinda	eucalypt	4	25.5	1200	3.0	700	12
Paracou	mixed tropical	unknown	25.7	2875	7.0	603	ca. 30

Table 2-3 Fitted parameters of equation [2] for the different sites and years.

site	date	a	Fc_opt	Reco	r ²
Hesse	June 1997	-0.064	-26.9	6.90	0.74
	June 1998	-0.063	-26.1	7.32	0.59
	June 1999	-0.073	-27.2	8.29	0.62
	June 2000	-0.127	-30.1	9.09	0.61
	June 2001	-0.096	-29.0	6.85	0.68
	June 2002	-0.069	-28.7	5.31	0.57
	July 2002	-0.124	-32.0	8.88	0.66
	Aug 2002	-0.100	-30.6	7.89	0.65
	Sept 2002	-0.060	-23.1	3.61	0.59
Le Bray	June 1997	-0.043	-23.6	5.89	0.73
	June 1998	-0.039	-20.4	5.72	0.60
	June 1999	-0.061	-21.2	7.78	0.72
	June 2000	-0.065	-27.6	8.87	0.67
	June 2001	-0.051	-23.0	6.00	0.53
Puéchabon	June 1999	-0.031	-11.6	4.63	0.59
	June 2000	-0.060	-14.7	5.23	0.50
Hinda	June 2001	-0.026	-22.8	2.44	0.69
Bilos	June 2001	-0.036	-10.4	4.41	0.46

Table 2-4 Estimated parameters of the relationship $Reco = a \exp(b T_{air})$, and coefficient of determination (r^2) values in 5 sites (year 2001). The column « maxi » corresponds to the estimated ecosystem respiration at the highest observed temperature in each site.

	a	b	r²	maxi
Puéchabon	1.13	0.031	0.31	2.52
Le Bray	1.39	0.040	0.64	3.88
Hesse	1.13	0.068	0.75	4.86
Hinda	0.02	0.205	0.82	3.07
Bilos	0.59	0.076	0.70	3.75

Table 2-5 Comparison of annual ecosystem fluxes between a clear-cut in 2001 and a mature pine stand at 28 in 1997-1998 and at age 31 in 2001 (Kowalski et al. 2003).

Annual exchange	Clear-cut	28 yr-old stand	31 yr-old stand
<i>NEE</i> (gC m ⁻²)	290	-575	-498
<i>GPP</i> (gC m ⁻²)	727	2255	2025
<i>Reco</i> (gC m ⁻²)	996	1680	1527

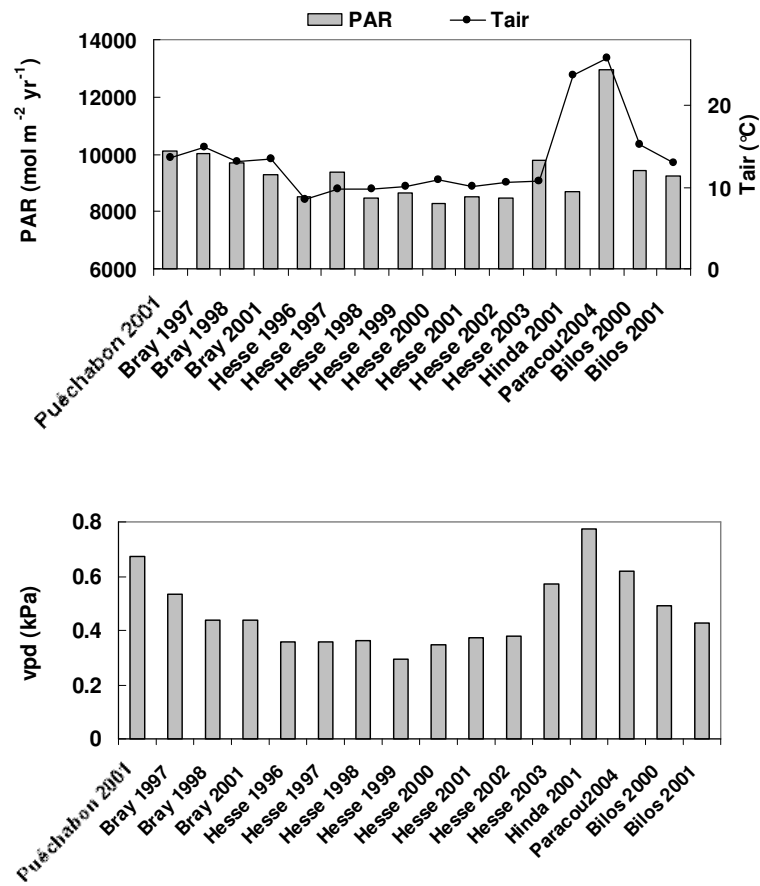


Figure 2 - 1. Top : Annual mean of air temperature and cumulated radiation (PAR) in the investigated sites. Bottom : annual mean of water vapour pressure saturation deficit (vpd).

