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Original article

Manipulating nutrient and water availability in a maritime pine plantation: effects on growth, production, and biomass allocation at canopy closure

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***Pinus pinaster* /**
stormdamage /
leaf area index /
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Abstract

• We present here the results of a water and nutrient manipulation experiment in a five-year-old plantation of maritime pine in south-western France.

• Water and nutrient levels were manipulated in a factorial design with two levels of irrigation (control receiving only rainfall (C) and irrigated (I)) and three levels of fertilisation (control with no added nutrients (C), P-only (P) and annual addition of a complete nutrient mix (F)) in order to quantify growth limitations of plantation forest in this particular area.

• The treatments applied during five years increased aboveground biomass annual increment by 4% (I) to 58% (IF) with respect to the control (C). The fertilised plots had a slightly non-significant lower root-to-shoot ratio. The effect of irrigation was maximal in 2002, resulting in 6%, 7% and 12% higher growth rate on the F, C and P plots, respectively. A windstorm disturbed the experiment in 1999 and has affected preferentially the fertilised plots, with IF plots displaying 60% damage.

• The higher growth rate of fertilised and irrigated plots was attributed to both an increase (estimated at 5 to 15%) in the amount of light absorbed by the canopy, and an increase (estimated at 26% for IF plots) in the amount of above-ground biomass produced annually per unit leaf area.

Mots-clés :
fertilisation /
irrigation /
optimisation de la nutrition /
***Pinus pinaster* /**
dégâts de tempête /
indice foliaire /
efficience de la croissance

Résumé – Manipulation de la disponibilité en eau et éléments minéraux dans une plantation de pins maritimes : effet sur la croissance, la production, l'allocation de la biomasse à la fermeture du couvert.

• Dans l'objectif de quantifier l'impact des facteurs limitant de la croissance du pin maritime dans le sud-ouest de la France, les apports d'eau et d'éléments minéraux sont manipulés selon un schéma expérimental factoriel à deux niveaux d'alimentation en eau (témoin recevant uniquement les pluies et irrigué) et à trois niveaux d'alimentation minérale (témoin, apport annuel de phosphore, apport annuel d'un mélange minéral complet).

• Les traitements appliqués pendant cinq ans ont entrainé une augmentation de l'accroissement annuel en biomasse aérienne allant de +4 % (I) à + 58 % (IF). Les arbres fertilisés ont un rapport biomasse aérienne sur racinaire légèrement mais non significativement supérieur à celui des arbres témoins. L'effet de l'irrigation a été maximal en 2002, avec des accroissements en biomasse aérienne plus élevés de 6 %, 7 %, 12 % pour les arbres fertilisés, témoins et fertilisés en P. Une tempête a endommagé le dispositif en 1999, affectant préférentiellement les arbres fertilisés avec 60 % des arbres touchés, contre 13 % pour les témoins.

• La plus forte croissance observée pour les placeaux fertilisés et irrigués a été attribuée à une augmentation d'une part de +5 à +15 % de la quantité de rayonnement absorbé par la canopée, et d'autre part de +26 % de la quantité de biomasse aérienne produite annuellement par unité d'indice foliaire.

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1. INTRODUCTION

Interest in the combined effects of fertiliser addition and irrigation on the primary productivity of forests has recently increased for areas in which long-term climate change may lead to longer, more severe summer droughts and in which the addition of fertiliser is already common, such as southern Europe (Loustau et al., 2005; Milne and Van Oijen, 2005). It has long been accepted that the availability of water and nutrient resources tightly controls forest productivity, but very few data quantifying the impacts of water and nutrients have been obtained (Benson et al., 1992; Jokela et al., 2004; Linder, 1987; Tamm, 1991).

These effects depend on the local climate and soil conditions, with irrigation having a more marked effect in Mediterranean-type climates, such as that of Australia. By contrast, fertilisation has the stronger effect on growth responses in the eastern USA and Sweden, where annual evapotranspiration rates are lower, and soil water storage capacity and precipitation levels are higher.

The application of various treatments combining irrigation and fertiliser in a 10-year-old stand of *Pinus radiata* D. Don in the pioneering Biology of Forest Growth experiment in Australia resulted in a 150% higher annual increase in stem volume for the best treatment (Snowdon and Benson, 1992). Other field experiments in which water and nutrient levels were manipulated showed that leaf area and production were greatly increased by the establishment of non-limiting conditions based on irrigation and fertilisation treatments. After ten years of nutrient optimisation, with or without irrigation, in young *Picea abies* (L.) Karst. stands, current annual stem volume increment (CAI) was increased by 366% in northern Sweden and 142% in southern Sweden (Bergh et al., 1999). In the south-eastern USA, the optimum fertilisation and irrigation of an eight-year-old *Pinus taeda* L. plantation doubled leaf area index (LAI) and increased CAI by 152% after four years of treatment (Albaugh et al., 1998). After eight years of treatment, fertilisation and irrigation had significantly increased standing stem mass, by 119% for fertilisation and 23% for irrigation (Albaugh et al., 2004).

In south-western Europe, the limitation of forest growth by water and nutrients has been quantified only for eucalyptus plantations in Portugal (Pereira et al., 1994). However, Maritime pine *(Pinus pinaster* Aït.), is the most widely planted forest tree species in this region (IEFC, 2002), covering 2.3 million hectares of intensively managed forest. The French "Landes de Gascogne" maritime pine forests account for 15.5% of the area under forest in France, 21% of national wood production, and 40% of softwood production (Lorette, 1996). The growth of these monocultures, established 150 years ago, is affected by nutrient and water limitations. These forests are mostly on sandy spodosols. These soils are highly acidic and have a low mineral nutrient availability, low cation exchange capacity and a superficial iron pan (Trichet et al., 1999a). The water regime is characterised by a permanent water table, fluctuating between the soil surface in winter and a depth of 1.8 m in summer, typically corresponding to a depth 1 m below the root layer, but the water balance is geographically variable (Loustau et al., 1999a). In the last 30 years of the 20th Century, the extension of drainage, tillage, phosphorus addition, vegetation control, and dynamic management practices increased the average productivity of this region from 4.8 m^3 ha^{-1} y^{-1} in 1960 to 11 m^3 ha^{-1} y^{-1} in 1998. However, the long-term productivity of maritime pine forests is predicted to decline in certain areas from 2050 onwards, due to the effects of increasing summer water deficit, in terms of both soil and atmospheric water (Loustau et al., 2005). More accurate quantitative data are therefore required concerning the combined effects of water and nutrient availability in a regional context.

We present here the results from a nutrient x water field experiment begun in 1998, in a five-year-old stand of maritime pine. We report the results obtained during the period preceding canopy closure, from 1998 to 2002. The objective of the experiment was to investigate the effects of water and nutrient availability on above- and belowground productivity. We also partitioned increases in growth and productivity into two productivity components: leaf area and light interception, and growth efficiency, which is the amount of above-ground biomass produced annually per unit leaf area.

2. MATERIALS AND METHODS

2.1. Study site

The site studied is located 20 km south-west of Bordeaux, France (44 ° 42' N, 0 ° 46' W), at an altitude of 60 m above sea level. Mean annual temperature is 13.2 °C and mean annual rainfall is 983 mm (1971–2000, Mérignac meteorological station, Météo-France). The soil is a sandy and hydromorphic humic podzol (spodosol) that has developed on an Quaternary Era aeolian sandy deposit. The water table fluctuates between a depth of 1.4 m in summer and 0.1 m in winter.

