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Understorey-overstorey biotic and nutrient interactions are key factors for *Pinus pinaster* growth and development under oligotrophic conditions

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ABSTRACT

The main objective of this study was to examine the interactive effects of nutrient availability and understorey plants, including a nitrogen(N)-fixing shrub, on growth, physiology and survival of commercial maritime pines (*Pinus pinaster* Ait.). Three experimental sites within the *Landes de Gascogne* forest were installed in two wet moorlands (one dominated by gorse, a leguminous shrub and one by a perennial grass), and in one dry moorland dominated by ericaceous plants. In dry moorland, the ericaceous understorey increased pine mortality and decreased pine growth, suggesting a competition for water, the most limiting resource of this ecosystem. In wet moorland, a decrease in pine growth suggested a strong competition for soil resources, with or without phosphorus addition. In the other wet moorland dominated by gorse, pines responded to competition for light through stem elongation and self-pruning, but not by reducing growth. The intercropped gorse improved pine N-nutrition and trees acclimated to shrubs by growing more fine roots. Gorse had a positive effect on stomatal conductance during spring, while pine water status decreased moderately with increasing shrub competition during summer. Our results provide new understanding of the feasibility of using gorse as an intercropping N-fixing plant in managed forests, and revealed the structural and physiological trade-offs that exist between increasing N-availability and competition for water and light.

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Introduction

Forests are considered as one of the most important sources of renewable bio-energy and woody material. Consequently, planted forests are expected to be more and more productive and currently make up less than 10% of world's forest cover, but account for over 40% of industrial wood production (FAO and UNEP 2020). Among the different forest practices that can potentially increase wood production, understorey crushing is commonly proposed (South et al. 2006). Understorey vegetation can compete with trees for resources (nutrients, water and light), which can potentially limit forest growth (Balandier et al. 2006), particularly in productive sites (Delerue et al. 2018). In managed forests, the highest resource availability is generally encountered after harvest and prior to planting (Lieffers et al. 1999; Fox et al. 2006). However, following site establishment this resource availability also coincides with a high level of competition from early successional vegetation (Kimmins 1974; Lieffers et al. 1999). In addition, the effects of competition are expected to increase when planted trees begin to grow and have higher nutrient and water demand and potentially lower physiological capacity to tolerate many stressors (Delzon et al. 2004; Guignabert et al. 2018).

In parallel, positive tree-understorey interactions can also exist. For instance, the presence of nitrogen (N₂) fixing

legumes is expected to increase soil fertility, tree nitrogen supply and plant growth (Crews and Peoples 2004). While the potential effects of mixed-species plantations on forest ecosystem productivity, which include N-fixing trees and fast-growing trees, have been assessed (Hansen and Dawson 1982; Laclau et al. 2008; Santos et al. 2017), few studies have quantified the role of N-fixing species present in the understorey stratum (Rodríguez et al. 2009; Hoogmoed et al. 2014; Li et al. 2016).

Maritime pine (*Pinus pinaster* Ait.) is a stress tolerant Mediterranean tree species able to live in water and nutrient limited ecosystems, making it one of the most planted species worldwide for productive afforestation. This species is intensively managed in the *Landes de Gascogne* forest, with extensive soil preparation and fertilisation before planting seedlings that are mostly coming from plant breeding programmes. Stands generally grow fast despite the local poor soils, leading to a canopy closure at 11–15 years after plantation. From this stage, foresters manage the stands to rapidly provide large amounts of woody material to the forest-wood chain by commercially thinning the stands 3–4 times before the final harvest (when trees are between 35 and 40 years old). In a previous study (Vidal et al. 2019), the technical feasibility of cultivating the common gorse shrub (*Ulex europaeus* L., hereafter referred to as gorse) as an inter-crop species, and its effect in a maritime pine plantation were

investigated in the *Landes de Gascogne* forest (SW France). The new concept of forest management proposed by Vidal et al. (2019) was to modify the understorey composition towards a mono-specific gorse intercrop in order to increase N availability for the pine trees. Indeed, even though phosphorus (P) strongly limits tree growth on those ecosystems, the soil is also deficient in N (Trichet et al. 2008). Before crushing and leaving the intercrop on the forest soil, the study measured an increase in needle N content. However, a long-term monitoring study showed that ecosystem N status was in a strong interaction with the local P availability (Vidal et al. 2019).

Building on this previous work, the main objective of the present study was to gain insights into the interactive effects of nutrient availability and different types of understorey plants on an early-rotation maritime pine plantation growing on poor soils. We specifically investigated the structural and physiological interactions occurring between gorse and maritime pine during the first years after planting. To reach our objective, we monitored pine water status and nutrition, as well as pine and understorey growth along a gradient of gorse biomass in an experimental forest site in a wet moorland. We compared this trial with two other sites to extend the feasibility of successfully growing maritime pine on oligotrophic soils characterised by different understorey vegetation types (grasses in a wet moorland and ericaceous species in a dry moorland). We hypothesised that during the early years (1) gorse and pine compete for light at the beginning of the rotation when heights are comparable, (2) gorse and pine compete for water during the drought periods, and (3) N fixed by gorse stimulates tree nutrition, mitigates the competition for water and light and increases site productivity.

Materials and methods

Site description

The study sites were located within the *Landes de Gascogne* forest in the south-west of France, characterised by a mean annual temperature of 12.7°C and a mean annual precipitation of 900 mm yr⁻¹. The soils are sandy podzols made of 9–14% fine sands, 80–89% coarse sands, and highly deficient in P (Trichet et al. 2009; Augusto et al. 2010; Bertran et al. 2011). Maritime pine plantations progressively replaced the native moorland vegetation, which remains still widespread in the understorey and defines, along with water table depth, the four principal ecological site classifications of this forest ecosystem (Augusto et al. 2010): *wet moorlands* (dominated by *Molinia caerulea* L., a perennial deciduous grass), *mesophyllous moorlands* (with *Pteridium aquilinum* (L.) Kuhn), *dry moorlands* (dominated by *Calluna vulgaris* L. and *Erica cinerea* L., two woody perennial *Ericaceae* shrubs), and *coastal sand dune woodlands* (with mosses, *Cytisus scoparius* L. and *Arbustus unedo* L.). Three experimental sites were installed in two wet and one dry moorlands (Figure 1). Hereafter, the aforementioned experimental sites are referred to as *wet-gorse site* (44.50°N, –1.00°E), *wet-grass site* (44.85°N, –0.9°E) and *dry-ericaceous site* (44.16°N, –1.03°

E). Before planting the six months old pine seedlings, sites were ploughed to remove any competing vegetation present. In one of the two wet moorland sites, we sowed common gorse to test the effects of this N-fixing shrub on pine growth and to evaluate soil N-P interactions (Augusto et al. 2005; Cavard et al. 2007). At this site, gorse plants were intercropped between pine lines with one sowing of 100 seeds m⁻² to increase the spontaneous density of gorse in the understorey (Figure 1).

Climatic data (temperature and precipitation) for all three sites were provided by regional weather stations run by INRAE (*Bilos* and *Cestas-Pierroton* sites). At the wet-gorse site, where plant-level physiological parameters were measured, climatic conditions and soil moisture were also directly monitored in two zones: one in a low and one in a high gorse density area. In each zone, a micrometeorological station consisting of a CS215 probe (Campbell Scientific®, UT, USA) and a quantum sensor (LI-190R, Licor, NE, USA) was installed at a height of 2 metres to measure light intensity, air temperature, relative humidity and to determine vapour pressure deficit (VPD). Soil water content (R_r) was measured using one 5-cm-long ML2X-Tetha probe (Delta-T Devices, Cambridge, UK) and two 30-cm-long CS616 water content reflectometers (Campbell Scientific®) installed in two soil profiles down to a depth of 70 cm, which corresponds to the soil layers where the majority of pine roots are located (Bakker et al. 2006; Achat et al. 2008). Moisture sensors were individually calibrated in the laboratory in different repacked soils corresponding to their *in situ* soil layers. Drought intensity is best quantified in the form of relative extractable water (REW, dimensionless), and therefore R_r was converted to REW as defined by Bréda et al. (2006):

$$\text{REW}(\%) = (R_r - R_{\min}) / (R_{\max} - R_{\min}) * 100 \quad (1)$$

The difference " $R_{\max} - R_{\min}$ " represents the soil water holding capacity, with $R_{\max}$ and $R_{\min}$ (4% for this sandy soil; Moreaux 2012) being the maximal soil water reserve and the soil wilting point, respectively.

Experimental design

The wet-grass and the dry-ericaceous sites were planted with maritime pine trees (1,250 stem ha⁻¹; 4x2 m spacing) in November 2008. Seedlings were grown in a nursery during one year, with regular water and nutrient applications. They originated from seeds produced by seed orchards that constitute the third generation of genetic selection of *Pinus pinaster*. Each of those two sites were divided into four blocks, and within each block the same four treatments were applied (Figure 1 and Figure S1). Each treatment was a combination of two factors: an initial P-supply (80 kg P₂O₅ ha⁻¹ in the wet-grass site and 60 kg P₂O₅ ha⁻¹ in the dry-ericaceous site) and mechanical crushing (using a bladed roller) of the understorey. Control treatments were applied in parallel to P-application and vegetation crushing. Between 2008 (initial ploughing) and 2017, understorey crushing was performed seven times for the wet-grass site and three times for the dry-ericaceous site. Hereafter, treatments are designated as follows: P/UD for Phosphorus supply Understorey

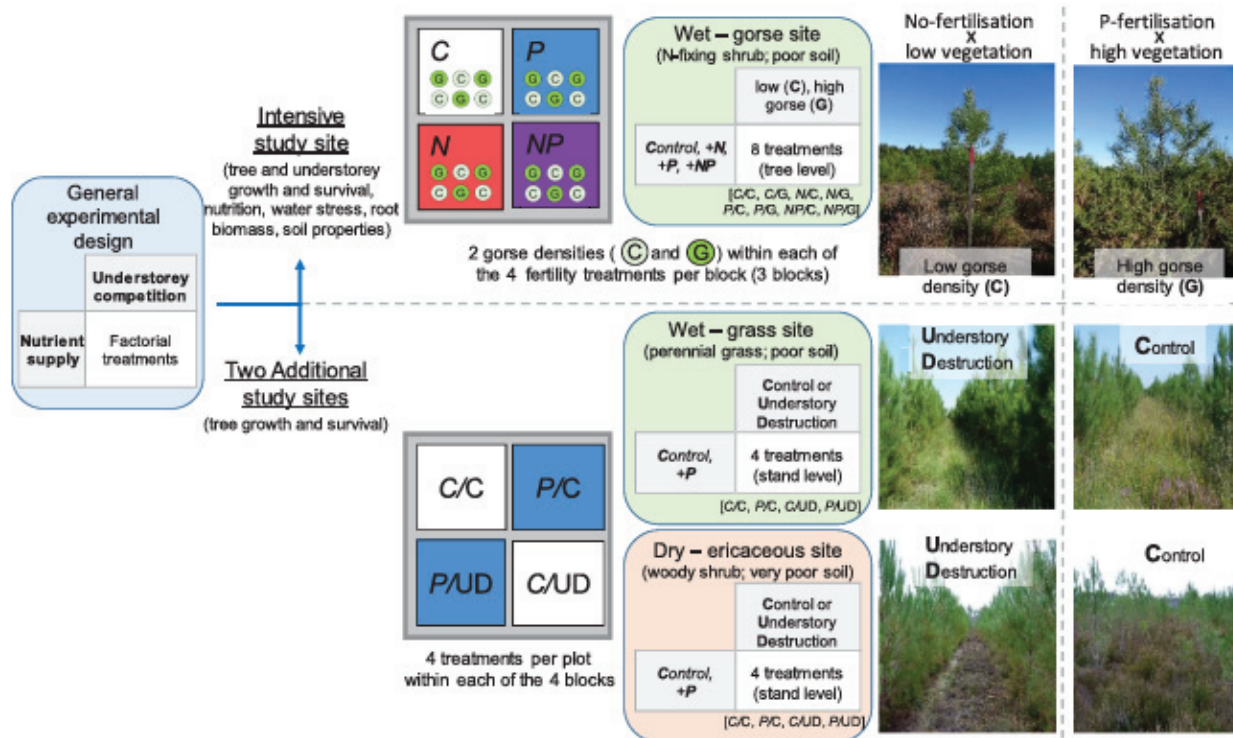


Figure 1. Description of the three understorey-overstorey experimental sites. Applied treatments and field illustrations are presented for the wet-gorse site, the wet-grass site and the dry-ericaceous site.

