Plasticity in growth, biomass allocation and root morphology in beech seedlings as induced by irradiance and herbaceous competition

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Abstract: Biomass increment, biomass allocation and fine-root morphology were compared on four-year old *Fagus sylvatica* seedlings growing under low (11% relative irradiance), medium (14-19%) or high (46%) irradiance under natural *Pinus sylvestris* canopies, and under full light in a weeded meadow in the French Massif Central. Significant differences in biomass increment were found among plots in relation to light regime and interspecific competition. Light regime had little effect on shoot-to-root ratio and biomass allocation, but had a clear impact on above- and belowground morphological variables. Beech seedlings displayed a lower specific root length (SRL) and a higher specific leaf area (SLA) under shade, thus indicating limited belowground competitive ability and poor morphological adjustment to shade. Similarly, competition from herbaceous vegetation had a negligible effect on seedling growth and biomass allocation, but significant impact on fine-root morphology. Low SLA and high SRL values at high irradiance coincided with high growth increments.

Key words: Biomass allocation, European beech (*Fagus sylvatica* L.), fine-root architecture, interspecific competition, irradiance

Résumé: L’accroissement de biomasse, les patrons d’allocation de biomasse et la morphologie des racines fines ont été comparés sur des plants de hêtre (*Fagus sylvatica* L.) de quatre ans installés sous un boisement naturel de pin sylvestre à faible, moyen et fort éclairement (11%, 14-19% et 46% d’irradiance relative), et en pleine lumière dans une prairie désherbée du Massif Central français. Les plants ont montré des différences significatives de croissance en biomasse selon l’éclairement relatif et l’intensité de la compétition avec le pin et les herbacées. L’éclairement a peu affecté le ratio biomasse aérienne / biomasse racinaire et l’allocation de biomasse au sein des différents compartiments, mais a eu un impact clair sur la morphologie aérienne et racinaire des plants. Les hêtres subissant un fort ombrage présentaient des racines fines peu ramifiées (faible longueur spécifique racinaire, SRL) et des feuilles peu épaisses (forte surface spécifique foliaire, SLA), ce qui suggère une faible capacité d’accès aux ressources du sol et un ajustement à une faible énergie lumineuse. De même, la végétation herbacée a eu un faible impact sur la croissance des hêtres et l’allocation de biomasse, mais a affecté significativement la morphologie de leur racines fines. Au total, des valeurs de SLA faibles et de SRL fortes à fort éclairement correspondent à de forts taux d’accroissement en biomasse.
Mots clés : Allocation de biomasse, Hêtre (*Fagus sylvatica* L.), morphologie des racines fines, compétition interspécifique, éclairement sous forêt
1. Introduction

European beech (*Fagus sylvatica* L.) is a major late-successional species able to replace early-
successional tree species in European temperate forests (e.g. [17, 51]). The ‘Chaîne des Puys’ volcanic
range of the French Massif Central presents a mosaic of wooded habitats (i.e., pioneer natural
woodlands and shrublands) that may provide suitable habitats for beech. Field surveys indicate that
beech seedlings establish sporadically under full-light conditions but mostly under the canopy of
ageing *Pinus* or *Betula* pioneer woodlands [16, 32]. They exhibit variable survival, growth, and
morphology [15, 16] across the mosaic of habitats caused by woody colonization and pioneer stand
dynamics. As a consequence, *Fagus* seedlings face variable irradiance levels and weed competition
according to canopy closure. The literature has long established *Fagus sylvatica* as a shade-tolerant
species [27] that appreciates shelterwood [5, 25, 54]. It is also considered as a drought-sensitive
species, given clear evidence that belowground competition for water and nutrients from surrounding
herbaceous vegetation severely limits seedling development under full-light conditions [9, 21, 34].

Theory in plant ecology assumes that adaptive strategies allow subordinate late-successional
and shade-tolerant species to establish under the canopy of shade-intolerant and pioneer species, in
particular: (i) preferential biomass allocation to the most efficient organs for acquiring light [22, 26],
water and nutrients [27]; and (ii) modification of the spatial arrangement and the efficiency of resource
capture by these organs [20, 29]. Biomass allocation strategy in response to stress is a central concern
in plant ecology, but the issue is still being debated [4]. Some authors hypothesize that shade entails
preferential allocation to stems at the expense of roots and constant allocation to the foliage [44],
while others indicate higher allocation to stem and leaves [48]. Morphological responses of aerial parts
to competition from overstory and understory vegetation have been widely investigated for most
temperate tree species. Converging evidence from the literature indicates that the aerial parts of *Fagus*
seedlings have a high morphological (and physiological) acclimation capacity to light regime at
crown-scale [33, 41] and branch-scale [11, 26] as well as at leaf-scale [5, 32, 37, 40]. Shading
especially is expected to result in leaves with higher specific leaf area (SLA) [44]. Such plasticity of
leaf traits has been proved to coincide with high relative growth rates (RGR) within the same habitat
Morphological plasticity in belowground parts has received much less attention although overstory species and grasses can outcompete beech [8, 10]. A previous study on naturally-regenerated saplings indicated that fine-root morphology, root biomass and rooting profile adapted to local crowding by the *Pinus* or *Betula* overstory [15, 16]. However, such studies are frequently unable to discriminate ontogenic effects of beech age from biotic (e.g. interspecific competition, browsing) and abiotic stresses (e.g. shade).