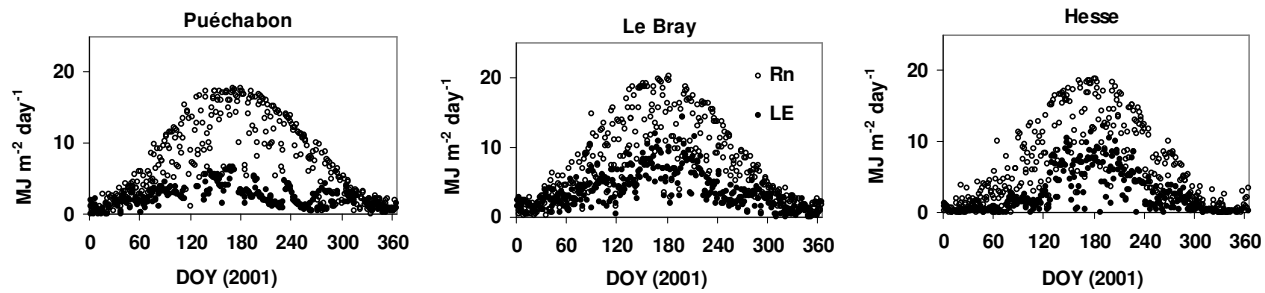


Figure 2 – 2. Annual courses of net radiation (R_n) and of latent heat flux (λE) in Puéchabon, Le Bray and Hesse (daily data).

