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Photosynthesis capacity of *Quercus petraea* (Matt.) saplings is affected by *Molinia caerulea* (L.) under high irradiance

Antoine Vernay [a,b], Philippe Balandier [c], Ludivine Guinard [a,b], Thierry Améglio [b,a], Philippe Malagoli [a,b,*]

[a] Clermont Université, Université Blaise Pascal, UMR547 PIAF, F-63000 Clermont-Ferrand, France
[b] INRA, UMR547 PIAF, 63100 Clermont-Ferrand, France
[c] Irstea, Research Unit on Forest Ecosystems (EFNO), Domaine des Barres, 45290 Nogent-sur-Vernisson, France

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ABSTRACT

Molinia caerulea (L.) Moench is a well-known resource competitor to the detriment of tree regeneration in many boreal or temperate forests of the Northern hemisphere. This study aimed to investigate to what extent soil nitrogen uptake in interaction with light availability drives the early (*i.e.* in two months) establishment of competition between oak (*Quercus petraea* (Matt.) Liebl.) and *M. caerulea* saplings. Two-year-old oak was grown in a greenhouse in 20 L pots, either alone or in combination with *M. caerulea*, at two irradiance levels (11% and 55% of incident photosynthetically active radiation, iPAR). Leaf photosynthesis measurements and soil ^{15}N-labeling were used to monitor changes in carbon assimilation and soil nitrogen uptake between and within species under well-watered conditions. Presence of *M. caerulea* had no significant effect on short-term oak sapling growth regardless of irradiance availability level. However, under 55% iPAR, *M. caerulea* had higher nitrogen uptake and photosynthesis capacity, whereas sessile oak grown with *M. caerulea* under 55% iPAR showed the same N uptake and a strong decrease in photosynthesis capacity compared to 11% iPAR. The findings reported here point to a very short-term response of photosynthesis and N uptake in a mixture of *M. caerulea* – oak saplings under 55% iPAR), which might partly result from greater nitrogen uptake by *M. caerulea*.

1. Introduction

Success in either natural regeneration or transplantation hinges on the ability of young trees to overgrow surrounding vegetation. Of the many interaction processes trees are exposed to (e.g. allelopathy and mechanical crushing), competition from understory shrubs, forbs and grasses for available resources (light and soil resources) may be critical to tree sapling growth and subsequent survival (Balandier et al., 2006). In the shelterwood system, it is well established that light is the most limiting resource driving tree sapling growth and survival (Nambiar and Sands, 1993; Gemmel et al., 1996; Löf, 2000; Gaudio et al., 2011b). Successful regeneration essentially relies on better tolerance to shading than the surrounding vegetation (Gaudio et al., 2011b). Moreover, reduction in uptake of soil resources (water and nutrients) in these low-light-availability conditions may result from a lower shoot C assimilation, thus leading to decreased carbohydrates available for both root growth and root nutrients uptake (Rundel and Yoder, 1998). In contrast, gap creation by cutting mature trees to sustain tree regeneration leads to greater light availability for mixed understory vegetation and tree seedlings and saplings. In this situation, regeneration sapling growth and survival can fail as understory vegetation competes for belowground resources that become the limiting factor (Harmer, 1996; Coll et al., 2004; Picon-Cochard et al., 2006; Harmer and Morgan, 2007; Provendier and Balandier, 2008). For instance, young oak trees (*Quercus petraea*) competing with grass (*Deschampsia flexuosa*) had reduced height, number of branches and size of root system saplings, despite greater investment of dry weight in the fine (<2 mm) roots (Collet et al., 1996b). Increase in incident light also changes soil water balance due to higher levels of incident radiation and concomitantly greater soil evaporation, whereas reduced standing tree volume decreases transpiration and rainfall interception (Aussenac, 2000). Competition for soil water between tree saplings and surrounding vegetation has been extensively studied in both natural regeneration and plantation settings (Collet et al., 1996a, 1996b; Picon-Cochard et al., 2001, 2006; Coll et al., 2004; Balandier et al., 2009; Berges and Balandier, 2010). Studies on oak (*Q. petraea*; Collet et al., 1996b) and beech (*Fagus sylvatica*;

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[*] Corresponding author.
E-mail address: Philippe.MALAGOLI@univ-bpclermont.fr (P. Malagoli).

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Coll et al., 2004; Picon-Cochard et al., 2006) also stress that competition for soil nutrients as an important factor. Hence, under semi-controlled conditions and temperate latitude, Collet et al. (1996b) found that the reduced saplings growth of sessile oak mixed with grasses was not due to competition for water during the two first years after sowing but may result from competition for soil inorganic nitrogen. On the other hand, Coll et al. (2004) concluded that the interplay between availabilities of soil water and inorganic nitrogen was responsible for competition in a mixture of beech saplings and grasses. The evidence thus suggests that soil inorganic nitrogen availability and uptake may also drive the establishment of dominance between tree saplings and understory vegetation, but there has been little research to address this issue (Fotelli et al., 2002). Moreover, responses of tree seedlings or saplings surrounded by competing vegetation are generally monitored after several years of growth (typically two or more) at either growth or survival level and for the (tree) species of interest based on basic measurements of stem diameter, height, and above- and below-ground compartment dry weights. However, as underlined by Collet et al. (1996b), physiological changes during a short period following the transplantation or emergence of young trees in natural regeneration are an equally critical factor in both young trees and understory species. Indeed, these early changes will define the subsequent ability to uptake soil resources and the extent to which these resources will be depleted, thus limiting the growth of forest tree saplings. The brunt of research to date has focused on carbon and water uptake after 1-year old growth following the establishment of the competition. However, there is debate over whether the growth of tree saplings and surrounding vegetation respond quickly (within months) to changes in available resources (light, water and nitrogen) through changes in carbon, water and nitrogen uptake. Furthermore, compared to carbon and water uptake, the contribution of soil inorganic nitrogen allocation between tree saplings and surrounding vegetation (especially grasses) under short periods during early growth has been relatively unexplored. A better understanding of the changes in processes involved in resource capture during early growth of tree saplings competing with understory vegetation would find practical applications in forest management. Indeed, cutting mature oak forest after acorns fall in order to increase incident light and subsequent growth and survival of oak saplings is a common forestry practice, but it may also enhance the growth of competing surrounding vegetation and, in turn, reduce soil water and nitrogen availability, thus jeopardizing tree sapling survival if not growth performance in the forest. Identifying a trade-off among resource availabilities to optimize tree sapling growth may help improve forest management.