Destruction, P/C for Phosphorus supply/Control treatment, C/UD for Control treatment/Understorey Destruction and C/C for Control/Control (Figure 1).

The wet-gorse site was set up in 2012–2013, following the same practices as the other two sites (Figure 1 and Figure S1). At this site, growth and tree physiology in response to site fertility were intensively monitored for three consecutive years (2016–2018, Figure S1). This site was divided into three blocks in November 2012 in which four fertility treatments were applied: nitrogen alone (N), phosphorus alone (P), nitrogen + phosphorus (NP) and absence of fertilisation (control C). Applications of P (80 kg P_2O_5 ha^{-1}) and N (60 kg N ha^{-1}) were made by hand in spring 2013. Additional N was applied in spring 2014 (60 kg N ha^{-1}), 2015 (60 kg N ha^{-1}), 2017 (50 kg N ha^{-1}) and 2018 (50 kg N ha^{-1}) because former studies showed that the effects of N fertilisation on tree growth tend to quickly disappear in the studied region (Trichet et al. 2009). Gorse sowing was performed on half of the plots comprising a P-supply (i.e. treatments P and NP), but that operation was delayed by one year compared to pine plantation because of bad weather conditions occurring in 2013. After germination, gorse cover was not homogeneous across the planted areas. Therefore, we could not study its effects at the stand scale and we decided to study gorse-pine interactions at the individual tree scale instead. In each of the four fertility levels (i.e. C, N, P, NP), we selected a low and a high density gorse understorey from which three pine trees were selected for a total of 72 individuals measured (3 blocks $\times$ 4 fertility levels $\times$ 2 gorse densities $\times$ 3 trees). Around each pine tree, a square sampling area

was delimited (4 m^2), inside which one gorse shrub was marked and later used for nutrition monitoring (hereafter referred to as the gorse-neighbour). In 2017 (when the trees were five years old), a supplement of P fertiliser (80 kg of P_2O_5 ha^{-1}) was added to each 4 m^2 sampling area (P and NP treatments).

Ecosystem aboveground production

The effect of the understorey shrubs on the overstorey trees was assessed by measuring tree height and mortality for nine years (2008–2016, Figure S1) at the dry-ericaceous and the wet-grass sites ($n = 80$ –120 trees per plot, depending on the site). In addition, circumference at 130 cm above the ground (C_{130}) was also measured in 2014 and 2016 at the wet-grass site and in 2014 and 2017 at the dry-ericaceous site. At the wet-gorse site, the 72 selected pines were tall and old enough to survive understorey competition and none of those trees died during the experiment. Pine height, C_{130} and diameter at 10 cm above ground level (D_{10}) were measured for three years (2016–2018). Pine stem volume was calculated from C_{130} and height (ht) in combination with an index of tree form. Tree form (corresponding to the ratio of tree volume and the volume of a cylinder of similar height and circumference) was estimated from C_{130} and tree hardness ($= C_{130}^{1/2}/ht$) as:

$$\text{form}(C_{130}, ht, \text{unitless}) = \alpha + \beta \times C_{130} + \gamma \times \frac{C_{130}^{1/2}}{ht}, \quad (2)$$

where for maritime pine α , β and γ can be taken as 0.396, 0.235 and 0.00097, respectively (Vallet et al. 2006).

Then, pine volume was calculated as described in Trichet et al. (2009):

$$\text{volume (cm}^3\text{)} = \frac{1}{(4 \times \pi)} \times C_{130}^2 \times ht \times \text{form} \quad (3)$$

Additionally, we tried to compare pine stem volumes among sites. Pine C_{130} was not measured each year in the additional two sites, so we used C_{130} measured in 2015 (seven years old pines). At the wet-gorse site we selected the last monitored year (2018), when trees were six years old. At the wet-gorse site, we also recorded three other structural tree variables in summer 2017: branching, stem verticality deviation and canopy expansion. Branching was characterised as the height of the lowest living branch (defined as having green needles). Using a pendulum, stem verticality deviation was defined as the angle formed at 1.5 m between the main stem and the vertical direction. Canopy expansion corresponded to the maximum elliptic surface centred on the stem occupied by the canopy in the horizontal plane. We measured the distance between the furthest extending branches in two directions: within the tree line and perpendicular to the tree line. To complete the morphological assessment, we calculated the height-to- D_{10} ratio (height: D_{10}) to investigate any effects on pine stem elongation relative to their diameter.

During the winters of 2017 and of 2018, we determined the height of the vegetation and the vegetation cover in each plot by separating the main species present per plant functional group (Fabaceae, Ericaceae or Poaceae; Albaugh et al. 2012). We then estimated the total understorey aboveground biomass in each of the 4 m² sampling area every year, and once for the entire site in 2016 by using the phytovolume method, which consisted for a given species in multiplying its ground area covered by its mean height (Gonzalez et al. 2013). We complemented these allometric relationships with a specific function determined on common gorse thickets as in Vidal et al. (2019):

$$\text{Biomass (gm}^2\text{)} = 1100.9 \times \text{Phytovolume}^{0.9983} (n = 37, r^2 = 0.86) \quad (4)$$

Ecosystem belowground soil chemistry and productivity

In each plot of the wet-gorse site, we collected four soil cores (0–15 cm) located one metre from the 72 sampled pine trees, and then made 72 composite samples (Figure S1). Soil samples were dried at 40°C and divided into three homogeneous aliquots. The first one was used to determine the P organic–inorganic total pools (hereafter referred to as P_{org} and P_{inorg} ; and P_{tot} the total pool; Saunders and Williams 1955). The second aliquot was used to measure pH_{H₂O} (as no differences were observed among treatments, pH values are not presented). The third was used to quantify soil organic matter and total soil carbon (C_{tot}) concentration (Augusto et al. 2010).

At the wet-gorse site, we also investigated root biomass and distribution of understorey species in each pine square (Figure S1). In April 2018, roots were collected from two soil cores (8 cm in diameter) taken at one point for each pine square: topsoil from 0 cm to 15 cm, and deeper soil from 15 cm to 30 cm ($n = 72$ pines $\times 2$ layers = 144). Each soil sample was washed and sieved (2 mm). Using reference samples taken for species recognition (composed of individual root systems collected on site for each species), we sorted roots into six different classes: fine pine roots (<2 mm of diameter), coarse pine roots (>2 mm), fine gorse roots (<2 mm), coarse gorse roots (>2 mm), other understorey species roots (fine+coarse roots), and necromass. Fine root length was estimated using the line intersect method (Tennant 1975). After drying the root samples at 65°C for 3 days, fine root biomass (g) and specific root length (m g⁻¹) were determined (Bakker et al. 2006). Using the volume of the cores, roots were expressed on a volume basis either as root length density (cm cm⁻³) or as root biomass density (g cm⁻³).

At the same time as root sampling and to infer the amount and rate of N-fixing, we labelled the soil in April 2018 at a soil depth of 2 cm around 24 trees (3 trees for each of the 8 treatments defined in Figure 1) by injecting 5.0 mg of non-fertilising ¹⁵N with a syringe at four points around the pines (corresponding to four volumes of 6.5 mL of NH₄Cl; 99% ¹⁵N) (Dawson et al. 2002). To avoid a leaching effect of a possible heavy rain episode, and because nitrogen is rapidly allocated to foliage (Augusto et al. 2011), we collected needles one week after labelling. Foliage samples were dried at 40°C for 72 h and then ground. We analysed $\delta^{15}\text{N}$ with an Elemental Analyser – Isotopic Ratio Mass Spectrometer (EA – IRMS), in the SILVA-TECH platform of INRAE.

Plant nutrition

To assess the effects of the fertilisation treatments combined with gorse densities on pine nutrition, each winter (2016, 2017 and 2018) we collected ten pairs of current-year green needles sampled from the upper south-facing part of the canopy (Figure S1). We also collected green twigs of a gorse-neighbour. Pine and gorse tissues were dried and then ground for determination of total N, P, K, Ca and Mg concentrations. N and P were analysed by colorimetry whereas K, Ca and Mg concentrations were measured with a flame atomic absorption spectrophotometer. These concentrations were then compared with the nutritional abacus for young maritime pines (Table S1; van den Burg 1985). We calculated needle-N:P ratios which provided a comprehensive index of soil nutrient limitations for plant nutrition (Augusto et al. 2017). Generally, a N:P ratio lower than 12 suggests N-limitation, while a N:P ratio higher than 16 suggests P-limitation (Koerselman and Meuleman 1996). We then combined aboveground and belowground biomass values with the values of nutrient concentrations (in corresponding plant compartments) to estimate the N and P stocks contained in the understorey layer (Augusto et al. 2005; Achat et al. 2018).