In spring 1993, after clear felling and site preparation (stump removal followed by ploughing to a depth of 0.3 m), the stand was planted with one-year-old maritime pine seedlings of local origin at a spacing of 4 × 2 m. The understorey was removed by chemical treatments in 1998 and 1999 and mechanically after 2001.

In December 1999, the site was severely damaged by a windstorm. A small number of trees were uprooted, but 37% of the remaining trees were left leaning by more than 20°. Within five months of the storm, the uprooted trees were cut down and the leaning trees were manually straightened up and secured with ropes tied around the bases of undamaged trees. Two years later, in December 2001, the ropes were cut and a few fallen trees were removed. The standing stocks (trees ha^{-1}) for each year and treatment are found in Table I.

2.2. Treatments and experimental design

The factorial combination of two irrigation (C, I) and three fertilisation regimes (C, P, F), resulted in six treatments (C, P, F, I, IP, IF), which were applied in a randomised complete block design with four replicates (blocks). Twenty-four rectangular plots, 60 × 36 m (0.216 ha) wide, were established within the five-year-old plantation in 1998. Plots were contiguous on the shorter axis, and separated by

Table I. Mean values (n = 4) for stocking, height, diameter at breast height, basal area (standing) and total cumulative production (standing + thinned) of stem volume (under bark), from 1997 (before treatment) to 2002. In the same column, values annotated with the same letter are not significantly different (P = 0.05) (Student Newman Keuls test after ANOVA, α = 0.05).

Year	Treatment	Stocking (Stems.ha^{-1})	Mean height (m)	Mean diameter (cm)	Basal area (m^2.ha^{-1})	Cumulative stem volume production (m^3.ha^{-1})
1997	IF	1232	4.5	8.2	6.7	10.4
	F	1233	4.4	8.0	6.4	9.8
	IP	1236	4.3	7.7	6.0	9.2
	P	1224	4.5	8.1	6.6	10.2
	I	1239	4.2	7.7	6.0	9.1
	C	1232	4.3	7.8	6.1	9.3
1998	IF	1230	5.7	10.0	9.8	18.0
	F	1233	5.5	9.5	9.0	16.5
	IP	1234	5.5	9.3	8.6	15.8
	P	1222	5.6	9.6	9.2	16.8
	I	1233	5.3	9.3	8.6	15.6
	C	1232	5.4	9.3	8.6	15.6
1999	IF	1230	7.0	12.6 a	15.7 a	34.5 a
	F	1233	6.6	12.2 ab	14.7 ab	31.8 ab
	IP	1234	6.6	11.7 ab	13.7 ab	29.4 ab
	P	1220	6.7	11.9 ab	13.9 ab	30.0 ab
	I	1231	6.4	11.2 b	12.4 b	26.5 b
	C	1232	6.5	11.2 b	12.3 b	26.2 b
2000	IF	1069	8.0 a	14.5 a	18.0	50.2 a
	F	1112	7.6 b	14.2 ab	17.8	47.8 a
	IP	1154	7.6 b	13.8 ab	17.5	45.4 ab
	P	1162	7.9 ab	13.9 ab	18.0	46.2 ab
	I	1210	7.6 b	12.9 b	16.1	39.7 b
	C	1214	7.6 b	12.9 b	16.1	39.4 b
2001	IF	1060	9.2 a	16.3 a	22.7	69.3 a
	F	1107	8.5 b	15.9 a	22.3	66.1 a
	IP	1143	9.0 a	15.6 a	22.1	63.8 a
	P	1154	8.9 a	15.4 a	22.1	63.2 a
	I	1192	8.5 b	14.4 b	19.8	55.0 b
	C	1207	8.5 b	14.2 b	19.6	53.8 b
2002	IF	969	10.0 a	18.0 a	25.1	88.7 a
	F	1038	9.6 b	17.4 ab	25.0	84.6 a
	IP	1125	9.6 b	16.9 ab	25.9	82.8 a
	P	1110	9.6 b	16.7 b	24.9	80.4 a
	I	1180	9.2 c	15.5 c	22.8	70.3 b
	C	1199	9.4 bc	15.3 c	22.5	68.3 b

a 6 m path on the longer axis. This experiment covered a total area of 5.8 ha. Measurements and growth data for the various treatments are shown in Table I. Trees at the edge of the plot were not used for measurement, to avoid edge effects; the effective net plot size was therefore 50 × 28 m (0.14 ha and 170 trees).

The nutrient treatments were optimum nutrition (F), addition of P only (P), and control (C). The optimum nutrition treatment was defined as maintaining dormant season foliar nitrogen concentration at 13 mg N per g^{-1} dry mass (d.m.), and other macronutrients in balance with N to maintain element-N ratios of 0.1 (P), 0.37 (K), 0.12 (Ca), and 0.06 (Mg) (cf. Adams and Allen, 1985, Hüttl, 1986; Linder, 1995). The nutrients were applied annually as a complete mixture of macro- (N, P, K, Ca, Mg) and micronutrients (B, Cu, Mn, Zn) (Table A in Appendix). The P treatment was consistent with "common practice" in the "Landes de Gascogne" area and involved the annual application of super-phosphate to maintain foliar P concentration at 1.2 mg g^{-1} (d.m.). The control plots (C and I) received no fertiliser. Fertilisers were applied in early July during the first year, and during the third week of March in all other years.

Half of the plots were irrigated (I, IP, IF,) from May to October with about 6 mm day^{-1}of water, based on average potential evapotranspiration for the region. The water was pumped from a depth of 35 m and distributed at night via sprinklers, placed 0.3 m above ground level in a 8 m × 8 m grid. No irrigation was carried out in 2000, because the major windstorm in December 1999 impeded the drainage of surface water, which remained close to the surface of the soil throughout the year. During the experiment, mean annual growing season precipitation for the 1971 to 2000 period was 526 mm y^{-1}; an excess of more than 100 mm was observed in 1998 and 1999, and a deficit of 150 mm was observed in 2002. The annual amount of water added varied within the range 800–1200 mm during the 1998 to 2001 period, due to different start dates and durations of the irrigation period.

2.3. Tree measurements

In December and January, between 1997 and 2002, the circumference at breast height (1.3 m), was measured on all trees. From 1997 to 1999, a complete tree height inventory was carried out annually. From 2000 onwards, individual heights were estimated using a regression-based model developed from 30 trees per plot. The sample trees were chosen from the plot diameter distribution, and parameters b_1 and b_2 of Equation (1) below were fitted, linking circumference and height for each treatment (Richards, 1959; Chapman, 1961). Thereafter, Equation (1) was applied to all measured circumferences.

$$H = 1.30 + a_1[1 - \exp(-b_1 \times C)] \quad (1)$$

where H is height, C is circumference at breast height (1.3 m), and $a_1$and b_1 are coefficients determined using the SAS procedure NLIN (SAS Software, 2002).

Assessment of the damage caused by the windstorm in December 1999

In December 1999, the experiment was partly damaged when the south-western part of France was hit by a high-intensity storm moving from west to east at a speed of 100 km h^{-1}, with horizontal wind speeds peaking at 144 km h^{-1} (Bordeaux-Mérignac weather station, Météo-France). The damage to each tree in the experiment was assessed, based on measurements of the angle of the stem from the vertical.