Here we performed a study under semi-controlled greenhouse conditions to investigate to (i) what extent growth of oak saplings (*Q. petraea*) mixed with *Molinia caerulea* responds to two contrasted irradiance levels in the short term (within 2 months) and more specifically, (ii) how physiological mechanisms linked to photosynthesis behind competition induce growth reduction and (iii) what extent soil mineral nitrogen uptake and allocation between species change under two contrasted irradiance levels. The hypothesis was that *M. caerulea* has a greater N uptake capacity compared to oak saplings under a higher irradiance level. Growth, biomass, N uptake through soil ^{15}N-labeling and photosynthesis capacity were measured to monitor early response of canopy under either low- or high irradiances, thus imitating growth in each species after or not a gap creation. Sessile oak was chosen as it is a well-spread and economically important forest species in France and in Europe. *M. caerulea* is a common gramineae that is strongly competitive for young tree saplings, especially oaks, as *M. caerulea* tolerate a wide range of irradiance levels ranging from 6% to 100% iPAR (Taylor et al., 2001; Gaudio et al., 2011c).

2. Materials and methods

2.1. Experimental design

The experiment was conducted in a greenhouse at the INRA, UMR PIAF research unit in Clermont-Ferrand (Auvergne, France, 45°45′N, 3°07′E, altitude: 394 m) from April to June 2011. Two-year-old bare root oak (*Q. petraea* Matt (Leib.) (26.5 ± 0.9 g fresh weight per tree) saplings sourced from a local tree nursery were planted on April 12th in 25 pots (20 L) filled with a clay-sandy soil (%clay = 20.3, %loam = 22.8, %sand = 56.9, pH = 6.15, N content = 1.45 g kg^{-1}, C content = 14.6 g kg^{-1}) before bud break. *M. caerulea* (L.) Moench tufts (above-ground parts + roots) were carefully collected from Saint-Augustin forest (Château-sur-Allier, Auvergne, France; 46°46′12.88″N, 02°57′52.48″E) before being transplanted into the pots on April 12th, 2011. Experimental set-up is presented in Fig. 1. Oak saplings were either grown without *M. caerulea* (two saplings per pot; Single Species (SSp); 10 replicates) or grown with *M. caerulea* (one sapling surrounded with 3 tufts of *M. caerulea* (69.2 ± 1.6 g per tuft fresh weight of *M. caerulea* and adhering soil); Mixed Species (MSp); 10 replicates; Fig. 2). In the SSp design, two oak saplings per pot were sown side-to-side to account for intraspecific competition compared to interspecific competition with *M. caerulea*. No pot contains only one sapling of oak under SSp treatment as inter- *vs* intra competition was investigated. Set-up of the experiment at the beginning and at the end of the experiment is shown in Fig. 2. All pots were placed in the greenhouse, with half of them under 11% iPAR by fitting a commercial dark green cloth to decrease solar incoming PAR (iPAR) from outside the greenhouse, this resulting in ~55% and 11% of iPAR availability to mimic a noticeable gap and a relatively dense mature oak stand, respectively. Shading started from one week after setting up the experiment in April, *i.e.* one week after bud break in oak until harvest of oak and *M. caerulea* in June. In oak, two shoot elongation flushes occurred under 55% iPAR whereas only one occurred under 11% iPAR during the experiment. In this split-plot design, the main factor was shading (11% and 55% iPAR), the subplot was the mixture design (SSp and MSp) with a randomized pot location within the shading and unshading plot. Pots were regularly watered to eliminate water stress as a confounding factor. Mean temperature over the experiment was 19.5 °C (min = 8.5 °C; max = 32.8 °C) under 55% iPAR and 19.3 °C (min = 9.8 °C; max = 30.3 °C) under 11% iPAR. Mean air humidity over the experiment was 23.8% (min = 22.8%; max = 27.5%) under 55% iPAR and 33.3% (min = 23%; max = 62.5%) under 11% iPAR. Any undesirable species appearing in the pots over the course of the experiment were manually weeded.

2.2. ^{15}N labeling procedure

To assess nitrogen uptake and allocation between oak and *M. caerulea*, on May 18th 2011 (4 weeks after sapling transplant), 30 mg ^{15}N was supplied as $K^{15}NO_3$ (At. %^{15}N = 99%; 1 mM) in solution in 20 pots (5 replicates for both SSp and MSp-grown oak under 11% or 55% iPAR). Furthermore, in the 55% iPAR treatment, 10 extra pots (5 MSp pots and 5 bare-soil pots) received the same amount of an unlabelled $K^{14}NO_3$ solution (Fig. 1) to assess ^{15}N natural abundance in each plant and soil compartment at the end of the experiment. Watering was controlled to match water amount added in each pot to water pot field capacity (*i.e.* no visible water leakage