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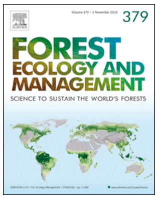

Carry-over benefit of high internal N pool on growth and function of oak seedlings (*Quercus petraea*) competing with *Deschampsia cespitosa*

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ABSTRACT

In contrast to N soil availability or carbon (C) reserves, the role of N reserves in plant interactions has been under-researched. The N-loading of tree seedlings in nurseries before plantation within a forest community to increase their survival and early growth is still controversial. We hypothesized that a larger N-loaded pool in oak seedlings during year $n - 1$ might favor growth and function during year n through higher N remobilization, and thus lessen the impact of competition from *Deschampsia cespitosa* (tussock grass).

In 2015, we cultivated two sets of one-year oak seedlings in 20 L pots with two nitrogen supply levels: no supply (N-unloaded) and 87 kg ha^{-1} (N-loaded), without competition and without water limitation. A greenhouse experiment was then undertaken in 2016 with the same two oak batches, but with 0, 1, 2 or 3 tillers of *D. cespitosa* in both N-loaded and N-unloaded batches. Half the pots were subjected to drought for one month (August 2016).

Soil water availability was the prime factor driving plant growth and photosynthetic responses in oak, both with and without competition. Under well-watered conditions, a greater internal N pool was correlated with higher oak photosynthesis. A high internal N pool was also beneficial to oak seedlings under low competitive pressure from *D. cespitosa*. However, when grass density increased, intraspecific competition outweighed interspecific competition, and attenuated the negative effect of *D. cespitosa* on oak seedlings.

A carry-over effect of N-loading thus had a positive effect on growth and function in oak seedlings when no water stress occurred under low competition by *D. cespitosa*: this effect may derive from more N storage in perennial tissues, resulting in more N mobilized during vegetative growth. Our results underline the importance of the internal N pool in plant competition, and are evidence that a higher potential regenerative success rate of oak seedlings is related to abiotic conditions, competitive pressure and internal N pool.

1. Introduction

Competition between tree seedlings and grass in forest ecosystems has been well characterized and documented (Picon-Cochard et al., 2001; Coll et al., 2003; Balandier et al., 2006). Tree seedling survival and early growth can be massively jeopardized by strong competition from understory species (Provendier and Balandier, 2004; Balandier et al., 2006). Common grass response to clear-cut results in severe soil resource depletion through very fast growth and extensive root systems that rapidly prospect large soil areas and profiles (Freschet et al., 2017). Tree seedlings are much less efficient than grasses in taking up soil resources: they develop less rapidly and face low soil resource levels due to grass preemption. This leads to high seedling mortality rate or at least very poor early growth (Balandier et al., 2006; Harmer and Morgan, 2007; Frochot et al., 2009; Cuesta et al., 2010). To survive, tree seedlings thus resort to a lower allocation of carbon (C) and nitrogen (N) resources to growth and more resource storage in perennial organs (Shea et al., 2004): this allows C and N recycling to meet nutrient demand for growth later on, as environmental conditions improve.

Limited availabilities of light, soil water and nutrients, and their interactions impair seedling growth (Davis et al., 1998; Gaudio et al., 2011). For instance, because most minerals are available only from soil solution, dryness can directly affect N availability (Gonzalez-Dugo et al., 2005; Giehl and von Wiren, 2014; He and Dijkstra, 2014), especially in well-lit plots where competition between grass and tree

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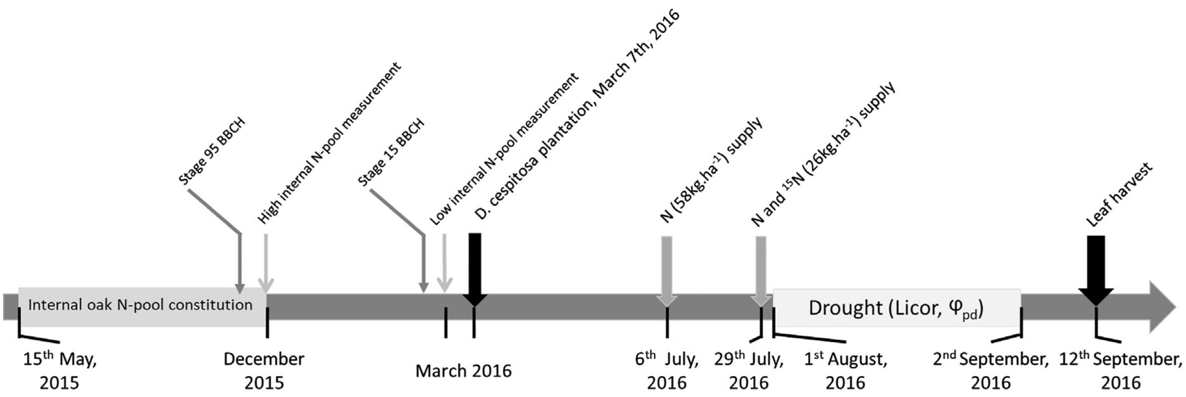

Fig. 1. Time line of all measurements and treatment applications (Ψ_{pd} stands for predawn leaf water potential).

seedlings for belowground resources is strongest (Vernay et al., 2016; Simon et al., 2017).

Competition from grass is likely to increase in the near future, because of (i) scarcer water resources, as drought frequency and intensity are expected to increase (IPCC, 2014), and (ii) the greater ability of grass to prospect and take up available N resources (Van Hees, 1997; Collet et al., 1999; Coll et al., 2003).