2.4. Needle nutrient concentrations

Current-year needles were collected in January each year from six (1997 to 2001) to nine (2002) codominant trees chosen from the three central rows of each plot. We sampled 30 to 40 fascicles from the central part of a lateral south-facing shoot from the upper third of the crown. These fascicles were dried at 65 °C and ground. In 2001 and 2002, a pair of needles was used for determination of the needle area to mass ratio. Before drying and weighing, total needle area was calculated from needle diameter and length, assuming a semi-cylindrical shape.

Nutrient levels were analysed after digestion in sulphuric acid and hydrogen peroxide. Nitrogen and phosphorus were determined colorimetrically with a Technicon auto analyser II, as described by O'Neill and Webb (1970), and potassium, calcium, and magnesium were determined with a Varian SpectrAA-20 flame atomic absorption spectrophotometer.

2.5. Biomass measurements

Tree biomass was estimated in January 1997, before the treatments began, and was re-assessed in January 2001 and January 2004, three and six years after the start of treatment.

In 1997, 30 trees representative of the stand height distribution were harvested, as described by Porté et al., (2002). The root systems were mechanically extracted from the soil and the biomass of the stump and coarse roots was calculated (Danjon et al., 1999). The fine root (diameter less than 2 mm) biomass was estimated from a sample of 96 soil cores (9.2 cm diameter, 60 cm depth). Cores were taken from within and between tree rows to take spatial variability into account.

In 2001, we sampled one tree per plot, representative of the average diameter and height per plot, corresponding to a total of 24 trees. Each tree was cut at ground level, separated into buds and cones, one-, two-, and three-year-old needle cohorts, branches, and stem. The samples were dried at 65 °C until constant weight was reached and were then weighed accurately. Stem biomass was separated into bark and wood, and a wood-to-bark biomass ratio was determined from four 10 cm-thick stem disks sampled at ground level, and at the base, middle, and top of the crown. Below-ground biomass was estimated as the sum of two components: (1) the biomass of the roots located within a 4 m^2 square area centred on the stem, determined for each tree by uprooting the stump and attached roots and sieving all soil material down to a depth of 0.6 m, and (2) in the remaining peripheral area, root biomass was estimated by obtaining four soil sample cores 92 mm in diameter and extending to a depth of 0.6 m. The effects of the treatments on tree allometry were assessed using a set of allometric equations relating the biomass of each tree component, W_i, where i corresponds to foliage, branches, bark and stem wood, to diameter at 1.3 m height, D, parameterised using the measured biomass data. The equations were:

$$W_i = a_2 D^{b2} \quad (2)$$

where a_2 and b_2 are the parameters to fit. The effects of treatments on these parameters were analysed for the 2001 data, by covariance analysis after the log transformation of Equation (1) (PROC GLM, SAS Institute, v8.2, 2002).

The same protocol was followed in 2004, except that 30 trees were chosen, five for each treatment, according to stem diameter distribution within each treatment.

2.6. Estimation of annual biomass and volume production, and LAI

The standing tree biomass W was estimated for every year from 1997 to 2002, using the allometric model, modified by Porté et al., (2002), as follows:

$$W = a_3 D^{b3} Age^{c3}. \quad (3)$$

Treatment did not affect the parameters a_3 and b_3 (see Sect. 3). The data collected in 1997, 2001 and 2004 were therefore pooled and a single set of values for parameters a_3, b_3 and c_3 was estimated by non-linear regression. These parameters were calculated for each biomass component and for entire tree biomass. Annual biomass production from 1997 to 2002 was calculated as the difference in standing biomass between two consecutive years.

Stem wood volume was calculated by dividing stem wood biomass by its specific gravity. No data were available concerning treatment and age effects on wood density, so a density value of 440 kg m^{-3} was used for all treatments and years (Delzon et al., 2004a).

The total needle area per tree was estimated from the needle biomass and specific leaf area (SLA) data obtained in 2001 and 2002. The mean SLA values for each treatment obtained in 2001–2002 were extrapolated to previous years for which no such data were available. The LAI was calculated as defined by Chen and Black (1992). For a given growing season, average annual LAI was defined as the mean value for two consecutive years. Above-ground and stem wood biomass growth efficiencies were calculated as the ratio of annual increase in biomass to annual mean LAI.

2.7. Statistical analysis

For all variables studied, the statistical significance of the block, fertilisation, irrigation, and interaction effects were tested, using the SAS-GLM procedure for analysis of variance (PROC GLM, SAS Institute, v8.2, 2002). We initially assessed interactions between block and fertilisation; these interactions were removed from subsequent analyses as they were found not to be significant for the variables tested.

For the analysis of variance for tree biomass components, an arcsine transformation was used, to make it possible to carry out statistical analyses on proportions (Dagnélie, 1975). Storm damage data were analysed by chi-squared tests. The allometric parameters of Equation (1) were calculated by non linear regression analysis, using the least-squares criteria of the NLIN procedure (SAS Institute, v8.2, 2002).

3. RESULTS

3.1. Needle nutrient concentrations

From 1998 onwards, the F treatment significantly increased needle N levels to the target value of 13 mg g^{-1} (d.m.) (Fig. 1). Unexpectedly, in 2000 and 2001, needle N levels on control plots reached a level close to that observed with complete fertilisation in 2000. We assume this was due to the lateral transport of mobile elements, such as nitrogen, between adjacent plots, either in the water table or by the cross-feeding of roots and root interconnections. In plots subjected to the P treatment, N levels remained low and no significant trend over time was observed. In 2002, the amount of nitrogen added was increased to 160 kg N ha^{-1} and needle N levels on F plots consequently increased to 15 mg g^{-1}, levelling off slightly below 13 mg. g^{-1} on control plots. Irrigation significantly decreased needle N content in 1999 and 2002, with a severe drought recorded in 2005 (Delzon et al., 2005). For most treatments in which fertiliser was applied, foliar P concentration also reached the target value of 1.2 mg g^{-1}. This value was maintained from 1998 onwards, with the exception of the year following the suspension of treatment (2001) in which P levels fell to 10 mg g^{-1}. This immediate response to the interruption of treatment shows that internal storage did not buffer the variation in nutrient availability.

One year after the initial fertiliser addition, only the P/N ratio was affected by the treatments. During subsequent years, fertiliser had an effect on all nutrient ratios (Fig. 2). In the complete fertilisation treatment (F), the needle concentrations of K, Ca and Mg were higher, such that target P/N Ca/N and Mg/N nutrient ratios were attained after two years of application, regardless of irrigation status. The overall effect of irrigation on nutrient ratios was to decrease K/N ratios in 1999 and 2002, and to increase P/N ratio for the complete fertilisation treatment (IF).

3.2. Individual tree biomass (2001)

Irrigation had no significant effect on any of the biomass components and its interaction with fertilisation was not significant. The fertilisation treatments, F and P, increased individual tree biomass by 32% and 16%, respectively (Fig. 3), affecting all biomass components. Current-year foliage and branches were the biomass components most affected by the treatments. P treatment increased bud biomass by 52%, needle biomass by 32%, living branch wood biomass by 35%, stem wood biomass by 11% and stump and coarse root biomass by 34%. F treatment increased bud biomass by 50%, needle biomass by 68%, living branch wood biomass by 63%, stem wood biomass by 13%, and stump and coarse root biomass by 57%. Root-to-shoot biomass ratio was highest for the irrigated control trees, however, the difference in root-to-shoot biomass ratio was not significant, due to the small number of replicates.