Pine water status and leaf physiology

We evaluated the effects of gorse and other understorey species on soil moisture, and on pine water status and leaf gas exchange. In 2017 and 2018, measurements were performed in spring when soil water was not limiting (i.e. high water table / full soil water holding capacity), and in the summer (dry season) when reduced soil moisture was expected to induce water stress (Figure S1). It was not possible to study all of the 72 trees because the measurements had to be done under the same environmental conditions. Time required for the field campaign restricted us to measure only one block ($n=24$ trees) in 2017, and two blocks in 2018 ($n=48$ trees). We used a Scholander pressure chamber (Precis 2000, Gradignan, France) to estimate water potentials (Ψ) at predawn (between 4 and 7 AM), and at midday (between 10 AM and 2 PM). We sampled sun-exposed needles ($n=4-5$ per tree), located in the upper part of the canopy. For each pine tree we then calculated the water driving force ($\Delta\Psi$) by subtracting midday Ψ from predawn Ψ values (Lambers et al. 2008). We measured stomatal conductance (g_s , $\text{mmol m}^{-2} \text{s}^{-1}$), at the same time as the midday Ψ measurements, on sun-exposed leaves using a leaf porometer (Decagon model SC-1*, Pullman, WA, USA). The observed g_s was corrected by the needle surface area located in the chamber. Leaf transpiration (E , $\text{mmol m}^{-2} \text{s}^{-1}$) was expressed from g_s and the leaf-to-air vapour pressure deficit (VPD , kPa) as follows:

$$E = g_s \times VPD \times kg(T) \quad (5)$$

where $kg(T)$ is the conductance coefficient (in $\text{kPa m}^{-3} \text{kg}^{-1}$) that depends on leaf temperature (Ewers et al. 2001). We estimated field tree hydraulic conductance on a leaf-area basis (K_{tree} in $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) from the relationship between E and $\Delta\Psi$ (Loustau et al. 1998; Domec et al. 2009a). The soil water potential was considered to be very close to predawn Ψ in the leaves (Bréda et al. 2006), and thus K_{tree} was calculated as:

$$K_{\text{tree}} = \frac{E}{\Delta\Psi} \quad (6)$$

Data analyses

Data analyses were performed with R.3.3.4 (R Core Team 2017). We used mixed modelling to take into account: (1) the spatial dependence of samples belonging to plots and blocks; or (2) the time dependence within repeated measurements made on the same individual (only for pine growth at the wet-gorse site where pines were clearly identified among years). When conditions for model application (normality and homoscedasticity) were not met, we then transformed our data (square, arcsine, logarithm). To test for treatment effects at the three sites, we first tested experimental factors (i.e. nutrition and understorey biomass) and their interactions, and then we considered the treatments (e.g. C/C versus P/C; Figure 1). In the wet-gorse site, we also consider the factors *understorey biomass* and *phytolume* in models to scrutinise more precisely the effects of

gorse biotic interactions on pines through pine morphology, physiology and fine root development. If at least two treatments were significantly different, we used a multiple pairwise comparison to test these differences (Tukey post-hoc test). For pine growth, contrasts between treatments and years were performed to test whether the slopes of regressions between years and treatments differed between treatments. When a linear regression was performed using a mixed model (Nakagawa and Schielzeth 2013), we provided the marginal R^2 (i.e. the variance explained by the fixed effects; noted as R_m^2) and the conditional R^2 (i.e. the variance explained by both fixed and random effects; noted as R_c^2).

Pine survival in the two additional sites (i.e. in the wet-grass site and in the dry-ericaceous site; Figure 1) was investigated (for four years old pines, when pines are considered established) using a General Linear Mixed Model to integrate both random effects and a binomial distribution of data.

Results

Understorey composition and production

Gorse phytovolume ranged from 0 to $1.92 \text{ m}^3 \text{m}^{-2}$ (corresponding to 0–2.11 kg m^{-2} of dry weight aboveground biomass). Gorse biomass was the highest where phosphorus (P) was supplied ($P < 0.001$). The presence of gorse enhanced the total understorey phytovolume, but decreased the phytovolume of the other species (*Ericacea* and *Molinia*, Figure 2). Overall, total nitrogen contained in the understorey (above + belowground compartment) increased with gorse phytovolume and ranged from 2.78 g m^{-2} –7.13 g m^{-2} of N ($P < 0.001$; $R_m^2 = 0.41$; $R_c^2 = 0.43$). In P-fertilised plots, gorse mean heights reached 170 ± 4 cm at age four and 203 ± 4 cm at age six. In comparison, pines were 66 ± 5 cm and 191 ± 12 cm taller than gorses at the same age.

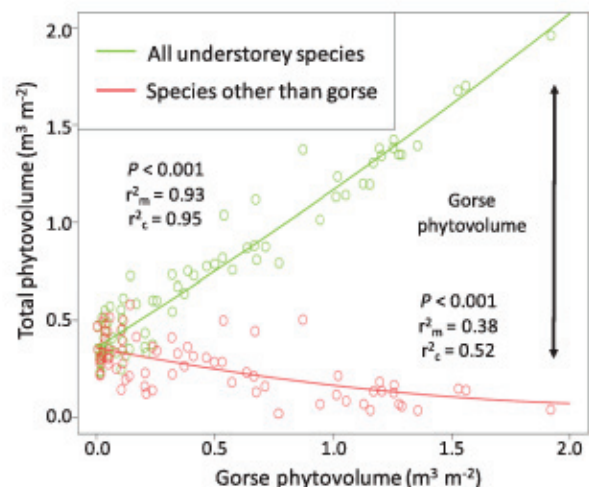


Figure 2. Understorey phytovolume surrounding maritime pines at the wet-gorse site ($n=72$ trees). The « Species other than gorse » group of species was mainly composed of *M. caerulea* and *C. vulgaris*. P -values are indicated for each fitted curve with the marginal R^2 (R_m^2) and the conditional R^2 (R_c^2).

Pine production and survival

Pine stem volumes are presented relative to treatments for the wet-grass site and the dry-ericaceous site (Figure 3a and b). Differences in volume in each site ($P < 0.001$) resulted from differences in height and circumference between treatments (Table S2). At the dry-ericaceous site, only understorey crushing increased stem volumes ($P < 0.001$). At the wet-grass site, both P-fertilisation ($P < 0.001$) and understorey crushing ($P = 0.004$) increased pine volumes. Final pine height was similar between the two sites (Figure S2a & b). At age four, more pines died in plots with an intact understorey at the dry-ericaceous site ($1.4 \pm 1.0\%$ vs. $0.4 \pm 0.0\%$ in plots with frequent understorey destruction, $P = 0.009$), while the opposite ($P = 0.003$) was observed at the wet-grass site ($5.6 \pm 3.6\%$ and $1.1 \pm 0.6\%$ mortality in plots with annual understorey destruction and in control plots, respectively).

P-fertilisation increased pine height at the wet-gorse site (Figure S2c; $P = 0.008$) although a high gorse density decreased pine C_{130} (Table S3; $P = 0.016$). The application of N + P combined with low gorse density increased pine stem volumes ($P < 0.01$; Figure 3c). There was no difference in tree height between sites (Figure S2d). There was an effect of the gorse phytovolume on several pine morphological traits (Figure 4). Gorse phytovolume increased the height: D_{10} ratio and the height of the lowest living branch (the branching), and decreased canopy expansion ($P < 0.01$).

Soil and root characteristics

At the wet-gorse site, P-fertilisation increased soil P_{tot} ($P < 0.001$; $70.6 \pm 5.1 \mu\text{g g}^{-1}$ with P-supply, $33.0 \pm 2.3 \mu\text{g g}^{-1}$ without P-supply) as well as both P_{inorg} ($P < 0.001$; 29.8 ± 3.0 vs. $2.15 \pm 0.1 \mu\text{g g}^{-1}$) and P_{org} ($P = 0.042$; 40.7 ± 3.2 vs. $30.9 \pm 2.2 \mu\text{g g}^{-1}$). We measured higher ($P < 0.01$) P_{tot} , P_{inorg} , and P_{org} in NP/G and P/G plots than in plots with similar fertility treatment but with low gorse phytovolume (NP/C and P/C).

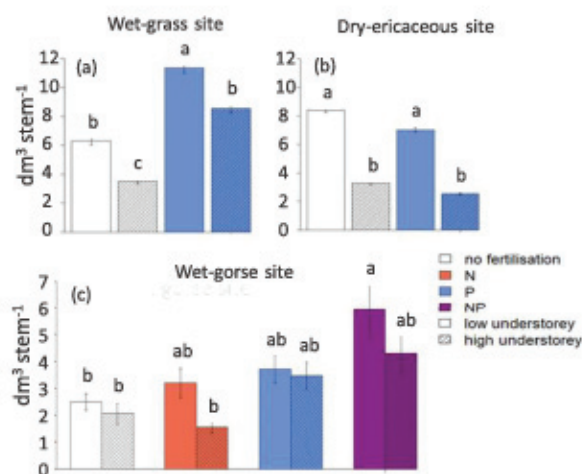


Figure 3. Effects of fertilisation and understorey composition on maritime pine stem volume growth ($\text{dm}^3 \text{ stem}^{-1}$). Mean volumes are shown for seven-year-old trees at the wet-grass site (panel a, $n = 1,280$ trees) and at the dry-ericaceous site (panel b, $n = 1,928$ trees), and for six-year-old trees at the wet-gorse site (panel c, $n = 72$ trees). Different letters indicate significant differences between treatments within a site (Tukey post-hoc test).

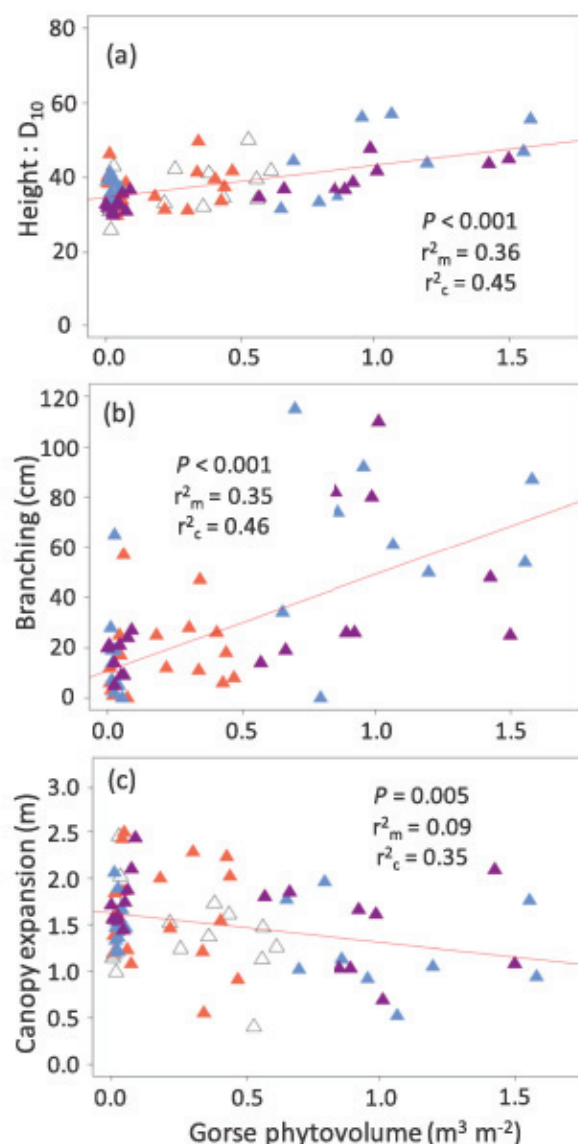


Figure 4. Effects of gorse phytovolume and fertilisation on maritime pine morphology at the wet-gorse site ($n = 72$ trees). Height: D_{10} ratio (panel a), height of the lowest living branch (panel b) and canopy expansion (panel c) are presented relative to gorse phytovolume. Data were collected in 2017 (pines were five years old). P-values are indicated for each linear fitted curve with the marginal R square (R^2_m) and the conditional R square (R^2_c). White triangles, orange triangles, blue triangles and purple triangles in panels indicate pines without fertility treatment, pines with nitrogen treatment, pines with phosphorus treatment and pines with nitrogen + phosphorus treatment, respectively.