To investigate beech response to irradiance and competition from the surrounding vegetation, we studied biomass increment, biomass allocation and belowground morphology over two seasons in two-year-old beech seedlings growing under experimental Scots pine stands, and on a weeded meadow. Seedlings had similar mass and age at the beginning of the experiment since plant morphology and biomass allocation patterns are hypothesized to change over tree developmental stages [24]. Although *in situ* field experiments face problems in separating the specific effects of multiple growth variables on the target species, this approach was used to stay close to realistic interactions between beech seedlings and their competitors (e.g. studying real herbaceous communities and multiple interactions with the overstory instead of simulated shade). The aim of this study was to test the following hypothesis: (i) beech would react strongly to competition from the over- and understory vegetation by modifying its morphology at leaf-level and fine-root level in order to improve its efficiency in acquiring light and soil resources [3, 20, 26]; (ii) these changes would correlate with biomass increments and allocation plasticity. More practical objectives were to assess the extent to which light and herbaceous interference affect beech development, and to gather information on the optimal growth conditions for this species within the study area.

### 2. Materials and methods

#### 2.1 Study sites and experimental design

The study area was the volcanic range of the Chaîne des Puys (French Massif Central, longitude 2°59’ E, latitude 45°42’ N). The stands selected for the experiment presented a range of
similar ecological features: elevation is 850 to 950 metres, physiographic positions are plateaux or moderate slopes, and climate is mid-oceanic (mean annual rainfall = 820 mm; mean annual temperature = 7°C). Soils are loamy Cambisols on basaltic tephras (FAO soil classification) with a typical mull or mull-moder humus form. They have no major nutritional constraints since mean pH<sub>water</sub> is 6.0, mean C:N ratio is 12, and CEC is 33 mEq per 100 g in the upper soil layer [15]. Native forest sites were mesic or gently acidic, with overstory dominated by Fagus sylvatica L., Abies alba Mill., and scattered Acer spp. or Prunus avium L.

The experimental design comprised six neighbouring stands located within a former agro-pastoral area typical of the ‘Chaîne des Puys’. Five forested stands were dominated by Scots pine, which established naturally after the cessation of grazing in the 1950s [43]. The last plot was a non-forested meadow, which was fully weeded with an initial glyphosate treatment, then manually harrowed during the whole experiment to maintain a bare soil and to avoid any competition with herbaceous. Stands were selected to form a gradient of light regime (= stand density) and stand age (Table 1) comprising: (i) three young and dense Pinus-dominated stands at pole stage with a sparse understory, which were left intact or thinned to achieve three light regimes: low (LL, 11% relative irradiance), medium (ML-V, 19.2% relative irradiance) and high irradiance (HL, 46.5% relative irradiance); (ii) a submature Pinus-dominated stand of medium light regime (ML+V, 16% relative irradiance) with an abundant understory vegetation; and (iii) a full-light regime (FL-V, 100% relative irradiance) control plot installed on a former meadow without tree colonization, which was weeded before setting up the experiment. This experimental design allowed not only comparison according to light gradient but also comparison between stands of medium light regime with very low vegetation competition (ML-V) and high vegetation interference (ML+V; Table 1). Relative irradiance of 11 to 46% is within the range of light regimes that commonly occur in heterogeneous and sparse-canopied natural Scots pine woodlands in the study area [16].

All pine-dominated stands had similar mesic ground vegetation associating dicotyledons such as Galium or Fragaria spp. and graminae such as Festuca rubra and Dactylis glomerata with presumably high competitive ability [9, 10]. To estimate the competition entailed by herbaceous species, we assessed aerial and fine-root (< 2 mm) biomass on five replicates of 1 m² on each stand.
These plots were installed in areas that were representative of the stand. Aerial biomass was estimated after clear-cutting, while fine-root biomass was collected on a 70-cm deep soil layer. In *Pinus*-dominated stands, vegetation cover correlated positively with light regime: it was very sparse at dense pole stage whereas it developed considerably in thinned stands at high light regime and under the submature plot ML+V (Table 1). Data analysis (data not shown) indicated that herbaceous fine-root biomass increased exponentially with light in the dense pine stands ($R^2_{adj} = 0.63$), and was about 13-fold higher in the submature stand (ML+V) than in the young stand of similar relative irradiance (ML-V).

On each stand we installed a fenced 18x18 m square plot. Each plot included a 12x12 m central zone surrounded by a 3-m buffer zone with similar stand characteristics. Central zones were subdivided in one-hundred 1.2m square units, with four units left apart and dedicated to seed sowing. On each plot, 96 two-year-old bare root seedlings (*Fagus sylvatica* L.) purchased from a local nursery were randomly distributed and planted in November 2000 in the centre of each 1.2x1.2m unit. Randomisation and utilisation of two-year-old seedlings allowed reducing possible ontogenic and size-dependent drift in biomass [24] since seedlings had the same age. An analysis of variance indicated that seedling biomass did not differ significantly among stands at the beginning of the experiment (data not shown). To avoid errors in computing individual biomass increment, we computed allometric relationships on a supplementary subset of 33 seedlings before plantation. Correlations between initial shoot and root biomass, stem height, and base diameter were very high ($R^2$ ranging from 0.95 to 0.99). Biomass within seedlings compartments before plantation was 0.31, 0.60, 4.71, 4.62 and 0.71 g (dry weight) for fine roots, main roots, taproot, stem and branches, respectively. Total aerial biomass was 5.32 g while total root biomass was 5.62 g, thus giving a balanced shoot-root ratio (mean = 0.95).

Mean global irradiance under the Scots pine canopy was measured with 16 TSL tube-solarimeters (1-m long, Delta-T™ device) distributed evenly over each plot at 0.7 m above ground. Each solarimeter was located at the centre of four seedlings. Measurements were integrated over 24 hours in June 2001, and expressed as relative values of incident radiation measured at the same time under full-light conditions at the vicinity of each stand in the weeded meadow. Complementary measurement of the near red-to-far-red ratio indicated limited change in light quality, i.e. high
correlation with the relative irradiance. Soil-water content was monitored weekly in the 0-20 cm soil layer with a TDR probe (Trime T3, IMKO™, Ettlingen, Germany) beside four beech seedlings per plot (see [8, 9]).