No treatment effect was found for the allometric coefficients a_2 and $b_2$in the material collected in 2001. This was true for all biomass components — foliage, branch wood, stem wood, roots, and bark — and for total biomass. A single set of allometric coefficient values was subsequently used to estimate the biomass of the different parts of the tree, at both individual tree and plot levels (Tab. II).

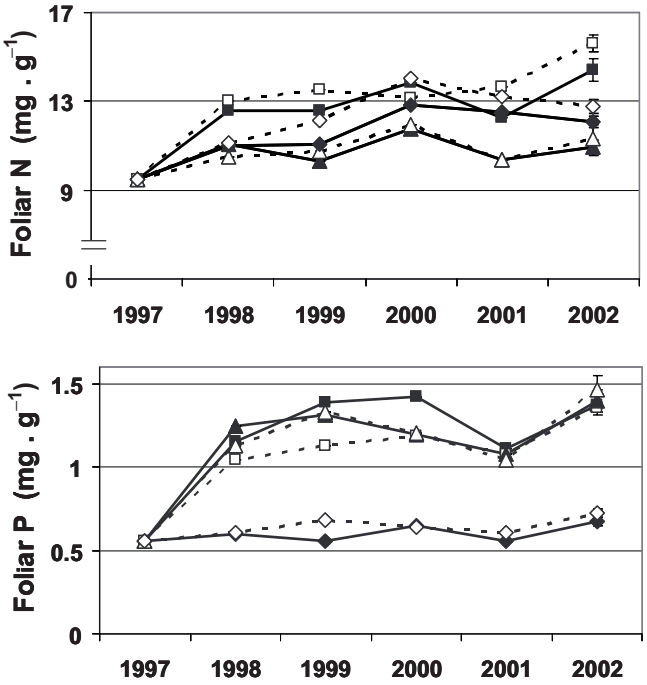


Figure 1. Dormant season foliar N and P concentrations for each treatment, from 1997 to 2002. The treatments were IF (closed square, solid line), F (open square, dotted line), IP (closed triangle, solid line), P (open triangle, dotted line), I (closed diamond, solid line), C (open diamond, dotted line). Mean values are shown and vertical bars indicate standard errors (n = 4).

3.3. Storm damage

Fertilisation increased the impact of storm damage whereas irrigation had no significant interaction on storm damage (Fig. 4). The proportion of trees uprooted by the wind or

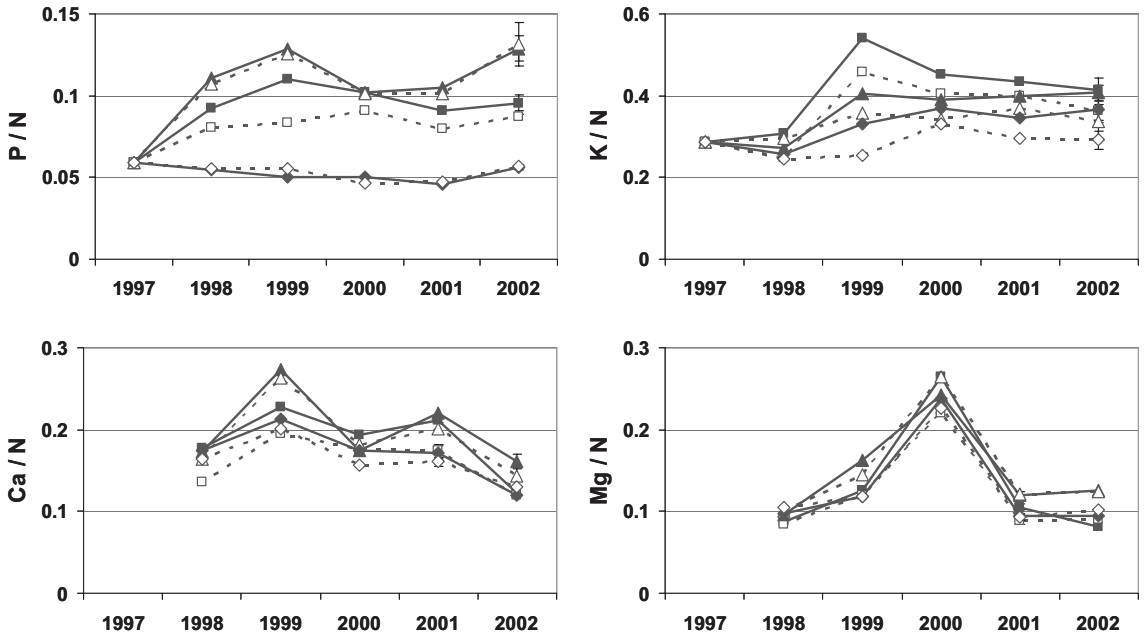


Figure 2. Dormant season P/N, K/N, Ca/N, Mg/N foliar concentration ratios for the fertilisation x irrigation treatment combinations, with P, K, Ca, Mg expressed in per cent N (by mass). In 2000, no treatments were applied. The treatments were IF (closed square, solid line), F (open square, dotted line), IP (closed triangle, solid line), P (open triangle, dotted line), I (closed diamond, solid line), C (open diamond, dotted line). Bars show one standard error of the mean.

Table II. Parameters of the allometric model $W_i = a_3 D^{b3} Age^{c3}$ (Eq. (3)) where W_i is the above-ground biomass and stem wood, bark, branch wood or needle biomass (kg tree^{-1}), D (mm) the stem diameter at 1.3 m height and Age the age of the trees (years). The parameters were determined by non linear regression, using the biomass data obtained in 1997, 2001 and 2004 (total number of trees = 84). Asymptotic standard errors are given in brackets.

	a_3 (kg.mm^{-1}.year^{-1})	b_3	c_3	$P > F$
Above-ground biomass	4.7×10^{-4} (1.8×10^{-4})	2.1 (0.1)	0.3 (0.2)	< 0.0001
Stem wood	3.8×10^{-5} (1.7×10^{-5})	2.3 (0.1)	0.8 (0.2)	< 0.0001
Bark	4.1×10^{-3} (1.7×10^{-3})	1.9 (0.1)	ns	< 0.0001
Branch wood	1.0×10^{-4} (6.4×10^{-5})	1.9 (0.1)	0.9 (0.3)	< 0.0001
Needles	1.7×10^{-2} (7.7×10^{-3})	1.9 (0.2)	–1.5 (0.3)	< 0.0001

leaning heavily was significantly higher for plots with optimal or P fertilisation. The trees on F treatment plots were larger than the control trees and were more strongly affected by the storm. Stand density was decreased by 120 to 160 trees ha^{-1} for F treatment plots and by 20 to 80 trees ha^{-1} for other treatments. The proportion of trees with broken stems was not influenced by fertilisation.

Trees that did not recover from storm damage were felled later in 2002, further reducing stand density by 70 to 90 trees ha^{-1} for F treatments, and 10 to 50 trees ha^{-1} for other treatments (Tab. I). Storm damage resulted in an underestimation of the effects of treatments for both data average spatially and data averaged on an individual tree basis. Data calculated on the basis of ground area, such as increases in volume and biomass, decreased most strongly on plots displaying the greatest decrease in stand density (plots subjected to F fertilisation). The effect of fertilisation, as averaged over the remaining trees, on mean diameter, mean height, and annual increments, was also biased because the storm preferentially damaged larger trees.

