Plant interactions as biotic drivers of intraspecific variability in leaf litter traits and decomposability of a foundation tree species (Quercus petraea)

Ludovic Henneron, Matthieu Chauvat, Frédéric Archaux, Marthe Akpa-Vinceslas, Fabrice Bureau, Yann Dumas, Laurent Mignot, Francois Ningre, Sandrine Perret, Claudine Richter, et al.

Plant interactions as biotic drivers of intraspecific variability in leaf litter traits and decomposability of a foundation tree species (*Quercus petraea*)

Ludovic Henneron[1,2], Matthieu Chauvat[1], Frédéric Archaux[3], Marthe Akpa-Vinceslas[1], Fabrice Bureau[1], Yann Dumas[3], Laurent Mignot[1], François Ningre[4], Sandrine Perret[3], Claudine Richter[5], Philippe Balandier[3] and Michaël Aubert[1]

[1] Normandie Univ, UNIROUEN, IRSTEA, ECODIV,FR-76000 Rouen, France; [2] UREP, INRA, Clermont-Ferrand, Auvergne, France; [3] IRSTEA, Unit Research on Forest Ecosystems, Domaine des Barres, F-45290 Nogent-sur-Vernisson, France ; [4] INRA-LERFoB, 54280 Champenoux ; [5] ONF, Research & Development department, Boulevard de Constance , 77300 Fontainebleau, France

ludovic_henneron@hotmail.com

Context & scientific issues

- **Leaf litter traits and decomposability** are increasingly recognized as an 'extended' phenotype affecting plant community dynamics and ecological processes through plant-litter-soil feedbacks.
- **Intraspecific trait variability** can be an important source of functional diversity. While the role of genetic variability and environmental conditions, *i.e.* mostly soil abiotic factors, as sources of intraspecific variation in leaf litter traits and decomposability has been explored, very few studies have focused on the effect of **biotic factors such as plant neighbor identity and abundance and plant-plant interactions.**
- **Removal experiments** can be useful tools to manipulate species abundance in real ecosystems and to study the effect of altering plant interactions. Hence, the **removal of oak canopy trees** can affect oak leaf litter quality by altering: competition for light among trees ($\mathbf{H_1}$); competition for nutrients among trees ($\mathbf{H_2}$); competition for nutrients between trees and coexisting understory plants ($\mathbf{H_3}$), either related to abundance changes ($\mathbf{H_{3a}}$) or shifts in species composition ($\mathbf{H_{3b}}$) of understory plants; soil abiotic properties alterations ($\mathbf{H_4}$).

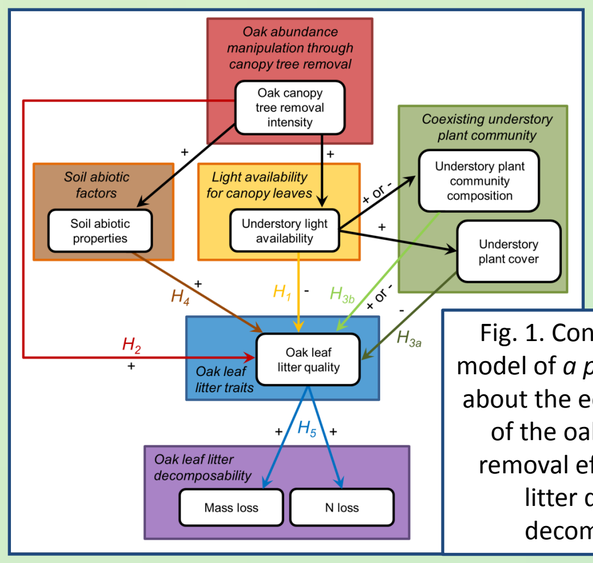

Fig. 1. Conceptual causal model of *a priori* hypotheses about the ecological drivers of the oak canopy tree removal effect on its leaf litter quality and decomposability

Aim of the study: *to assess how plant interactions control intraspecific variation in oak leaf litter traits and decomposability*

Material & methods

Study sites & treatments:

- **Experimental manipulation of oak abundance through the removal of oak canopy trees** using silvicultural-thinning regimes of contrasting intensity (Fig. 2)
- 5 Forest sites located throughout northern France on **contrasted pedoclimatic contexts** (Fig. 3) :
  - Oceanic to continental temperate climate
  - Very acidic (moder) to slightly acidic (mull) soil conditions
- Utilization of two complementary **experimental networks** :
  - The Scientific Interest Group - French national cooperative for data on forest growth - oak group (GIS-Coop)
  - The oak network of the Forest and Wood Resource Laboratory (LERFob)
- 19 sessile oak (*Quercus petraea*) stands studied covering a wide gradient of :
  - **Oak abundance** → 3 to 44 $m^2.ha^{-1}$ (oak canopy tree basal area used as a proxy)
  - **Forest successional stage** → 18 to 171 years old stands
    - ✓ **Aggradation** stage (< 90-year-old) → intense tree height growth and plant competition
    - ✓ **Biostatic** stage (>90-year-old) → maturity of trees

Oak leaf litter sampling and analyses:

- Sampling by **litter traps** (Fig. 4)
- A large set of 26 **litter chemical and biochemical traits** to characterize oak leaf litter quality
- Decomposability of oak leaf litter determined using **standardized *ex situ* decomposition bioassays** (Fig. 5)

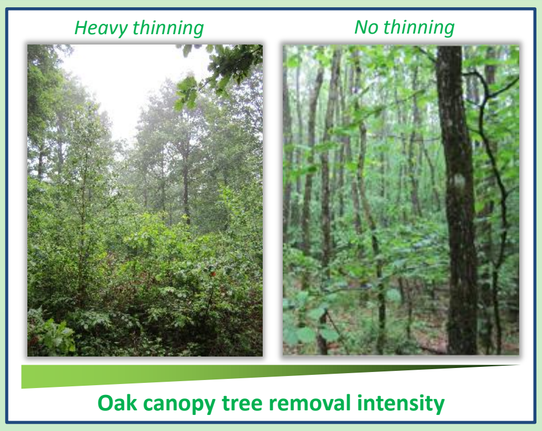

Fig. 2. Illustration of oak abundance manipulation

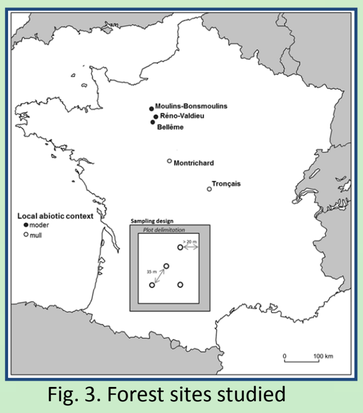

Fig. 3. Forest sites studied

Fig. 4. Litter trap

Fig. 5. Standardized *ex situ* decomposition bioassay

Results & discussion

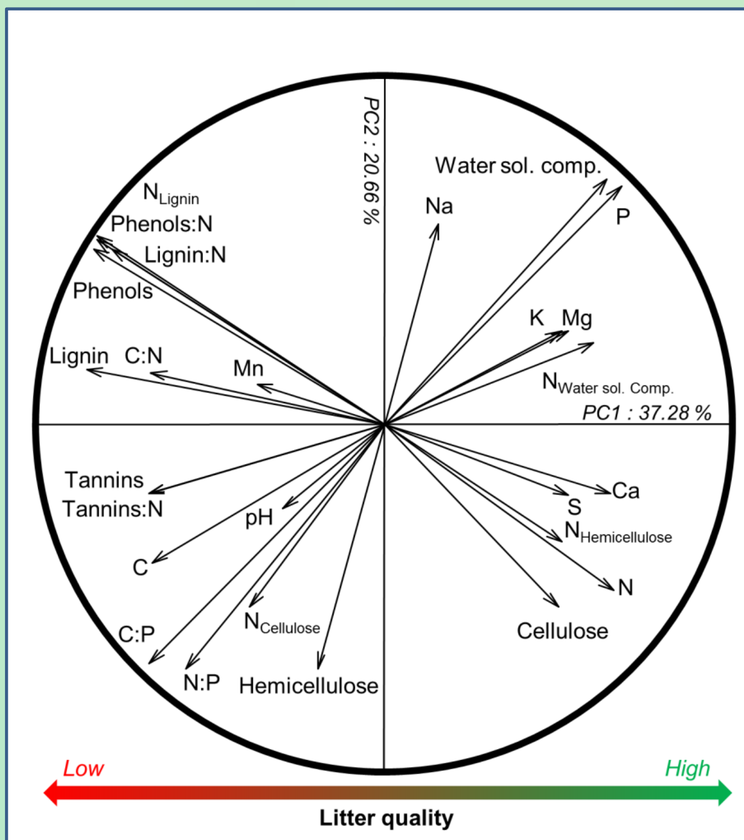

Fig. 6. Ordination of the 26 oak leaf litter traits based on within-site PCA (n = 19) Phenols: Total phenols; Tannins: Condensed tannins; Water sol. Comp.: Water-soluble compounds.