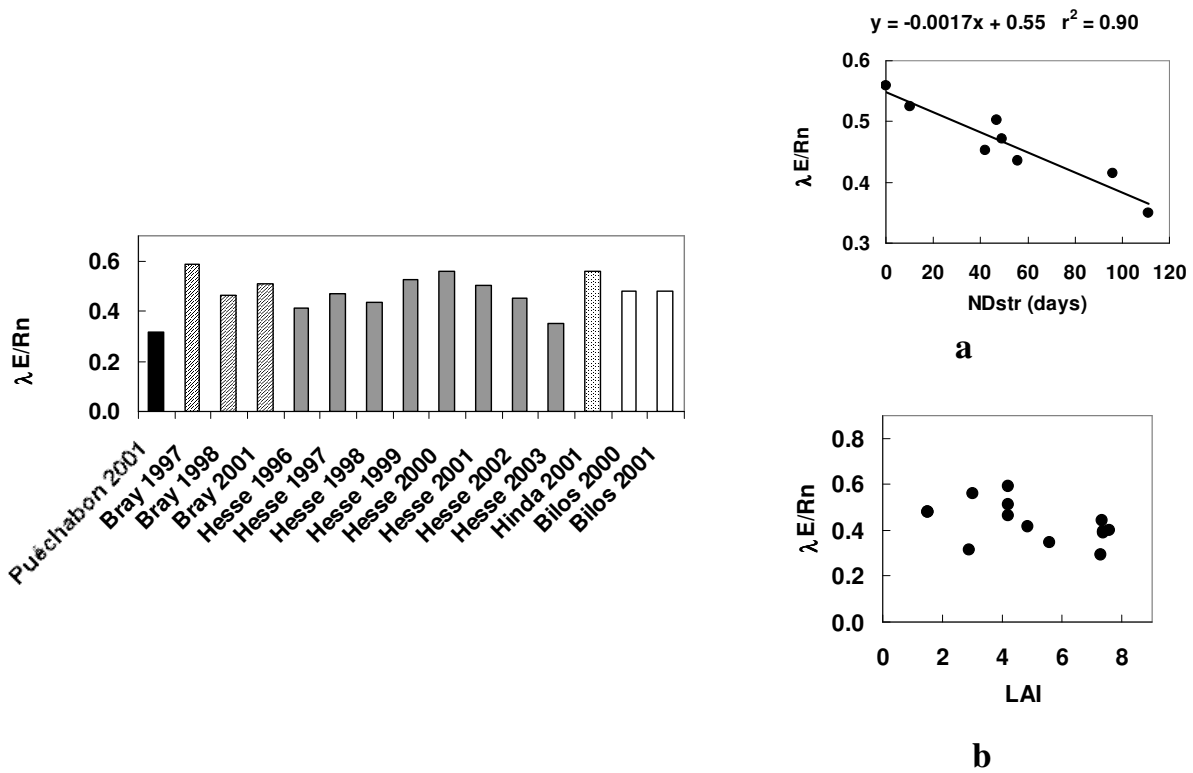


Figure 2 – 3. Between-site and years variation in the ratio of latent heat flux to net radiation ($\lambda E/R_n$). Calculation was performed on complete years, except at Hesse where it was restricted to the leafy period (May to October). Right-hand graphs: a) effect of water stress on the ratio $\lambda E/R_n$ at Hesse, expressed as the number of days (NDstr) during which the relative extractable water in the soil is below 0.4; b) relationship between $\lambda E/R_n$ and the leaf area index (LAI) for the same sites and years.

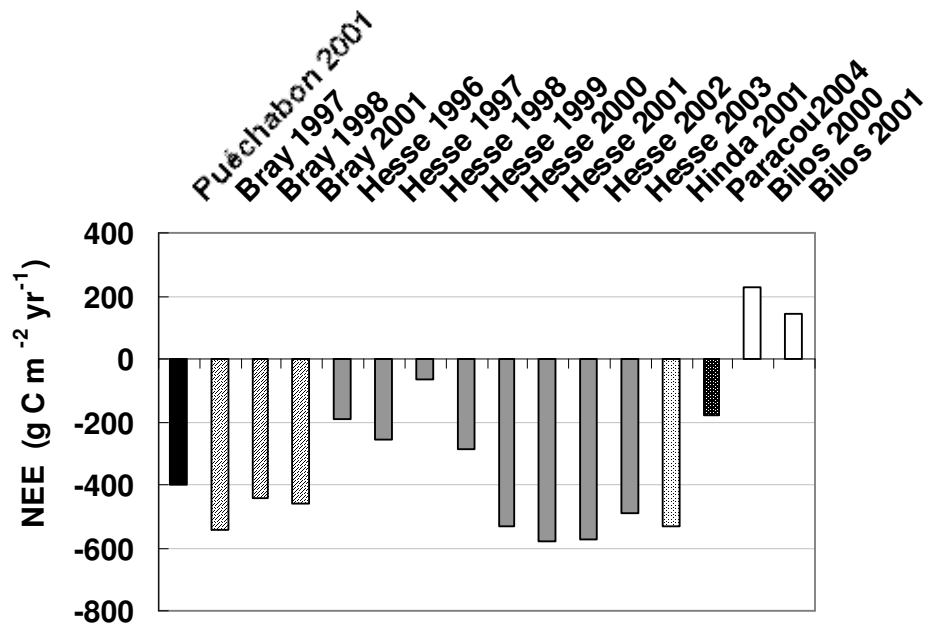


Figure 2 – 4. Variation of the annual net carbon balance (*NEE*) of 6 forest ecosystems. At Le Bray and Hesse, 3 and 7 years of measurement are presented, respectively. Negative values indicate a carbon uptake, and positive values a carbon release from the ecosystem to the atmosphere.

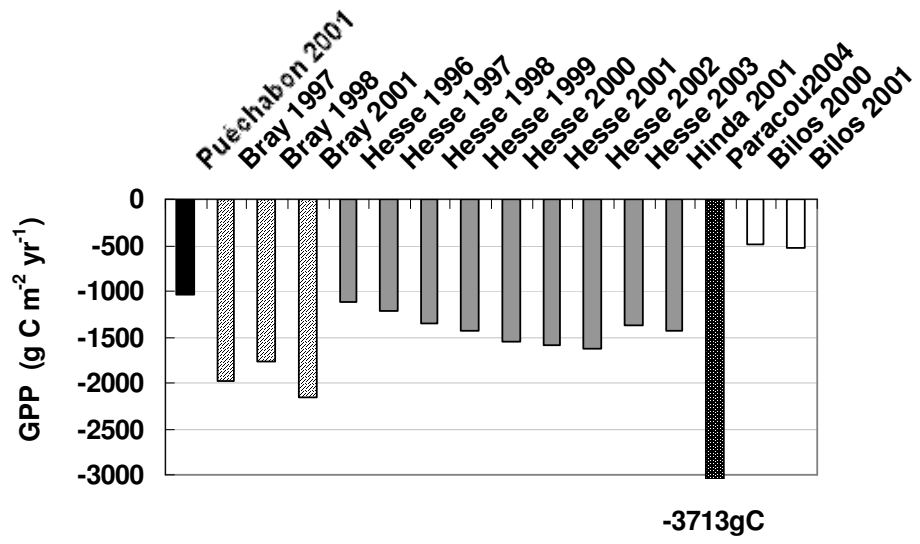


Figure 2 – 5. Annual gross assimilation (*GPP*) among sites and years.

