Effet du type de sol, du génotype et du climat sur le microbiote racinaire du Peuplier noir (*Populus nigra* L.)

I. Contexte général

En comparaison avec le microbiote des plantes de grandes cultures qui ont fait l'objet d'études approfondies au cours des dernières années, peu de travaux ont été réalisés concernant le microbiote des arbres. Ceci peut notamment s'expliquer par le fait que les recherches en foresterie soient moins développées qu'en agriculture et par le cycle de vie des arbres très différents de celui des plantes herbacées.

Selon les études qui ont été menées sur le microbiote racinaire de plusieurs espèces d'arbres tels que le hêtre, le chêne, le peuplier et le pin, nous savons que les principaux facteurs qui influencent les communautés de micro-organismes associées aux racines sont les propriétés physico-chimiques du sol, la physiologie de l'arbre hôte qui affectent directement la qualité et la quantité des exsudats racinaires, les champignons ectomycorhiziens et la saison (Uroz et al., 2016). De plus, nous savons que le génotype est également un facteur de structuration et de composition du microbiote racinaire (Cregger et al., 2018 ; Gallart et al., 2018).

Ces principaux facteurs peuvent être régulés par les conditions climatiques. Par conséquent, nous pouvons nous attendre à ce que le changement climatique actuel ait un impact conséquent sur le microbiote racinaire des arbres.

Le rapport de conférence suivant, publié dans la revue *New Phytologist* et auquel j'ai contribué, montre l'importance de développer des projets de recherches multidisciplinaires pour améliorer notre connaissance sur les effets globaux du changement climatique.

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Meetings

Facing global change: the millennium challenge for plant scientists

41st New Phytologist Symposium 'Plant sciences for the future', Nancy, France, April 2018

Introduction

We entered the Anthropocene with the industrial revolution. This geological era is defined by the unprecedented impact of human activities on the planet's geochemical cycles, making us the main driving force of Earth environmental changes (Crutzen, 2002; Steffen *et al.*, 2011). Since the middle of the twentieth century the human population has tripled, reaching seven billion today and probably 10 billion by 2050 (United Nations, 2015). This dramatic increase, associated with the improvement in the welfare of the population, has led to the overexploitation of natural resources. Intensive agriculture and industrialization has resulted in global warming, modification of nutrient cycles, pollution and reduction of wilderness; and endangering the preservation of eco- and agro-systems (Tilman *et al.*, 2002; Steffen *et al.*, 2011; Ehrlich & Harte, 2015). Today, the challenge is not only to intensify agro-productions to feed, fuel and shelter the growing population; but to do so in spite of the consequences of climate change while lessening our impact on the supporting ecosystems (Godfray *et al.*, 2010; Ehrlich & Harte, 2015; Byrne *et al.*, 2018).

Plant sciences can play an important part in mitigating both the causes and consequences of the pressure population growth imposes on the environment. As the primary producer of eco- and agro-systems, plants are essential to assess and understand human-driven environmental changes (Loreau *et al.*, 2001; Lin *et al.*, 2008). They are also central tools to develop sustainable production methods (Godfray *et al.*, 2010; Ehrlich & Harte, 2015; Byrne *et al.*, 2018).

In this context, the 41st New Phytologist Symposium 'Plant sciences for the future' was set as an experimental interdisciplinary platform. Bringing together early career and leader scientists from different fields of plant sciences, it aimed to promote the development of transdisciplinary research projects to build a better understanding of the multiple aspects of the upcoming environmental challenges; and to produce robust solutions for society. A special debate chaired by Marc-André Selosse (Natural History Museum of Paris, France) and Richard Norby (Oak Ridge National Laboratory, TN, USA) highlighted the critical topics and knowledge gaps the scientific community needs to fill in order to harness plant sciences to solve these societal issues. This event, held in Nancy, France on 11–13 April 2018, hosted researchers from 70 universities, research institutes and companies representing 29 countries in the fields of Developmental biology, Evolutionary biology, Ecology, Plant–microorganism interactions, Physiology and Genetic engineering (Fig. 1). In this article we outline how all plant science fields contribute to understand the effects of global change and to developing innovative solutions to maintain agro-productions, promote sustainability and counteract climate change.

Exploring biogeochemical cycles

Human activities have altered global biogeochemical cycles. Colin Brownlee (Marine Biological Association, Plymouth, UK) illustrated the role of marine phytoplankton in the carbon (C) cycle, reminding that coccolithophores are responsible for much of the calcium carbonate formation on Earth. The increasing input of CO_2 into the atmosphere since the industrial revolution, which is responsible for ocean warming and acidification, is compromising the ability of coccolithophores to form calcium carbonate and therefore affecting the completion of the global C cycle (Orr *et al.*, 2005). Brownlee demonstrated the role of proton channels in the calcification process of calcite coccoliths. Elucidating the cellular mechanisms involved in biomineralization is essential to minimize human impact on these critical species.

Forests represents a major C sink (Pan *et al.*, 2011). Björn Lindahl (Swedish University of Agricultural Sciences, Uppsala, Sweden) highlighted the importance of plant–fungi interactions in nutrient cycling and soil fertility in boreal forests. Using high-throughput sequencing to elucidate boreal forest mycobiome and combining it with climatic, edaphic and forest productivity parameters, Lindahl's group showed that the composition of the fungal community is the principal driver of organic matter storage in those environments. Lindahl proposed that intensification of forest practices by changing soil fungal communities could improve the soil C stock in boreal forest but presents long-term soil fertility risks.

From the boreal forest to the steppe, Amy Austin (University of Buenos Aires, Argentina) demonstrated that photodegradation is a dominant force controlling C losses in semi-arid ecosystems (Austin & Vivanco, 2006). Recent findings of her team suggests that photodegradation of the leaf litter promotes its subsequent biotic degradation by increasing accessibility of labile C compounds to microbes (Austin *et al.*, 2016). Land-use or climate change altering vegetation cover could largely influence the effect of sunlight on C cycling in these ecosystems. Croplands

are an anthropogenic biome that we could manage to increase potential C sequestration. Carbon dioxide reaction with minerals naturally moderates atmospheric CO_2 and this effect has been enhanced since the emergence of land plants (Berner, 1997). David Beerling (University of Sheffield, UK) proposed to exploit this natural phenomenon by adding fast-reacting silicate rocks on croplands to trap CO_2. Eventually, weathering products could run-off in to oceans and enhance alkalinity, counteracting acidification, and sustaining the growth of marine phytoplankton that we presented as crucial for the completion of C cycle earlier in this paragraph. Together, these results highlight the importance of expanding our knowledge about C and nutrient turnover on Earth to predict and actively minimize our impact on climate.

Assessing the effects of climate change on plant physiology

Global warming has increased the intensity and frequency of extreme climactic events. High amplitude of temperature variation is the major cause of important plant losses in eco- and agro-systems (Eiche, 1966; Boyer, 1982; Hatfield & Prueger, 2015).

Plant pre-adaptation to climate variations could limit losses (Wikberg & Ögren, 2007; Yordanov *et al.*, 2000). Drought acclimation of trees involves structural changes in wood formation and abscisic acid (ABA) is a key plant regulator of this acclimation (Gupta *et al.*, 2017). Andrea Polle (University of Göttingen, Germany) showed the importance of ABA signal perception and response in wood formation of drought-stressed trees. Cecilia Brunetti (CNR, Sesto Fiorentino, Italy) demonstrated how trees limit xylem conduits embolism by modulating their carbohydrate metabolism and how ABA is involved in restoring xylem transport ability.

Limiting water loss by modulating stomatal aperture is another plant survival response to drought. Predicting plant responses to different levels of drought is still difficult. Belinda Medlyn (University of Western Sydney, Australia) reviewed recent advances in 'optimal stomatal theory' and presented a new *in silico* model to understand and predict stomatal responses to drought and heat.

Environmental stresses such as changes in temperature can affect plant metabolism and growth (Sampaio *et al.*, 2016). Shuhua Yang (China Agricultural University, Beijing, China) showed that stomatal conductance and, in consequence, leaf photosynthesis and respiration are affected by cold stress via the regulation of the CBF-dependent cold signalling pathway in Arabidopsis (Zhou *et al.*, 2011). Owen Atkin (Australian National University, Canberra, Australia) suggested that, by boosting plant respiratory metabolism, global warming could increase CO_2 release and influence the future atmospheric CO_2 concentrations.

Understanding plant physiological and metabolic adaptive responses to climate change are key factors for the production of efficient prediction models. These models are necessary to improve or develop novel management methods of eco- and agro-systems that could limit plant losses in the future.

Maintaining plant productivity

In our demographic context, maintaining population welfare depends on our ability to intensify agro-production. Environmental changes are threats to the maintenance of crop yields in both agricultural and forests agro-systems. They have direct impacts on plant mortality and biomass (Lobell & Field, 2007; Schlenker & Roberts, 2009), and indirectly affect plant productivity by altering population dynamics of plant pests, symbiotic microorganisms and competitive species (Gregory *et al.*, 2009; Lindner *et al.*, 2010). Biotechnological or agronomic solutions are necessary to lessen the consequences of global change on plant production.

In this frame, understanding the genetic basis of wood production in different tree lineages may help to mitigate the repercussions of abiotic stress on forest productivity through adapted management plans. Andrew T. Groover (US Forest Service and University of California, Davis, CA, USA) reviewed the genetic basis of evolution of woody plants and highlighted species-specific or conserved gene modules regulating the development of dicot and monocot cambium (Zinkgraf *et al.*, 2017).