2.2 Growth, biomass allocation and root architecture of beech seedlings

All beech seedlings were monitored throughout two growing seasons (2001, 2002) to assess shoot growth. We measured stem height, base diameter, and crown dimensions. Relative growth increments were computed at individual-scale in reference to the initial values at planting date. Specific leaf area (SLA, cm$^2$.g$^{-1}$) was assessed following a standardized protocol [23]. Ten leaves were selected on each seedling according to the upper, median and lower part of the tree. Leaf blades were cool-stored in airtight bags until processing. Each leaf was dried with tissue paper to remove any surface water, and immediately weighed to determine their saturated fresh mass. The area of the fresh blade was determined using WinFolia™ software (Regent Instruments, Quebec, 2000), and dry mass was measured after oven-drying for five days at 70°C.

We manually harvested six random seedlings at the end of the first growing season (November 2001) and ten at the end of the second season (November 2002). Seedlings were harvested taking care to prevent root breaking [16], then cool-stored before treatment. They were divided into six compartments: leaves, branches, stems, taproots, coarse-roots (diameter > 2 mm) and fine roots (diameter < 2 mm), then weighed after oven-drying (70°C) for five days. Biomass allocation for each compartment was computed in g per compartment per g of total plant biomass (see [44]; Table 4). Since the relative biomass distribution to plant compartments is sensitive to the whole plant biomass, this allometric approach allowed separating changes resulting from plant size from changes due to real shifts in partitioning [35].

Fine-root morphology was assessed on three intact sub-samples per seedling. Samples corresponded to first- to third-order roots [20] to prevent morphological variations according to the position and the branching order [3, 42]. Specific root length, mean fine-root diameter (mm) and internode length (mm) were assessed with the WinRhizo™ image analysis software V 5.0A (Regent...
Instruments, 2000) since these variables were proved efficient for characterizing the soil exploitation strategy of forest tree species [3, 15, 16, 19].

2.3 Belowground development of over- and under-story vegetation

Root biomass and the fine-root morphology of competitor plants (i.e. *Pinus sylvestris* and herbaceous species) were assessed to investigate their impact on beech growth and morphology. Four root cores were extracted at a distance of 40 cm around each target seedling (i.e., harvested) with a 7x15 cm root corer, in the 0-15 cm and 15-30 cm soil layers. Roots were extracted from the mineral and organic soil using a 4-mm mesh sieve, and sorted according to their diameter (fine roots < 2 mm, other roots > 2 mm) and to the species (Scots pine *versus* herbaceous species). Root identification used morphological criteria such as colour, branching and flexibility. We used databases from the literature, our own reference materials and dichotomic keys [16]. Morphological measurements were performed using WinRhizo™ on pine and herbaceous fine-root subsamples as on beech. Root elongation over the active vegetation period was monitored for all species (beech, pine, weeds) on a pair of 1x0.8 m rhizotrons per plot. Root drawings on transparent sheets were scanned then analysed using WinRhizo™. In addition, fine-root colonization within ingrowth bags was surveyed on five seedlings per stand. The 40x7.5 cm bags with a 0.5 cm nylon mesh were installed around five randomly selected beeches per plot in March 2001 (see [52]), and the fine roots that had colonized the bags were removed twice a year to assess their biomass and morphology as described above.

As *Pinus*-dominated natural woodlands were spatially heterogeneous, each seedling experienced a specific degree of competition from the pine overstory, depending on pine number, size and distance. Aboveground competition by pines was assessed by measuring the distance, the diameter at breast height (dbh) and the height of all surrounding pines within a 3 m competition radius around each seedling. This enabled computing of different competition indices that were proven efficient in predicting interspecific competition in pine stands (see [38, 43]). In particular, we tested the efficiency of distance-dependent *versus* distance-independent indices, and the correlation between irradiance and local crowding. Aboveground competition by the herbaceous layer was estimated by harvesting the
aerial herbaceous biomass of each 1.20 x 1.20 m square plot after extraction of seedlings. Dry biomass was weighed (± 0.1 g) after five days of drying in an oven (70°C).

2.3 Data analysis

In this experimental design, individuals (i.e., *Fagus* seedlings) were considered as the experimental units since the various thinning treatments were not replicated. In fact, the small-scale mosaic of stands within the study area prevented exact replications. Confounding factors due to site variations were largely avoided, making it possible to take radiation transmittance as the main source of variation, and vegetation competition as a co-variable. Seedling growth and morphology were also compared between the different treatments.

Responses of beech seedlings to ecological variables were assessed using simple and multiple linear regression analyses (i.e. nested variables) at individual scale and stand scale, and analysis of variance (ANOVA) at stand scale. Beech biomass increment was correlated with co-variables and nested variables describing interspecific competition at individual scale, such as pine and herbaceous root biomass, or relative irradiance. We used the natural data or log-transformed data when necessary in order to meet conditions of normality. A Fisher’s LSD-procedure and a multiple range test were used to compare means between the stands. Probability values of *P*<0.05 were considered significant.

Tests of biomass allocation strategies were performed on a constant mass basis, i.e. on the proportion of biomass in an organ relative to the whole seedling biomass.