3.4. Stand growth and production

Only small effects of treatment were observed one year after the first nutrient application in 1998, but larger differences in the annual increase in stem wood and biomass were observed in 1999. The combined fertilisation and irrigation (IF) treatment increased the annual increment in above-ground biomass by 58% and stem wood production by 55% with respect to the control (Fig. 5). From 1999 onwards, storm damage reduced the effect of treatment, giving an overall gain in above-ground biomass increment over 1997–2002 of 34%.

As expected, treatment had no effect on mean tree size or stand production after one year, but significant differences

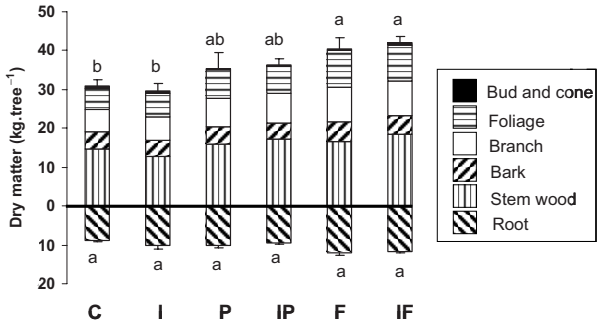


Figure 3. Mean dry matter of biomass components in mean trees for each treatment (n = 4) three years after the start of the experiment. Each bar is the mean value of four trees per treatment. Letters above and below each bar indicate significant differences between treatments for total above- and below-ground biomass, respectively (SNK test after ANOVA, α = 0.05).

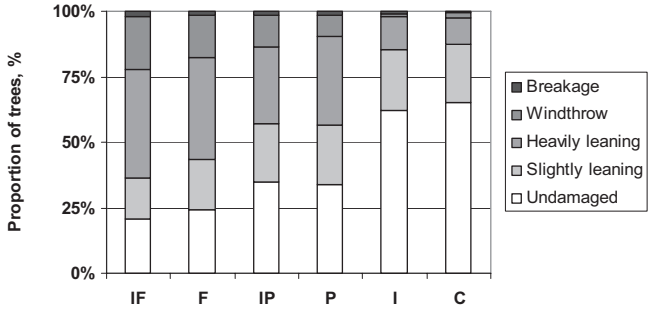


Figure 4. Mean proportion of trees (n = 4) per damage class after the 1999 windstorm. The damage classes are: undamaged; 0° < leaning angle (LA) < 9°; slightly leaning: 10° < LA < 19°; heavily leaning: 20° < LA < 59°; windthrow: LA > 60°; breakage: stem broken.

appeared after two years, for all variables except height (Tab. I). In 1999, P treatment increased cumulative stand production by 13%, with F treatment increasing stand production by an additional 12%, suggesting that P and the other nutrients were equally limiting for productivity. Significant differences in stem height, diameter, and stand production were observed in 2001 and 2002, following the interruption of treatment due to the storm. In 2002, P fertilisation increased stand production by 19% and the application of other nutrients gave an additional increase of 8% with respect to control plots. Irrigation had a smaller effect on biomass production, but this effect was significant for all years except 1998 and 2000. In 2002 — the driest year of the period — the gain in production due to irrigation reached 6, 7 and 12% for the C, F and P fertilisation treatments, respectively.

3.5. Productivity and leaf area index (LAI)

LAI was increased by treatment, due to an increase in needle biomass, but not through changes in leaf area-to-mass ratio, which differed only slightly from that of the control (data not shown). F treatment increased LAI by 15% in 1998, 28%

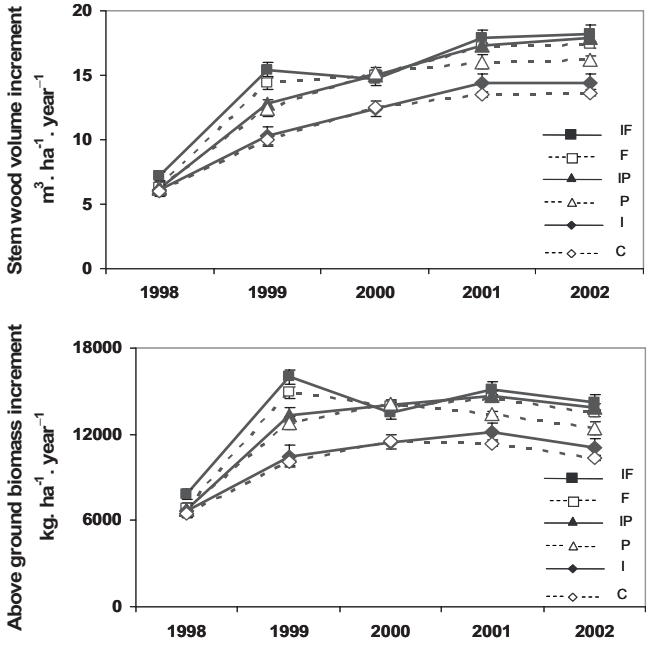


Figure 5. Annual increases in stem wood biomass and above-ground biomass from 1998 to 2002. Each symbol is the mean value per treatment (n = 4). Bars give the standard error of the mean.

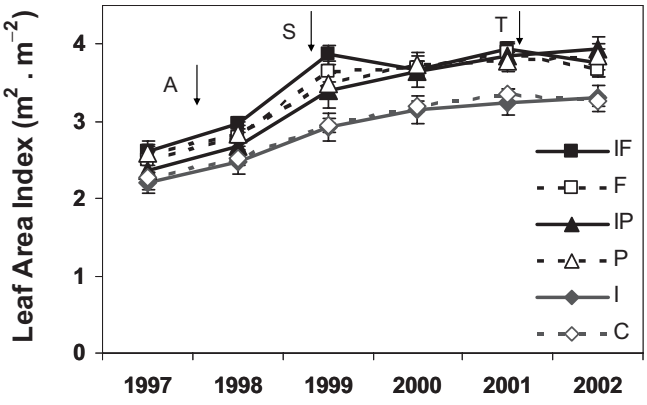


Figure 6. Mean leaf area index for each treatment (n = 4 replicates) from 1997 to 2002. First treatment application (A) in 1998, windstorm in 1999 (S) and post-storm thinning in 2001 (T) are indicated with arrows.

in 1999, 16% in 2000, 19% in 2001 and 13% in 2002, with respect to the control value which was 3.2 in 2002 (Fig. 6). P treatment increased LAI by 10% in 1998, 18% in 1999, 16% in 2000, 16% in 2001, and 18% in 2002. Irrigation had no significant effect on LAI during this period.

Above-ground biomass growth efficiency peaked for all treatments in 1999, and decreased thereafter (Fig. 7). The F treatment increased growth efficiency by 26% in 1999, 11% in 2001 and 19% in 2002, with respect to the control value which was 0.35 kg.m^{-2}/unit of LAI in 1999. Irrigation (for all fertilisation treatments considered together) increased growth efficiency by 8% in 2001 and 2002.

