



HAL
open science

How nutrient availability influences acclimation to shade of two (pioneer and late-successional) Mediterranean tree species?

Yogan Monnier, Anne Bousquet-Mélou, Bruno Vila, Bernard Prévosto,
Catherine Fernandez

► To cite this version:

Yogan Monnier, Anne Bousquet-Mélou, Bruno Vila, Bernard Prévosto, Catherine Fernandez. How nutrient availability influences acclimation to shade of two (pioneer and late-successional) Mediterranean tree species?. *European Journal of Forest Research*, 2013, 132 (2), pp.325-333. 10.1007/s10342-012-0677-7 . hal-01756415

HAL Id: hal-01756415

<https://amu.hal.science/hal-01756415>

Submitted on 10 Apr 2018

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

How nutrient availability influences acclimation to shade of two (pioneer and late-successional) Mediterranean tree species?

Yogan Monnier · Anne Bousquet-Mélou ·
Bruno Vila · Bernard Prévosto · Catherine Fernandez

Abstract Examining ecological limits to shade acclimation at whole-plant level is determinant for evaluating the success of sapling establishment in low-light environments. We studied nutritional effects on whole-plant development in response to shade in two Mediterranean forest tree species with different successional status: the early-successional *Pinus halepensis* Mill. and the late-successional *Quercus pubescens* Wild. Through a nursery-based factorial experimental design approach, we measured height increment along 2 years and final leaf, stem and root biomass in both species saplings subjected to two lights and two soil nutrient availability treatments. The shade avoidance response was exclusive to *P. halepensis*, appeared as timely dependent, and persisted longer in saplings exposed to higher nutrient availability. *Q. pubescens* benefited from the higher nutrient availability by lowering the light-driven plastic response in aerial support investment and below-ground carbon allocation, whereas *P. halepensis* heightened its light-driven plastic response. These contrasted responses are thus clearly related to the shade acclimation

strategy of each species: the shade-intolerant *P. halepensis* enhances shade avoidance when non-nutrient-limited, whereas the shade-tolerant *Q. pubescens* assumes a conservative strategy by limiting phenotypic plasticity-induced costs. Maintaining greater shade avoidance in non-nutrient-limited soil conditions might be an adaptive advantage for *P. halepensis* seedlings growing in the understory, in response to gap formation in the overstory. In contrast, the more conservative and less costly shade responsiveness of *Q. pubescens* may confer it a better adaptive advantage in long-term light-limited environments.

Keywords *Pinus halepensis* · *Quercus pubescens* · Phenotypic plasticity · Biomass partitioning · Allocation · Forest regeneration

Introduction

For most terrestrial plants, light availability is a major environmental constraint in successional habitats (Tilman 1985). Although water stress is a strong limiting factor in Mediterranean ecosystems, the main factor determining species coexistence along forest dynamics is interspecific difference in juvenile responsiveness to light (Valladares and Niinemets 2008). With the successional decrease of understory light availability, the performance of juvenile trees is primarily based on their ability to acclimate to shade, and this light-driven plasticity (sensu Bradshaw 1965) is a key determinant of regeneration success in Mediterranean forest understory (Sanchez-Gomez et al. 2006a).

Plastic response to shade is recognized as following one of two contrasted strategies: shade tolerance and shade avoidance (Henry and Aarssen 1997). Shade tolerance

Y. Monnier (✉) · A. Bousquet-Mélou · B. Vila · C. Fernandez
Institut Méditerranéen de Biodiversité et d'Ecologie marine et
continentale (IMBE, UMR CNRS 7263), Aix-Marseille
Université, Centre St-Charles, 3 place Victor Hugo,
13331 Marseille Cedex 03, France
e-mail: yogan.monnier@imbe.fr; yoganmonnier@gmail.com

Y. Monnier · B. Prévosto
IRSTEA-CEMAGREF, UR EMAX, 3275 Route de Cézanne CS
40061, 13182 Cedex 5, Aix en Provence, France

(defined as long-term ability to survive and grow under low light) is essentially expressed through morphological and physiological changes at leaf level (Grime 1979; Valladares and Niinemets 2008). Shade avoidance involves maximizing light interception through plastic crown adjustments and strong vertical growth (Henry and Aarssen 2001), known as 'shade avoidance syndrome' (Franklin 2008). Morphological plasticity at whole-plant level is thought to be an important adaptation to shade (Messier and Nikinmaa 2000), and recent insights into shade acclimation have led to recognition of the importance of crown and whole-plant biomass partitioning plasticity and plant ontogeny (Niinemets and Valladares 2006; Portsmouth and Niinemets 2007; Valladares and Niinemets 2008). These shade-induced adjustments could procure an important adaptive advantage by higher niche preemption and occupation during forest succession.

The trait value expressed between different environments at a given point in time is the result of plasticity in the plant's developmental trajectory between the different environments, thus creating the need to adopt an ontogenic approach (Moriuchi and Winn 2005). Indeed, it is now broadly assumed that the light-driven plasticity of morphological or crown traits is plant life-cycle-dependent (Gedroc et al. 1996; Greenwood et al. 2009; Niinemets 2004; Lusk and Warton 2007). Although this appears obvious at leaf level (Lusk and Warton 2007) and in terms of root:shoot ratio (Delagrange et al. 2004; Gedroc et al. 1996; Valladares et al. 2005), there is still a lack of knowledge on the evolution of the shade avoidance response (gauged through shade-induced height increase) in the early stages of ligneous plant growth. Sumida and Komiyama (1997) asserted that branching height (involved in shade avoidance response) increased more rapidly in the shade-intolerant species. However, the developmental trajectories of the plasticity of shade-avoidance traits in ligneous plants between low and high light regimes are still poorly understood.