3. Results

3.1 Beech growth and stand competition

Stand-scale comparisons revealed clear differences in beech growth two years after plantation (Table 2). Aboveground, belowground, and total biomass of beech seedlings increased with irradiance, from deep shade to full light. The mean seedling biomass at full light was three-fold greater than that measured at low light (LL). Stands of medium light regime showed similar biomass increment, although one had an abundant herbaceous cover (ML+V) whereas the other had limited cover (ML-V).
Beech growth and plasticity

Beech had a high growth at high light (HL) despite the presence of an abundant herbaceous cover. The full-light weeded plot (FL-V) showed the highest overall biomass increment despite severe intra-plot variability. Relative biomass increments were higher for roots than for shoots in a same stand (Table 2).

At individual scale, shoot growth correlated strongly with root growth (Fig. 1-a,b,c). Fine-root biomass (Fig. 1-a,c) or fine-root biomass increment (Table 3) correlated strongly with shoot biomass or relative stem-diameter increment. Relative irradiance had a positive impact on shoot and root biomass, and relative stem-diameter increment (Table 3). Competition indices experienced variable success in predicting beech growth. Indices based on vertical or horizontal angle sums within the 3 m competition radius explained about 40-50% of beech biomass (e.g. Vast3, Fig. 1-d) whereas weighted indices including the distance of neighbours were inefficient (e.g. SBD, Table 3). Pinus sylvestris root biomass had a depletive effect on shoot and root development of Fagus, unlike herbaceous fine-root biomass (Table 3). Since pine fine-root biomass accounted for the vast majority of stand root biomass, the total fine-root biomass of both competitors had an effect on beech growth.

A general linear model displayed a moderate prediction of beech relative biomass increment (R²_adj = 0.40) with a strongly predominant effect of relative irradiance (P<0.001), a very limited effect of pine root biomass (P=0.6209), and a null effect of the herbaceous root biomass (P=0.9921). Influential points and high residuals corresponded to seedlings growing in stands with low herbaceous cover at medium- or at full-light (ML-V, HL-V) irradiance. Regression and covariance-nested analyses on shoot and root biomass considered separately gained similar results.

3.2 Biomass allocation

Biomass allocation within plants (corrected from seedling size effects) varied little among stands after two years of the experiment (Table 4). Shoot-to-root ratios varied insignificantly among stands. Similarly, relative biomass allocation to leaves and branches did not differ markedly (Table 4). Variations were slightly higher within the root system than within the shoot. In stands with limited herbaceous competition (LL, ML-V and FL-V), increasing light enhanced allocation to coarse- and
fine-roots at the expense of the taproot, while allocation within aerial parts varied insignificantly. For seedlings planted at full light without vegetation competition, more biomass was allocated proportionally to stem than to branches and leaves. At medium irradiance (ML-V, ML+V) allocation patterns were similar irrespective of vegetation competition. Regression analyses (data not shown) confirmed that: (i) relative irradiance did not correlate with allocation to stem and branches, which remained constant among stands; (ii) light enhanced coarse and fine roots ($R^2_{adj}$ was 0.68 and 0.52, respectively) at the expense of the taproot; (iii) higher allocation to fine roots corresponded to higher beech growth both above- and belowground; and (iv) total root weight ratio was maximal at low- and full-light regime, and minimal at medium-light regime.

The fine-roots-to-leaves biomass ratio increased with irradiance (Fig. 3). Values ranged from 0.93 g g$^{-1}$ in low light with sparse herbaceous cover to 1.17 g g$^{-1}$ in the full-light weeded plot. This ratio was little affected by herbaceous competition at medium irradiance since it was not significantly different in the ML-V and ML+V stands (Fig. 3).

### 3.3 Above- and belowground morphological plasticity

Fine-root morphology varied strongly among stands for beeches. SRL and average diameter varied considerably ($P<0.0001$) while internode length varied less, but significantly ($P=0.0297$, data not shown). Seedling fine roots had a lower SRL, a higher average diameter and a lower internode length under shade in comparison to medium- or full-light regime (Fig. 2). At medium irradiance, the presence of an abundant herbaceous biomass (i.e., ML+V versus ML-V) produced roots with a lower average diameter and a higher SRL and internode length. Conversely, *Pinus sylvestris* had thick and little-ramified fine roots with almost constant morphology among stands ($P>0.05$, Fig. 2). Herbaceous fine roots were very thin and densely ramified, with considerable variations among stands. Overall, herbaceous fine roots tended to be finer and more ramified in stands with high irradiance and abundant graminae in comparison to forest dicots (ML+V, HL+V).

The SRL values for *Fagus* correlated slightly positively with the herbaceous fine-root biomass ($R^2_{adj}=0.24$, $P<0.001$), and negatively with the vertical ($R^2_{adj}=0.31$, $P<0.001$) and horizontal ($R^2_{adj}=0.36$, $P<0.001$) biomass.
0.25, \(P<0.001\) competition indices. Average fine-root diameter correlated negatively with herbaceous fine-root biomass \(R^2_{adj} = 0.30, P<0.001\). The abundance of \(Pinus\) fine roots had no significant effect on \(Fagus\) fine-root morphology.

Acclimation to shade at leaf level (i.e., high SLA) coincided with thicker and less-ramified roots (i.e., high average diameter, low SRL and low internode length). In the denser stands (LL, ML-V and HL) shading clearly resulted in an increase in SLA, paralleled by a decrease in SRL (Fig. 3). The full-light and weeded plots had a very low SLA and a high SRL, although SRL was lower than expected owing to the light regime. Both stands at medium irradiance had similar SLA, while the dense herbaceous cover (ML+V) entailed an increase in SRL in comparison to that existing under the sparse herbaceous cover (ML-V). At the same time, the fine-roots-to-leaf-mass ratio slightly increased with light regime and slightly decreased with the abundance of herbaceous vegetation (Fig. 3). Low SLA and high SRL values correlated positively with the relative diameter increment (Fig. 4; \(P<0.001\)).