We did not measure any differences in soil organic matter nor C_{tot} between treatments. Soils of the wet-grass site and the dry-ericaceous site appeared different: C_{tot} , N_{tot} and P_{tot} were higher in the wet-grass site (24.9 g kg^{-1} of C, 0.85 g kg^{-1} of N, 0.101 g kg^{-1} of P and $C:N = 29$) than in the dry-ericaceous site (18.3 g kg^{-1} of C, 0.48 g kg^{-1} of N, 0.088 g kg^{-1} of P and $C:N = 38$).

We observed that gorse fine root biomass (FRB) density increased with gorse phytovolume (Figure S3; $P < 0.001$) but no variation in total FRB appeared along the gorse phytovolume level gradient. In the 0–15 cm soil layer, gorse phytovolume increased pine SRL (Table 1; $P = 0.021$) and tended to increase pine fine root length density ($P = 0.079$). Topsoil labelling increased $\delta^{15}\text{N}$ -needle values along the gorse

Table 1. Species and treatment differences in fine-root characteristics for the 0–15 cm soil depth at the wet-gorse site (FRB, FRL and SRL represents fine root biomass, fine root length and specific root length, respectively).

	Treatments	FRB density (mg cm ⁻³)	FRL density (cm cm ⁻³)	SRL (m g ⁻¹)
Fine-root traits as a function of gorse phytovolume level	Very low	0.177 ± 0.031 n.s.	0.155 ± 0.026 n.s.	9.58 ± 0.91 b
	Low	0.164 ± 0.024 n.s.	0.154 ± 0.023 n.s.	9.79 ± 0.69 b
	High	0.198 ± 0.050 n.s.	0.172 ± 0.027 n.s.	11.86 ± 1.22 ab
	Very high	0.201 ± 0.029 n.s.	0.262 ± 0.043 n.s.	14.26 ± 1.59 a
Fine-root traits as a function of P-fertilisation level	No P fertilisation	0.110 ± 0.041 n.s.	0.232 ± 0.101 a	23.11 ± 2.41 a
	P fertilisation	0.148 ± 0.027 n.s.	0.511 ± 0.075 b	44.87 ± 4.59 b

Note: FRB, FRL and SRL were analysed as function of the four gorse phytovolume levels, and as a function of P-fertilisation for fine gorse roots. Different letters within a column indicate significant differences between groups (Tukey post-hoc test) ([*] $P < 0.1$; * $P < 0.05$; ** $P < 0.01$).

phytovolume gradient (Figure S4; $P = 0.019$; $r_m^2 = 0.23$; $r_c^2 = 0.26$). Regarding gorse roots in the 0–15 cm layer (Table 1), P-supply increased both gorse fine root length density ($P = 0.013$) and gorse specific root length ($P = 0.007$).

Pine and whole-ecosystem nutrition

The N and P (as well as K, Ca and Mg) concentrations in the needles indicated that pines were not nutritionally stressed (Table S1). Gorse phytovolume, as well as N-supply, increased pine needle N-concentrations ($P < 0.001$). In addition, pines in N/G and NP/G treatments had greater needle N-concentrations ($P < 0.001$) than in N/C or NP/C treatments, respectively (Figure 5a). The effect of site characteristics on P dynamics was weaker than for N, as revealed by the marginal increase ($P = 0.064$) in needle P-concentration with increasing gorse density (Figure 5b). Consequently, needle N:P ratio increased in treatments with a N-fertilisation (Figure 5c; $P < 0.001$) and with high gorse densities ($P < 0.001$). In addition, P fertilisation improved gorse P concentration in twigs (Figure S5; $P < 0.01$), while both P fertilisation and N fertilisation modified the twig N:P ratio ($P < 0.05$).

Meteorological conditions, pine water status and leaf physiology

Periods of moderate water stress were recorded during the summer season in the wet-grass site and the dry-ericaceous site when pines were three and four years old (years 2010 and 2011; Figure S6). At the wet-gorse site, the 2016 and 2018 growing seasons experienced a summer drought when pines were four and six years old (Figure S7a). Values of whole tree hydraulic capacity (K_{tree}) varied from 0.47–1.23 mmol m⁻² s⁻¹ MPa⁻¹ but did not show any differences between treatments or years ($P > 0.1$).

The year 2017 was relatively wet (Figure S7a) and no severe drought occurred. During spring, soil water availability (Figure S7b) was high with a mean relative extractable water (REW) of 38% (corresponding to 14.4% soil water content). In spring, we did not detect any effect of the gorse phytovolume on predawn water potential values (predawn Ψ), midday water potential (midday Ψ), delta psi ($\Delta\Psi$), and stomatal conductance (g_s) (Figure 6). Midday Ψ values were comprised between –1.45 MPa and –2.38 MPa. In summer 2017, as soil was drier than in spring (REW = 7.7%; soil moisture = 6.1%), pine predawn Ψ values became more negative ($P < 0.01$) than those of spring. Those summer predawn Ψ values decreased linearly with increasing gorse phytovolume

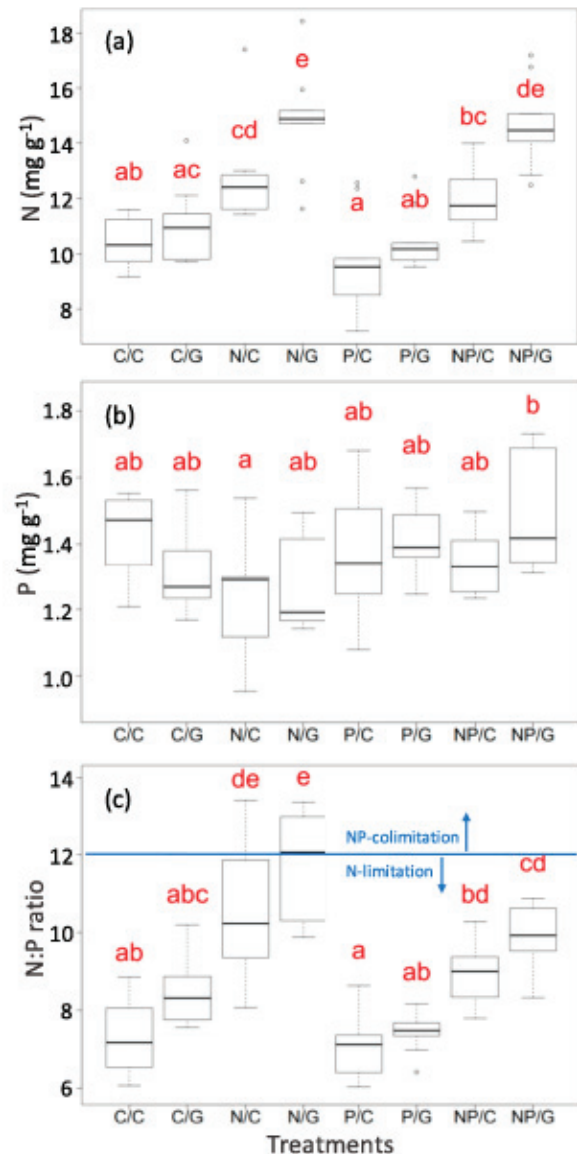


Figure 5. Effects of site characteristics on maritime pine needle nitrogen (N; panel a), phosphorus (P; panel b), and N:P (panel c) concentrations at the wet-gorse site ($n = 72$ trees). For each site treatment, the upper letters represent the level of fertilisation (C=control, N=nitrogen addition, P=phosphorus, NP=nitrogen plus phosphorus) and the lower letters the type of understorey (C=control and G=gorse addition). N and P concentrations (panel a and b, respectively) and N:P ratio (panel c) are shown for current green needles sampled in November 2017 from five years old pines. Different letters indicate significant differences between treatments (Tukey post-hoc test). Likely soil nutritional limitations are indicated: "N-limitation" could occur if N:P ratio is lower than 12 while "NP-colimitation" could occur if the N:P ratio exceeds this threshold (Koerselman and Meuleman 1996).