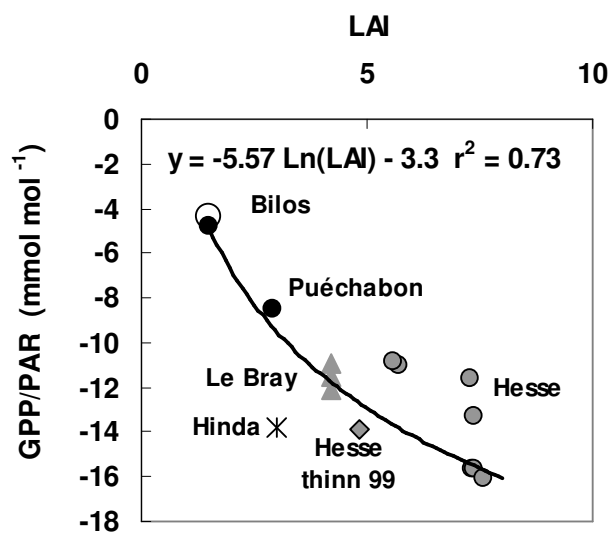


Figure 2 – 6. Relationship between the gross assimilation to photosynthetically active radiation ratio (*GPP/*PAR, annual values) and the leaf area index (LAI). Data of Paracou are not included here.

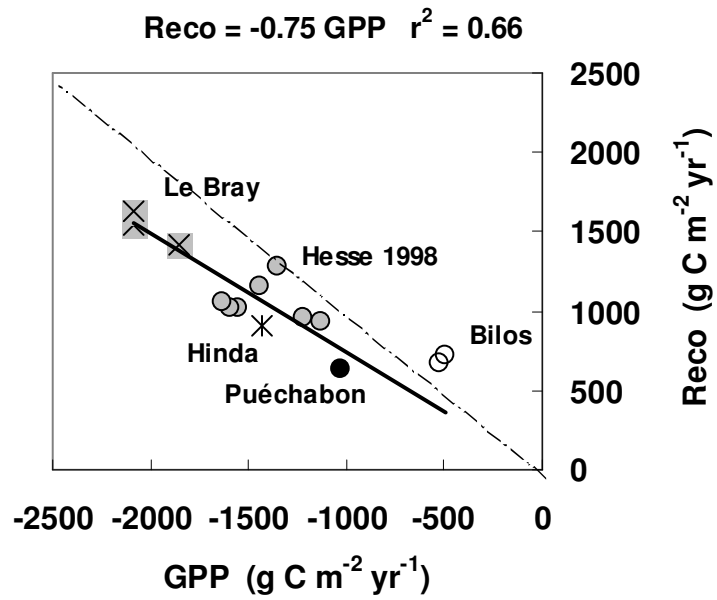


Figure 2 - 7 Relationship between ecosystem respiration (*Reco*) and gross assimilation (*GPP*) (annual sums). The regression line does not take into account the data of Bilos.

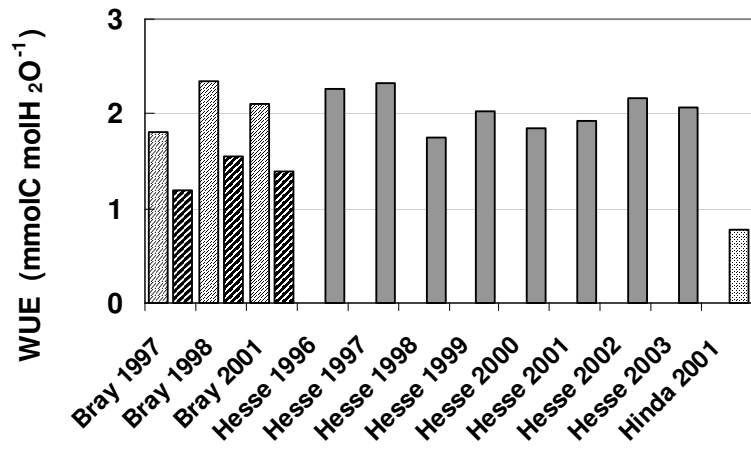


Figure 2 - 8. Water use efficiency (annual values) in 3 sites over several years of measurements. At Le Bray, WUE is calculated either: 1) with the total evapotranspiration (see text) : right bars, or 2) with an estimate of the pines transpiration, only (left bars).