Shade avoidance syndrome, and more generally an extensive foliar area in response to shade, is a mechanism that is sustained by a greater investment in support structure. As this plastic response to shade entails high costs (due to resource uptake and allocation), nutrient availability may interact with light availability to affect whole-plant resource allocation patterns. Many works highlighted the need to examine plastic responses to shade in the context of nutrient-dependence (Grassi and Minotta 2000; Valladares et al. 2000; Portsmouth and Niinemets 2007). Here, we propose to study the intrinsic and ecological limits of the shade acclimation of regenerating forest trees, highlighting developmental and nutritional effects on whole-plant response to shade. We assessed the light-driven plasticity of crown and biomass partitioning in saplings

of two Mediterranean forest tree species with different successional status: *Pinus halepensis* Mill., a strongly shade-intolerant pioneer species, and *Quercus pubescens* Wild., a late-successional species thought to possess a greater shade tolerance. Several hypotheses were tested: (1) The pioneer *Pinus halepensis* has a greater light-driven plasticity at whole-plant level than the more late-successional species *Quercus pubescens*; (2) this shade-avoidance syndrome (height increase) would be proved nutrient-dependent and timely limited; (3) the magnitude of light-driven biomass partitioning patterns is more responsive to nutrient availability for the greater plastic species.

These hypotheses were tested using a nursery-based experimental design following two methodological approaches: (1) an ontogenic approach designed to assess temporal variations in the shade-avoidance syndrome and to compare the developmental trajectories of this plastic response in two nutrient availability treatments; (2) a snapshot approach to test whether higher nutrient availability similarly enhances the light-driven plastic adjustments of the two species through similar biomass partitioning at whole-plant level.

Materials and methods

Plant material

The two study species belong to the *Pinaceae* and *Fagaceae* families and are common in the Mediterranean forests of southern France. *Pinus halepensis* (hereafter *Pinus*) is a shade-intolerant coniferous species that regenerates under high-light conditions after forest fires and in large forest gaps and abandoned croplands. *Quercus pubescens* (hereafter *Quercus*) is a late-successional winter deciduous hardwood species that regenerates under a wide range of light spanning forest understory to open land (Barbero et al. 1990). In mature *Pinus* forests, *Quercus* seedlings reportedly regenerate better than *Pinus* seedlings in understory conditions (Quézel and Barbero 1992).

Experimental design and treatment application

The study was conducted in a plant nursery at Aix-en-Provence, Southern France (43°30'N, 5°24'E). Seeds of both species were collected in nearby sites exhibiting comparable ecological conditions. In May 2006, the experiment was set up with 1-year-old nursery-grown *Pinus* and *Quercus* seedlings of uniform size ($p > 0.05$) germinated and transplanted one per pot in 10-L plastic pots filled with a draining substrate made of 25 % calcareous sand, 25 % siliceous sand, and 50 % mineral soil from

Provence Granulat quarry. The seedlings were grown outdoors and regularly drip irrigated over the year to prevent water stress. The factorial experimental design included two factors: light availability and nutrient availability. For light availability, half of the pots were placed in full sunlight (High Light HL $n = 30$), while the other half were placed under a shade cloth (Low Light LL $n = 30$, EMIS France, ref. 1077) giving 23 % light transmittance below the shading nets to reproduce the light conditions under a dense pine wood canopy (Valladares et al. 2006). The shade cloth was placed 2.5 m aboveground to cover the entire plot area, and four additional pieces of netting were placed vertically to cover all plot orientations. Transmittance and light quality (R:FR ratio and blue light), both under shade and in sun, were measured with a spectrometer (SpectroVio C5210-C5220, K-MAC), since light quantity and quality play central roles in the shade avoidance response (Franklin 2008). In line with Gasque and García-Fayos 2004, red to far-red ratio (R/FR) at 660/730 nm was 1.54 for the HL treatment and 1.11 for the LL treatment, that is, similar to values observed under *Pinus halepensis* cover (Gasque and García-Fayos 2004). Following Aphalo and Lehto (1997), the photon flux density of blue light measured at 450 nm was 22 % of the photon flux density measured under full-light conditions. The nutrient availability treatments consisted in supplying (1) fertilization at rate of 75 mg N, 8.2 mg P, and 20.74 mg K (Low Nutrient: LN $n = 20$) or (2) a second fertilization rate fivefold higher than LN (High Nutrient: HN, $n = 40$). Nutrients were weekly applied in liquid form.