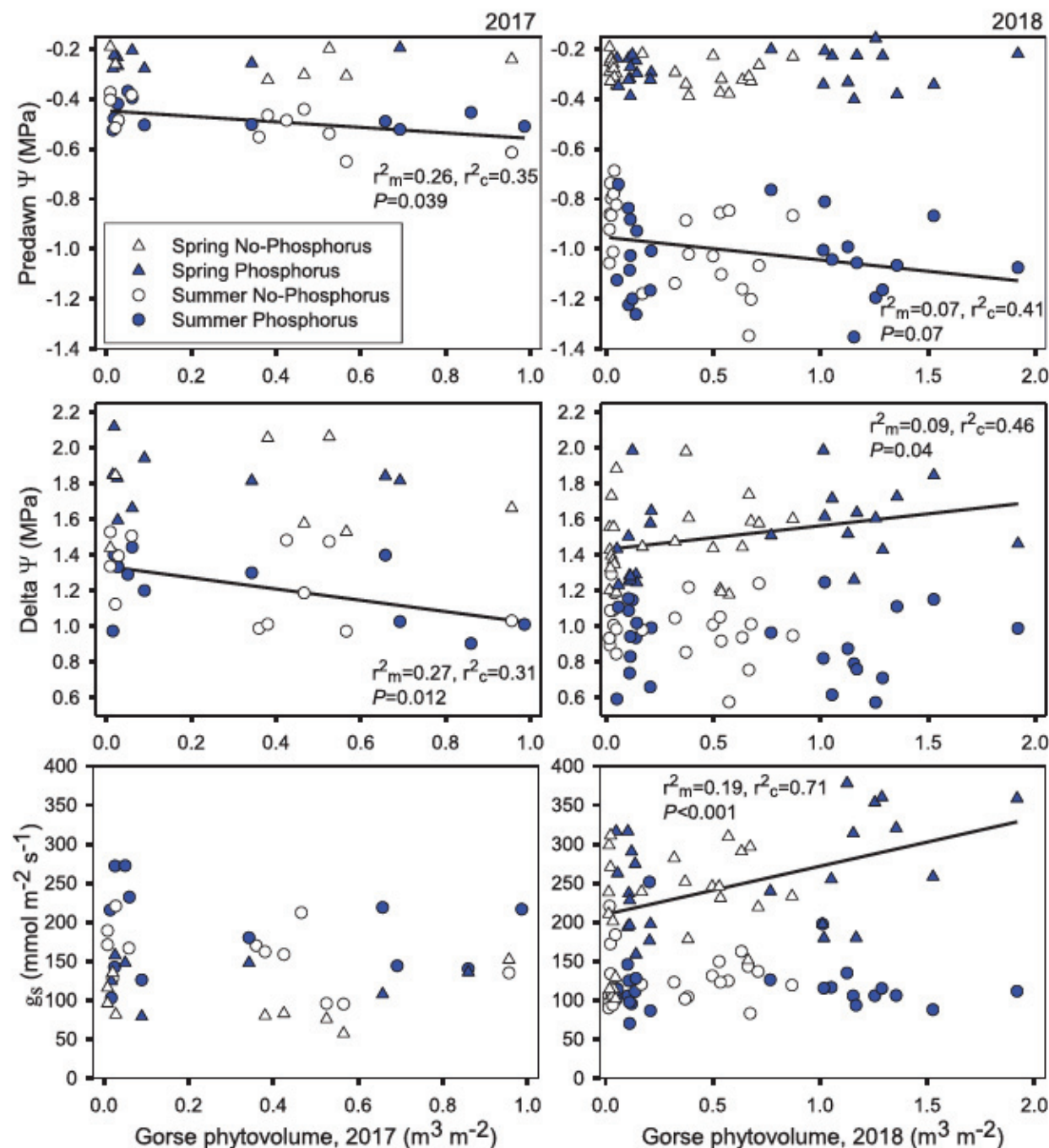


Figure 6. Effects of gorse phytovolume and phosphorus levels on leaf-level physiological parameters measured on maritime pine trees from the wet-gorse site. Pine predawn water potentials (Predawn Ψ), soil to leaf water potential gradient (Delta Ψ) and stomatal conductance (g_s) are presented for spring and summer of 2017 (five years old pine, $n = 24$ trees) and of 2018 (six years old pine, $n = 48$ trees). Linear regressions, along with the marginal R square (R^2_m) and the conditional R square (R^2_c), are represented for P -values < 0.1 .

by being 0.2 MPa lower when pines were surrounded by a dense gorse understorey (Figure 6). Midday Ψ values increased (less negative) with gorse phytovolume ($P = 0.038$; $r^2_{\text{marginal}} = 0.18$; $r^2_{\text{conditional}} = 0.18$) and values ranged between -1.36 MPa and -2.01 MPa (data not shown). Consequently, summer pine $\Delta\Psi$ values decreased ($P = 0.012$) with gorse phytovolume (Figure 6).

Hydric conditions during 2018 were more contrasted than in 2017 (Figure S7) with a flooded soil in spring followed by a severe drought in summer. The spring campaign took place when soil began to dry, and while no effects were detected

on predawn Ψ (Figure 6), a trend of decreasing midday Ψ values was recorded with greater gorse phytovolume ($P = 0.073$; $r^2_m = 0.07$; $r^2_c = 0.08$) and values ranged between -1.49 MPa and -2.33 MPa (data not shown). Consequently, $\Delta\Psi$ values increased with gorse phytovolume ($P = 0.04$). In spring of 2018, we observed a large increase of g_s with gorse phytovolume ($P < 0.001$) that was independent of P-application (Figure 6). In the summer of 2018, water potentials and g_s were measured during a drought period (REW = 3.3%, soil water content = 4.8%). While midday Ψ values remained in the same range as in spring (between

–1.42 MPa and –2.35 MPa), predawn Ψ values dropped and tended to be lower ($P=0.07$) with increasing gorse phytovolume (Figure 6). Finally, predawn Ψ , midday Ψ and $\Delta\Psi$ values measured in summer 2018 were lower than in 2017 ($P < 0.001$). Values of g_s in summer 2018 were lower than in spring ($P < 0.001$). We also observed that g_s in summer 2018 was lower than in summer 2017 ($P = 0.03$).

Discussion

Shade avoidance in a dense canopy

Gorses in the wet-gorse site quickly formed tall dense thickets around pines. Following studies by Balandier et al. (2006) and Vidal et al. (2019), this would induce competition for light during the early years, specifically because maritime pine is a shade intolerant species (Rameau et al. 2003; Valladares and Niinemets 2008). The first sign of competition was a delay in maritime pine diameter growth when gorse was abundant (see also Balandier et al. 2007), but no effect was measured on height. An increase in stem slenderness (height to diameter ratio) is often a structural response of shade intolerant species to a decrease in light received (Chen and Klinka 1998; Zavala et al. 2011; Gaudio et al. 2011a). Trees may also adapt their canopy to lower light conditions by reducing crown size (Weisberg et al. 2005; Jucker et al. 2015; Vidal et al. 2019). In our study, tree self-pruning induced by gorse expansion resulted in higher lowest living branches during the early stage of pine growth, but this effect disappeared when most pines became taller than the understorey canopy.

Water consumption under conditions of stress and competition

We first hypothesised that pines and gorses grown together would compete for soil water (Watt et al. 2003; Vidal et al. 2019), which was somehow verified by the decline in predawn Ψ during the summer in plots with high gorse phytovolume (Figure 6). On similar sites, Loustau et al. (1990) measured that below 20% of REW, predawn Ψ began to drop sharply with values going from –0.6 MPa at the beginning of the water stress to –1.2 MPa under severe drought. In 2017, predawn Ψ values indicated that a weak stress was imposed as gorse phytovolume increased, which was explained by significant summer rain events that mitigated the competition for water (Figure S7). In 2018, soil water storage was close to the wilting point (around 4% of soil water content down to 80 cm deep; Moreaux 2012), pine trees became more water-stressed than in 2017, and the stress severity also increased slightly with the presence of gorse. However, we expected that gorse phytovolume would have a stronger effect on pine water status during a dry year than a wet year, and it is possible that in 2018, once the soil wilting point was reached, the severity of the drought erased the stress differences between plots. It should be noted that in this ecosystem the presence of a hardpan layer and a high water table from early winter to mid spring limits deep root proliferation below 70 cm

(Bakker et al. 2006; Achat et al. 2008), which imposes a seasonal water deficit (Figure S7b).

The more negative predawn Ψ values measured in summer than in spring reflected the diminution in soil water content. The decreasing in predawn Ψ as gorse phytovolume increased implied a low level of competition for water from the shrubs, but the similar values of whole hydraulic tree capacity (K_{tree}) between seasons indicated that tree water transport capacity was not impacted (Domec et al. 2009b). However, because in the meantime the soil to leaf water potential (i.e. the driving force for water movement, $\Delta\Psi$ in Figure 6) tended to decrease from spring to summer, it likely reduced the pine water uptake during summer, with a concomitantly reduction of g_s values (Lambers et al. 2008). The close coordination that exists between K_{tree} and water flow within and among species implies that the maintenance of a rather constant K_{tree} as gorse competition increased, may have been the inherent component of the hydraulic system acting as a signal to regulate water uptake (Meinzer 2002). Maritime pine is qualified as a water-conservator species (Duursma et al. 2008; Moreaux et al. 2011) that can limit transpirational water loss by closing stomata (Loustau et al. 1990; Bréda et al. 2006), and this isohydric response is very pronounced in young individuals (Delzon et al. 2004). At moderate water stress (summer 2017 and spring 2018), g_s remained high and did not limit pine transpiration whether or not the trees were P-fertilized (Figure 6). During a more severe drought (summer 2018), stomata closed in order to limit further drop in Ψ and to maintain a high K_{tree} (Sperry and Tyree 1990; Knipfer et al. 2020).

Tree nutrition as influenced by leguminous understorey

As expected, P stimulated pine and gorse growth (Delerue et al. 2015; Vidal et al. 2019), but did not affect the response of plant physiological traits to gorse phytovolume or seasonal conditions (Figure 6). Selecting pine plots with high values of gorse phytovolume may have led to selecting plots with higher soil P content ($P < 0.01$ for all soil P pools) because available P could increase gorse recruitment and growth (Delerue 2013). The high gorse fine root length density and specific root length in the topsoil (where P was supplied) likely indicated stronger root and mycorrhizal prospection for P uptake. This may be driven by the overall P limitation for this forest type (Trichet et al. 2009) and be further reinforced by the specific needs of P for symbiotic N fixation (Augusto et al. 2013).

We observed that both N fertilisation and gorse understorey improved pine N nutrition. Several studies have shown that leguminous species increased soil N content (Slesak et al. 2016; Winsome et al. 2017) and plant N nutrition (Paula et al. 2015). In our study, the denser pine root systems and the results of the ^{15}N labelling indicated that gorse induced a faster N uptake by pines (El Zein et al. 2011). We suggest that this root growth plasticity may reflect an acclimation to more fertile soil patches with higher N concentrations (Hodge 2004).

Gorse-pine coexistence: a biotic interactions balance

Gorse-pine interactions varied over time, with gorse understorey strongly affecting resource availability for pines. Following our first hypothesis, gorse competed with pines for light at the beginning of the rotation, then understorey competition was strongly reduced four years after plantation, when pines started to dominate the shrubs. Before this threshold age, pines avoided competition for light by morphological plasticity such as stem slenderness and self-pruning. Similarly to competition for light, we speculate that competition for water occurred at the early stage for pine because thick gorse stands probably increased whole-site water use (Moreaux et al. 2011), as indicated by the higher level of water stress with increased gorse competition in 2017. Thus, once pines were established, gorse continued to compete with pines during drought periods but the effects remained weak, which partly confirmed our second hypothesis.

Site productivity and pine nutrition were substantially favoured by gorse in interaction with nutrient availability, as hypothesised (third hypothesis). Competition for light and water decreased as trees got older, with eventually no negative consequences on growth or on pine hydraulic capacity (K_{tree}). We also suggest that the absence of negative impact recorded at this stand stage could be due to the gorse fertility benefits (third hypothesis). Conversely, the gorse presence did not improve tree growth, despite an overall positive effect on tree N nutrition. These processes support the idea that a gorse understorey could be an advantage for pine forestry.

Pine production in different environments

The wet-grass site is ecologically close to the wet-gorse site and its understorey can be taken as a proxy for the potential understorey composition in the wet-gorse site without gorse sowing. Pine growth is constrained here predominantly by the phosphorus scarcity and, to a lesser extent, by competition with the understorey stratum. Purple-moor grass is a perennial, deciduous, and herbaceous species. Crushing this herbaceous species to reduce its presence in the understorey is generally partly effective, and hence actual competition from purple-moor grass could be larger than expected despite crushing. In general purple-moor grass negatively affects soil water reserves (Loustau et al. 1990) and could then be an efficient competitor by decreasing tree water availability and soil nutrient solubility (Balandier et al. 2006; Delerue et al. 2018).

At the dry-ericaceous site, pine growth and survival indicated strong competition by ericaceous shrubs. The absence of P fertilisation effects between treatments would exclude nutrient competition. Similarly, competition for light could also be diminished because of the low growth and low leaf area of this shrub (Gimingham 1960; Gaudio et al. 2011b). In contrast, we suspect that there was a high competition for soil water because water holding capacity in dry moorlands is lower than in humid ones that are also characterised by a higher water table (Moreaux 2012). The

perennial character of *Ericaceae* species leads to a progressive accumulation of aboveground biomass (Gimingham 1960), creating small thickets, which increase total evapotranspiration while the ecosystem is strongly constrained by water.