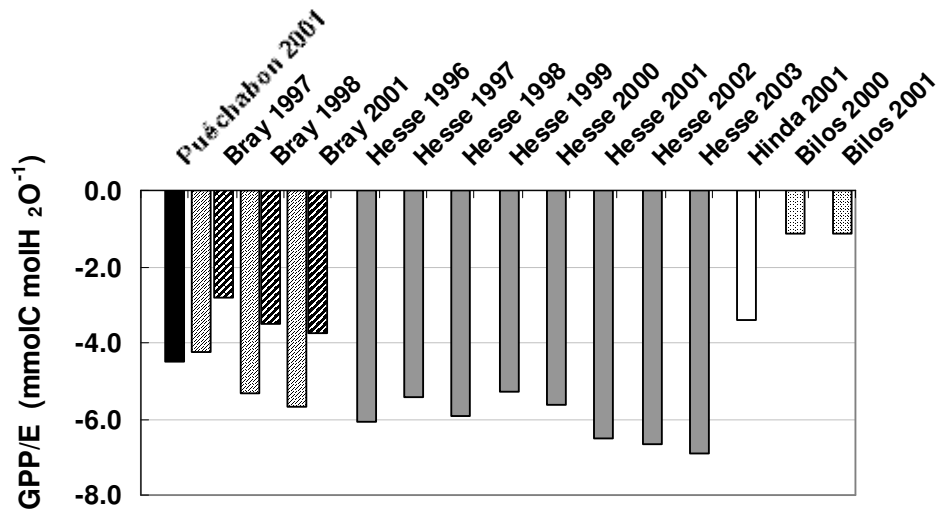


Figure 2 – 9. Canopy water use efficiency WUEc, calculated as GPP/E in 5 sites. At Le Bray, WUEc was calculated in two ways (see figure 2-8).

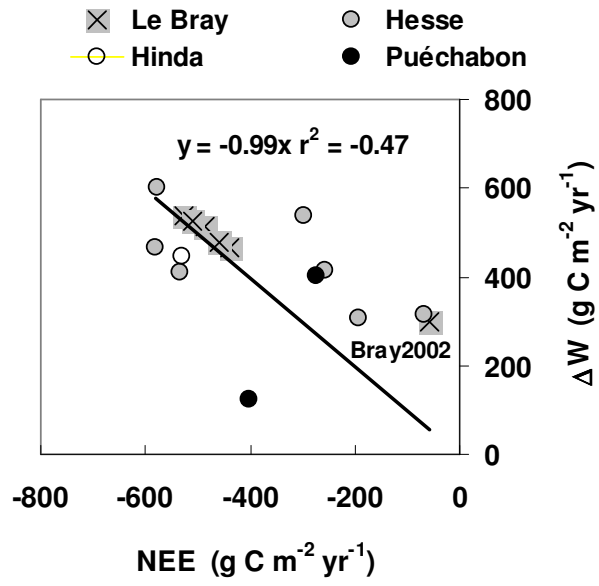


Figure 2 – 10. Relationship between the annual net carbon balance (*NEE*) and biomass increment of the stands.