4. Discussion

4.1 Beech development in response to competitive stress

Marked differences in the biomass of \(Fagus\) seedlings were found two years after plantation, our data being within the range reported in the literature at similar age [6, 11, 45, 51]. This confirms current indications that although \(Fagus\) tolerates shade and appreciates shelterwood, it responds favourably to canopy opening with enhanced growth [11]. Seedlings in full light in the weeded meadow had a three-fold higher biomass than those planted at shade in dense \(Pinus\) stands. Light regime is likely to be the main driving factor behind beech growth in our experiment since irradiance varied strongly among stands while edaphic and climatic constraints were similar. Shade reduced both shoot and root development, as reported elsewhere [36, 39, 51, 54]. Limited growth at low light (11% relative irradiance) presumably results from reduced leaf area and photosynthetic activity [50], although \(Fagus\) has been proved to regenerate at a much lower irradiance of 3 to 5% [12, 30, 37]. Such limited growth is also hypothesized to maintain a positive carbon balance in reducing the loss by respiration or photorespiration [4], thus allowing late-successional species to survive for long periods.
Biomass and diameter increments suggest that ideal practice would be to install seedlings in full light in fully weeded parcels. Maximum light supply and the removal of herbaceous competition allow a three-fold increase in seedling biomass over two years. However, such plantation entails cost- and time-consuming weeding that is unrealistic with respect to current forestry practices [15]. At the same time, plantations in unweeded plots in high or full light generally experience very low growth or high mortality [8, 9, 25, 34]. A compromise solution should be to favour beech installation in low-density stands similar to the ageing natural pine woodlands. They provide a lateral shelterwood and an incidental radiation of about 40%, reported as optimal for beech growth [8, 25, 36], although such irradiance also favours dense herbaceous cover.

Our experimental design suggested a limited impact of weed competition on seedling biomass. At medium irradiance, biomass increments were similar among stands having contrasted herbaceous covers. Moreover, the overall abundance of herbs above- or belowground did not affect beech growth, in contradiction with some data from literature [8, 21, 34, 36]. At the same time, pine fine roots had a moderate but unquestionably depletive effect. First, this apparent inconsistency can be explained by the predominance of pine competition over herbaceous competition owing to disproportionate biomass amounts. The herbaceous cover remained lower than seedling height, and climatic demand remained moderate during the experiment. Enhanced weed cover with increasing irradiance also enhances beech growth potential, thus balancing the positive and negative effects of light regime. Sparse herbaceous cover under shade obviously results in limited competition with *Fagus* (e.g. [31]). Distance-weighted indices based on the horizontal dimension of competitors failed to explain beech growth, thus confirming their inability to accurately reflect the complex interactions between stand variables, and possibly the ability of *Fagus* root systems to escape competition by exploiting non-colonized soil volumes [15]. Indices based on vertical dominance by pines explain a large part of shoot and root growth since they mostly reflect aerial competition for light, and they include the height of the subject tree [16].
4.2 Allocation plasticity

The theory on global allocation for biomass partitioning in plants [47] assumes that shading results in higher relative biomass allocation to the stem, constant allocation to the foliage and lower allocation to the fine roots in comparison to high- or full-light [29, 51] conditions. Almost all plants produce thinner leaves (i.e., higher SLA) when grown in shade in order to maximize their net carbon gain [14, 26, 53]. As a consequence, the shoot-to-root ratio is expected to increase in shade for both shade-tolerant [39, 54] and shade-intolerant boreal tree species [31, 44]. Our results indicated a depletive impact of shade for all beech compartments (see [2, 39]), a low impact of light regime on biomass allocation within plants on a constant mass basis, and insignificant variation in shoot-to-root ratio among stands (see [2]). Our estimates for shoot-to-root ratio are in accordance with the literature for shade-tolerant species [29]. In contrast to aerial compartments, biomass allocation varied slightly within the root system, thereby contradicting scarce data from the literature [51]. Both light and herbaceous competition enhanced allocation to fine and coarse roots at the expense of taproot, in agreement with previous findings [7, 16, 35, 51].

Recent debates are about determining whether morphological adjustments predominated or not on allocation plasticity along life-cycle in higher plants [4, 22, 24, 46, 48]. Our findings support the opinion that, for constant seedling mass, allocation to leaves, stems and roots varied little with light availability [28, 31, 35, 44] or herbaceous competition [28] in woody perennials. Most studies indicate that changes are mostly ontogenic and size-dependent, thus variable along tree life [24, 51]. As a late-successional species, beech is expected to preferentially adjust its above- and belowground morphology [37, 51], and to show a progressive shift in biomass allocation along its life-cycle [4, 29]. Balanced shoot-to-root ratios amongst our stands (i.e. 1.03 to 1.23) would thus mostly indicate a limited and progressive shift in biomass from nursery seedlings (mean = 1.39) to young (mean = 2 at 20 yrs. [16]) or mature trees (mean about 5). This is consistent with the statement that the shoot-to-root ratio is highly integrative and poorly indicates environmental conditions [18].
4.3 Morphological plasticity

Morphological adjustments at leaf level and root level in relation to irradiance and herbaceous competition predominated over allocational adjustments, thus agreeing with recent reports [1, 3, 5, 27]. *Fagus* responded to changes in light environment by adjusting its leaf morphology, especially increasing the SLA under shade (e.g. [5, 29, 37, 40]). Thinner leaves at shade are often hypothesized to allow an efficient use of the limited light resource in forest understory [35, 37, 44, 53], especially when coinciding with optimal leaf spatial arrangement and orientation [40]. This also generally coincides with an increase in leaf area ratio, lateral crown expansion, and plasticity in the spatial arrangement of leaves [22, 49], which are typical features of shade-tolerant species [26, 37, 41, 51].