Evidence of variations in biotic interactions among sites suggested that the functional group dominating the understorey influences tree growth by modulating the availability of resources (Balandier et al. 2006; Craine and Dybzinski 2013; Forrester 2014). Nevertheless, site comparisons should be interpreted with caution because of the differences in age and environmental conditions. Maritime pine is a stress tolerant species able to grow on poor soils, which probably makes this species sensitive to interspecific competition and biological invasion (Grime 1977; van Etten et al. 2020). This sensitivity could explain the prominence of competition effects in young plantations, supporting our first two hypotheses. Interactions between species for nutrient uptake could also potentially switch to facilitation when the N-fixing functional strategy is dominant. However, in contradiction to our third hypothesis, neither indirect facilitation, nor direct facilitation, had a significant influence on pine dynamics, even though a positive trend was observed.

Concluding remarks

Maritime pines can establish in unfertile and dry conditions, even though in its sapling stage this species can be sensitive to competition. As a consequence, regular understorey mechanical controls appear suitable to enable high site productivity in young plantations, especially with understorey dominated by fast-growing woody perennial species. At young stand stages, light competition clearly impacts pine growth and morphology, while competition for water remains weak and only significant during drought periods. Plant phenotypic plasticity probably enables trees to mitigate most of the negative effects of competition. In the case of an understorey dominated by leguminous species, tree nutrition can likely benefit from improved N availability, which can be taken into account in forest resource management planning.

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Supplementary Information Tables S1 & S2

Table S1: Young maritime pine (*Pinus pinaster* Ait) nutritional threshold values (dry mass basis) of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg). Optimum and low reference values are calculated after van den Burg (1985).

	N (mg g ⁻¹)	P (mg g ⁻¹)	K (mg g ⁻¹)	Ca (mg g ⁻¹)	Mg (mg g ⁻¹)
Optimum value	13.7	1.4	5.2	2.9	1.9
Low value	12.2	1.0	3.4	2.0	1.2

Table S2: Growth of seven-year-old maritime pine trees at the wet-grass and the dry-ericaceous sites. Mean values of tree height, circumference at breast height (C₁₃₀) and volume are shown for the wet-grass (n = 1,280 trees) and the dry-ericaceous (n = 1,928 trees) sites as a function of treatments ('P' and 'C' stand for phosphorus fertilisation and control, respectively; 'UD' and 'NC' for understory crushing and no understory crushing, respectively). Different letters indicate significant differences between groups (Tukey post-hoc test; ***P < 0.001; ANOVA).

Treatments	Wet-grass					Dry-ericaceous				
	Height (cm) ***	C ₁₃₀ (cm) ***	Volume (dm ³ stem ⁻¹) ***	Height (cm) ***	C ₁₃₀ (cm) ***	Volume (dm ³ stem ⁻¹) ***	Height (cm) ***	C ₁₃₀ (cm) ***	Volume (dm ³ stem ⁻¹) ***	Volume (dm ³ stem ⁻¹) ***
P/UD	500.8 ± 5.3 a	30.0 ± 0.4 a	11.4 ± 0.39 a	469.9 ± 3.5 a	25.0 ± 0.2 a	7.03 ± 0.15 a				
P/NC	469.3 ± 4.7 a	26.8 ± 0.4 ab	8.54 ± 0.30 b	324.2 ± 4.8 b	16.1 ± 0.3 b	2.54 ± 0.11 b				
C/UD	409.5 ± 4.8 b	23.7 ± 0.4 b	6.32 ± 0.28 b	503.1 ± 4.3 a	26.4 ± 0.2 a	8.41 ± 0.18 a				
C/NC	352.3 ± 5.1 c	18.4 ± 0.3 c	3.54 ± 0.20 c	364.7 ± 4.7 b	17.8 ± 0.3 b	3.29 ± 0.12 b				

Supplementary Information Table S3

Table S3: Maritime pine growth at the wet-gorse site ($n = 72$ trees). Circumference at breast height (C_{130}) and volume per stem are shown as a function of treatment (fertilizer application is represented by the upper letters, i.e. control 'C', nitrogen 'N' or phosphorus 'P'; gorse abundance is represented by the lower letters i.e. control 'C' or gorse addition 'G'). Different letters indicate significant differences between groups within one year (Tukey post-hoc test: [NS] non significant; [*] $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; ANOVA).

Treatments	Four years old pine (2016)			Five years old pine (2017)			Six years old pine (2018)		
	C ₁₃₀ (cm) [NS]	Volume (dm ³ stem ⁻¹) [NS]	C ₁₃₀ (cm) [*]	Volume (dm ³ stem ⁻¹) [*]	C ₁₃₀ (cm) *	Volume (dm ³ stem ⁻¹) **			
C/C	5.3 ± 0.8 a	0.15 ± 0.03 a	11.5 ± 0.8 ab	0.84 ± 0.12 ab	17.4 ± 1.0 ac	2.48 ± 0.31 ab			
C/G	6.6 ± 0.9 a	0.25 ± 0.06 a	10.9 ± 1.2 ab	0.86 ± 0.19 ab	15.3 ± 1.6 bc	2.06 ± 0.40 b			
N/C	7.8 ± 1.0 a	0.35 ± 0.08 a	13.3 ± 1.3 ab	1.27 ± 0.24 ab	18.9 ± 1.6 ac	3.19 ± 0.55 ab			
N/G	5.6 ± 0.6 a	0.16 ± 0.03 a	9.9 ± 0.9 b	0.60 ± 0.10 b	14.2 ± 1.0 c	1.55 ± 0.23 b			
P/C	7.4 ± 1.1 a	0.37 ± 0.11 a	13.9 ± 0.9 ab	1.44 ± 0.30 ab	20.2 ± 1.1 ac	3.71 ± 0.54 ab			
P/G	8.6 ± 0.6 a	0.42 ± 0.05 a	13.6 ± 0.8 ab	1.33 ± 0.18 ab	19.3 ± 1.2 ac	3.46 ± 0.50 ab			
NP/C	8.3 ± 0.9 a	0.40 ± 0.09 a	16.0 ± 1.4 a	1.98 ± 0.40 a	24.2 ± 1.9 a	5.93 ± 1.05 a			
NP/G	8.2 ± 0.8 a	0.40 ± 0.08 a	14.4 ± 1.2 ab	1.56 ± 0.38 ab	21.2 ± 1.4 ab	4.29 ± 0.70 ab			

Supplementary Information Figure S1

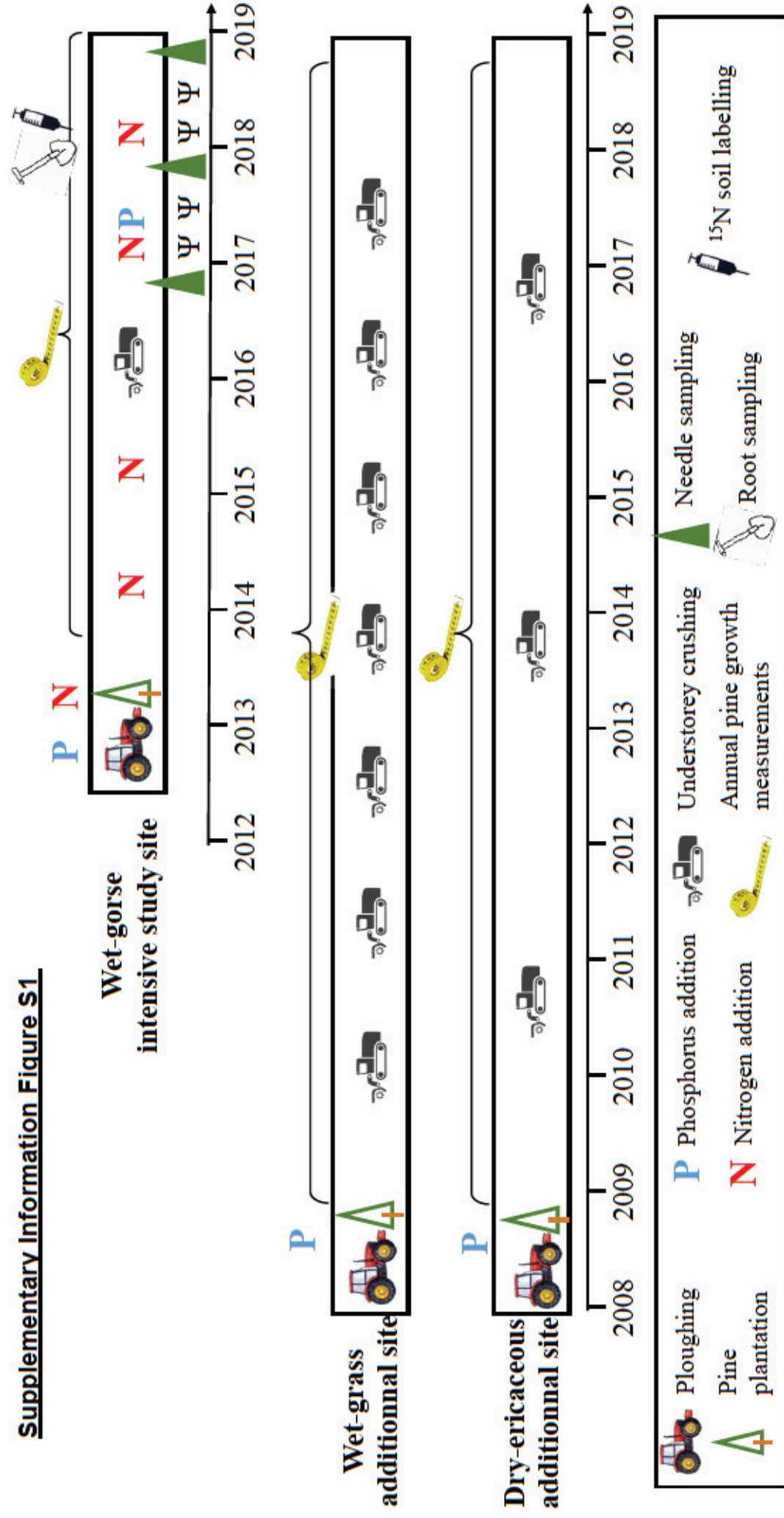


Figure S1: Timing of site preparation, soil and tree sampling for the wet-gorse, wet-grass and the dry-ericaceous sites.