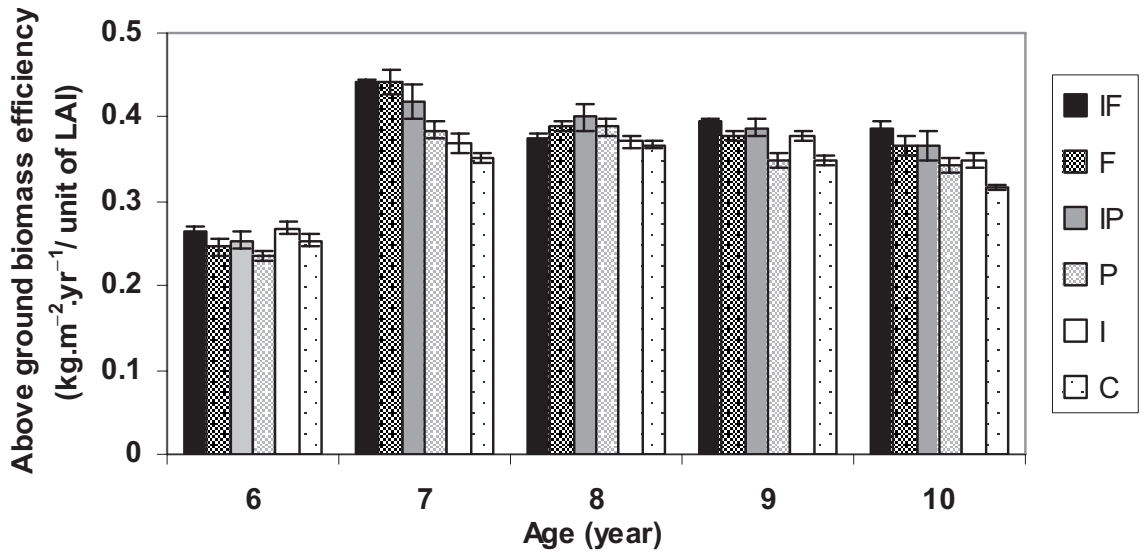


Figure 7. Mean values (n = 4) for above-ground biomass growth efficiency from 1998 to 2002. Bars show the standard error of the mean.

4. DISCUSSION

Our results document growth dynamics due to fertilizer and irrigation treatments during the period of stand development preceding canopy closure. Mean tree biomass, for all treatments combined, increased from 12.8 to 71.8 t ha^{-1} during the period reported, 1998–2002. The annual increase in above-ground biomass increased from 1998 to 2000, peaked in 2001 and levelled off from 2002 onwards (data not shown). This suggests that a period of maximal growth was reached at the end of the study. This finding was confirmed by the pattern observed for LAI, which was almost maximal in 2002. LAI was still increasing slightly in 2002, but had already exceeded a value of 3.0 for control plots, this value being higher than that typically found in mature stands of fertility class-1 (Delzon and Loustau, 2005), and exceeded 3.9 for fertilised plots (Fig. 6).

The fertiliser treatments successfully kept foliar nutrient levels close to target concentrations. N levels for the foliage of control trees (11 to 13 mg g^{-1}) were high with respect to values available for this region — typically from 9 to 12 mg g^{-1} (cf. Bonneau et al., 1968; Loustau et al., 1999a; Saur, 1989). The foliar P content of the control trees, 0.6–0.7 mg g^{-1}, is typical of values observed in unfertilised stands in this area (Loustau et al., 1999a, Delzon et al., 2005) and is close to the critical values at which the P-induced limitation of photosynthesis has been observed (Loustau et al., 1999b). These results confirm that P is a growth-limiting nutrient at this experimental site.

The doubling in N fertiliser input in 2002 led to foliar N concentration reaching 1.5 g g^{-1}, corresponding to the upper limit of the optimal value assumed for maritime pine (Bonneau, 1995). The P/N ratios of the P-fertilised trees were close to 0.125, exceeding the value obtained by Adams and Allen (1985) for a loblolly pine plantation in the south-eastern USA (P/N ratio of 0.1), and the recommended target value for field-grown trees (Hüttl, 1986; Linder, 1995). Similarly, K/N ratios exceeded 0.35–0.4 for trees given the optimal fertilisation treatment and were below recommended target values for the control trees (cf. Adams and Allen, 1985; Bonneau, 1995; Hüttl, 1986; Linder, 1995).

The optimal fertilisation and irrigation treatment increased above-ground biomass increment, with growth responses up to 58% that of the control. This value is lower than that reported for plantations of young conifers in the south-eastern USA, where nutrient optimisation increased biomass growth by 130 and 177% (Albaugh et al., 1998) and in Sweden, where growth was increased by 142% to 366% (Bergh et al., 1999). These differences may reflect differences in initial site fertility and climate, as well as the responsiveness of the species to nutrient treatments.

The strong and significant effect of P and F treatments showed that nutrients other than P limit maritime pine production in the Landes de Gascogne region. The additional effect of complete nutrient addition was similar to that of P fertilisation alone. In a previous experiment, Gelpe and Guinaudeau (1974) observed similarly that treatments with N and K in addition to P led to a significant increase in vertical growth with 58%, 22%, and 21% greater height responses reported after 2, 6, and 16 years, respectively.

The marginal effect of irrigation may be accounted for by the high levels of precipitation observed in the first three years of the experiment. Growing season water deficit (rainfall minus Penman's evaporation) was close to zero in 1998 and 1999, at 16 and 36 mm, respectively, but reached 192 and 303 mm in 2001 and 2002, respectively. This accounts for the effect of irrigation becoming significant only in 2002. A larger effect might be expected under the standard climatic conditions in this area.

The response of planted forest stands to the addition of water and nutrients is variable and depends on seasonal site water balance and initial soil fertility (McMurtrie et al., 1990). Our experimental conditions were different from those of the

Biology of Forest Growth experiment in Australia (Benson et al., 1992), in which irrigation had a greater impact because severe water stress occurred during the foliage expansion period (Linder et al., 1987). Our site was closer to the SETRES experiment (Albaugh et al., 1998), or studies in Sweden (Bergh et al., 1999), in which irrigation had little or no effect.

The effects of treatment on growth and biomass production, as assessed in our experiment, may underestimate the actual effects of optimal fertilisation because first, the control trees grew faster than available local references (Lemoine and Decourt, 1969; Lemoine et al., 1986) and second, the 1999 storm affected the fertilised plots and control plots differently, with the fertilised plots more severely affected. This impact is clearly shown by the deviation from the expected trajectory of LAI and biomass increment for all plots other than control in 1999 (Figs. 5 and 6).

Regarding the process involved in the response to treatments, it is clear that the effects on growth and production observed cannot be entirely attributed to differences in LAI and the amount of light intercepted. The difference in LAI between fertilised and control plots ranged between 0.4 and 1.0 units of LAI, corresponding to a potential relative increase of 5 to 15% in the amount of visible light intercepted annually by the tree canopy as estimated using a light extinction coefficient of 0.47 (Berbigier and Bonnefond, 1995). This cannot entirely account for the additional annual increment in biomass observed (58% in 1999 for IF), implying an important role of the 26% increase in growth efficiency in 1999 for IF (Fig. 7), and changes in carbon allocation between the parts of the plant above and below ground.

In 2002, stem volume growth efficiency was 4.1 m^3 ha^{-1} $year^{-1}$ per unit LAI for control trees and 5.0 m^3 ha^{-1} $year^{-1}$ per unit LAI for trees on optimally fertilised and irrigated plots. These values are lower than those reported by Albaugh et al., (1998) for loblolly pine (7.1 m^3 ha^{-1} $year^{-1}$ for control and 9.2 m^3 ha^{-1} $year^{-1}$ per unit LAI for the irrigated and fertilised plots) or Vose and Allen (1988) for nine-year old loblolly pine plantations (6.7 m^3 ha^{-1} $year^{-1}$ for control and 7.5 m^3 ha^{-1} $year^{-1}$ per unit LAI for the fertilised plots). The decline in biomass growth efficiency observed during the course of this experiment may be due to mutual shading, resulting from the higher LAI in 2002 (Jarvis and Leverenz, 1983).