Morphological plasticity of roots in response to shade and herbaceous competition has been poorly investigated in the literature for *Fagus* [15, 16] and other tree species (e.g. [3]). Causes for coarser roots at shade remain unclear, although a previous study indicated that slow-growing trees generally exhibit thick and low-ramified roots at shade [13]. This may result from direct effects, i.e. that low shoot growth may correspond to low root growth. Conversely, fast-growing species would logically have large organs for resource acquisition both above- and belowground [44]. From a whole plant perspective, the ‘functional equilibrium’ theory [49, 51] predicts that the capacity of leaves and fine roots to acquire resources has to be balanced. The SRL/SLA ratio would be a good indicator for morphological adjustments at shade. Shade slightly reduced the fine roots-to-leaf mass ratio since leaves were thinner but biomass allocation to fine roots varied little. These results agree with the affirmation that *Fagus sylvatica* holds an intermediate reaction to shading between highly-reactive species such as *Betula pendula* that show a strong acclimation in terms of biomass partitioning and morphological adjustment of leaves, and low-reactive species such as *Quercus robur* that react little aboveground but demonstrate enhanced root foraging [51]. Changes in *Fagus* fine-root morphology could also result from indirect effects owing to the ‘multiple resource limitation theory’ [26]. Shading would also correspond to lower available soil resources reducing root foraging, but this argument is not likely since edaphic characteristics were similar among stands.
Herbaceous competition produced thinner and more ramified roots in beech, thus stimulating a foraging strategy to better exploit soil resources, and probably to resist to resource depletion [27, 37]. In fact, high foraging strategy belowground presumably correlates with high competitive ability [3, 27, 45]. In the absence of herbaceous competition (HL-V) SRL is much lower than expected due to irradiance. Maximal root foraging occurred at high irradiance with maximal herbaceous competition. Regression analysis (data not shown) indicated that beech fine-root morphology varied strongly with the herbaceous fine-root abundance, little with the relative irradiance, and did not vary with the root biomass of *Pinus*. In contrast to *Fagus*, *Pinus* had an almost null adaptive strategy for improving its soil exploitation efficiency according to changes in light and belowground competition, thus confirming that it is more conservative [3, 15, 16].

High SRL and low SLA at high irradiance corresponded to high growth potential for *Fagus*, in accordance with the literature on many plant species [13, 14, 44, 55]. High SRL is hypothesized to allow beech to capture the limiting soil resources to maintain (or enhance) its growth [48], while low SLA is typical of sun leaves with limited transpiration [40]. High SLA values would conversely allow an efficient use of the limited light resource in forest understory by maximizing the leaf area displayed per unit of leaf biomass [35, 40, 44, 53]. While early-successional and shade-intolerant species would demonstrate very rapid morphological adaptation [5, 37], competitive and shade-tolerant species such as *Fagus* should demonstrate morphological and, to a lesser extent, allocational traits favouring its survival and growth in shade [27, 41]. Investigating to what extent leaves and fine roots may increase their physiological efficiency to maintain a balanced carbon-nutrient uptake within beech saplings would provide an interesting complement to this study [4]. Shade tolerance in European beech could rely more on an enhanced plasticity in light-harvesting variables such as crown morphology and chlorophyll content than on enhanced physiological plasticity in relation to photosynthetic activity [50]. Machado *et al.* [35] clearly reminded that the coined ‘shade tolerance’ of forest trees encompasses a collection of traits that maximize survival at shade via the efficient use of limiting resources in forest understories (i.e., soil resources as well as light) in reference to the ‘multiple resource limitation theory’ [26]. In our experiment, light gradient had a predominant effect on the development of beech saplings due to limited edaphic and climatic constraints. Shade resulted chiefly
in morphological adjustments at leaf and root level, and limited changes in biomass allocation
patterns. The ecological and silvicultural implications of this study are that beech seedlings clearly
benefit from shelterwood in relation to their shade tolerance (e.g. [54]). Our results cannot conclude in
an optimal irradiance level since the experimental design did not investigate a continuous range of
variation. In our experimental programme, a compromise solution would correspond to a high-light
regime (42% relative irradiance) and a mid-density herbaceous layer similar to that existing in ageing
pine stands. Since mowing [34] and systematic herbicide treatments are partially inefficient in
reducing vegetation competition and cannot be considered as practical tools for common forestry
practice, this alternative represents a low-cost solution to favour beech installation.

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anonymous reviewers for their essential help to improve the manuscript. This research was funded by
the French Ministry for Land Management (contract # N° 043/2000).
References


Beech growth and plasticity


[53] Walters M.B., Reich P.B., Seed size, nitrogen supply, and growth rate affect tree seedling


<table>
<thead>
<tr>
<th>Stand</th>
<th>LL</th>
<th>ML-V</th>
<th>HL</th>
<th>ML+V</th>
<th>FL-V</th>
</tr>
</thead>
<tbody>
<tr>
<td>Description</td>
<td>Young pine stand (pole stage)</td>
<td>Submature pine stand</td>
<td>Weeded meadow</td>
<td></td>
<td></td>
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<tr>
<td>Light regime</td>
<td>Low</td>
<td>Medium</td>
<td>High</td>
<td>Medium</td>
<td>Full light</td>
</tr>
<tr>
<td>Herbaceous cover density</td>
<td>Low</td>
<td>Low</td>
<td>High</td>
<td>Medium</td>
<td>Null</td>
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</table>