Environmental changes are modifying development and distribution of plant pests, threatening crop and forest productivity (Porter *et al.*, 1991; Logan *et al.*, 2003). Plant diseases are now responsible for *c.* 25% of crop losses (Martinelli *et al.*, 2015). Controlling their outbreak is crucial to maintain plant productivity. A strategy to contrast future pest spread is to engineer crops resistant to a wide variety of pathogens. Ralph Panstruga's team (University of Aachen, Germany) explores the role of the MILDEW RESISTANCE LOCUS O genes (Jørgensen, 1992) – encoding members of a family of membrane integral proteins conserved in plants – in conferring multiple resistances. They showed that mutations in MLO genes improved *Arabidopsis thaliana* resistance to several leaf epidermal cell penetrating pathogens, but increased susceptibility to microbes with different invasion strategies (Acevedo-Garcia *et al.*, 2017). Stella Cesari (INRA, France), 2017 Tansley Medal winner, proposed to exploit the complex mechanistic and structural variability of nucleotide-binding domain and leucine-rich repeat-containing proteins (NLRs) to increase sensitivity or extend specificity of pathogen effector recognition (Cesari, 2017).

Understanding plants adaptive strategies to global change

Plants are increasingly exposed to new environmental stresses such as habitat degradation, climate change and the expanding range of invasive species and pests (Anderson *et al.*, 2011). To predict the consequences of global change on ecosystems, it is necessary to understand the different levels of plant adaptation (phenotypic plasticity, dispersion capacity and evolution) to new threats.

Plants can modulate the phenotypic plasticity of their neighbours by emission of volatile organic compounds (VOCs). André Kessler (Cornell University, Ithaca, NY, USA) showed that VOCs emitted by *Solidago altissima* upon herbivore attack alter herbivore dispersal and feeding behaviour through the modification of the

Fig. 1 Group photograph of the attendees of the 41st New Phytologist Symposium 'Plant sciences for the future' in the entrance of the Hôtel de Ville, Nancy (France). Photograph by Steven White, Leeds Media Services.

metabolism of non-attacked plants. This indicates spreading the risk of herbivory to neighbours as a fitness-optimizing strategy. The high variability of VOC types and levels in the field suggests the possibility of herbivore-driven natural selection on chemical communication (Morrell & Kessler, 2017). This might modulate crop adaptability to newly introduced pests.

Linda F. Delph (Indiana University, Bloomington, IN, USA) reminded the audience that the phenotype is the direct interface between the organism and its environment and therefore at the centre of evolution. She showed that genetic selection on key fitness traits such as flower number and height was strongly influenced by the environmental conditions in *Silene latifolia*. In-depth investigation of environmental factors influencing plant evolution may help predict phenotypic traits and fitness of plants in changing ecosystems.

Flower development is one of the most intricate and finely tuned processes influencing plant reproductive success. The floral organ must acquire specialized structures, bloom at the right time of the year and bear coevolving traits with its pollinators. By taking advantage of the -omics technologies, several groups found that specific transcription factors (TFs) evolved to allow the formation of elaborate and diverse floral petals. Elena Kramer (Harvard University, Cambridge, MA, USA) presented the role of the AqJAGGED gene, a TF involved in multiple key aspects in *Aquilegia* flower morphogenesis (Min & Kramer, 2017), while Hongzhi Kong (Institute of Botany, Beijing, China) showed that NpLMI1 and NpYAB5-1 are involved in the control of *Nigella* petal shape.

Since the first observations of pollination systems by Darwin (1862), researchers have been seeking for evidence of pollinator-promoted selection for diverse floral shapes. Babu Ram Paudel (Yunnan University, China) showed how two alpine gingers (*Roscoea purpurea* and *R. tumjensis*) occur sympatrically and have similar morphology, but are reproductively isolated through a combination of phenological displacement of flowers and different attracted pollinators. Global change might reshape these evolutionary boundaries and modify population or speciation dynamics.

Human impacts on the environment will influence plant traits and drive their evolution by modulating plant fitness (resistance to pathogens, pollination, population dynamics). However, plant plasticity might provide a key for plant adaptability on the short term.

Innovative plant technology: a role for basic and applied science

Understanding the genetic and molecular basis of phenotypes is key to groundbreaking biotechnological applications; hence the importance of tight coordination and synergy between basic and applied sciences. The Symposium hosted researchers interested in fundamental biological mechanisms, scientists involved in both basic and applied research and developers employed in biotechnology companies, aiming to bridge their complementary mindsets.

Understanding the molecular aspects of nutrient uptake and storage by plants is crucial to improving the yield or nutritional

properties of crops. By investigating the developmental biology of rooting systems in early land plants, Liam Dolan (University of Oxford, UK) showed that the development of rooting structures in land plants is tightly controlled by some conserved TF networks (Breuninger *et al.*, 2016; Proust *et al.*, 2016). Such highly conserved key regulators can be used to enhance crops ability to access nutrients (Dolan *et al.*, 2011; US Patent Application no. 12/451,574). The fine-tuning of lateral root emergence is another central aspect of root systems development. Keith Lindsey (Durham University, UK) showed how the 36-aa peptide POLARIS, orchestrating the auxin–ethylene crosstalk, modulates lateral root emergence (Chilley *et al.*, 2006). These signalling mechanisms affect plants' access to water and nutrients and mediate plant plasticity in a changing environment. The regulation of the level of reserves is also fundamental to plant nutrition. Alison M. Smith (John Innes Centre, Norwich, UK) highlighted the importance of clock genes, which modulate starch production and degradation for efficient plant sustainment (Graf *et al.*, 2010; Scialdone *et al.*, 2013). Arabidopsis leaves modulate the rate of starch degradation according to the duration of the night, in order not to starve before dawn (Fernandez *et al.*, 2017). A better understanding of the dynamics of plant nutrient reserves may help engineering stress-resistant or nutrient-rich crops.

Examples of basic sciences translated into innovative plant technologies were given at the symposium. As presented earlier, David Beerling is exploiting silica weathering to counter accumulation of excess atmospheric CO_2. These results involved integrative studies spanning through geology, chemistry, economy and plant sciences, demonstrating once more the inestimable power of transdisciplinary research. Anne Osbourn (John Innes Centre) showed that through coexpression, evolutionary co-occurrence and epigenomic coregulation genomes can be mined for biosynthetic gene clusters involved in production of secondary metabolites (Medema & Osbourn, 2016). Their genetic manipulation allows the production of specific chemicals at a lower cost than conventional synthetic chemistry (Owen *et al.*, 2017). Technical platforms and start-ups are being born in the exciting field of plant chemistry (Reed *et al.*, 2017).

In conclusion, the symposium highlighted the need of integrative research to (1) understand, model, predict the consequences of global change on ecosystems and plant physiology, productivity, epidemiology; (2) create innovative solutions to future challenges in the fields of food security, sustainable crop management and efficient production; (3) diffuse knowledge and know-how among specialists and the general public. To this purpose, the symposium was closed by a public talk on plant–microorganism interactions, given by Marc-André Selosse with the beautiful background of the Hôtel de Ville of Nancy.

Acknowledgements

The authors thank the New Phytologist Trust and the Lab of Excellence ARBRE for organizing this symposium. The authors are grateful to all attendees who contributed to the stimulating atmosphere of this conference. A special acknowledgement to M-A. Selosse and R. Norby for leading the debate on the role of plant sciences in solving societal issues. The authors thank A. Austin, A. Polle, B. Medlyn, L. Wingate and A. Kessler for their time and advice during the mentoring session on Gender equality in plant sciences. The authors are grateful to F. Martin and the New Phytologist Trust for their support and helpful comments on the report. This work was supported by the LabEx ARBRE (ANR-11-LABX-0002-01), the Région Grand-Est, the University of Lorraine, the Genomic Science Programme of the US Department of Energy as part of the Plant–Microbe Interfaces Scientific Focus Area and, the ANPCyT (PICT 2015-1231, PICT 2016-1780), the University of Buenos Aires (UBACyT) and the CONICET of Argentina.

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References

Acevedo-Garcia J, Gruner K, Reinstädler A, Kemen A, Kemen E, Cao L, Takken FLW, Reitz MU, Schäfer P, O'Connell RJ *et al.* 2017. The powdery mildew-resistant Arabidopsis *mlo2 mlo6 mlo12* triple mutant displays altered infection phenotypes with diverse types of phytopathogens. *Scientific Reports* **7**: 1–15.

Anderson JT, Willis JH, Mitchell-Olds T. 2011. Evolutionary genetics of plant adaptation. *Trends in Genetics* **27**: 258–266.

Austin AT, Méndez MS, Ballaré CL. 2016. Photodegradation alleviates the lignin bottleneck for carbon turnover in terrestrial ecosystems. *Proceedings of the National Academy of Sciences, USA* **113**: 1–6.

Austin AT, Vivanco L. 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature* **442**: 555–558.

Berner RA. 1997. The rise of plants and their effect on weathering and atmospheric CO_2. *Science* **276**: 544–546.

Boyer JS. 1982. Plant productivity and environment. *Science* **218**: 443–448.

Breuninger H, Thamm A, Streubel S, Sakayama H, Nishiyama T, Dolan L. 2016. Diversification of a transcription factor family led to the evolution of antagonistically acting genetic regulators of root hair growth report diversification of a transcription factor family led to the evolution of antagonistically acting genetic regulators of root hair growth. *Current Biology* **26**: 1622–1628.