The improvement in biomass growth efficiency on fertilised and irrigated plots can be attributed to an increase in leaf photosynthetic capacity in fertilised trees and a decrease in stomatal limitation due to the effects of drought in irrigated trees. P addition may be particularly important in this respect, as Loustau et al., (1999b) and Delzon et al., (2005) demonstrated a positive relationship between needle P concentration and photosynthetic capacity within a range of values similar to those reported here. The improvements in nitrogen status lead to improvements in photosynthetic performance in many cases (cf. Coll et al., 2007 Linder and Rook, 1984; Teskey et al., 1994). For maritime pine, Medlyn et al., (2002) found that seasonal changes in photosynthetic capacity were related to needle N content in 18- and 29-year-old trees.

We could not evidence any difference in tree allometry among treatments. The significant shift from below-ground to above-ground biomass allocation with fertiliser application therefore suggests that treatments increased growth rather than changing tree ontogeny. This shift in allocation may account for the increase in stem growth efficiency from 1998 to 2002, and the higher efficiency observed in fertilised trees. For above-ground biomass, the proportion of total above-ground biomass consisting of woody tissues (76%) and needles (22%) were similar to those reported by Gower et al., (1994), for 11 young temperate pine stands, with average values of 83% and 17%, and by Albaugh et al., (1998) for nine-year-old *Pinus taeda*, with average values of 76% and 24%, respectively. For below-ground biomass, the average root/shoot ratio of 0.29 is similar to the value of 0.26 reported by Albaugh et al., (1998) for nine-year-old *Pinus taeda*, and to the root/shoot ratio of 0.25 measured by Ritson and Sochacki (2003) in closely spaced maritime pine, for a similar range of shoot biomass values.

We interpret the higher sensitivity of fertilised trees to wind as resulting from an imbalance between above- and below-ground parts of the plant due to the fertilisation. Fertilised plantations have already been shown to have a greater sensitivity to wind, for a number of species, including Monterey pine (Barker, 1978), Scots pine and Norway spruce (Hirvela and Hynynen, 1990; Laiho, 1987), and maritime pine (Lefrou, 1979). The lower resistance to wind of N-fertilised plantations is commonly accounted for by higher levels of foliage and branch production. Our results are consistent with this hypothesis, with 60%, 43%, and 13% of trees on F, P, and C plots, respectively, damaged, and trees subjected to optimal or P addition having 62% more branch biomass and 30% more needle biomass than control trees. Lefrou (1979) made a similar observation in a fertilisation experiment on mature maritime pine trees after the 1977 storm in south-western France.

Our results demonstrate that, given the site fertility and climate of the "Landes de Gascogne", growth appears to be limited primarily by nutrients (P and other major elements) and secondarily by water. The observed increase in stand biomass production at canopy closure may be attributed to increases in leaf area and above-ground biomass growth efficiency.

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REFERENCES

Adams M.B. Allen and H.L., 1985. Nutrient proportions in foliage of semi-mature loblolly pine. Plant Soil 86: 27–34.

Albaugh T.J. Allen H.L. Dougherty, P.M. Kress, L.W., and King, J.S., 1998. Leaf area and growth responses of loblolly pine to nutrient and water additions. For. Sci. 44: 317–328.

Albaugh T.J., Allen H.L., Dougherty P.M., and Johnsen K.H., 2004. Long term growth responses of loblolly pine to optimal nutrient and water resource availability. For. Ecol. Manage. 192: 3–19.

Barker J.E., 1978. Some sylvicultural effects of fertilisation. N.Z. J. For. Sci. 8: 160–177.

Berbigier P., and Bonnefond J.M., 1995. Measurement and modelling of radiation transmission within a stand of maritime pine (*Pinus pinaster* Ait.). Ann. Sci. For. 52: 23–42.

Bergh J., Linder S., and Lundmark T., Elfving, B., 1999. The effect of water and nutrient availability on the productivity of Norway spruce in northern and southern Sweden. For. Ecol. Manage. 119: 51–62.

Benson M.L., Landsberg J.J., Borough C.J., and 1992. The Biology of forest growth experiment: an introduction. For. Ecol. Manage. 52: 1–16.

Bonneau M., 1995. La fertilisation des forêts dans les pays tempérés. ENGREF, Nancy, 367 p.

Bonneau M., Gelpe J.,and Le Tacon F., 1968. Influence des conditions de nutrition minérale sur le dépérissement du Pin maritime dans les Landes de Gascogne. Ann. For. Sci. 25: 251–289.

Chapman D.G., 1961. Statistical problems in dynamics of exploited fisheries populations. In: Proceedings of the 4th Berkeley Symposium of Mathematics, Statistics and Probability 4: 153–168.

Chen J.M. and Black T.A., 1992. Defining leaf area index for non-flat leaves. Plant Cell Environ. 15: 421–429.

Coll L., Messier C., Delagrange, S., and Berninger, F., 2007 Growth, allocation and leaf gas exchanges of hybrid poplar plants in their establishment phase on previously forested sites: effect of different vegetation management techniques, Ann. For. Sci. 64: 275–285.

Dagnélie P., 1975. Théorie et méthodes Statistiques, Vol. 2. Les Presses Agronomiques de Gembloux.

Danjon F., Bert D., Godin C., and Trichet, P., 1999. Structural root architecture of 5-year-old *Pinus pinaster* measured by 3D digitising and analysed with AMAPmod. Plant Soil 217: 49–63.

Delzon S., and Loustau D., 2005. Age-related decline in stand water use: sap flow and transpiration in a pine forest chronosequence. Agric. For. Meteorol. 129: 105–119.

Delzon S., Sartore M., Granier A., and Loustau D., 2004a. Radial profiles of sap flow with increasing tree size in maritime pine. Tree Physiol. 24: 1285–1293.

Delzon S., Sartore M., Burlett R., Dewar R., and Loustau D., 2004b. Hydraulic responses to height growth in maritime pine trees. Plant Cell Environ. 27: 1077–1087.

Delzon S., Bosc A., Cantet L., and Loustau D., 2005. Variation of the photosynthetic capacity across a chronosequence of maritime pine correlates with needle phosphorus concentration. Ann. For. Sci. 62: 537–543.

Gelpe J. and Guinaudeau J., 1974. Essai de fertilisation minérale sur Pins maritimes à Mimizan (Landes), résultats après la 16 année. Rev. For. Fr. XXVI: 459–463.

Gough C., Seiler J.R., Johnsen K.H., and Sampson D.A., 2004a. Seasonal photosynthesis in fertilized and nonfertilized loblolly pine. For. Sci. 50: 1–9.

Gough C., Seiler J.R., and Maier C.A., 2004b. Short-term effects of fertilization on loblolly pine physiology. Plant Cell Environ. 27: 876–866.

Gower S.T., Ghloz H.L., Nakane K., and Baldwin V.C., 1994. Production and carbon allocation pattern of pine forests. Ecol. Bull. (Copenhagen) 43: 115–135.

Hirvela H. and Hynynen J., 1990. Effect of fertilization on the growth, top damage and susceptibility to windthrow of Scots pine stands in Lapland. Folia For. 764: 1–16 (in Finnish, with English summary).

Hüttl R., 1986. Forest fertilisation: result from Germany, France and the Nordic countries. The Fertiliser Society, Proceedings No. 250, 40 p.

IEFC, 2002. Forest Atlas of the South Atlantic Arc, 78 pp.