Measurements

The growth experiment was conducted with *Pinus* and *Quercus* in two consecutive growing seasons (years 2007 and 2008) to estimate the evolution in plant growth responses to light and fertilization treatments. Each individual was tagged, and height (along the stem from base to apical bud) and basal diameter were measured four times, that is, in February 2007, May 2007, March 2008, and July 2008. *Pinus* height was measured as length from stem collar to the highest apex. In *Quercus*, as most individuals were multi-stemmed with no clear leader shoot, we measured the cumulated length of all stems. In July 2008, each sapling was excavated, carefully washed of its substrate to avoid loss of fine roots, and then separated into roots, stems, and leaves. All samples were then dried (60 °C for at least 72 h) and weighed (Online resource 1). The following growth parameters were then established: leaf, stem and root biomass, stem/leaf ratio (S/L, g g^{-1}), root/shoot ratio (shoot = stem + leaf biomass, R/S g g^{-1}), leaf mass fraction (LMF, proportion of

whole-plant biomass assigned to leaves, g g^{-1}), root mass fraction (RMF, proportion of whole-plant biomass assigned to roots), and stem mass fraction (SMF, proportion of whole-plant biomass assigned to stems). An index of phenotypic plasticity for selected variables was calculated for each species at treatment level as a mean across individuals from each treatment, rather than at genotype level (Pigliucci 2005). The plasticity index was computed as the difference between the minimum and the maximum mean values between the two levels of light treatment divided by the maximum mean value, that is, $\text{PI} = (\text{max mean value} - \text{min mean value}) / \text{max mean value}$. This phenotypic plasticity index is useful for comparing environmental responses of variables with different units and with contrasting ranges (Valladares et al. 2000; Valladares et al. 2006). The index scales from 0 to 1, where a higher index value indicates a more plastic response of the individual/population to a given combination of factors (Valladares et al. 2006).

Data analysis

Repeated measures two-way ANOVA (for height data obtained throughout years 2007 and 2008) were used to establish significant differences between means after applying a Levene test to check for homogeneity of variances. Two-way ANOVA was used to determine whether Biomass S/L, Biomass R/S, LMF, SMF, and RMF differed significantly between light treatments (HL vs LL) and nutrient treatments (HN vs LN) in each species. If the analysis yielded a significant factor effect, differences between mean values were examined using a Bonferroni post hoc test. Analysis of covariance (ANCOVA) was used to assess the effects of treatment (light combined with nutrient), species, and size (stem length at the end of the experiment as covariate), and the treatment \times species interaction, on the various traits recorded. The stem length at the beginning of the experimental treatment period was used as an additional covariate in ANCOVA in order to statistically consider the effects of initial plant size on the two traits. Stem/Leaves ratio was Box-Cox transformed prior to analyses of variance to ensure homogeneity of variances. A significant main effect of light indicates shade-induced phenotypic plasticity for the studied trait. A significant interaction between light and nutrient indicates that the magnitude of the plastic response to shade is dependent on the nutrient availability treatment. In this case, t tests were used to test significant differences between light treatments in each nutrient treatment. All statistical analyses were performed using GraphPad Prism version 5.00 for Windows, GraphPad Software, and Statgraphics Centurion XV (StatPoint, Inc., USA) software.

Results

Developmental trajectories of the shade avoidance response

We first focused on the low-nutrient availability treatment to exclusively consider the developmental effect (Fig. 1a, b). At the first two harvesting dates (Feb-07 and May-07), shade conditions significantly increased height in 2-year-old *Pinus* saplings (two-way RM ANOVA, $F = 17.49$; $p < 0.001$, Bonferroni t test) but had no effect on *Quercus* saplings ($p > 0.05$) (Fig. 1a, b). As a result, 2-year-old *Pinus* saplings exhibited stronger height plasticity between the two light regimes (0.27 and 0.25 in Feb-07 and May-07) than *Quercus* (with non-significant differences between shade and high light regimes in year 2007). However, the height of both species was strongly positively influenced by full-light conditions in the 3-year saplings (Mar-08 and Jul-08), which reached significantly greater height than in shade treatments (two-way RM ANOVA, $p < 0.001$ in each case, Bonferroni t test) (Fig. 1a, b).

Then, we assessed the effects of nutrient availability on the developmental trajectories of the shade avoidance response (Fig. 1c, d). In *Pinus*, high soil nutrient availability led to significantly height differences between the two light treatments ($F_{\text{Light} \times \text{Nutrient}} = 10.32$, $p = 0.0015$, Bonferroni t test; Fig. 1c). With higher nutrient availability, 3-year-old *Pinus* saplings maintained a higher height under shade conditions than under full light (two-way RM ANOVA, $F = 10.70$; $p < 0.0001$, Bonferroni t test). In

contrast, *Quercus* sapling height remained unaffected by fertilizer uptake ($p = 0.32$; Fig. 1d).

Differential effects of fertility on light-dependent biomass partitioning

Overall, plant response to shade varied strongly between nutrient availability, species, and trait involved (Fig. 2). The two species showed the same light-driven plastic response in terms of S/L and LMF, with no significant effect of light regime on S/L or LMF in Low nutrient and a similar shade-induced increase of LMF in High nutrient (PI = +0.22 and +0.21 for *Pinus* and *Quercus*, respectively; Table 1). In contrast, the two species showed a reversal of light-driven plastic response in R/S, RMF, SMF. In *Quercus* saplings, most traits showed a light-driven plasticity in Low nutrient, while in *Pinus* saplings the same traits showed a light-driven plasticity in High nutrient. Moreover, *Quercus* saplings showed a shade-induced increase in R/S and RMF (PI = +0.43 and +0.24, respectively) and a shade-induced decrease in SMF (PI = -0.26) when limited by N availability (Low nutrient), while *Pinus* saplings showed the reverse pattern in the same traits (PI = -0.58, -0.47 and +0.16, respectively).