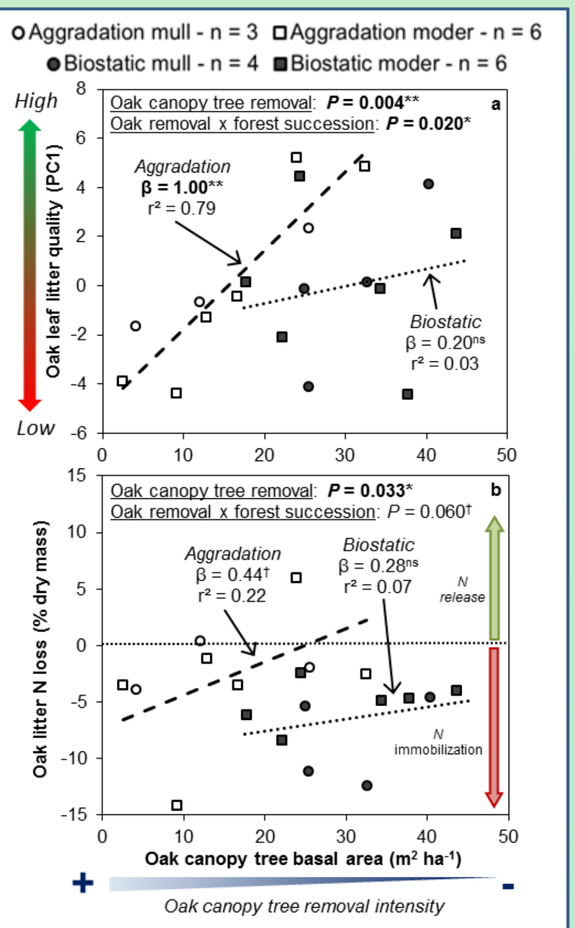

Fig. 7. Response pattern of oak leaf litter quality (a) and N loss (b) to the removal of oak canopy trees (n = 19)

- Oak leaf litter quality strongly declined with tree removal in early forest successional stage, which had important negative consequences for litter decomposability
  - Litter became poorer in nutrients such as N and Mg and richer in secondary metabolites such as total phenolics, condensed tannins and lignin (Fig 6, 7a)
  - Importantly, litter N loss switched from N release to N immobilization (Fig 7b)
- Variance partitioning indicated that oak abundance explained as much variation in oak leaf litter traits as oak age and twice as much as soil abiotic factors
  - This underlines that biotic factors can be more important sources of intraspecific variation in tree leaf litter traits than more commonly recognized soil abiotic factors

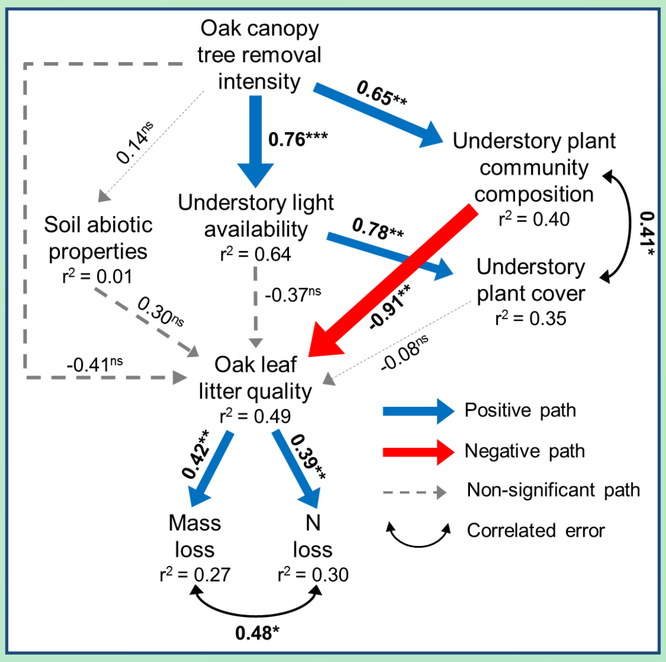

Fig. 8. Path analysis about the mechanisms through which oak canopy tree removal could drive changes in oak leaf litter quality and decomposability.

- The decline of oak leaf litter quality induced by tree removal was most likely driven by a shift in understory plant community composition ($\mathbf{H_{3b}}$, Fig. 8).
  - This could be due to an increased competition with a more abundant and faster-growing understory plant community with an higher leaf N content
  - We propose that this plasticity of leaf litter traits could be an adaptive strategy of ectomycorrhizal tree species consisting in 'short-circuiting' the N cycling through plant-litter-soil feedbacks in order to preserve their pre-empted nutrient pool of the capture by competing understory plants in the context of treefall gaps.

Conclusions & broader implications

- Our large-scale, multi-site study involving long-term oak canopy tree removal provides clear experimental evidence that **biotic factors such as plant-plant interactions can be strong drivers of plasticity in leaf litter traits**, with important consequences for litter decomposability.
- This finding contributes to the emerging view that **phenotypic plasticity** is fundamentally related to biotic interactions for sessile organisms, especially for long-lived and large plant species such as trees.
  - Taking this source of functional diversity into account could help us to better understand plant community dynamics and ecological processes in terrestrial ecosystems.

Acknowledgements:
This study was funded by a grant provided by the Upper-Normandy region via the Wide Area Network Research (TERA: Territory, Environment, Risk, Agronomy) and by the French Ministry of Ecology, Sustainable Development and Energy (Convention No. 10-MBGD-BGF-3-CVS-081, BGF program, IMPREBIO Research Project). We greatly thank P. Delporte, M. Le Gall, C. Abgrall, J. Lainé, A. Follin, M. Colombel and S. Mascré for laboratory, technical and field support. We also thank M. Makkonen for sharing their data, J. Messier for their advice in statistical analysis as well as N. Fanin for their helpful comments.
We also thank the 'French data cooperative on forest growth' (GIS Coop) and the 'oak network of the Forest and Wood Resource Laboratory' (LERFob), supported by AgroParisTech, INRA, ONF and Irstea with the financial support of the French Ministry of Agriculture and Forest, for the management of several sites studied and for providing data.