| Mean overstorey density (n.ha\(^{-1}\)) | 4012 | 1451 | 496 | 1420 |
| Mean overstorey basal area (m\(^2\).ha\(^{-1}\)) | 52 | 31 | 15 | 49 |
| Mean overstorey age (yrs.) | 25 | 25 | 25 | 40 | Non forested |
| Pine fine-root biomass (dw, g.m\(^2\)) 0-30 cm | 3632 ± 541 \(a\) | 3260 ± 567 \(a\) | 2666 ± 367 \(a\) | 2573 ± 421 \(a\) |
| Pine root length increment (2001), m | 158 \(c\) | 117 \(b\) | 28 \(a\) | 2 \(a\) |
| Herbaceous aboveground biomass (dw, g.m\(^2\)) | 2 ± 0.4 \(a\) | 7 ± 2 \(a\) | 219 ± 44 \(c\) | 48 ± 13 \(ab\) |
| Herbaceous fine-root biomass (dw, g.m\(^2\)) 0-30 cm | 7 ± 0.4 \(a\) | 17 ± 4 \(a\) | 143 ± 32 \(b\) | 215 ± 45 \(c\) | Weeded |
| Herbaceous root length increment (2001), m | 6 \(a\) | 69 \(a\) | 1141 \(b\) | 563 \(c\) |
| Relative irradiance (%) | 11.0 ± 0.4\(a\) | 19.2 ± 0.7\(c\) | 46.5 ± 1.2\(d\) | 16.0 ± 0.6\(b\) | 100.0 |
| Soil water content 0-20 cm (%) | 11.2 ± 0.2\(a\) | 12.9 ± 0.1\(c\) | 12.3 ± 0.1\(bc\) | 12.5 ± 0.1\(bc\) | 12.9 ± 0.4\(c\) |

Table 1. Main stand characteristics (mean ± standard error). LL: low irradiance; ML-V: medium irradiance and sparse herbaceous cover; HL: high irradiance; ML+V: medium irradiance and dense herbaceous cover; FL-V: full-light weeded. Different letters in a row indicate statistically significant differences (LSD procedure, 95% confidence interval).
<table>
<thead>
<tr>
<th>Variable</th>
<th>LL</th>
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<th>ML+V</th>
<th>HL</th>
<th>FL-V</th>
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<tbody>
<tr>
<td>Shoot biomass (dw, g)</td>
<td>14.4 ± 1a</td>
<td>28.7 ± 4ab</td>
<td>24.6 ± 2ab</td>
<td>38.0 ± 3b</td>
<td>44.5 ± 9c</td>
</tr>
<tr>
<td>Root biomass (dw, g)</td>
<td>14.2 ± 1a</td>
<td>22.8 ± 3ab</td>
<td>19.8 ± 1ab</td>
<td>33.4 ± 3b</td>
<td>40.1 ± 6c</td>
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<tr>
<td>Total plant biomass (dw, g)</td>
<td>28.6 ± 2a</td>
<td>51.5 ± 7bc</td>
<td>44.4 ± 3b</td>
<td>71.4 ± 6cd</td>
<td>84.6 ± 14d</td>
</tr>
<tr>
<td>Shoot biomass increment (%)</td>
<td>34 ± 7a</td>
<td>94 ± 12ab</td>
<td>80 ± 11ab</td>
<td>124 ± 15b</td>
<td>254 ± 63c</td>
</tr>
<tr>
<td>Root biomass increment (%)</td>
<td>61 ± 7a</td>
<td>111 ± 13ab</td>
<td>96 ± 13ab</td>
<td>169 ± 20b</td>
<td>295 ± 56c</td>
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<tr>
<td>Total biomass increment (%)</td>
<td>45 ± 6a</td>
<td>102 ± 11ab</td>
<td>87 ± 11ab</td>
<td>142 ± 16a</td>
<td>270 ±56c</td>
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<tr>
<td>Stem diameter increment 2000-2002 (%)</td>
<td>20.4 ± 6a</td>
<td>34.3 ± 11b</td>
<td>31.7 ± 11b</td>
<td>47.2 ± 12c</td>
<td>56.3 ± 25d</td>
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</tbody>
</table>

Table 2. Growth of *Fagus* seedlings two years after plantation (mean ± standard error). Data gathered the shoot, root and total biomass, biomass increment, and stem diameter increment between 2000 and 2002. Different letters in a row indicate statistically significant differences (LSD procedure, 95% confidence interval). LL: low irradiance; ML-V: medium irradiance and sparse herbaceous cover; HL: high irradiance; ML+V: medium irradiance and dense herbaceous cover; FL-V: full-light weeded.
Table 3. Correlation matrix for seedling biomass two years after plantation and other measured variables. Correlation significant at P<0.001 are shown in bold, P<0.005 in bold and italic, and P<0.01 in italic. Variables are total seedling biomass (TOB), shoot biomass (SHB); root biomass (ROB), relative stem diameter increment (SDI), relative irradiance (RIR), total herbaceous root biomass (RHT), total Scots pine root biomass (RPT), stand root biomass including pine and herbs (RCT), herbaceous aerial biomass (HAB), HASA3 competition index (HAS), VAST3 competition index (VAS), SBA competition index (SBA) and SBA distance-weighted competition index (SBD).