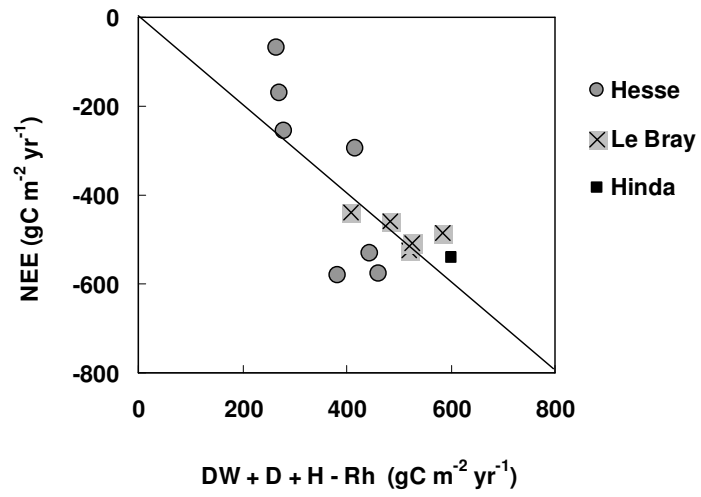
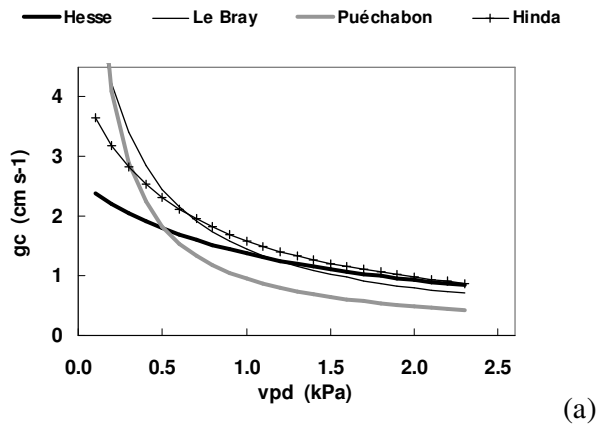
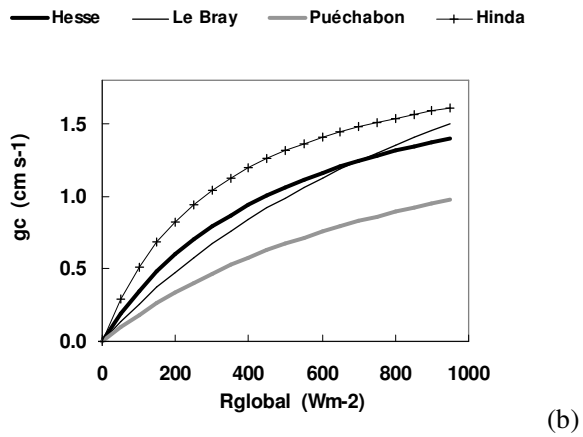


Figure 2 – 11. Relationship between the sum of biomass increment plus fine root and leaf production less the heterotrophic respiration ($\Delta W + D - Rh$) and the annual carbon balance (NEE).



(a)



(b)

Figure 2 – 12. Variation of canopy conductance to water vapour (g_c) for 4 Carbofor sites, fitted according to the equation [1]. Effects of air vapour pressure deficit at $R_g=900 \text{ Wm}^{-2}$ (a) and of global radiation (b) at $vpd=1\text{kPa}$.

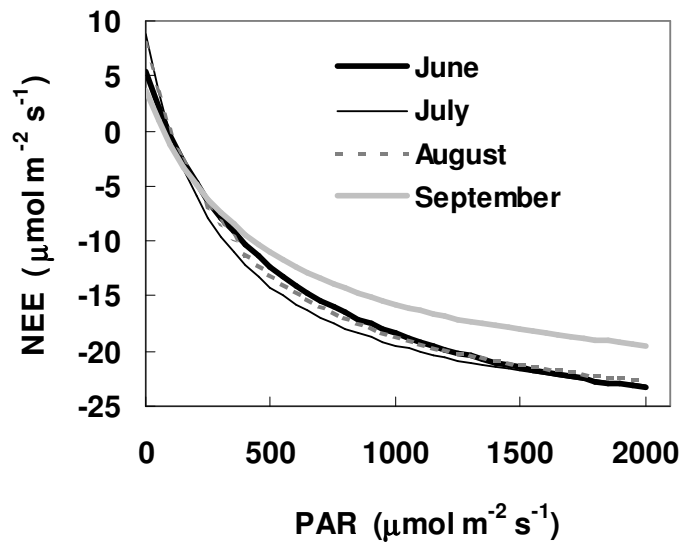


Figure 2 - 13 Variation of *NEE* as a function of PAR at Hesse for the June to September period in 2002 (wet year), from the model [2]. The coefficients of determination R^2 range between 0.6 and 0.7.