Byrne PF, Volk GM, Gardner C, Gore MA, Simon PW, Smith S. 2018. Sustaining the future of plant breeding: the critical role of the USDA-ARS National Plant Germplasm System. *Crop Science* **58**: 1–18.

Cesari S. 2017. Multiple strategies for pathogen perception by plant immune receptors. *New Phytologist* **219**: 17–24.

Chilley PM, Casson SA, Tarkowski P, Hawkins N, Wang KL, Hussey PJ, Baele M, Ecker JR, Sandberg K, Lindsey K. 2006. The POLARIS peptide of Arabidopsis regulates auxin transport and root growth via effects on ethylene signaling. *Plant Cell* **18**: 3058–3072.

Crutzen PJ. 2002. Geology of mankind. *Nature* **415**: 23.

Darwin C. 1862. *On the various contrivances by which British and foreign orchids are fertilized by insects.* London, UK: Murray.

Dolan L, Menand B, Yi K. 2011. *Composition and method for modulating plant root hair development.* US Patent Application no. 12/451,574.

Ehrlich PR, Harte J. 2015. Opinion: To feed the world in 2050 will require a global revolution. *Proceedings of the National Academy of Sciences, USA* **112**: 1–2.

Eiche V 1966. *Cold damage and plant mortality in experimental provenance plantation with Scots Pine in Northern Sweden.* Stockholm, Sweden: Studia Forestalia Suecica 0039-3150.

Fernandez O, Ishihara H, Georges MG, Mengin V, Flis A, Sumner D, Arrivault S, Feil R, Lunn JE, Zeeman SC *et al.* 2017. Leaf starch turnover occurs in long days and in falling light at the end of the day. *Plant Physiology* **174**: 2199–2212.

Godfray HCJ, Beddington JR, Crute IR, Haddad L, Lawrence D, Muir JF, Pretty J, Robinson S, Thomas SM, Toulmin C. 2010. Food security: the challenge of feeding 9 billion people. *Science* **327**: 812–819.

Graf A, Schlereth A, Stitt M, Smith AM. 2010. Circadian control of carbohydrate availability for growth in Arabidopsis plants at night. *Proceedings of the National Academy of Sciences, USA* **107**: 9458–9463.

Gregory PJ, Johnson SN, Newton AC, Ingram JSI. 2009. Integrating pests and pathogens into the climate change/food security debate. *Journal of Experimental Botany* **60**: 2827–2838.

Gupta A, Hisano H, Hojo Y, Matsuura T, Ikeda Y, Mori IC, Senthil-Kumar M. 2017. Global profiling of phytohormone dynamics during combined drought and pathogen stress in *Arabidopsis thaliana* reveals ABA and JA as major regulators. *Scientific Report* **4**: 4017.

Hatfield JL, Prueger JH. 2015. Temperature extremes: effect on plant growth and development. *Weather and Climate Extremes* **10**: 4–10.

Jørgensen JH. 1992. Discovery, characterization and exploitation of Mlo powdery mildew resistance in barley. *Euphytica* **63**: 141–152.

Lin BB, Perfecto I, Vandermeer J. 2008. Synergies between agricultural intensification and climate change could create surprising vulnerabilities for crops. *AIBS Bulletin* **58**: 847–854.

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolström M *et al.* 2010. Climate change impacts, adaptive capacity and vulnerability of European forest ecosystems. *Forest Ecology and Management* **259**: 698–709.

Lobell DB, Field CB. 2007. Global scale climate-crop yield relationships and the impacts of recent warming. *Environmental Research Letters* **2**: 014002.

Logan JA, Réginière J, Powell JA. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment* **1**: 130–137.

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B *et al.* 2001. Biodiversity and ecosystem functioning: current knowledge and future challenge. *Science* **294**: 804–808.

Martinelli F, Scalenghe R, Davino S, Panno S, Scuderi G, Ruisi P, Villa P, Stroppina D, Boschetti M, Goulard LR. 2015. Advanced methods of plant disease detection. *Agronomy for Sustainable Development* **35**: 1–25.

Medema MH, Osbourn A. 2016. Computational genomic identification and functional reconstitution of plant natural product biosynthetic pathways. *Natural Product Reports* **33**: 951–962.

Min Y, Kramer EM. 2017. The *Aquilegia JAGGED* homolog promotes proliferation of adaxial cell types in both leaves and stems. *New Phytologist* **216**: 536–548.

Morrell K, Kessler A. 2017. Plant communication in a widespread goldenrod: keeping herbivores on the move. *British Ecological Society* **41**: 1049–1061.

Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RA, Gnanadesikan A, Gruber N, Ishika A, Joos F *et al.* 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* **437**: 681–686.

Owen C, Patron NJ, Huang A, Osbourn A. 2017. Harnessing plant metabolic diversity. *Current Opinion in Chemical Biology* **40**: 24–30.

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG. 2011. A large and persistent carbon sink in the World's forest. *Science* **333**: 988–993.

Porter JH, Parry ML, Carter TR. 1991. The potential effects of climatic change on agricultural insect pests. *Agricultural and Forest Meteorology* **57**: 221–240.

Proust H, Honkanen S, Jones VAS, Morieri G, Prescott H, Kelly S, Ishizaki K, Kohchi T, Dolan L. 2016. RSL Class I genes controlled the development of epidermal structures in the common ancestor of land plants. *Current Biology* **26**: 93–99.

Reed J, Stephenson MJ, Miettinen K, Brouwer B, Leveau A, Brett P, Goss RJM, Goossens A, O'Connell MA, Osbourn A. 2017. A translational synthetic biology platform for rapid access to gram-scale quantities of novel drug-like molecules. *Metabolic Engineering* **42**: 185–193.

Sampaio BL, Edrada-Ebel R, Batista F, Costa D. 2016. Effect of the environment on the secondary metabolic profile of *Tithonia diversifolia*: a model for environmental metabolomics of plants. *Scientific Report* **6**: 1–11.

Schlenker W, Roberts MJ. 2009. Nonlinear temperature effects indicate severe damages to U.S. crop yields under climate change. *Proceedings of the National Academy of Sciences, USA* **106**: 15594–15598.

Scialdone A, Mugford ST, Feike D, Skeffington A, Borrill P, Graf A, Smith AM, Howard M. 2013. Arabidopsis plants perform arithmetic division to prevent starvation at night. *eLife* **2**: 1–24.

Steffen W, Grinevald J, Crutzen P, Mcneill J. 2011. The Anthropocene: conceptual and historical perspectives. *Philosophical Transactions. Series A: Mathematical, Physical, and Engineering Sciences* **369**: 842–867.

Tilman D, Cassman KG, Matson PA, Naylor R, Polasky S. 2002. Agricultural sustainability and intensive production practices. *Nature* **418**: 671–677.

United Nations. 2015. World population prospects: the 2015 revision. *United Nations Department of Economic and Social Affairs.* **33**: 1–66.

Wikberg J, Ögren E. 2007. Variation in drought resistance, drought acclimation and water conservation in four willow cultivars used for biomass production. *Tree Physiology* **27**: 1339–1346.

Yordanov I, Velikova V, Tsonev T. 2000. Plant responses to drought, acclimation and stress tolerance. *Photosynthetica* **38**: 171–186.

Zhou MQ, Shen C, Wu LH, Tang KX, Lin J. 2011. CBF-dependent signaling pathway: a key responder to low temperature stress in plants. *Critical Reviews in Biotechnology* **31**: 186–192.

Zinkgraf M, Gerttula S, Groover A. 2017. Transcript profiling of a novel meristem, the monocot cambium. *Journal of Integrative Plant Biology* **59**: 436–449.

Key words: biochemical cycles, climate change, food security, holobiont, phenotypic plasticity, plant adaptive strategies, plant productivity, plant sciences.

II. Objectifs

D'après la littérature existante sur les plantes herbacées, il est désormais clairement établi qu'une diminution de la disponibilité en eau et une augmentation de la température modifie la composition et la structure du microbiote racinaire (Wallenstein & Hall, 2012). Chez les arbres, le lien entre les propriétés physico-chimiques du sol, les besoins physiologiques de l'arbre et les communautés microbiennes associées aux racines demeure encore peu étudié.

Parmi les espèces d'arbres qui sont naturellement confrontées aux effets du changement climatique, le peuplier noir d'Europe (*Populus nigra* L.) est un bon exemple. Il s'agit d'une espèce pionnière colonisant les sédiments alluviaux le long des fleuves dans les zones climatiques tempérées du continent Asie-Europe et d'Afrique du Nord. Avec d'autres espèces d'arbres riverains, *P. nigra* occupe une position clé dans l'écosystème riverain, mais sa pérennité et sa diversité génétique sont menacées pour deux raisons principales : l'absence de sites de régénération en raison de l'activité humaine sur les plaines inondables et l'impact du changement climatique. L'augmentation de la fréquence des événements naturels extrêmes liés aux changements climatiques est susceptible d'entraîner des variations plus fréquentes et plus intenses des nappes phréatiques et des régimes d'écoulement des cours d'eau qui affectent le développement des semis et la physiologie des arbres. Il existe de grandes variations dans la capacité de réaction au stress climatique au sein des populations de *P. nigra* et entre elles, ce qui suggère un important potentiel d'adaptation (Chamaillard et al., 2011). On pourrait supposer que le microbiote de la racine du peuplier noir contribue à cette adaptation, mais aucune étude n'a été réalisée jusqu'à présent pour évaluer son rôle relatif. Des études sur le microbiote des racines de peuplier d'autres espèces (e.g. *P. deltoides*, *P. trichocarpa*) ont déjà été faites mais jamais sur des écosystèmes riverains (Hacquard & Schadt, 2015).