Size dependence of the shade-induced plasticity

It appeared only a size dependence of R/S ratio in *Quercus* (Table 2). In *Quercus* saplings, there was a significant negative relationship between height and R/S ratio for the

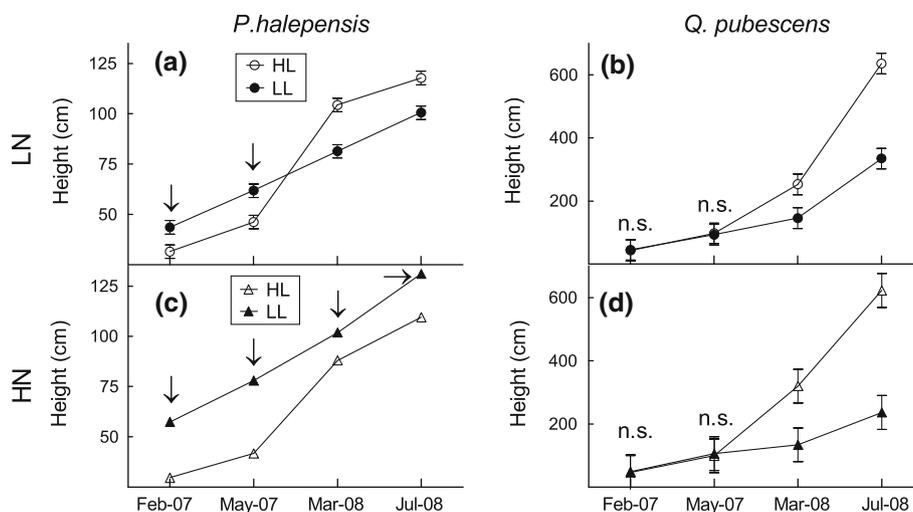
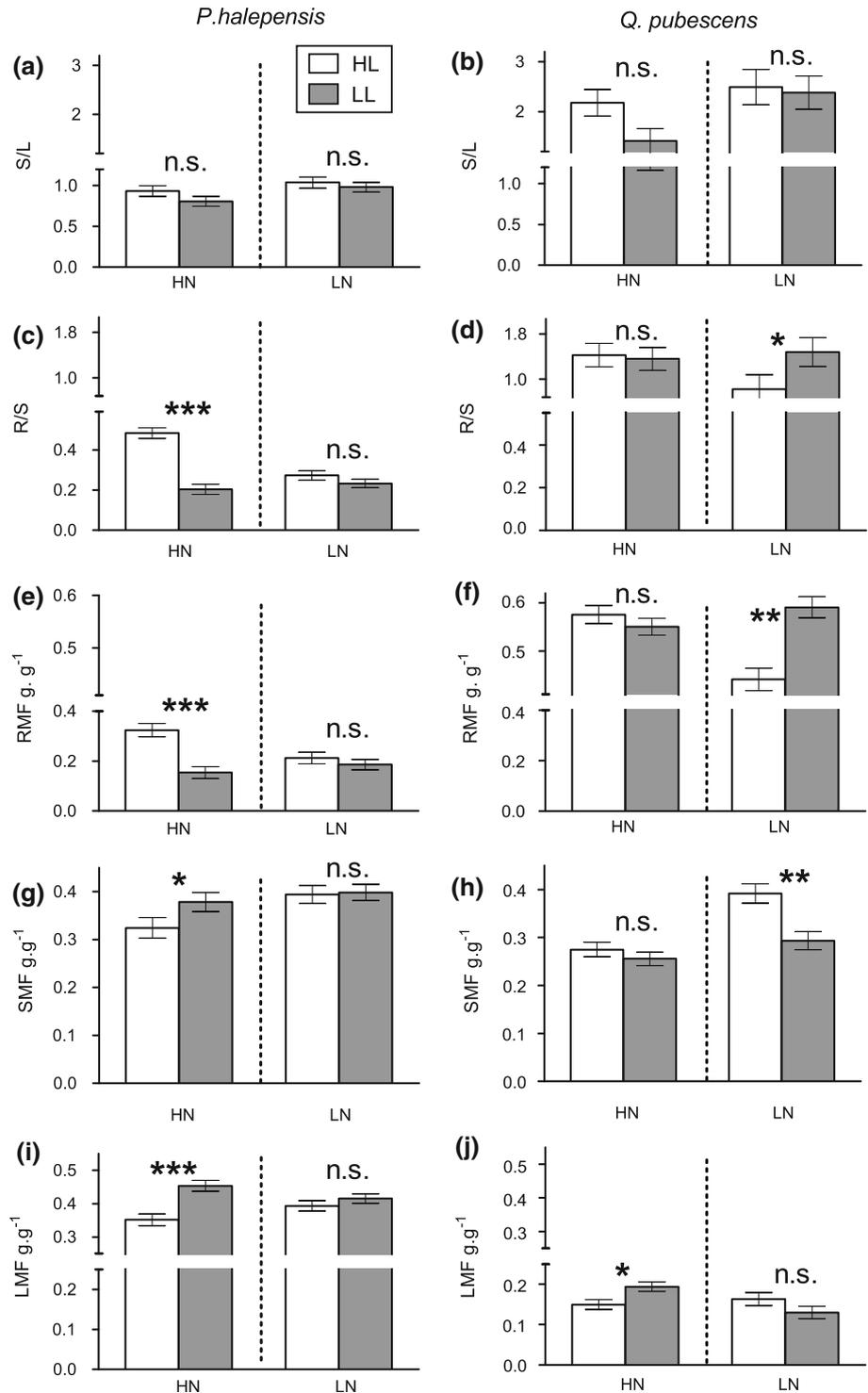