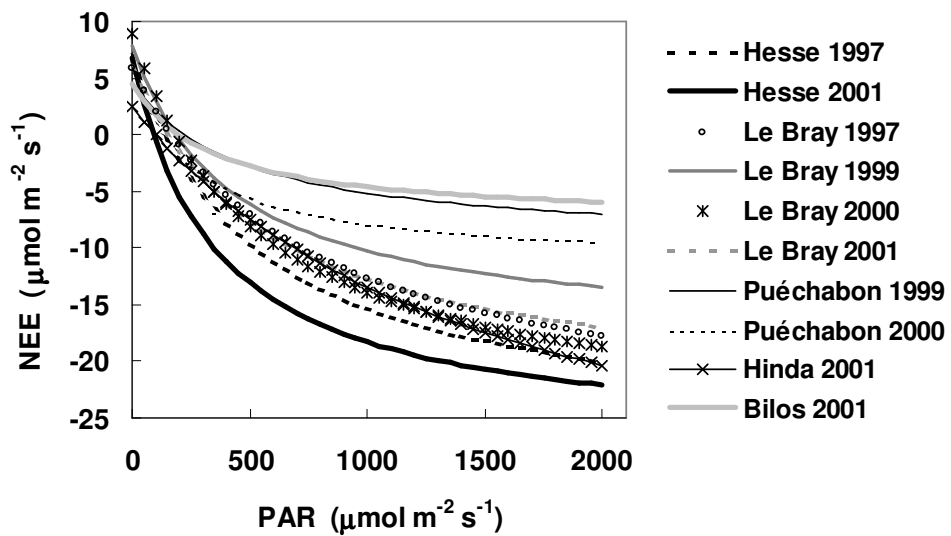


Figure 2 – 14. Variation of net ecosystem exchange (*NEE*) as a function of PAR during June in several sites and years. Curves are the best fits of equation [2], obtained for the June measurements. The coefficients of determination R^2 range between 0.6 and 0.7.

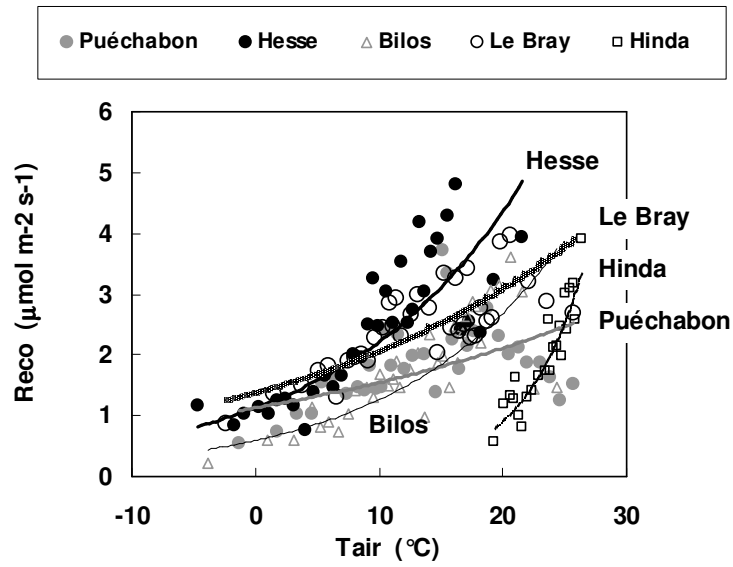


Figure 2 – 15. Relationship between ecosystem respiration (*Reco*, night measurements) and air temperature in 5 Carbofor sites, during 2001. Data points are bin averages of 10 measurements.