<table>
<thead>
<tr>
<th>Variables</th>
<th>TOB</th>
<th>SHB</th>
<th>ROB</th>
<th>SDI</th>
<th>RIR</th>
<th>RHT</th>
<th>RPT</th>
<th>RCT</th>
<th>HAB</th>
<th>HAS</th>
<th>VAS</th>
<th>SBA</th>
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<tr>
<td>TOB</td>
<td>-</td>
<td>0.97</td>
<td>0.95</td>
<td>0.73</td>
<td>0.59</td>
<td>0.07</td>
<td>-0.36</td>
<td>0.15</td>
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<tr>
<td>SHB</td>
<td>-</td>
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<td>0.85</td>
<td>0.68</td>
<td>0.51</td>
<td>0.08</td>
<td>-0.34</td>
<td>-0.25</td>
<td>0.16</td>
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<td>-0.56</td>
<td>-0.57</td>
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<tr>
<td>ROB</td>
<td>-</td>
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<td>0.74</td>
<td>0.62</td>
<td>0.04</td>
<td>-0.37</td>
<td>-0.31</td>
<td>0.14</td>
<td>-0.57</td>
<td>-0.52</td>
<td>-0.57</td>
<td>-0.34</td>
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<tr>
<td>SDI</td>
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<td>-</td>
<td>0.74</td>
<td>-0.08</td>
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<td>0.38</td>
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<td>0.94</td>
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<td>-</td>
<td>0.46</td>
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<tr>
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Table 4. Biomass allocation within plant compartments in 2002. Abbreviations are: Leaf weight ratio (LWR), branches weight ratio (BWR), stem weight ratio (SWR), taproot weight ratio (TWR), coarse-roots weight ratio (>2mm, cRWR), fine-roots weight ratio (<2mm, fRWR), total roots weight ratio (RWR). LL: low irradiance; ML-V: medium irradiance and sparse herbaceous cover; HL: high irradiance; ML+V: medium irradiance and dense herbaceous cover; FL-V: full-light weeded.

<table>
<thead>
<tr>
<th>Variable Abbreviation</th>
<th>LL</th>
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<th>ML+V</th>
<th>HL</th>
<th>FL-V</th>
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<td>LWR (g(^{-1}) g(^{-1}))</td>
<td>0.08 (ab)</td>
<td>0.09 (ab)</td>
<td>0.10 (b)</td>
<td>0.10 (b)</td>
<td>0.07 (a)</td>
</tr>
<tr>
<td>BWR (g(^{-1}) g(^{-1}))</td>
<td>0.13 (a)</td>
<td>0.14 (a)</td>
<td>0.13 (a)</td>
<td>0.13 (a)</td>
<td>0.12 (a)</td>
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<tr>
<td>SWR (g(^{-1}) g(^{-1}))</td>
<td>0.30 (a)</td>
<td>0.32 (ab)</td>
<td>0.32 (ab)</td>
<td>0.31 (a)</td>
<td>0.33 (ab)</td>
</tr>
<tr>
<td>TWR (g(^{-1}) g(^{-1}))</td>
<td>0.38 (b)</td>
<td>0.32 (ab)</td>
<td>0.29 (a)</td>
<td>0.29 (a)</td>
<td>0.29 (a)</td>
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<tr>
<td>cRWR (g(^{-1}) g(^{-1}))</td>
<td>0.04 (ab)</td>
<td>0.05 (abc)</td>
<td>0.09 (c)</td>
<td>0.08 (bc)</td>
<td>0.09 (c)</td>
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<tr>
<td>fRWR (g(^{-1}) g(^{-1}))</td>
<td>0.08 (a)</td>
<td>0.09 (ab)</td>
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<td>0.10 (b)</td>
<td>0.10 (b)</td>
</tr>
<tr>
<td>RWR (g(^{-1}) g(^{-1}))</td>
<td>0.50 (b)</td>
<td>0.45 (a)</td>
<td>0.45 (a)</td>
<td>0.47 (ab)</td>
<td>0.48 (b)</td>
</tr>
<tr>
<td>Shoot-root ratio</td>
<td>1.03 (a)</td>
<td>1.23 (a)</td>
<td>1.23 (a)</td>
<td>1.18 (a)</td>
<td>1.12 (a)</td>
</tr>
</tbody>
</table>
**Figure captions**

Fig. 1. Relative stem diameter increment vs biomass increment (a), relative stem diameter increment vs relative seedling biomass increment (ln-transformed data; b), relative shoot biomass increment vs relative root biomass increment (ln-transformed data; c), and final seedling biomass vs the VAST6 Competition Index. All results were computed after two years of experiment. The Vast3 competition index was the sum of vertical angles between the top of a seedling and the top of surrounding pines within a 3-m competition radius (explanations in the text).

Fig. 2. Variation in specific root length (SRL, m.g\(^{-1}\)), average fine-root diameter (mm) and mean internode length (mm) for *Fagus sylvatica* seedlings, *Pinus sylvestris* and herbaceous species among stands. LL: low irradiance; ML-V: medium irradiance and sparse herbaceous cover; HL: high irradiance; ML+V: medium irradiance and dense herbaceous cover; FL-V: full-light weeded. Different letters in a graph indicate statistically significant differences (LSD procedure, 95% confidence interval).

Fig. 3. Variation among stands for: (a) specific leaf area (SLA) versus specific root length (SRL); and (b) relative irradiance versus fine-root to leaves biomass ratio. Vertical bars correspond to the standard error.

Fig. 4. Relationships between relative diameter increment and specific leaf area (a) or specific root length (b) for *Fagus* seedlings. Relative diameter increment was computed as the ratio between the initial diameter (2000) and the final diameter (2002) in percentage.
Fig. 1.

**Belowground**

\[ y = 0.0753x + 16.774 \]

\[ R^2 = 0.7436 \]

**Aboveground**

\[ y = 9.873x - 105.88 \]

\[ R^2 = 0.7436 \]
Fig. 2.
Fig. 3.
Fig. 4.

(a) 

\[ y = -43.112 \ln(x) + 279.27 \]

\[ R^2 = 0.4998 \]

(b) 

\[ y = 1.9964x - 14.972 \]

\[ R^2 = 0.4168 \]