Fig. 1 Effect of shade on height of *Pinus halepensis* and *Quercus pubescens* saplings under a shade cloth at February 2007, May 2007, March 2008, and July 2008 (Low Light, filled symbols) compared to saplings under full-light conditions (High Light, empty symbols). For height analyses, we distinguished plants under low nutrient availability (Low nutrient, circle plots) ($n = 10$) (a, b) from plants under

high nutrient availability (High nutrient, triangle plots) ($n = 20$) (c, d). Bars indicate standard deviations (SD). At each date, difference in means between shade and full light are significant, unless marked *n.s.* Arrows indicate significant shade avoidance responses (higher height under Low Light than under High Light) for a given date (two-way RM ANOVA, $p < 0.05$, Bonferroni post hoc)

Fig. 2 Biomass stem/leaf ratio (S/L) (a) and (b); biomass root/shoot ratio (R/S) (c) and (d); root mass fraction (RMF) (e) and (f); stem mass fraction (SMF) (g) and (h); leaf mass fraction (LMF) (i) and (j), in *Pinus halepensis* and *Quercus pubescens* under light (High Light, Low Light) and fertility (High nutrient, Low nutrient) treatments. Bars represent means and SDs of individual saplings. The variation in sample size resulted from the small number of samples for biomass harvesting and chemical analysis



entire data set (simple regression, $F_1 = 7.25$, $R^2 = 0.13$, $p < 0.01$, Fig. 3a) and low nutrient treatments (ANCOVA, $F_1 = 7.37$, $R^2 = 0.60$, $p < 0.01$, Fig. 3b) but not for high nutrient plants (Fig. 3c). The slopes for regression using ANCOVA differed significantly between high-light and low-light plants ($F_1 = 6.21$, $p = 0.016$), with the low-light plants having a steeper slope; slopes did not

significantly differ between high- and low-nutrient plants ($F_1 = 0.11$, $p = 0.745$). Further, within low nutrient plants, there was significant difference in slopes between low- and high-light plants ($F_1 = 5.32$, $p = 0.035$ (Fig. 3b), while within high nutrient plants, slopes differ not significantly between low- and high-light plants ($F_1 = 1.95$, $p = 0.174$) (Fig. 3c).

Table 1 Effects of nutrient availability on light-driven phenotypic plasticity index [PI = (max – min)/max] in five traits (stem/leaf ratio (S/L), root/shoot ratio (R/S), leaf mass fraction (LMF), root mass

fraction (RMF) and stem mass fraction (SMF) of *Pinus halepensis* (*Pinus*), and *Quercus pubescens* (*Quercus*)

Trait	<i>Pinus</i> plasticity			<i>Quercus</i> plasticity			PI Differences (fertilizer)		PI Differences (species)	
	PI	F_{df}	p	PI	F_{df}	p	<i>Pinus</i>	<i>Quercus</i>		
Plastic responses to shade										
S/L	HF	-0.02	1.76 ₁₄	0.2079	-0.35	3.51 ₂₉	0.0716	-0.13	0.39	0.33
	LF	+0.11	0.18 ₁₉	0.6779	+0.04	0.09 ₁₆	0.7644			0.07
R/S	HF	-0.58	59.91 ₁₄	0.0000	+0.07	0.14 ₂₉	0.716	-0.43	0.36	-0.65
	LF	-0.15	1.58 ₁₉	0.2248	+0.43	10.37 ₁₆	0.0057			-0.58
RMF	HF	-0.47	68.25 ₁₄	0.0000	-0.05	0.68 ₂₉	0.4171	-0.38	-0.29	-0.42
	LF	-0.09	1.75 ₁₉	0.2019	+0.24	10.92 ₁₆	0.0048			-0.33
SMF	HF	+0.16	8.05 ₁₄	0.0140	-0.04	0.70 ₂₉	0.4097	0.15	-0.22	-0.2
	LF	+0.01	0.04 ₁₉	0.8456	-0.26	9.03 ₁₆	0.0089			-0.27
LMF	HF	+0.22	45.46 ₁₄	0.0000	+0.21	6.03 ₂₉	0.0205	0.15	-0.4	0.01
	LF	+0.07	0.68 ₁₉	0.4218	-0.19	4.11 ₁₆	0.0607			-0.26

In each species, columns give the light-driven PI of the corresponding trait in High-Nutrient and Low-Nutrient with F_{df} and p values of t test testing for light effect in High and Low nutrient availability. The table also gives the light-driven PI differences between nutrient treatments for each species (bold values for ANOVA light x nutrient $p < 0.05$) and between species under each nutrient treatment (values in bold highlight a dissymmetric effect of light treatment between species)

Table 2 Analysis of covariance for the fixed effects of species and treatment (light x nutrient), and the interactions between them, on stem/leaf ratio (S/L), root/shoot ratio (R/S), leaf mass fraction (LMF), root mass fraction (RMF), and stem mass fraction (SMF)