Les travaux présentés dans ce chapitre font partie du projet POPMICROCLIM (soutenu par le métaprogramme ACCAF). Les objectifs de ce projet sont de caractériser le microbiote des sédiments de deux rivières françaises, habitats naturels du peuplier noir, le microbiote racinaire du peuplier noir, l'impact du climat sur ces microbiotes et le rôle potentiel du microbiote dans l'adaptabilité des jeunes plants aux variations climatiques. Ce projet est réalisé en collaboration avec les équipes du Dr Lional Ranjard (INRAE UMR Agroécologie Dijon) en charge de l'analyse du microbiote du sol, du Dr Marc Villar (INRAE UMR BioForA) et du Dr Régis Fichot (Université d'Orléans) en charge des analyses génétiques et écophysiologiques. Au moment du dépôt de mon manuscrit, l'ensemble des données expérimentales a été acquis mais les analyses couplant études écophysiologiques et études microbiologiques n'ont pas encore été réalisées. Ne seront donc présentées ici que les données concernant l'étude du microbiote.

Nous avons essayé de répondre à plusieurs questions

- Quelle est la composition du microbiote racinaire du peuplier noir ?
- Y a-t-il un effet de l'origine du sol sur la composition du microbiote racinaire et du microbiote du sol ?
- Y a-t-il un effet de la transplantation de sol dans un nouveau climat sur le microbiote racinaire ?
- Le microbiote du sol et le microbiote racinaire du peuplier noir sont-ils influencés par les conditions climatiques de la Loire et de le Drôme ?

III. Démarche expérimentale

Afin de répondre à ces questionnements, nous avons profité d'une expérience de transplantation réciproque mise en place par l'UAGPF (Unité Mixte de Recherche Biologie intégrée pour la valorisation de la diversité des arbres et de la forêt, INRAE Val de Loire) au printemps 2017. Dans le but d'étudier les mécanismes génétiques d'adaptation des plants de peupliers noirs au changement climatique, des graines de peupliers noirs génétiquement caractérisés (via des marqueurs SSR et SNP) provenant de deux régions de France climatiquement contrastées (Drôme et Loire) ont été prélevées sur 2 x 10 arbres mères et plantées dans des conteneurs contenant les sédiments bruts des deux rivières. Des copies de chaque conteneur ont été faites et transportées dans les deux sites aux climats contrastés.
Les paramètres de développement (croissance, mise en dormance) et des paramètres éco-physiologiques pertinents pour l'acquisition de l'eau (efficacité de l'utilisation de l'eau, répartition de la biomasse, architecture des racines, anatomie du xylème) ont été mesurés sur deux saisons de croissance. En novembre 2017, les systèmes racinaires ont été échantillonnés afin de mesurer leur développement et d'évaluer la composition du microbiome racinaire des différents génotypes.

Les résultats de cette étude sont décrits sous la forme d'un article scientifique actuellement en préparation.
Les tableaux et tableaux supplémentaires sont disponibles en Annexe (Annexe 2 de la page 9 à la page 26).

A mesocosm transplant experiment to investigate how climate, soil properties and plant genetics determine the structure of the root microbiome of *Populus nigra* seedlings

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Abstract

Trees and their root-associated microorganisms are tightly interconnected. They play important roles in each other's nutrition and protection against stresses. Host factors such as tree genotype but also environmental factors particularly soil matrix and climate are key determinants of root microbiome structure and composition. Our understanding of the effects of soil origin and climate on the soil and the root microbiome and on tree physiology is incomplete. In the current context of climate change, it is not clear whether the soil and root microbiome react directly to the climatic variations and to the soil physico-chemical properties and indirectly to the tree physiology alteration. To address this question, we analysed the sediments of two French rivers located in two climatically contrasted regions Drôme and Loire and the root microbiome structure and composition of a pioneer tree from riparian ecosystem, the European black poplar (*Populus nigra* L.) cultivated in mesocosms in different sets of soil and climate conditions. Seeds were collected in the two contrasted regions and belonged to genetically characterized *Populus nigra* trees in order to study the relative contribution of host genotype on the root microbiome. After a season of growth, the above-ground size of seedlings was measured and sediment-, rhizosphere- and root-associated fungal and bacterial communities were characterized by high throughput MiSeq sequencing of rDNA ITS and 16S rRNA amplicons. Significant shifts of bacterial and fungal community composition were observed between native and transplant conditions of the seedlings culture. Enrichment of specific microbial communities in the rhizosphere and roots were correlated with increase of the aerial part growth of seedlings.

Keywords : Microbiome, metabarcoding, climate change, *Populus nigra*, sediments, genotype

Introduction

The European black poplar, *Populus nigra* L., is a natural and pioneer tree species colonizing alluvial sediments along rivers, where it often exists as a series of metapopulations (Villar & Forestier, 2009). *Populus nigra* occupies a keystone position within the riparian ecosystem thanks to its highly developed root system that allow it to be an efficient sediment trapper, riverbank fixative and natural nutrient purifier (Ruffinoni et al., 2003). However, its position is currently hindered by the lack of regeneration due to human pressure on flood plains and the impact of climate change (Lefevre et al., 1998; Cottrell, 2004). It is important to remind that for most riparian tree species, the regeneration is achieved through the colonization of river sediment along the riverbank according to the natural periodic flooding of the ecosystem and the lateral movement of the river bed. Seed dispersal combines an initial wind-mediated phase with the transport of seeds from the maternal tree to the ground or the water, followed by a secondary hydrochorous phase (Barat-Segretain, 1996; Imbert & Lefèvre, 2003). The *P. nigra* offprings are therefore often found several kilometres downstream of the mother tree on river bank or sediments islands subject to very variable environmental conditions. *Populus nigra* is considered as a fast-growing and opportunistic species, with a good tolerance to submersion, sediment burial and high temperature (Chamaillard, 2011; Corenblit et al., 2014). These abilities are important to adapt to the fluvial environment, which differs in space and time. Indeed, the place where *Populus nigra* seedlings begin their life cycle is more frequently disturbed during annual flood events compared to the place where they reached maturity (Corenblit et al., 2014). Climate change such as rising temperature and modifications of precipitation patterns could therefore have consequences on natural regeneration and genetic structuration of the populations of black poplars. The juvenile stage (i.e., seedling) is a key step in the development of trees but our knowledge of the parameters that determine the success of the installation and development remains limited.

In most of plant and tree species, extrinsic factors such as soil properties and climate, but also intrinsic factors such plant genotype are important determinants of the adaptation of tree seedlings to their environment. In addition, the root-associated microbiome, which corresponds to the complex microbial communities occurring on the surface and inside the roots, is known to increase nutrient and water acquisition and to protect host tree against biotic and abiotic stresses, improving by these ways the growth of the trees (Hacquard & Schadt, 2015; Timm et al., 2018). As several *Populus* species represent ecologically important species (e.g., *P. trichocarpa* or *P. deltoides* in the USA, *P. nigra* in Europe) and/or are used in plantations to produce wood biomass, recent efforts have been made to characterize their root microbiome and their potential role in the promotion of the growth of poplar (Germaine et al., 2004; Gottel et al., 2011; Danielsen et al., 2012; Shakya et al., 2013; Beckers et al., 2017; Durand et al., 2017; Durand et al., 2018; Cregger et al., 2018; Veach et al., 2019). Notably, Bonito et al., (2014) showed that the soil origin had a stronger effect on the fungal root community composition than on the bacterial communities, which were more tightly structured by host species (*Populus*, *Quercus* and *Pinus*) than by the soil origin. Considering mature trees of *Populus deltoides*, another riparian poplar tree species, Shakya et al., (2013) revealed that both the soil type, the season and the geographic distance (i.e., several tens of kilometres)

between trees were important drivers shaping bacterial and fungal communities in the rhizosphere and the endosphere. Comparatively to *P. trichocarpa* or *P. deltoides*, the composition and the structure of the root-associated microbiome of *P. nigra* has never been or rarely (Tesar et al., 2002) investigated nor how the *P. nigra* holobiont (i.e., the assemblage formed by the tree host and its associated microbiome; Hacquard & Schadt, 2015), could adapt to changing environments. The ecology of *Populus nigra* is currently well-known. The large-scale analysis of its distribution revealed that this species colonizes naturally alluvial sediments along rivers in several temperate climate zones of the Asian-European continent, such as in France, but also in Northern Africa. Those studies evidenced that *P. nigra* is able to adapt to different edaphic properties and to variable climates. Studies on phenotypic plasticity have been less discussed for black poplar, but this process has been demonstrated to be inheritable and has provided an evolving short-term response to climate change (Aitken et al., 2008; Nicotra et al., 2010). In this context, we can wonder whether the development of the tree seedlings of this species is linked to the selection of specific poplar populations (i.e., genetic adaptation), phenotypic plasticity and/or to the recruitment of particular microorganisms (i.e., the root-associated microbiome).