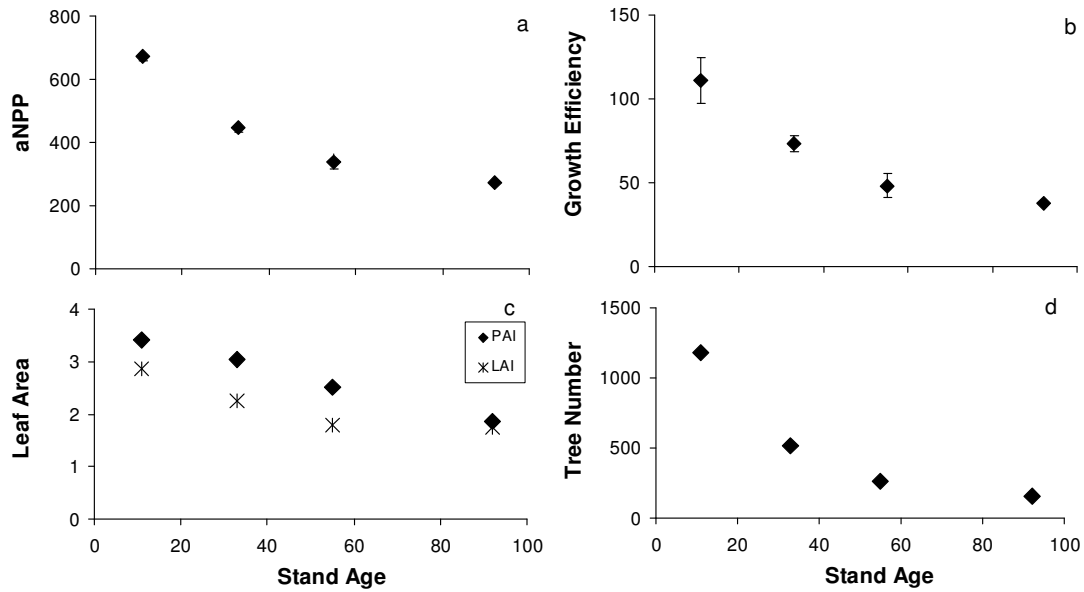


Figure 2-16. Changes in productivity as function of stand age in a maritime pine chronosequence in the Landes de Gascogne of south-western France, by various measures: (a) *aNPP* ($\text{gC m}^{-2} \text{yr}^{-1}$) represents above-ground Net Primary Production estimated using biomass increments and litterfall measurements per stand; (b) Growth Efficiency ($\text{gC m}^{-2} \text{yr}^{-1}$) corresponds to the above-ground annual tree biomass increment expressed per unit leaf area, (c) stand leaf area (LAI: Leaf Area Index and PAI: Plant Area Index; $\text{m}^2 \text{m}^{-2}$) and (d) Tree Number (ha^{-1}).

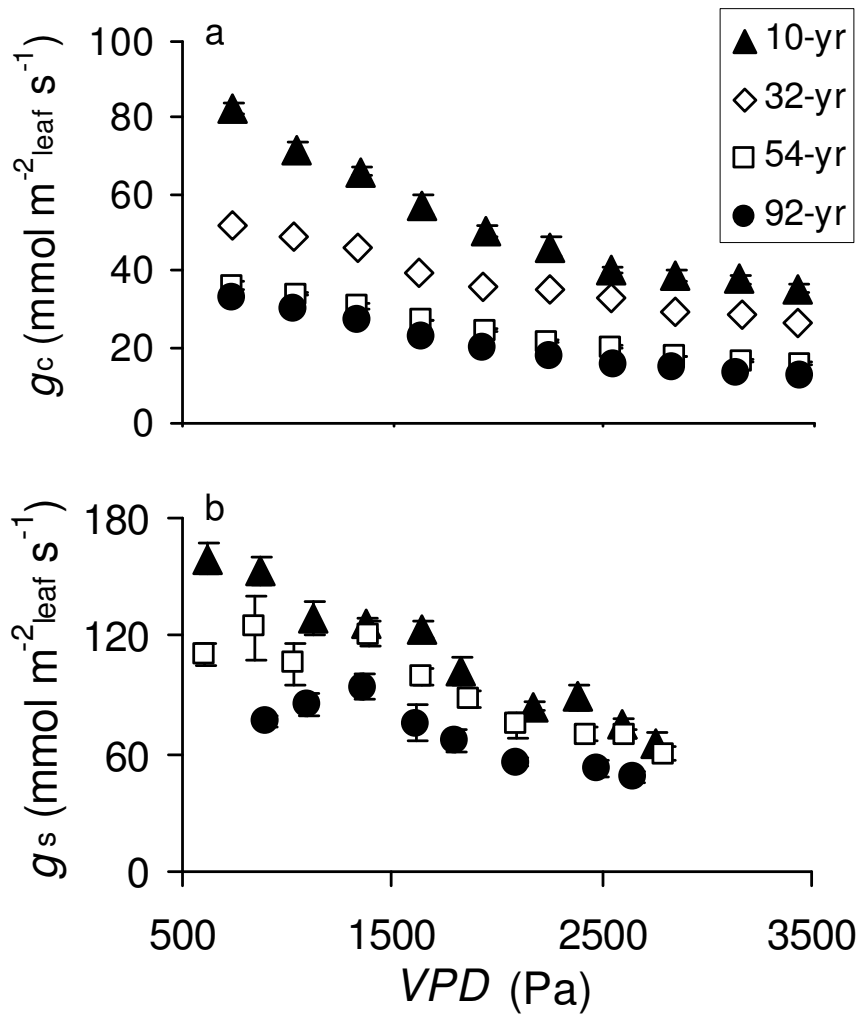


Figure 2-17. Mean values of canopy (a; g_c) and stomatal (b; g_s) conductance versus air vapour pressure saturation deficit (VPD) for four maritime pine stands of different age. g_c was determined from sap flow measured on six to seven trees per stand and g_s was measured on 1-year-old needles using a steady-state null balance porometer.