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Response of black poplar (*Populus nigra* L.) to hydrogeomorphological constraints: a semi-controlled *ex situ* experiment

Réponse du peuplier noir (*Populus nigra* L.) aux contraintes hydrogéomorphologiques : une expérimentation *ex situ* semi contrôlée

Virginia Garófano-Gómez^{1,2}; Dov Corenblit^{1,2}; Johannes Steiger^{1,2}; Bruno Moulia³; Stéphane Ploquin³; Patrice Chaleil³; Olivier Forestier⁴; André Evette⁵; Eduardo González⁶; Borbála Hortobágyi^{1,2} and Luc Lambs⁶

¹Clermont Université, UBP, MSH, 4 rue Ledru, 63057 Clermont-Ferrand Cedex 1, France (corresponding author: virginia.garofano_gomez@univ-bpclermont.fr).

²CNRS, UMR 6042, GEOLAB – Laboratoire de géographie physique et environnementale, 63057 Clermont-Ferrand, France. ³INRA Clermont Ferrand, UMRA547 Laboratoire de physique et physiologie intégrative de l'arbre fruitier et forestier, Site de Crouël 234, avenue du Brézet 63100 Clermont Ferrand, France. ⁴Pépinière Forestière de l'Etat, DRAAF Pays-de-la-Loire, route de Redon, 44290 Guémené Penfao, France. ⁵Irstea, UR EMGR, 2 rue de la papeterie BP 76, 38402 Saint-Martin-d'Hères, France. ⁶Ecolab CNRS, 118 route de Narbonne, F-31062 Toulouse Cedex, France.

RÉSUMÉ

Basé sur l'hypothèse d'existence d'une rétroaction éco-évolutive entre les espèces végétales riveraines ligneuses et la géomorphologie fluviale, une expérimentation *ex situ* en conditions semi-contrôlées a été planifiée afin de quantifier les traits de réponses fonctionnels (morphologique et biomécanique) de boutures de *Populus nigra* L. soumises à des contraintes hydrogéomorphologiques simulées : l'enfouissement sédimentaire, la force de traînée, et la combinaison des deux contraintes. Les questions scientifiques et le protocole expérimental sont présentés ici. L'hypothèse d'une construction de niche positive de *P. nigra* est testée à un certain degré. Les résultats de cette recherche contribueront à améliorer notre compréhension du fonctionnement des écosystèmes riverains et plus particulièrement du rôle de cette espèce ligneuse pionnière clé au sein de la bande active des cours d'eau.

ABSTRACT

Based on the hypothesis of an eco-evolutionary feedback between woody riparian species and fluvial geomorphology, a semi-controlled *ex situ* experiment has been planned to quantify key response functional traits (morphological and biomechanical) of *Populus nigra* L. cuttings to simulated hydrogeomorphological constraints, as well as to dissociate the specific responses to them. The constraints tested are sediment burial and drag force exerted by floods. The characteristics of the experiment are presented as well as the experimental design. The hypothesis of a positive niche construction by *P. nigra* is tested to a certain degree. The results from this research will improve our understanding of riparian ecosystem functioning and specifically of the role of this key woody pioneer species within active floodplain rivers.

KEYWORDS

Mechanical constraints, *Populus nigra* L., positive niche construction, response traits, sediment burial.

1 EVOLUTIONARY FEEDBACK BETWEEN WOODY RIPARIAN SPECIES AND HYDROGEOMORPHOLOGICAL CONSTRAINTS

As ecological systems localized at the land-water interface, riparian ecosystems are some of the most dynamic, heterogeneous and species-diverse ecosystems on the terrestrial portion of the planet. Different hydrogeomorphological factors (topography, flow and sediment transport regimes) control vegetation dynamics. These external abiotic factors have a direct effect on vegetation through their total or partial destruction, the dispersion of diaspores and the creation of new habitats for vegetation colonisation. But they also have an indirect effect on internal processes of succession (recruitment, establishment and growth, modulated by the water table depth and flood regime). However, this is not only a one-way relationship. Vegetation also has an impact on the flow and sediment transport regimes, basically through its canopy resistance to flow and the capacity of roots to modify substrate cohesion, which in turn causes an effect on the plant phenotype.

At an evolutionary timescale, this reciprocal interaction between vegetation and hydrogeomorphology has promoted the selection of certain plant traits (morphological, biomechanical, physiological and phenological) to increase the persistence of certain woody riparian species within highly disturbed fluvial environments. These traits improve species' adaptations to the original, unmodified hydrogeomorphological conditions, and potentially to their own modifications of the hydrogeomorphological environment within rivers. This functional connection between organisms and geomorphic forms and processes has led to the concept of 'ecosystem engineers' (Jones et al. 1994), as those species are able to modulate the supply of resources to other species by modifying their habitat. When the fitness of the ecosystem engineer is improved by its modification of the habitat and the modified environment also induces an evolutionary response, i.e. the selection and evolution of traits, of the ecosystem engineer or other organisms, this phenomenon is conceived as 'positive niche construction' (*sensu* Odling-Smee et al. 2003).