Supplementary Information Figure S2

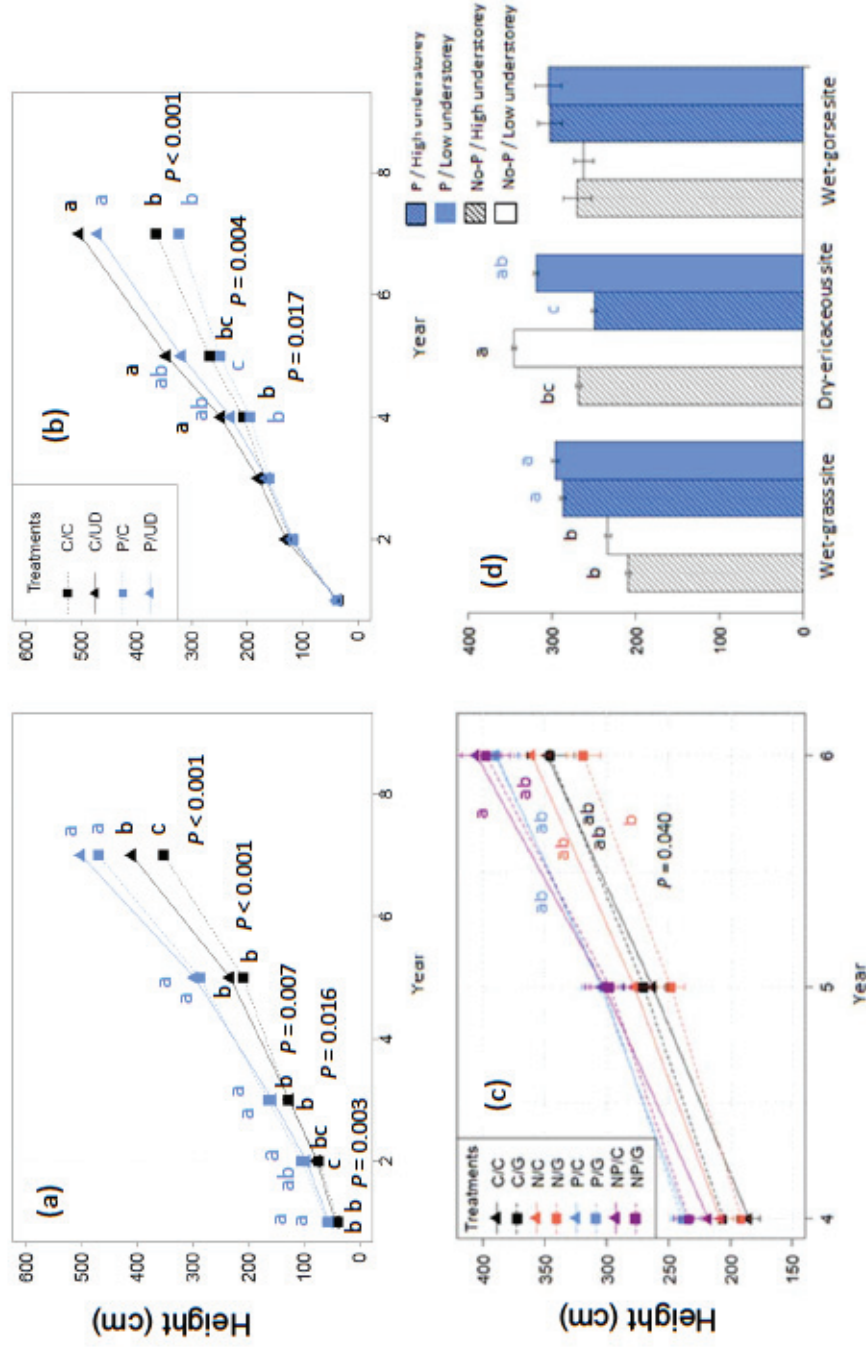


Figure S2: Maritime pine (*Pinus pinaster* ait.) height as a function of age for the three sites studied. Panels a, b and c represent pine heights for the wet-grass ($n = 1,280$ trees), the dry-ericeaceous ($n = 1,928$ trees) and the wet-gorse site ($n = 72$ trees), respectively. Note that in (a) and (b) pine heights of the dry-ericeaceous and the wet-grass site are shown from the first year after planting, while in (c) values start four years after planting. A comparison of the pine heights at five years old at each site is shown in panel d. Different letters indicate significant differences between groups within a site (Tukey post-hoc test).

Supplementary Information Figure S3

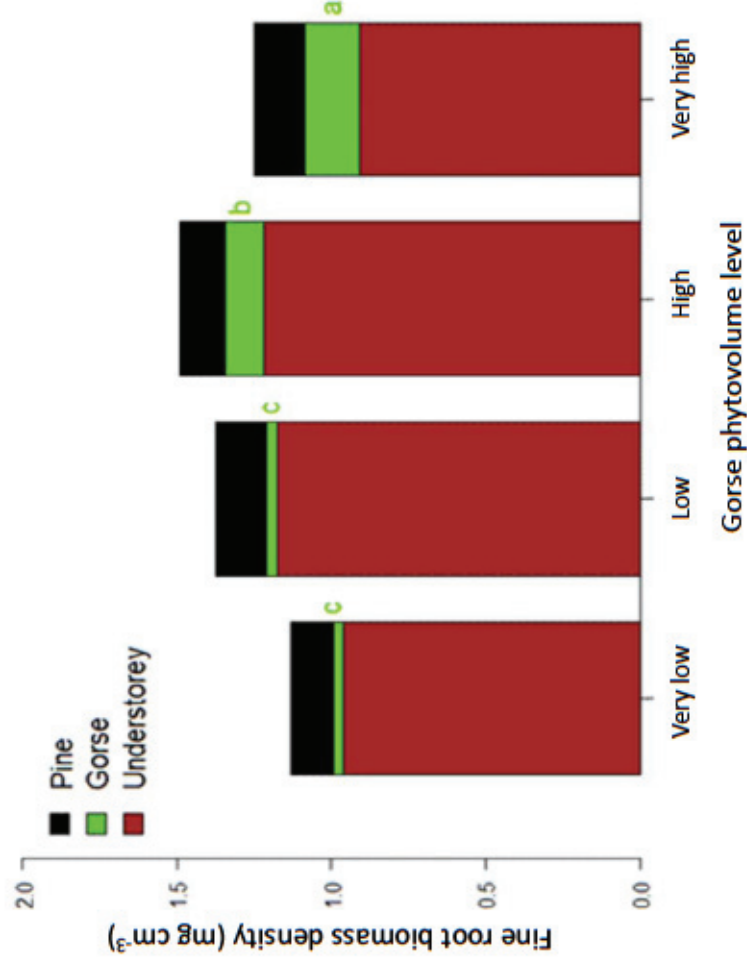


Figure S3: Fine root biomass density of maritime pine trees, gorse and the remaining understorey species. Total fine root biomass is presented as a function of gorse phytovolume levels and according to the three groups of vegetation: pine, gorse and the other species (named « Understorey »). Different letters indicate significant differences between gorse phytovolume levels (Tukey post-hoc test, $n = 72$ soil samples). Note that gorse fine root biomass increased significantly with gorse phytovolume (green letters).

Supplementary Information Figure S4

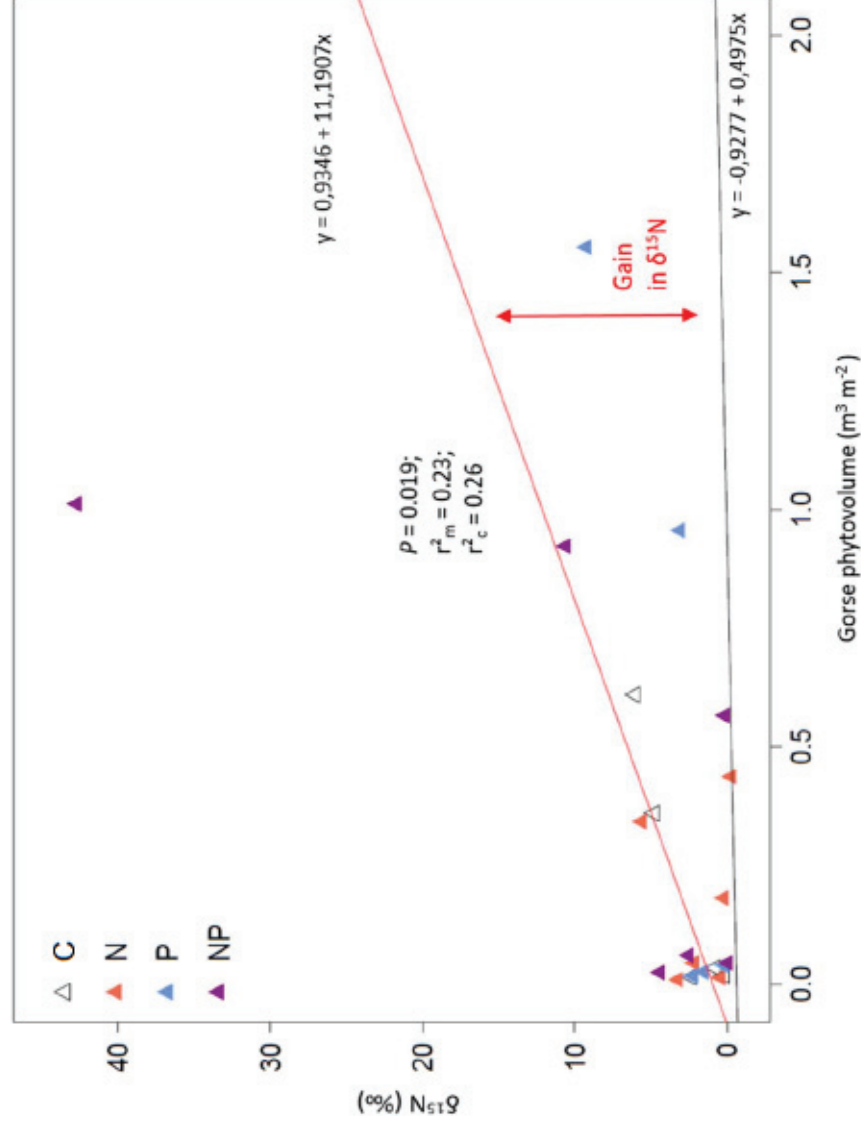


Figure S4: Gain in needle- $\delta^{15}\text{N}$ following soil ^{15}N labelling at a depth of two cm as a function of the four fertilisation treatments (C = control, N = nitrogen, P = phosphorus, NP = nitrogen plus phosphorus). The black line represents the initial needle- $\delta^{15}\text{N}$ and the red line represents the gain in needle- $\delta^{15}\text{N}$ after the ^{15}N labelling ($n = 24$ trees).