Source of variation	ddf	S/L (g.g ⁻¹)		R/S (g.g ⁻¹)		LMF (g.g ⁻¹)		RMF (g.g ⁻¹)		SMF (g.g ⁻¹)	
		MS	p								
Initial stem length	1	0.00	0.943	0.23	0.161	0.00	0.9628	0.01	0.2744	0.01	0.157
Final stem length	1	0.02	0.735	0.65	0.020	0.00	0.3904	0.02	0.0646	0.01	0.114
Species (S)	1	10.86	<0.001	14.97	<0.001	0.71	<0.001	1.33	<0.001	0.10	<0.001
Treatment (T)	3	1.23	0.001	0.57	0.003	0.02	<0.001	0.06	<0.001	0.03	<0.001
S x T	3	0.25	0.215	0.23	0.129	0.01	0.0713	0.02	0.0095	0.01	0.094
Residual	75	0.16		0.12		0.00		0.00		0.00	

Initial and final stem lengths (cm) were used as covariates. S/L was Box-Cox transformed prior to analysis
 df degrees of freedom, MS mean squares (variance)

Significant differences ($p < 0.05$) are highlighted in bold

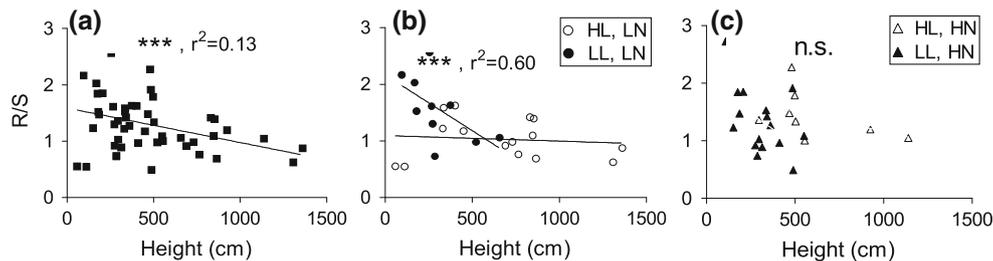


Fig. 3 Relationship between height and R/S ratio in *Quercus pubescens* saplings in **a** all treatments (Simple Regression Model: $p = 0.009$, $R^2 = 0.13$, dark squares), **b** low nutrient treatments only (ANCOVA model: $p = 0.0029$, $R^2 = 0.60$, Low Light: filled circles;

High Light: empty circles), **c** High Nutrient treatments only (ANCOVA model: $p = 0.059$, $R^2 = 0.24$, Low Light: filled triangles; High Light: empty triangles)

Discussion

Ontogenic variations of the shade avoidant response

As expected for the less shade-tolerant species, we found that 2-year-old *Pinus* saplings exhibited higher light-driven height plasticity than *Quercus* counterparts that demonstrate stronger shade avoidance features that maximize light interception (King 1990; Henry and Aarssen 2001). In low nutrient conditions (mimicking the fertility conditions commonly found in natural Mediterranean ecosystems), we also found that *Pinus* saplings grew higher under a low light than a high light regime at 2 years of age but not at 3 years of age. This reveals that the shade avoidance response was timely dependent since it was no longer found in 3-year-old saplings. Changes in the height response to shading during development are likely to reflect adaptive responses to the plant environment responsible for the shade avoidance cues (modifications in amount and quality of light). Our shading treatment simulated understory light conditions beneath an adult *Pinus* canopy. A time-decreased shade avoidance response, in the conditions where saplings were unable to reach the canopy, could increase fitness by diminishing the costs of carbon allocation to stem growth (Causin and Wulff 2003; Weinig 2000). However, it is equally possible that higher resource availability could prolong the shade avoidance response by decreasing the costs of the plastic response. Our findings thus showed that high nutrient seems to change the developmental trajectory of the shade avoidance trait (height enhancement), which persisted longer in *Pinus* (continuing in 3-year-old saplings) under higher nutrient availability. These results confirm our second hypothesis, and such process may have implications in highly fertile forest stands where *Pinus* and *Quercus* seedlings coexist, enduringly favoring the shade escape strategy of *Pinus*, which can reliably overtop neighbors in the expectation of canopy gap formation.

Nutrient availability differentially influenced the light-driven plasticity of the two species

In both species, nutrient availability influenced the whole-plant plasticity in response to shade in terms of aerial support investment (SMF), light-harvesting abilities (LMF), and belowground carbon allocation (RMF, R/S), but not the ratio between investments in aerial support and light harvesting (S/L). Variation in the S/L ratio has been described as a main process of the shade avoidance response (Morgan and Smith 1979), as the increment in stem growth comes with a reduction in biomass allocation to leaf tissue. It was thus surprising not to find any influence of nutrient availability on the shade-induced

variations of this trait in *Pinus*, which was the more shade avoidance species in this study. Focusing on SMF and LMF, one explanation for the relatively similar shade-induced increase (under high nutrient conditions, PI = 16 and 22, in SMF and LMF, respectively) could be that long-lived woody species need to make durable investment in structural plant tissue, consequently providing them greater light availability once they have overtopped competing vegetation (Niinemets 2010) (Table 2).