As, *P. nigra* is widespread in France along different rivers under different climates, we took the opportunity to study the factors that may explain their adaptation to a changing environment at the seedling stage. To do it, we used a mesocosm transplant experiment approach considering two different river sediments (i.e., Loire vs Drôme) as soil substrate, two different climates and several different tree progenies. Sediments of the Drôme and the Loire were conditioned in mesocosms, planted with different *P. nigra* progenies coming from the Drôme or the Loire region and incubated in natural conditions under the Drôme and the Loire climates with a constant irrigation. In this experiment, we evaluated the impact of these different parameters (sediment type, plant progeny, and climate) on the composition and structure of the root-associated microbiome of black poplar and on tree phenology and development. We characterized the microbial communities (*i.e.*, bacteria and fungi) colonizing sediment (BS), rhizosphere (R) and endosphere (E) of the three *Populus nigra* progenies per origin (i.e., 3 from the Drôme and 3 from the Loire) using amplicon 16S rRNA and ITS rDNA gene-targeted Illumina sequencing. In each location, the 3 progenies (i.e., the offsprings of *P. nigra* mother trees originating from Drôme and Loire) considered have been selected due to their contrasted above ground growth (i.e., low, medium and high) in their native sediment. In our experiment, their growth (roots and shoots) was monitored under each climate and in the two sediments considered and the chemical characteristics of the sediments were determined. We hypothesized that the growth of black poplar seedlings is influenced by the microbiome recruited in the root system. To test, this hypothesis, we organized our analyses to answer to three main questions: (i) Is there an effect of the soil origin on the microbiome composition occurring in the black poplar root system and in the surrounding soil? (ii) Do the genetic characteristics (i.e., progeny) influence the composition and structure of the root-associated microbiome? (iii) Are the black poplar soil and root-associated microbiome influenced by the contrasted climates and/or the soil conditions?

Material & Methods

Seed collection

For our transplant experiment, seeds from *Populus nigra* trees have been collected in two climatically contrasted regions of France (Drôme and Loire), along the Loire and Drôme rivers. In each location, seeds were specifically collected on *Populus nigra* mother trees previously genetically characterized based on single nucleotide polymorphism (SNP) or microsatellite analyses and presenting a flowering phenology out of step with the black poplar cv. Italica (Faivre-Rampant et al., 2016). The sampling period was determined to avoid as much as possible the hybridization with black poplar cv. Italica and to maximize the genetic differentiation of the *Populus nigra* seedlings progenies. In each region, the progeny of 10 mother trees has been collected.

For the experiments presented in this study, only 3 progenies per site have been considered. The Loire progenies were selected to present contrasted growth (low, medium and high) in the Loire sediment and under the Loire climate. The Drôme progenies were selected to present contrasted growth (low, medium and high) in the Drôme sediment and under the Drôme climate.

In the Loire region, the seeds from L04 progeny were collected from a mother tree located in the Natural reserve of Saint Pryvé Saint Mesnin (1.8415°/ 47.8824°) while the seeds from L06 and L08 progenies were collected from a mother tree located Guilly (2.2877°/ 47.8069°).

In the Drôme region, the seeds from D11, D13 and D15 were collected from mother trees located in Natural reserve of Les Ramières (4.9488°/ 44.7427°). Seeds collections were performed in May 2017. Seeds were stored in 4°C until germination assays in Petri dish with filter paper and water in order to check the seed viability.

Plant and soil material

In each location, raw sediments were collected using an excavator in the river bed. Although, these sediments did not follow paedogenesis steps, we will refer in our manuscript to BS as bulk sediment, in the sense of bulk soil (i.e., soil without roots). In the Loire region, sediment sampling was done in Saint Père sur Loire (2.3667°/47.7667°) in October 2016. In the Drôme region, the sampling was done in Livron (4.8399°/44.7682°) in December 2016. After the sampling of the sediments were transferred to the INRA Center of Orléans and conserved 4 months under ambient conditions and below a canvas sheet to let the sediments dry. After 4 months, the sediments were homogenised and conditioned in mesocosms (1m x 1m x 1m). A total of 12 mesocosms (6 containing the Drôme sediment and 6 containing the Loire sediment) has been prepared to permit our transplant experiment. A sediments sample (called “T0”) was collected in each mesocosm and conserved at -20°C until DNA extraction. After conditioning, half of the mesocosms was installed at the INRAE Center of Orléans (1.5452°/47.4942°; Loire region), while the other mesocosms were installed in the Natural reserve of Les Ramières (RMN) in Allex (4.9151°/44.7621°; Drôme region). The details of the experimental design are presented in Figure 26.

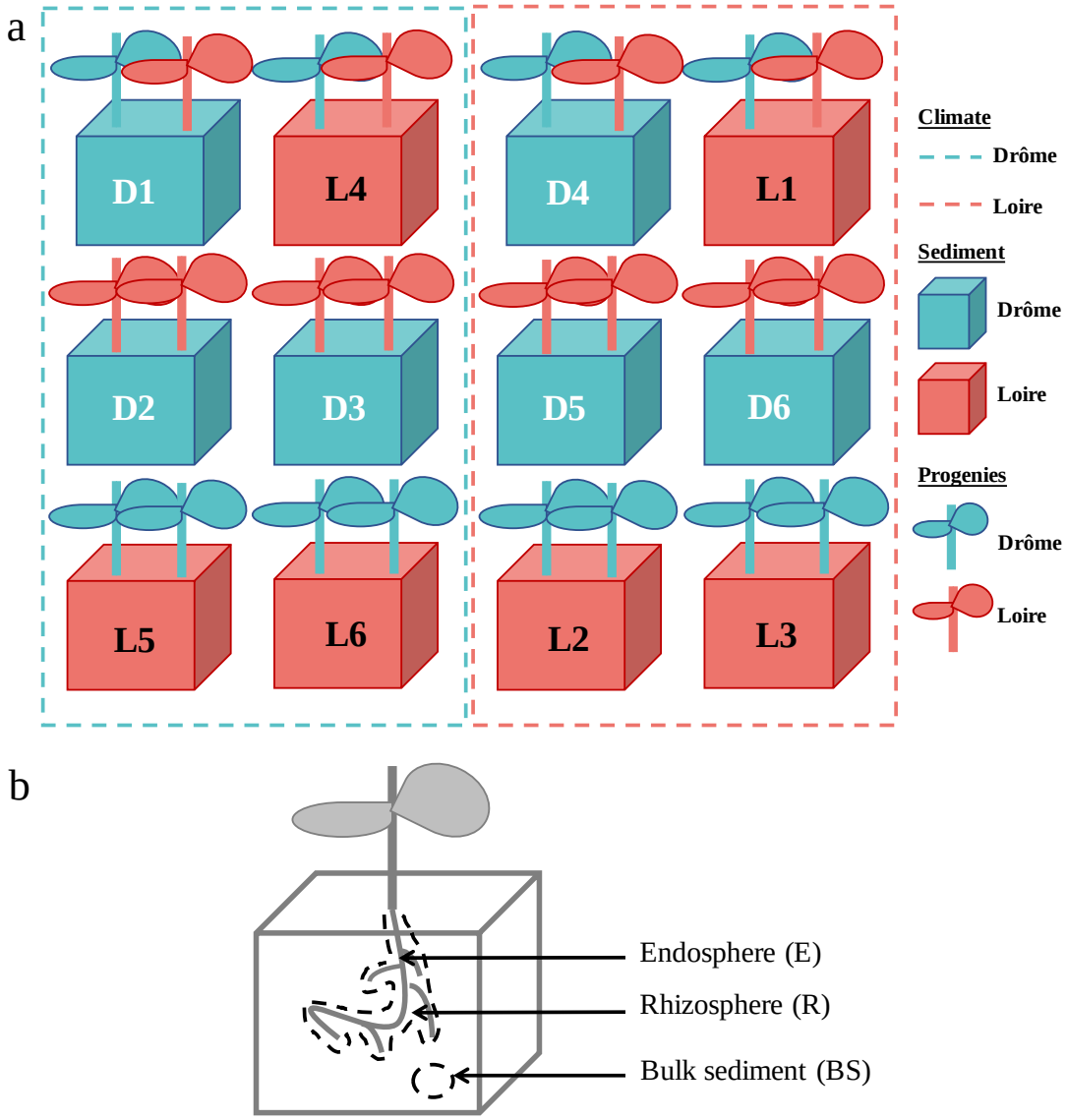

Figure 26 - Experimental design. In function of the question, the number of mesocosms treated varied from 1 to 4. To allow analysis, a minimum of n=3 samples have been collected for each sample type (compartment, progenie, climate; 3<n<6) (a). Comparmentalization of the different samples (BS, R and E) collected in each Populus nigra seedlings (b).

To avoid seedlings mortality or an absence of germination, seeds were first planted in soil plugs and incubated in greenhouse (20°C, 16 h light) at the end of the spring in 2017 with an unlimited watering. After two weeks of germination, seedlings were acclimated by shading with watering for one week. These seedlings were then transferred in the different mesocosms (Figure 26). Mesocosms were heavily watered along the full length of the experiment. Mesocosms located in Loire were watered 5 times a day for 5 minutes while mesocosms located in Drôme were watered 5 times a day for 10 minutes due to a lower pressure of the pump. Mesocosms were sprinkled from above with 5 sprinklers in unlimited quantities.

Physico-chemical analyses of the sediments and temperature and luminosity monitoring

The physico-chemical properties of the two sediments used in our study were determined by the Laboratoire d'Analyses des Sols (INRAE Arras, France) according to standard procedures. Briefly, exchangeable cations were extracted in either 1M KCl (Magnesium, Calcium, Sodium, Iron, Manganese) or 1M NH4Cl (Potassium) and determined by ICP-AES (JY180 ULTRACE). The 1M KCl extract was also titrated using an automatic titrimeter (Mettler TS2DL25) to assess exchangeable H+ and aluminium cations (Al^{3+}). The pH of the soil samples was measured in water at a soil to solution ratio of 1:2 (pH meter Mettler TSDL25). Exchangeable acidity was calculated by taking the sum of H^+ and Al^{3+}. The cation-exchange capacity (CEC) was determined by using cobaltihexamine chloride. Titration of the cobaltihexamine chloride soil extract was performed at 472 nm and compared to a reference of 0.05 N cobaltihexamine chloride extract.