Supplementary Information Figure S5

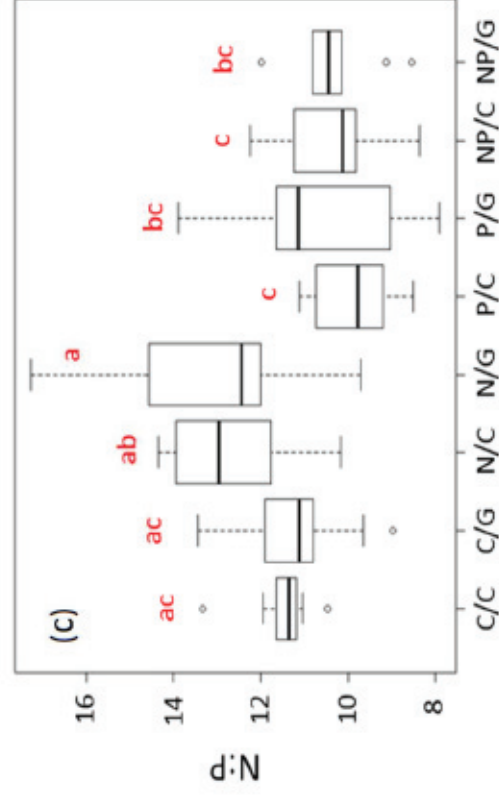
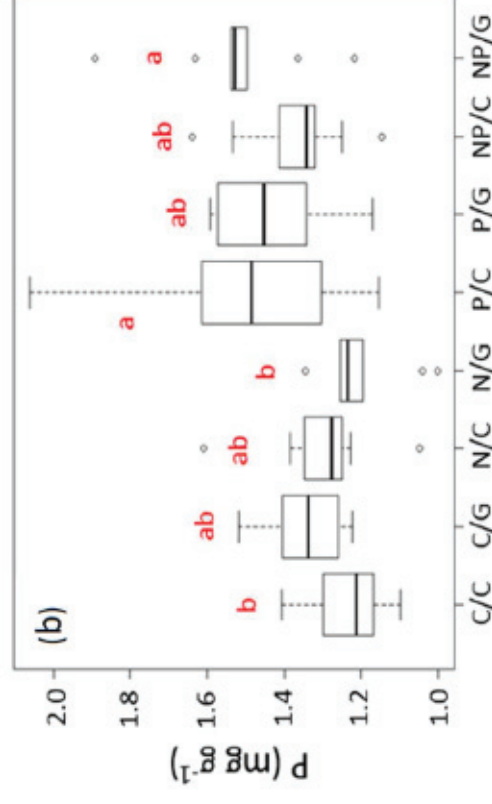
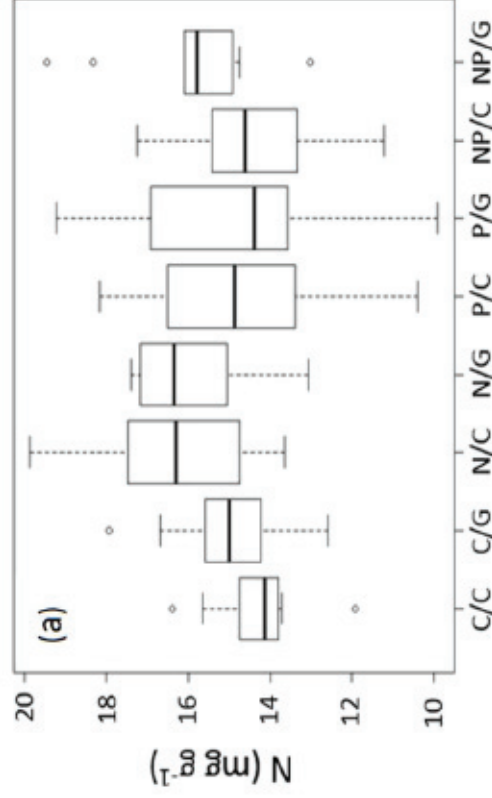


Figure S5: Effects of site characteristics on (a) nitrogen (N), (b) phosphorus (P), and (c) N:P concentrations ($P = 0.017$ for P, $P < 0.001$ for N:P) of green gorse twigs at the wet-gorse site (sampled in 2018 when stand age was seven, $n = 72$ gorse shrubs). For each site modality, the upper letters represent the level of fertilisation (C = control; N = nitrogen addition; P = phosphorus; NP = nitrogen plus phosphorus) and the lower letters the type of site undersory (C = control and G = gorse addition). Different letters indicate significant differences between modalities (Tukey post-hoc test).

Supplementary Information Figure S6

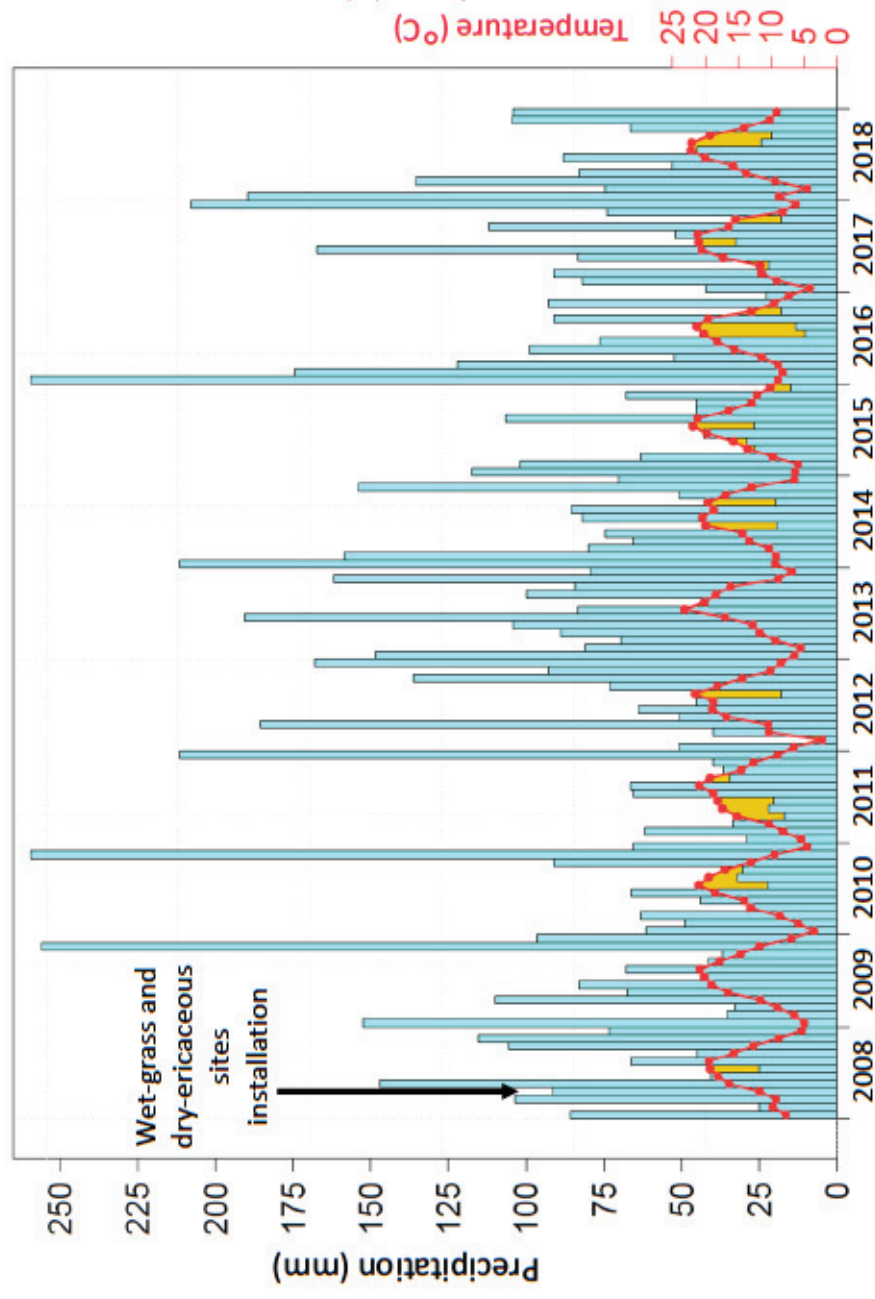


Figure S6: Walter-Lieth climate (ombrothermic) diagram showing the monthly variations in precipitation (blue) and air temperature (red) at the wet-grass site and the dry-ericeaceous sites from 2008 to 2018. Areas shaded in yellow indicate that mean temperatures were higher than twice the monthly precipitation and represent drought periods.

Supplementary Information Figure S7

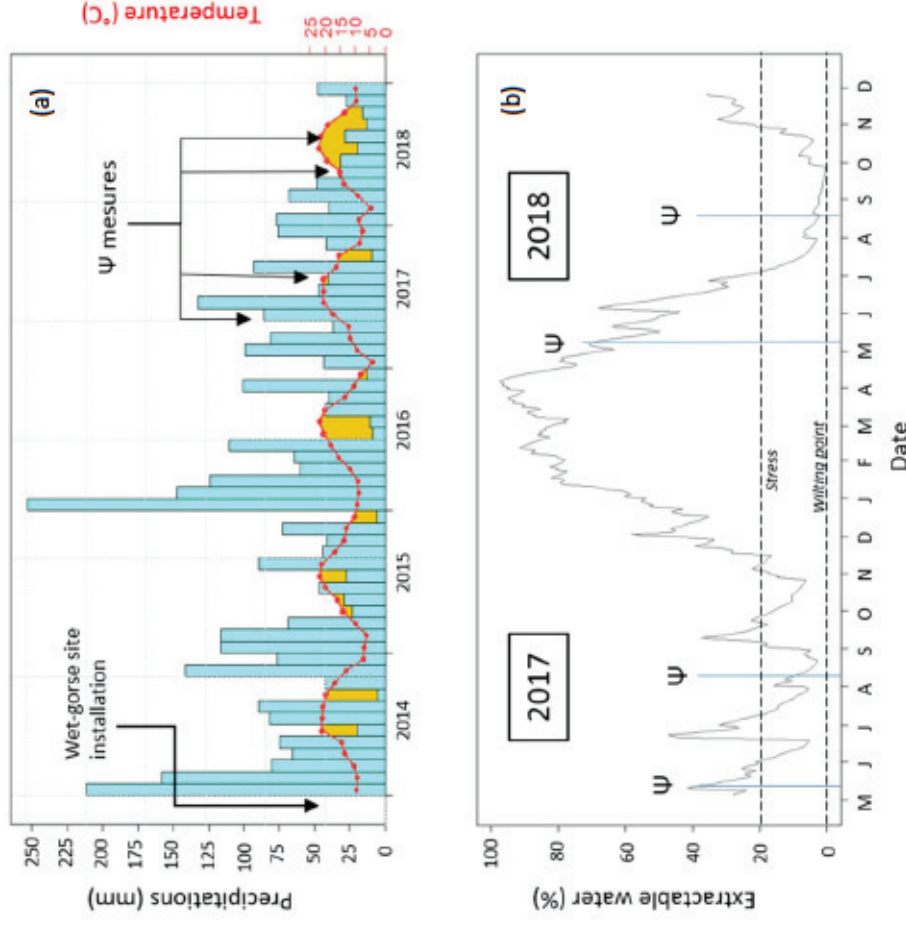


Figure S7: (a) Monthly variations in precipitation (blue bars) and temperature (red line) at the wet-gorse site. This ombrothermic diagram is presented from the first year after site establishment and treatment applications (2014) to the last monitoring year (2018). Areas shaded in yellow indicate that mean monthly temperatures were higher than twice the mean monthly temperatures and represent drought periods. In (b) the relative extractable water (REW) averaged over the 70 cm of soil is presented from May 2017 to December 2018, when ecophysiological measurements were performed (ψ symbols; Figure S1). REW thresholds for the onset of water stress (20% REW equivalent to 9% soil moisture) and for the soil wilting point (0% REW or 4% soil moisture) are also indicated.