Overall, the two species showed reverse response patterns to nutrient availability. *Quercus* benefit from higher nutrient availability by lowering the light-driven plastic response in aerial support investment and belowground carbon allocation, whereas *Pinus* benefited from higher nutrient availability by increasing the light-driven plastic response (except for LMF). Under the lower nutrient availability treatment, *Quercus* actually allocated proportionally less biomass to aerial parts and more to belowground parts in the shaded environment (LL) than under the less stressful high-light environment (HL). This allocational pattern is representative of the conservative strategy routinely described in shade-tolerant species. Resource allocation is directed away from growth abilities and toward efficient light-harvesting processes, storage organs, or chemical and structural defences that protect against mortality from starvation, drought, or predation—all of which are characteristics that maximize survival in the understory (Delagrange et al. 2004; Henry and Aarssen 2001; Moriuchi and Winn 2005; Portsmouth and Niinemets 2007). There is a different pattern under higher nutrient availability, where *Quercus* diminished its shade-induced plasticity, thus avoiding the costs associated with plastic responses to shade in non-limited soil resource environments (Auld et al. 2010; DeWitt et al. 1998). These two different behaviors of *Quercus* saplings to shade between high and low nutrients are illustrated by the relationship between size and R/S ratio. The decrease of R/S ratio with size (height) did not differ between high- and low-light plants in high-nutrient treatment. In contrast, in low nutrients and low-light plants, the trade-off between aerial and belowground allocation was illustrated by a strong decrease of R/S ratio with size compared to high-light plants.

Hence, while *Quercus* diminish intensity of light-driven plasticity in high nutrient, *Pinus* strengthen its shade acclimation strategy by increasing shade avoidance and aerial development. This nutrient-dependence of the shade avoidance syndrome has already been showed in *Pinus halepensis* saplings (Monnier et al. 2011), consistently with the fact that the light-driven plasticity of crown and architectural traits is dependent on nutrient availability (Burton and Bazzaz 1995; Lortie and Aarssen 1996; Portsmouth and Niinemets 2007). Regarding these both

species, the contrasted response patterns in light-driven plasticity to the nutrient availability seem related to the shade acclimation strategy of each species (tolerance vs avoidance). The shade-intolerant species (*Pinus*) enhanced shade avoidance when it was not limited by nutrient availability, whereas the more shade-tolerant species (*Quercus*) adopts a conservative strategy by limiting phenotypic plasticity-induced costs.

Conclusion

Shade-induced plasticity was previously reported to be lower in shade-tolerant than shade-intolerant Mediterranean species (Sanchez-Gomez et al. 2006a), but we have shown here that the magnitude of this shade responsiveness was nutrient-dependent. Gap formation in the canopy is a random event, and maintaining a stronger shade avoidance strategy in non-soil resource-limited conditions may confer adaptive advantages in the events of rapid changes in light environment. However, we showed that this strategy was limited by ontogeny and resource availability. *Q. pubescens* demonstrated a more conservative and less costly shade responsiveness by allocating more resources to below-ground parts under limited nutrient availability and by decreasing phenotypic plasticity-associated costs under non-limited nutrient availability. This strategy may provide it a long-term advantage in forest regeneration dynamic, as the shade avoidance of *P. halepensis* may be proved to be too costly to ensure a suitable development in dense understory. However, the full expression of plasticity strongly depends on the co-occurrence of multiple stresses, and further investigations are needed in order to improve our understanding of the linkages between light-driven phenotypic plasticity and environmental stresses such as drought (Sanchez-Gomez et al. 2006b), herbivory (Valladares et al. 2007), or plant–plant interactions (Callaway et al. 2003).

Acknowledgments We thank the staff of the Les Milles plant nursery (Bouches-du-Rhône Departmental Directorate of Agriculture and Forestry) for their technical assistance, and particularly Patrice Brahic for his valuable comments. We also thank Sylvie Dupouyet, Stéphane Greff, Caroline Lecareux, Céline Pemin, Willy Martin, Roland Estève, Aminata N'Dyaye, Christian Ripert, Diane Cattenoz, and Sylvain Bernard for their help with field and lab work. This study was funded by the CNRS under the Zone Atelier “Arrière-pays Méditerranéen” framework.