Temperature and luminosity monitoring was performed on each site. The temperature and the Photosynthetically Active Radiation (PAR) of each site was taken once an hour from the beginning of the experiment (June 2017) until the seedlings were harvested (October 2017).

Seedlings aerial growth monitoring

In each location (Loire or Drôme) and after 10 weeks of growth in the mesocosms, the aerial growth of *Populus nigra* seedlings of each progeny from Loire (L04, L06, L08) and Drôme (D11, D13 and D15) was measured on September the 4th (Table S1).

Sampling strategy

Before the transplant experiment, a total of 3 spatially distant BS samples were collected in each mesocosm from 3 spatially distant areas free of seedlings roots. The BS samples of each mesocosm were pooled, giving a total of 12 BS samples corresponding to the T0 in our study.

After five months of growth in the Loire and Drôme regions, all the mesocosms were transferred to the INRAE Center of Orléans. Each mesoscosm was opened to collect: bulk sediment (BS), root adherent soil (i.e the rhizosphere; R) and root sample (i.e. the rhizoplane and the endosphere; E). In each mesocosm, a total of 3 spatially distant BS samples were collected in each mesocosm from 3 spatially distant areas free of seedlings roots. The BS samples were pooled, giving a total of 12 BS samples. For each seedling considered, the root system was harvested, shaken over a sieve of 2 mm to remove non-adherent soil. The rhizosphere (R) was

recovered by washing the root system with 40 mL of a sterile solution of NaCl (10 mM), as previously described by Gottel et al., 2011. Finally, the washed roots were conserved for each seedling to access to the endosphere (E). After conditioning, all the sample types were stored at -20°C until DNA extraction.

DNA extraction

Total soil DNA was extracted using the DNeasy PowerSoil Kit following the protocol provided by the manufacturer (Qiagen, Venlo, the Netherlands). For each DNA extraction, 250 mg of BS and R samples have been used. For the endopshere (E), 50 mg of root tissues were crushed in liquid nitrogen and DNA was extracted using the DNAeasy PowerPlant Kit (Qiagen, Venlo, the Netherlands). DNA was quantified with a NanoDrop 1000 spectrophotometer (NanoDrop Products, Wilmington, DE, USA).

DNA amplification and Illumina MiSeq sequencing

A two-step PCR approach was chosen to barcode tag templates with frameshifting nucleotide primers (Lundberg et al., 2013). Primer mixtures for tagging bacterial amplicons were composed of 4 forward 515F (Universal, Chloroflexi, TM7, Nano; Table S2) and 2 reverse 806R (Universal, Nano; Table S2) primers covering the 16S rRNA V4 gene region mixed in equal concentrations (0,1 μM) (Cregger et al., 2018). Primer mixtures for tagging fungal amplicons were composed of six ITS3 forward primers (ITS3NGS1, ITS3NGS2, ITS3NGS3, ITS3NGS4, ITS3NGS5 and ITS3NGS10; Table S2) and one ITS4 reverse primer (ITS4NGS; Table S2) for ITS2 rRNA region mixed in equal concentrations (0.1 μM; Cregger et al., 2018). To inhibit plant material amplification (i.e., mitochondria and chloroplast), PCR reaction mix was implemented by a mixture of peptide nucleotide acids (PNA, Panagene Korea) blockers. These PNA blockers targeted plant mitochondrial and chloroplast 16S rRNA genes (mtPNA_717-1B4, pPNA_717-1B4; Lundberg et al., 2013; Table S2) and plant ITS nuclear rRNA gene (ITSspacePNA_717-1B4; Cregger et al., 2018; Table S2). The mitochondrial PNA blocker (mtPNA_717-1B4; Table S2) of Lundberg et al., 2013 was adjusted for a 1 bp mismatch. Although these PNA blockers have been designed to block mitochondrial and chloroplastic sequences of *Populus tremula x alba*, they can also be used for *Populus nigra*.

Polymerase chain reactions (PCR) were performed for two replicates of each sample by mixing 12 μl of 2.5x Phusion flash high fidelity master mix (ThermoScientific) with 1.5 μl of forward and reverse primer mix (5 nM final concentration) and 20 ng of total DNA in a final reaction volume of 30 μl. For bacteria, 0.75 μl of PNA probe (5 nM) was added. PCR, primer and probes dilutions were performed in DNA free water (0.2 μm filtered and UV treated; Carl Roth, France). For the first amplification of bacterial 16S rRNA, the following cycle parameters were used for bacterial amplification were 30 cycles of 98°C for 5s, 78°C for 10s, 52°C for 20s and 72°C for 15s. Primary PCR condition for fungal amplification were 30 cycles of 98°C for 5s, 78°C for 10s, 55°C for 20s and 72°C for 15s. PCR products without addition of microbial DNA (negative control) or corresponding to mock communities of known fungal or bacterial compositions were added as quality controls. After checking concentration of PCR products and amplicons size (350 pb for 16S rRNA amplicon and 420 pb for ITS amplicon) on agarose electrophoresis gel, samples of 50 μl (30 ng DNA per μl) were sent for tagging and MiSeq Illumina

Next Generation Sequencing (GeT PlaGe INRAE sequencing platform, Toulouse, France). Sequencing was done on MiSeq 2500 system.

Bioinformatic analyses

Bacterial sequences were further processed with FROGS (Find Rapidly OTU with Galaxy Solution) (Escudié et al., 2018) based on the Galaxy analysis platform (Afgan et al., 2016). The 16S rRNA amplicon sequences were demultiplexed, dereplicated and sequence quality was checked. The oligonucleotides, linker, pads and barcodes were removed from sequences. In addition, sequences were removed from the dataset, if non-barcoded, if they exhibited ambiguous bases or did not match expectations in amplicon size. The remaining sequences were clustered into operational taxonomic units (OTUs) based on the iterative Swarm algorithm. Chimeras and singletons (OTUs supported by one sequence) were removed. Bacterial double affiliation was performed by blasting OTUs against the SILVA database v132 (Quast et al., 2012) and the ribosomal database project (RDP) classifier (Wang et al., 2007). OTUs with affiliation <100% at the phylum level (indicated by a RDP bootstrap value <1) and corresponding to chloroplasts or mitochondria were removed from the data set. OTUs at lower taxonomic ranks than the phylum level were considered as "unidentified", when the RDP bootstrap value was < 0.70 OTUs with high relative abundances in negative controls were excluded from further analysis. The quality of the sequencing, and of the affiliation were evaluated based on the results obtained for the bacterial mock community.

Fungal sequences were processed as following. After demultiplexing and quality checking (QC quality score = 30, minimal size = 200 bp), bioinformatics analyses were performed using standard procedures as described in Pérez-Izquierdo et al. (2017) by using USEARCH. Briefly, the ITS2 was extracted with the Fungal ITSx v1.0.3 and partial ITS sequences were discarded. After de-replication, sequences were shorted by decreasing relative abundance and singletons discarded. OTUs were generated from abundance-sorted sequences with 97 % similarity threshold. Extracted sequences were then mapped against the OTU representative sequences. Taxonomic assignation of these representative sequences for each OUT was done by using the Basic Local Alignment Search Tool (BLAST) algorithm against the UNITE database.

For both fungal and bacterial data, per-sample rarefaction curves were calculated to assess sampling completeness, using function *rarecurve()* in package Vegan v3.5-1 (Oksanen et al., 2015) in R (version 3.4.3 ; R Core Team, 2016). Based on these, subsequent analyses of diversity and community structure were performed on datasets where samples have been rarefied with the Phyloseq (McMurdie, PJ. and Holmes, S., 2013) package to achieve equal read numbers according to the minimum number of total reads in any sample. In our study, the samples were rarefied to 10,733 sequences per sample for the bacteria and 4,162 sequences per sample for the fungi.

FUNGuild (Nguyen et al., 2016) was used to classify each fungal OTU into an ecological guild. We followed the same procedure as Cregger et al., 2018. OTUs identified to a guild with a confidence ranking to "highly probable" or "probable" were conserved in our analysis, whereas those ranking to "possible" or with multiple assignations were considered as unclassified.

Statistical analysis

Statistical analyses and data representations were performed using R software (R Core Team, 2016). After checking normal distribution of each dataset with Shapiro-Wilk test, Student t-tests were used to determine if the relative abundance of fungal guilds differed between the different compartments considered [sediments (BS), the rhizosphere (R) and the endosphere (E)] and/or according to the different treatments. A One-way ANOVA followed by Tukey HSD post-hoc test was used to determine if the relative abundance of dominant bacterial and fungal phyla and genera detected in the different compartments considered [sediments (BS), the rhizosphere (R) and the endosphere (E)] differed between the different treatments (sediments and climate conditions). Comparison of the relative abundance of bacterial and fungal OTUs in R and in E between two conditions was based on one-way ANOVA followed by Tukey HSD post-hoc test. Venn diagrams were created on http://bioinformatics.psb.ugent.be/webtools/Venn/. Microbial community structures were analysed using nonmetric multidimensional scaling analysis (NMDS) and permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity matrices.