2 THE BIOGEOMORPHOLOGICAL LIFE CYCLE OF *POPULUS NIGRA* L.

Black poplar (*Populus nigra* L.) has been identified as a keystone ecosystem engineer species shaping western European fluvial systems. Recently, the concept of 'biogeomorphological life cycle' of *P. nigra* (Corenblit et al. 2014) has highlighted how specific ranges of hydrogeomorphological conditions control the successive phases of the entire life cycle of this species. These phases depend on physical environmental conditions such as flow and sediment dynamics, which provide resources and constitute constraints to plant development.

Our research is based on the hypothesis that over an evolutionary perspective, *P. nigra* has developed certain traits that have helped this species to better resist the constraints of highly disturbed river environments. Traits such as rapid germination and root elongation reduce drought mortality during the first summer following germination and increase resistance to up-rooting during winter floods. During the first growing season and while still exposed to a high degree of hydrological connectivity, the young cohorts within the active corridor develop rapidly the aerial structures increasing surface roughness which may favour the trapping of fine sediment, organic matter and nutrients, both downstream of and within the cohorts. This trapping of sediment and resources in the poplars' vicinity occurs at least during the first ten years of its life cycle, thus favouring their establishment and clonal expansion. At this stage, an extensive feedback between biological and hydrogeomorphological components leads to the emergence of biogeomorphological entities such as vegetated islands. We hypothesise that the impact of poplars on the landform structure strongly modulates its growth performance, biomass and architecture (number of shoots, suckers and adventitious roots) until it reaches sexual maturity (10-15 years) in adequate stable conditions.

3 SEMI-CONTROLLED *EX SITU* EXPERIMENT

3.1 Hypothesis, objective and research questions

This research is based on the hypothesis that a specific biogeomorphological feedback between sediment deposition, landform construction and *P. nigra* development occurs. We wish to understand how *P. nigra* responds to hydrogeomorphological constraints (mainly drag force and sediment burial), and if these responses could be biologically useful, i.e. functional for the engineer species. Hence, we need to test if *P. nigra* is able to modulate its phenotype in order to reach a trade-off between the necessity to improve its resistance to mechanical constraints and the opportunity to improve its resource acquisition, biomass production and eventually, the chances to reach sexual maturity within a

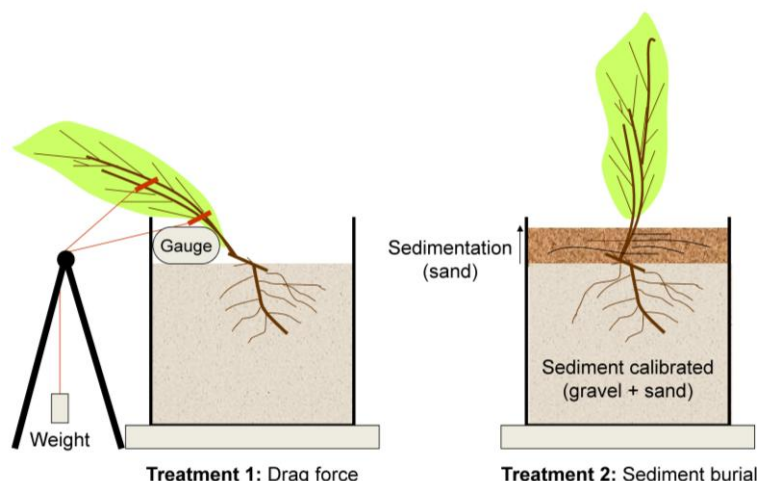
bioconstructed environment. Therefore, based on the theory of the positive niche construction by *P. nigra*, this study aims to analyse and quantify the expression of response functional traits of *P. nigra* cuttings to simulated hydrogeomorphological constraints through a semi-controlled *ex situ* experimental approach. We ask three main research questions: (1) How and to what extent do the hydrogeomorphological constraints (drag force and sediment burial) affect the growth of *P. nigra* at an early stage of the biogeomorphic life cycle? (2) Which are the responsive traits and which are the most significant responsive traits? (3) Is it possible to dissociate the traits affected by drag force from those affected by sediment burial?

3.2 Experimental design

An equilibrated experiment is being designed with 30 samples (i.e., cuttings of *P. nigra*, variety Jean Pourtet) per treatment. Each cutting (approx. 10 cm long) will be planted in a woven polypropylene bag from which water can exfiltrate, filled with a mix of gravel and sand (calibrated grain size 0-16 mm). Four bags will be installed within a pallet (as a block) with an irrigation system attached.

A completely randomized experimental design will be employed with cuttings and treatments assigned randomly to each one of the bags within the pallets. Three treatments will be applied: (1) drag force; (2) sediment burial; (3) drag force + sediment burial; and finally (4) control (no treatment application).

The mechanical constraint treatment will consist in the application of a calibrated force on the cutting to simulate the drag force exerted by floods. The sediment burial treatment will consist in the application of a layer of fine (calibrated grain size 0-4 mm) sediment around the main stem to simulate the deposited sediment after a flood event. To mimic the conditions in nature, the water level within the bag will be modulated along the experiment. Our null-hypothesis consists in the absence of differences in the response traits values in the treatments and control conditions.



Implementation schema of the different treatments: drag force (left) and sediment burial (right).

The treatments will be applied according to the temporal occurrence and average duration of floods in the region where the genotype comes from.

Different integrative aboveground morphological and biomechanical traits will be monitored during the course of the experiment and others (aboveground and belowground, as well as ratios between these two) will be measured once the experiment is finished.

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