References

- Aphalo PJ, Lehto T (1997) Effects of light quality on growth and N accumulation in birch seedlings. *Tree Physiol* 17:125–132
- Auld JR, Agrawal AA, Relyea RA (2010) Re-evaluating the costs and limits of adaptive phenotypic plasticity. *Proc R Soc Lond Ser B* 277:503–511
- Barbero M, Bonin G, Loisel R, Quézel P (1990) Changes and disturbances of forest ecosystems caused by human activities in the western part of the Mediterranean basin. *Vegetatio* 87:151–173
- Bradshaw AD (1965) Evolutionary significance of phenotypic plasticity in plants. *Adv Genet* 13:115–155
- Burton PJ, Bazzaz FA (1995) Ecophysiological responses of tree seedlings invading different patches of old-field vegetation. *J Ecol* 83:99–112
- Callaway RM, Pennings SC, Richards CL (2003) Phenotypic plasticity and interactions among plants. *Ecology* 84:1115–1128
- Causin HF, Wulff RD (2003) Changes in the responses to light quality during ontogeny in *Chenopodium album*. *Can J Bot* 81:152
- Delagrange S, Messier C, Lechowicz MJ, Dizengremel P (2004) Physiological, morphological, and allocational plasticity in understory deciduous trees: importance of individual size and light availability. *Tree Physiol* 24:775–784
- DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. *Trends Ecol Evol* 13:77–81
- Franklin KA (2008) Shade avoidance. *New Phytol* 179:930–944
- Gasque M, García-Fayos P (2004) Interaction between *Stipa tenacissima* and *Pinus halepensis*: consequences for reforestation and the dynamics of grass steppes in semi-arid Mediterranean areas. *For Ecol Manag* 189:251–261
- Gedroc JJ, McConnaughay KDM, Coleman JS (1996) Plasticity in root/shoot partitioning: optimal, ontogenetic, or both? *Funct Ecol* 10:44–50
- Grassi G, Minotta G (2000) Influence of nutrient supply on shade–sun acclimation of *Picea abies* seedlings: effects on foliar morphology, photosynthetic performance and growth. *Tree Physiol* 20:645–652
- Greenwood MS, Day ME, Berlyn GP (2009) Regulation of foliar plasticity in conifers: developmental and environmental factors. *J Sustain For* 28:48–62
- Grime JP (1979) *Plant strategies and vegetation processes*. Wiley, Chichester
- Henry HAL, Aarssen LW (1997) On the relationship between shade tolerance and shade avoidance strategies in woodland plants. *Oikos* 80:575–582
- Henry HAL, Aarssen LW (2001) Inter- and intraspecific relationships between shade tolerance and shade avoidance in temperate trees. *Oikos* 93:477–487
- King DA (1990) The adaptive significance of tree height. *Am Nat* 135:809–828
- Lortie CJ, Aarssen LW (1996) The specialization hypothesis for phenotypic plasticity in plants. *Int J Plant Sci* 157:484–487
- Lusk CH, Warton DI (2007) Global meta-analysis shows that relationships of leaf mass per area with species shade tolerance depend on leaf habit and ontogeny. *New Phytol* 176:764–774
- Messier C, Nikinmaa E (2000) Effects of light availability and sapling size on the growth, biomass allocation, and crown morphology of understory sugar maple, yellow birch, and beech. *Ecoscience* 7:345–356
- Monnier Y, Vila B, Montès N, Bousquet-Mélou A, Prévosto B, Fernandez C (2011) Fertilization and allelopathy modify *Pinus halepensis* saplings crown acclimation to shade. *Trees Struct Funct* 25:497–507
- Morgan DC, Smith H (1979) A systematic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. *Planta* 145:253–258
- Moriuchi KS, Winn AA (2005) Relationships among growth, development and plastic response to environment quality in a perennial plant. *New Phytol* 166:149–158
- Niinemets Ü (2004) Adaptive adjustments to light in foliage and whole-plant characteristics depend on relative age in the perennial herb *Leontodon hispidus*. *New Phytol* 162:683–696

- Niinemets Ü (2010) A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. *Ecol Res* 25:693–714
- Niinemets Ü, Valladares F (2006) Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecol Monogr* 76:521–547
- Pigliucci M (2005) Evolution of phenotypic plasticity: where are we going now? *Trends Ecol Evol* 20:481–486
- Portsmouth A, Niinemets Ü (2007) Structural and physiological plasticity in response to light and nutrients in five temperate deciduous woody species of contrasting shade tolerance. *Funct Ecol* 21:61–77
- Quézel P, Barbero M (1992) Le pin d'Alep et les espèces voisines: répartition et caractères écologiques généraux, sa dynamique récente en France méditerranéenne. *Forêt méditerranéenne* XIII:158–170
- Sanchez-Gomez D, Valladares F, Zavala MA (2006a) Functional traits and plasticity in response to light in seedlings of four Iberian forest tree species. *Tree Physiol* 26:1425–1433
- Sanchez-Gomez D, Valladares F, Zavala MA (2006b) Performance of seedlings of Mediterranean woody species under experimental gradients of irradiance and water availability: trade-offs and evidence for niche differentiation. *New Phytol* 170:795–805
- Sumida A, Komiyama A (1997) Crown spread patterns for five deciduous broad-leaved woody species: ecological significance of the retention patterns of larger branches. *Ann Bot* 80:759–766
- Tilman D (1985) The resource-ratio hypothesis of plant succession. *Am Nat* 125:827–852
- Valladares F, Niinemets Ü (2008) Shade tolerance, a key plant feature of complex nature and consequences. *Annu Rev Ecol Evol Syst* 39:237–257
- Valladares F, Martinez-Ferri E, Balaguer L, Perez-Corona E, Manrique E (2000) Low leaf-level response to light and nutrients in Mediterranean evergreen oaks: a conservative resource-use strategy? *New Phytol* 148:79–91
- Valladares F, Arrieta S, Aranda I, Lorenzo D, Sánchez-Gómez D, Tena D, Suárez F, Pardos JA (2005) Shade-tolerance, photoinhibition sensitivity and phenotypic plasticity of *Ilex aquifolium* in continental Mediterranean sites. *Tree Physiol* 25:1041–1052
- Valladares F, Sanchez-Gomez D, Zavala MA (2006) Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. *J Ecol* 94:1103–1116
- Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. *New Phytol* 176:749–763
- Weinig C (2000) Plasticity versus Canalization: population differences in the timing of shade-avoidance responses. *Evolution* 54:441–451