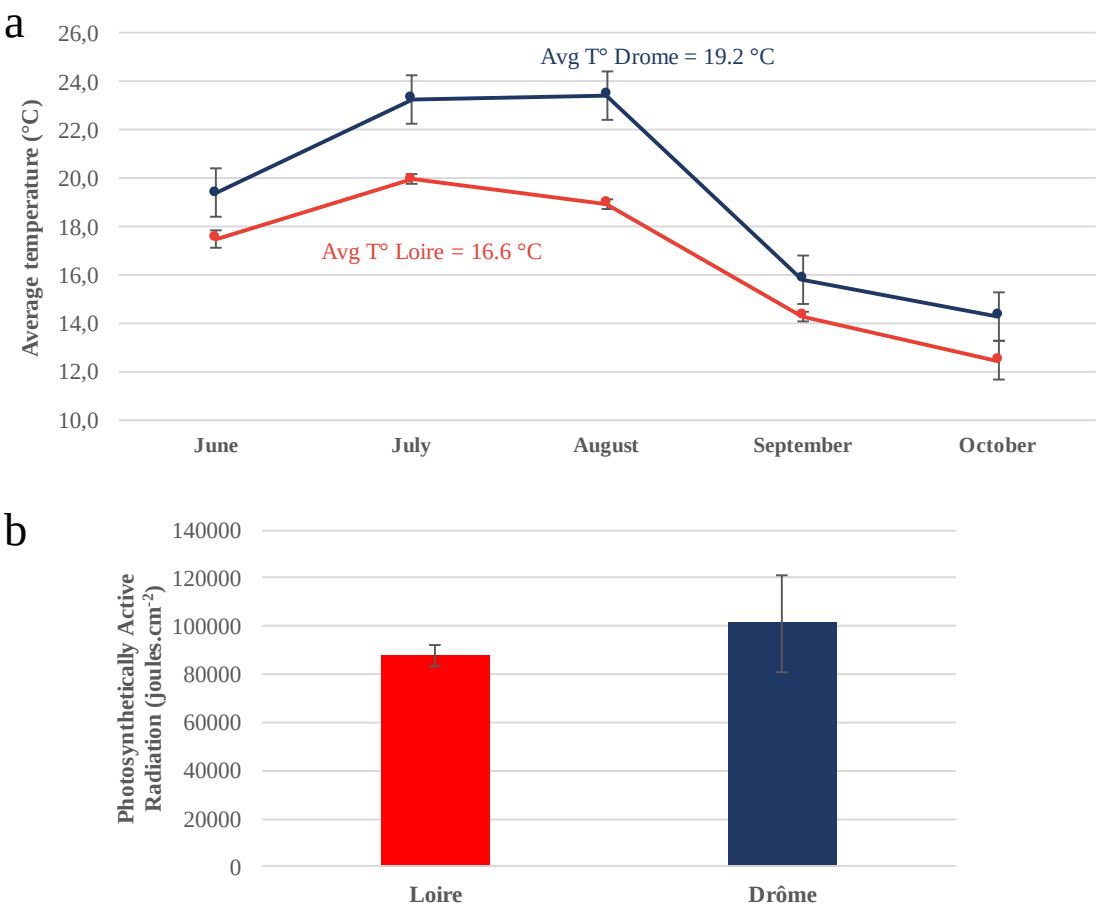

Figure 27 - Monitoring of temperature in Loire and Drôme regions. Average monthly temperature recorded by the meteorological station of INRAE (Loire, in red) and RMN (Drôme, in blue) from June to October 2017 (a). Cumulated PAR measures recorded from June to October 2017 in the Loire (red) and in the Drôme (blue) sites (means of daily measure ± SE) (b).

Results

Physico-chemical analyses of the sediment, temperature and luminosity monitoring and plant growth

Based on the physico-chemical analyses performed, the two sediments were characterized as silty-clayey for the Drôme and sandy for the Loire (Table S3) with alkaline pH. The two sediments strongly differed in terms of texture, cationic exchange capacity and amount of available nutrients. Estimated fertility was much higher in Drôme soil than Loire one.

The temperature monitoring performed from June to October 2017 revealed a warmer temperature (+2.6 °C) in the Drôme site compared to the Loire site (Figure 27). The luminosity (cumulated PAR measure from June to October 2017) was not significantly different between the Loire (87.5 ± 4.4 joules/cm^2) and the Drôme (101.2 ± 20.3 joules/cm^2) sites (Figure 27).

The measures done on the aerial parts of the poplar seedlings of the 3 progenies considered per site (i.e., Drôme and Loire) revealed significant differences of growth (ANOVA, $P<0.05$, Figure 28). Under their native conditions of culture (i.e., sediment and climate), D11 and L08 were the taller progenies, while L04 and D15 were the smaller ($P<0.05$), giving a specific pattern of distribution of the progenies according to their above ground size and for each site (Drôme: D11>D13>D15; Loire: L06>L08>L04).

We then considered the potential effect of the two sediments on the growth of the seedlings. When the measures were done considering the seedlings growing under their native climate, but in the transplanted sediment, both the Drôme and Loire progenies presented a different growth pattern than in their native conditions. For the Drôme seedlings we observed the following pattern (D11>D15>D13), while for the Loire seedlings no difference was observed (L04=L06=L08). Notably, the D15 progeny grew better in Loire sediment than in their native soil (+ 41 %; % expressed according to the native conditions; $P<0.05$), while the two other Drôme progenies grew less on the Loire sediment than in their native sediment (- 39 % for both D11 and D13; $P<0.05$). Similarly, the L06 seedlings grew better in Drôme sediments than their native sediments (+ 70 %; $P<0.05$), while no sediment effect was observed for the growth of the two other progenies.

The potential effect of climate on the growth of the seedlings was then considered. When the measures were done considering the seedlings growing under their non-native climate, but in their native sediment, the initial patterns were conserved (Drôme: D11>D13>D15; Loire: L06>L08>L04). However, the D15 seedlings grew better under their native climate than under the Loire climate (+ 75 %), while there was no climate effect for the two other Drôme progenies (D11 and D13).

Finally, when the combined effects of the transplant conditions (non-native climate + non-native sediment) were tested, the same patterns of growth were observed than under the native climate and the non-native sediment (D11>D15>D11; L04=L06=L08; Figure 28). All the Loire seedlings presented a significantly increased growth when transplanted in the Drôme soil and climate (L04 = + 69 %, L06 = + 48 %, L08= + 54 %), while D13 seedlings had a reduced aerial development when transplanted in the Loire soil and climate (- 200 %).

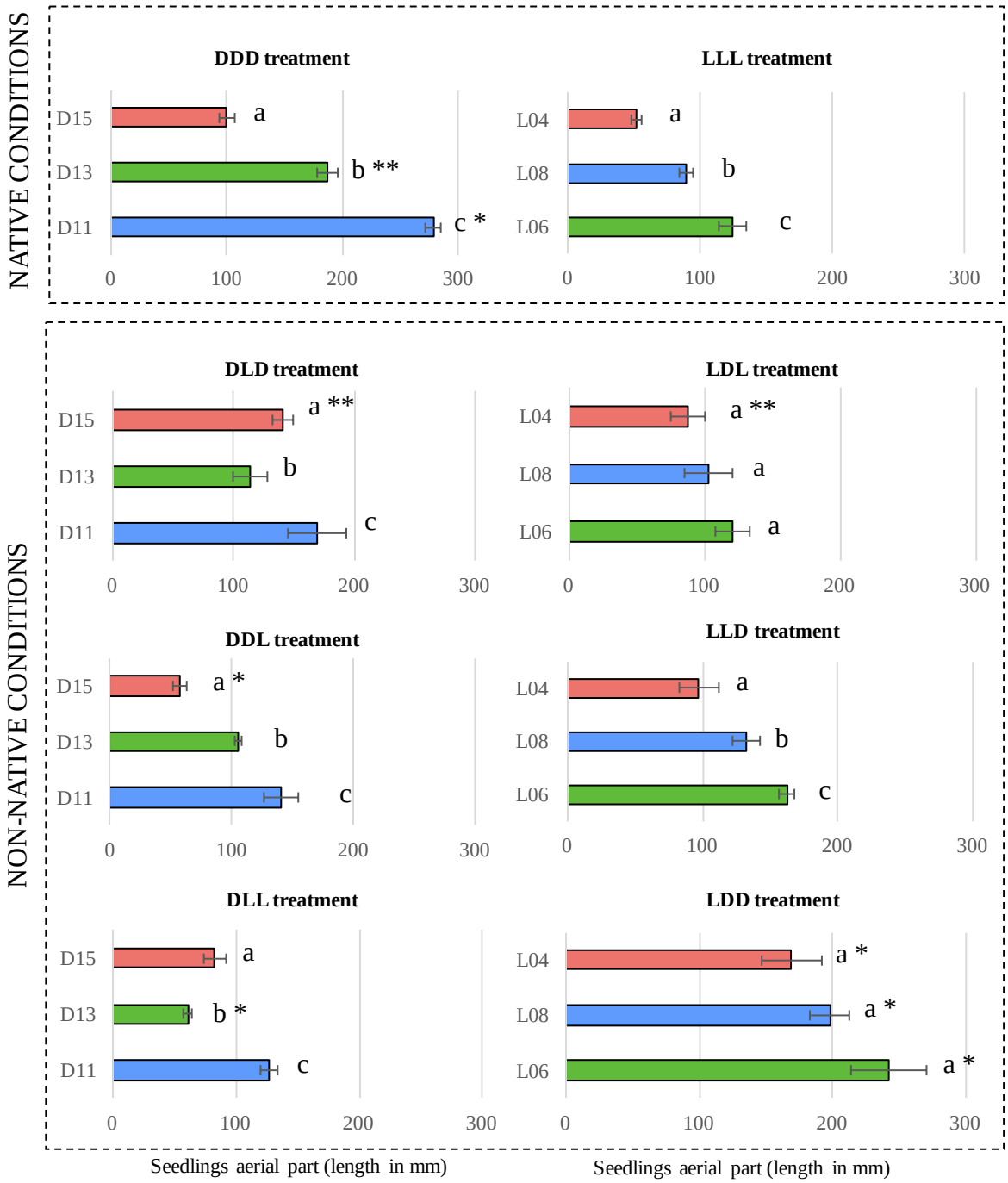

Figure 28 - Monitoring of the growth of the aerial part of Populus nigra seedlings. Length of aerial part of the seedlings of the Drôme (D11, D13, D15) and the Loire (L04, L06, L08) progenies cultivated in different climate and sediments conditions after 10 weeks of growth. The letters denote significant different in aerial part length of seedlings according to origin (i.e, Loire or Drôme) (ANOVA, P<0.05). The asterisks denote significant different in aerial part length of seedlings between treatment (ANOVA, P<0.05).