Jarvis P.G. and Leverenz J.W., 1983. Productivity of temperate, deciduous and evergreen forests. In: Lange, O.L. Nobel, P.S. Osmond, C.B. Ziegler, H. (Eds.), Physiological Plant Ecology IV. Ecosystem Processes, Mineral Cycling, Productivity and Man's Influence. Springer-Verlag, pp. 233–280.

Jokela E. J., Dougherty P.M., and Martin, T.A., 2004. Production dynamics of intensively managed loblolly pine stands in the southern United States: a synthesis of seven long-term experiments. For. Ecol. Manage. 192: 117–130.

Laiho O., 1987. Susceptibility of forest stands to windthrow in southern Finland. Folia For. 706: 1–24 (in Finnish, with English summary).

Lefrou G., 1979. Résultats, après dix ans d'expérimentation de deux essais de fertilisation de regonflage sur pin maritime dépérissant dans les Landes de Gascogne. Rev. For. Fr. XXXI: 127–133.

Lemoine B., Decourt N., 1969. Tables de production pour le pin maritime dans le sud ouest de la France. Rev. For. Fr. XXI: 5–16.

Lemoine B., Gelpe J., Ranger J., Nys C., 1986. Biomasse et croissance du pin maritime. Étude de la variabilité dans un peuplement de 16 ans. Ann. For. Sci. 43: 67–84.

Linder S., 1987. Responses to water and nutrition in coniferous ecosystems. In: Schultze E.-D., Zwölfer H. (Eds.), Potentials and limitations of ecosystem Analysis. Springer–Verlag, Ecol. Stud. 61: pp. 180–202.

Linder S., 1995. Foliar analysis for detecting and correcting nutrient imbalances in Norway spruce. Ecol. Bull. (Copenhagen) 44: 178–190.

Linder S., Rook D.A., 1984. Effects of mineral nutrition on carbon dioxide exchange and partitioning of carbon in trees. In: Bowen G.D., Nambiar E.K.S. (Eds.), Nutrition of Plantation Forests. Academic Press, New York, pp. 211–236.

Linder S., Benson M.L., Myers B.J. and Raison R.J., 1987. Canopy dynamics and growth of *Pinus radiata*. I. Effects of irrigation and fertilisation during a drought. Can. J. For. Res. 10: 1157–1165.

Lorette D., 1996. La forêt française et son bois, CRDP.

Loustau D., Bert D. and Trichet P., 1999a. La productivité forestière du massif landais et sa gestion durable. Rev. For. Fr. LI: 571–591.

Loustau D., Ben Brahim M., Gaudillère J.P. and Dreyer E., 1999b. Photosynthetic responses to phosphorus nutrition in two-year-old maritime pine seedlings. Tree Physiol. 19: 707–715.

Loustau D., Bosc A., Colin A., Ogée J., Davi H., François C., Dufrêne E., Déqué M., Cloppet E., Arrouays D., Le Bas C., Saby N., Pignard G., Hamza N., Granier A., Bréda N., Ciais P., Viovy N. and Delage F., 2005. Modeling climate change effects on the potential production of French plains forests at the sub-regional level. Tree Physiol. 25: 813–823.

McMurtrie R.E., Benson M.L., Linder S., Running S.W., Talsma T., Crane W.J.B. and Myers B.J., 1990. Water/nutrient interactions affecting the productivity of stands of *Pinus radiata*. For. Ecol. Manage. 30, 415-423.

Medlyn B.E., Loustau D. and Delzon, S., 2002. Temperature response of parameters of a biochemically based model of photosynthesis. I. Seasonal changes in mature maritime pine. Plant Cell Environ. 1155–1165.

Milne R. and van Oijen M., 2005. A comparison of two modelling studies of environmental effects on forest carbon stocks across Europe. Ann. For. Sci. 62: 911–923

O'Neill J.V. and Webb R.A., 1970. Simultaneous determination of nitrogen, phosphorus, and potassium in plant material by automatic methods. J. Sci. Food Agric. 21: 217–219.

Pereira J.S., Madeira M.V., Linder S., Ericsson T., Tomé M. and Araujo M.C., 1994. Biomass production with optimised nutrition in *Eucalyptus globulus* plantations. In: "Eucalyptus for Biomass Production", Peirera J.S., Peirera, H. (Eds.), Commission of the European Communities, pp 13–30.

Porté A., Trichet P., Bert D. and Loustau D., 2002. Allometric relationships for branch and tree woody biomass of maritime pine (*Pinus pinaster* Aït.). For. Ecol. Manage. 158: 71–83.

SAS Software, 2002. SAS/STAT User's Guide, Version 8.1.

Richards F.J., 1959. A flexible growth function for empirical use. J. Exp. Bot. 10: 209–300.

Ritson P. and Sochacki S., 2003. Measurement and prediction of biomass and carbon content of *Pinus pinaster* trees in farm forestry plantations, south-western Australia. For. Ecol. Manage. 175: 103–117.

Saur E., 1989. Alimentation oligo-minérale du Pin maritime en relation avec quelques caractéristiques physico-chimiques des sols sableux des Landes de Gascogne. Ann. For. Sci. 46: 119–129.

Snowdon P. and Benson M.L., 1992. Effect of combinations of irrigation and fertilisation on the growth and above-ground biomass production of *Pinus radiata*. For. Ecol. Manage. 52: 87–116.

Tamm C.O., 1991. Nitrogen in terrestrial ecosystems, questions of productivity, vegetational changes, and ecosystem stability. springer–verlag, Ecol. Stud. 81 115 p.

Teskey R.O., Withehead D. and Linder S., 1994. Photosynthesis and carbon gain by pines. Ecol. Bull. (Copenhagen) 43: 35–49.

Trichet P., Jolivet C., Arrouays D., Loustau D. and Ranger J., 1999a. Le maintien de la fertilité des sols forestiers landais dans le cadre de la sylviculture intensive du pin maritime. Revue bibliographique et pistes de recherches. Étude et Gestion des Sols 6 (4): 197–214.

Trichet P., Vauchel V., Bert D. and Bonneau M., 1999b. Fertilisation initiale et réitérée du Pin maritime (*Pinus pinaster* Ait.): Principaux résultats de l'essai de Berganton. Rev. For. Fr. LII: 207–222.

Vose J.M. and Allen H.L., 1988. Leaf area, stem wood growth, and nutrition relationships in loblolly pine. For. Sci. 34: 547–563.

APPENDIX

Table A.1. Rate of application of nutrients (kg ha^{-1} $year^{-1}$), 1998 to 2002, and type of fertiliser used (in brackets), for the P only (P) and optimal fertilised (F) treatments.

	1998		1999		2000		2001		2002	
Element (kg ha^{-1} $year^{-1}$)	P	F	P	F	P	F	P	F	P	F
N (urea)	–	80	–	81	–	–	–	80	–	159
P (triple superphosphate)	40	40	41	41	–	–	22	22	68	68
K (KSO_4)	–	60	–	57	–	–	–	60	–	118
Ca (dolomite)	–	25	–	28	–	–	–	25	–	55
Mg (dolomite)	–	14	–	16	–	–	–	5	–	12
B (borate)	–	–	–	–	–	–	_	0.3	–	3
Cu ($CuSO_4$)	–	–	–	–	–	–	–	3	–	13
Mn ($MnSO_4$)	–	–	–	–	–	–	–	0.3	–	13
Zn ($ZnSO_4$)	–	–	–	–	–	–	–	0.5	–	–