Stocking internal resource pools in tree seedlings, especially for N, has been proposed to counteract nutrient starvation due to rapid N depletion by competitive grass root uptake (Salifu and Timmer, 2001; Salifu et al., 2009; Ya-Lin et al., 2015): a rich internal N pool will thus act as a buffer compartment. N (and C) pools are well known to have a positive effect on plant functions under abiotic constraints, such as a better frost resistance (Morin et al., 2007; Mei et al., 2015), and an earlier and faster spring regrowth in roots (Millard and Proe, 1992; Malik and Timmer, 1998; Salifu and Timmer, 2001). Tree seedlings can also rely on this internal N pool to build new aerial organs during and after bud break (Staswick, 1994; Gomez and Faurobert, 2002; Millard and Grelet, 2010; Bazot et al., 2016). N-loaded oaks (*Quercus ilex* L.) exhibited a higher N concentration at whole plant level, resulting in higher leaf area and photosynthesis performance (Cuesta et al., 2010; Mei et al., 2015). Overall, an internal N pool may thus be a rescue option to cope with premature abiotic stress or nutrient starvation (Millard et al., 1990; Iqbal et al., 2012).

The beneficial effect of an internal N pool may have a residual effect: it has been shown that N-loaded trees such as Sitka spruce (*Picea sitchensis*) exhibit better aerial growth later in the season after bud break, two flushes being observed against only one for N-unloaded Sitka spruce (Millard and Proe, 1992). This could be interpreted as a carry-over effect of higher internal N pool recycling. Nevertheless, no study has yet evidenced any ecophysiological process related to the internal N pool that would explain this growth difference.

In grass, plants can also use N recycling to ensure regrowth in spring and keep a high level of growth and function irrespective of environmental nutrient availability. N reserves are stored in cord roots, internodes and seeds after aboveground biomass production ceases in summer. They are then recycled to new leaves after winter, as shown in *Molinia caerulea* in a fertile environment (van Heerwaarden et al., 2005). During the growing season, retranslocation of old leaf nutrients to new leaves enables grasses such as *D. cespitosa* (Davy, 1980) or *Festuca rubra* and *Agrostis capillaris* (Bausenwein et al., 2001) to offset nutrient soil deficiency.

To our knowledge, no study has yet explored the carry-over effect of the internal N pool on tree seedling growth and function during the subsequent vegetative season, in competition with grass. Some limited studies have focused on the functional role of the internal N pool in tree seedlings (Barbaroux et al., 2003; Millard and Grelet, 2010).

In this study we examined the role of the internal N pool of sessile oak seedlings (*Quercus petraea*) in competition with *D. cespitosa*. Two levels of internal N pools of oak seedlings were tested during the early interaction phase, a critical period for young trees, which drives their successful establishment and survival (Hangs et al., 2002). Two contrasting water regimes and three competitor densities were the other two factors of our experimental design. Both species are common in temperate forests, and are frequently found together in temporarily flooded stands (Davy, 1980). *D. cespitosa* often causes regeneration failure of *Q. petraea*, an oak species fairly tolerant to drought (Becker and Levy, 1982; Breda et al., 1993); *D. cespitosa*, though known as a hygrophilous species, is also reported to cope well with dry periods (Rahman, 1976; Davy, 1980). We focused on the early response of both species during six months of interaction.

We hypothesized that a well-stocked internal N pool in oak would improve seedling performance (growth and function) compared with a low internal N pool during early competition with *D. cespitosa* in both non-stressful and stressful contexts (here, drought and high grass density). The N pool accumulated during the previous year would be expected to produce higher leaf and root biomass and/or richer foliar tissues. More efficient first leaves would foster growth and resource capture early in the vegetative season, enhancing global plant performance under strong neighbor density and water stress.

2. Materials and methods

2.1. Experimental design and location

A greenhouse experiment with 20 L pots was set up at the INRA, UMR PIAF research unit in Clermont-Ferrand (Auvergne, France, 45°45′ N, 3°07′ E, altitude: 394 m). The experiment lasted from mid-May 2015 to September 2016 (Fig. 1). On 15 May 2015 we planted 144 one-year-old bare root oak seedlings (*Quercus petraea* Matt (Leib.) (23 ± 0.5 g fresh weight per tree) sourced from a local tree nursery in 20 L pots (one seedling per pot) filled with a clay-sandy soil (clay 20.3%, loam 22.8%, sand 56.9%, pH 6.15, total N content 1.45 $g\,kg^{-1}$, total C content 14.6 $g\,kg^{-1}$). They were cultivated in a sunny outdoor location in full light in 2015, and then transferred to a greenhouse in November 2015. Half the pots (72) received N fertilizer at an average rate of 29 $kg\,ha^{-1}$ in May, June and July 2015 (*i.e.* 87 $kg\,ha^{-1}$ in all, or 927 mg of inorganic N per pot) ($N_{INT}+$), while the other pots (72) received no N supply (N_{INT-}) (Fig. 1). Our purpose was to favor the formation of N reserves in half the oak seedlings. To make sure this was achieved, we collected ten oaks in December 2015 and eight in March 2016. After drying and grinding, N content (%N) was measured in trees from harvested root systems (fine roots + taproot mixed as a single sample) and stems in $N_{INT}+$ and N_{INT-}, by a CHN elemental analyzer (Flash EA 1112 Series, THERMO-ELECTRON).

N amount per plant (N_m) was calculated by

$$N_m = \%\ N \times DW_{organ}, \tag{1}$$