Sequencing results

After quality filtering, and chimera and singleton removals a total of 7,370,000 bacterial and 2,740,000 fungal reads with an average of 25,000 bacterial reads per sample (± 234 reads SE) and 9,830 fungal reads per sample (± 135 reads SE) remained. After taxonomy assignment, elimination of contaminants and singletons and completion of rarefactions, 2,479 bacterial and 3,197 fungal Operational Taxonomic Units (OTUs) with an average of 1,253 bacterial OTUs (± 21 SE) and 1,609 fungal OTUs (± 41 SE) per sample were considered for further analysis.

Structure and composition of the microbial communities of the Loire and Drôme sediments

The NMDS and PERMANOVA analyses revealed that in both sediments (*i.e.*, Loire and Drôme) the fungal and bacterial community structures varied significantly (P<0.05) between the preconditioning stage of the sediment in mesocosms and after the 5 months-incubation period (Figure 29, Table S4).

The same analyses only done on the 5 months-incubation period-related samples revealed that the Loire and Drôme BS microbiome were significantly different. In addition, the alpha-diversity indices (i.e., number of OTU observed and Shannon index) appeared significantly higher in the Drôme sediment than in the Loire sediment, for both the bacteria and fungi (One-way ANOVA, P<0.05, Figure 30 a, b). Our analyses also revealed that the climate did not significantly affect the structure of the Loire and Drôme BS microbiomes when the native and transplant conditions were compared (P>0.05, Table S4).

A detailed analysis evidenced that the differences between the two sediments (after the 5 months-incubation period) were significant only for the bacteria. Indeed, several phyla showed significantly different relative abundances between the Loire and Drôme sediments [Proteobacteria (26.4 ± 1.5 % in Loire vs 34.0 ± 1.7 % in Drôme), Acidobacteria (20.4 ± 0.6 % in Loire vs 16.3 ± 1.3 % in Drôme), Actinobacteria (14.8 ± 1.5 % in Loire vs 10.2 ± 2.4 % in Drôme), Chloroflexi (11.8 ± 1.5 % in Loire vs 16.1 ± 2.0 % in Drôme) and Firmicutes (5.5 ± 0.5 % in Loire vs 0.1 ± 0.0 % in Drôme)] (Figure 30 c). For the fungi, Ascomycota tended to be more abundant in the $BS_{Drôme}$ than in the BS_{Loire}. (P>0.05; Figure 30 d). The Loire and Drôme sediments appeared dominated by ectomycorrhizal fungi (EcM; 25.9 ± 18.8 % in Loire and 6.3 ± 2.0 % in Drôme), saprotrophic fungi (3.3 ± 0.9 % in Loire and 8.0 ± 3.0 % in Drôme) and fungal plant pathogen (2.7 ± 1.4 % in Loire and 1.8 ± 0.5 % in Drôme, Figure 30 e).

At the genus level (>1 % relative abundance), no significant difference was observed between the two sediments for both the bacteria and the fungi (P>0.05). However, at the OTU level, a high proportion of the OTUs appeared significantly enriched in only one sediment, as indicated by Venn diagram analyses. Indeed, only 61 % of the OTUs (=72 % of the 16S rRNA sequences) for bacteria and 17 % of the OTUs (=24 % of the ITS sequences) for the fungi appeared common to the two sediments (Figure 30 f).

Structure and composition of the rhizosphere and endosphere microbial communities in the native conditions

The NMDS and PERMANOVA analyses revealed the rhizosphere ($R_{Drôme}$ vs R_{Loire}) and the endosphere ($E_{Drôme}$ vs E_{Loire}) microbial (fungal and bacterial) community structures varied significantly ($P<0.05$) between the two sites (Table 1). A detailed analysis evidenced that these differences were explained by significant variations of the abundances of several bacterial (Chloroflexi [$R_{Drôme} > R_{Loire}$], Verrucomicrobia [$E_{Loire} > E_{Drôme}$] and Proteobacteria [$E_{Drôme} > E_{Loire}$]) (Figure 31 a) and fungal (Glomeromycota [$R_{Drôme} > R_{Loire}$], Chytridiomycota [$E_{Loire} > E_{Drôme}$], Ascomycota [$E_{Loire} > E_{Drôme}$] and Basidiomycota [$E_{Drôme} > E_{Loire}$]) (Figure 31 b) phyla. At the genus level, *Acidibacter*, *Azohydromonas* and *Steroidobacter* were significantly more abundant in $R_{Drôme}$ and $E_{Drôme}$ than in the Loire samples, while *Ohtaekwangia* was significantly more abundant in R_{Loire} and E_{Loire} than in the Drôme samples (ANOVA $P<0.05$, Table S5).

For the fungi, *Tomentella* and *Tetracladium* were significantly more abundant in Drôme samples (R and E) than in the related Loire samples (ANOVA $P<0.05$, Table S5). The funguild analyses revealed that the arbuscular mycorrhizal (AM) fungi were significantly more abundant in the R_{Loire} than in the $R_{Drôme}$ (ANOVA, $P<0.05$, data not shown), while saprotrophic fungi and plant pathogen were more abundant in the E_{Loire} than in the $E_{Drôme}$ (ANOVA, $P<0.05$, Figure 31 c).

Based on OTU analyses, the rhizosphere samples harboured the highest diversity (Shannon) and richness (OTUobs) values than the endosphere. In addition, the Drôme samples showed significantly higher values than the Loire samples (R and E). Notably, Venn diagram analyses revealed that 84 % and 36 % of the bacterial and fungal OTUs (= 92 % of the 16S rRNA 16S and 80 % of the ITS sequences) were common to the two rhizospheres ($R_{Drôme}$ vs R_{Loire}). Similarly, 54 % and 43 % of the bacterial and fungal OTUs (= 88 % of the 16S rRNA and 93 % of the ITS sequences) were common to the two rhizospheres ($E_{Drôme}$ vs E_{Loire}).

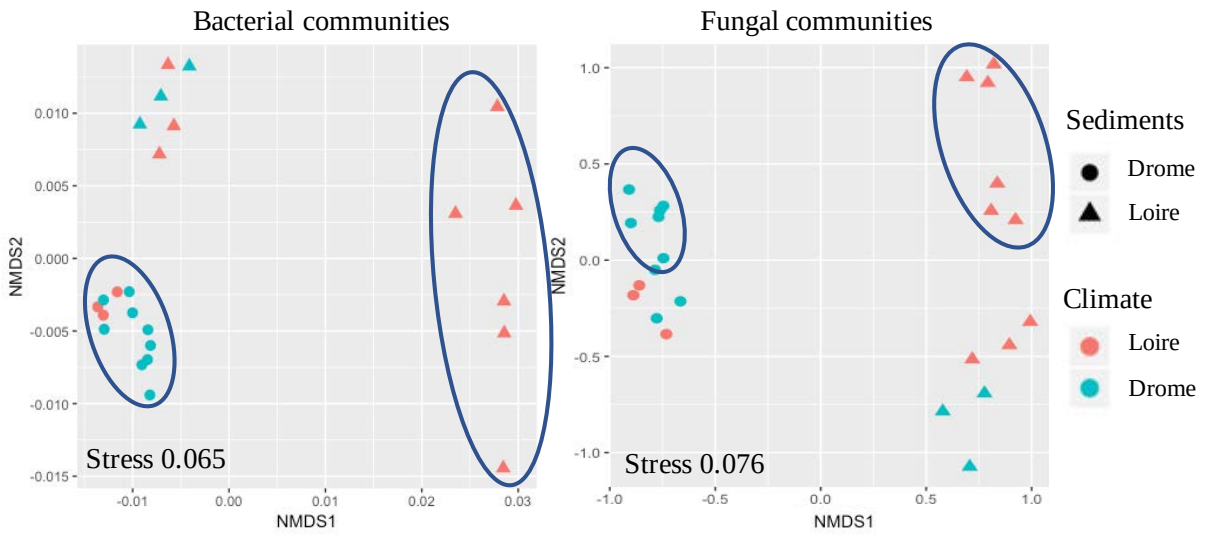

Figure 29 - Impact of pre-conditioning stage on the Loire and Drôme sediments microbiome. NMDS ordinations of bacterial and fungal OTUs across sediment type (Drôme and Loire) and climate (Drôme and Loire). Blue circles correspond to BS_T0 samples. Variances explanation based on permutational multivariate analysis using Euclidean dissimilarity matrix for bacterial and fungal OTUs are available in Table S4.

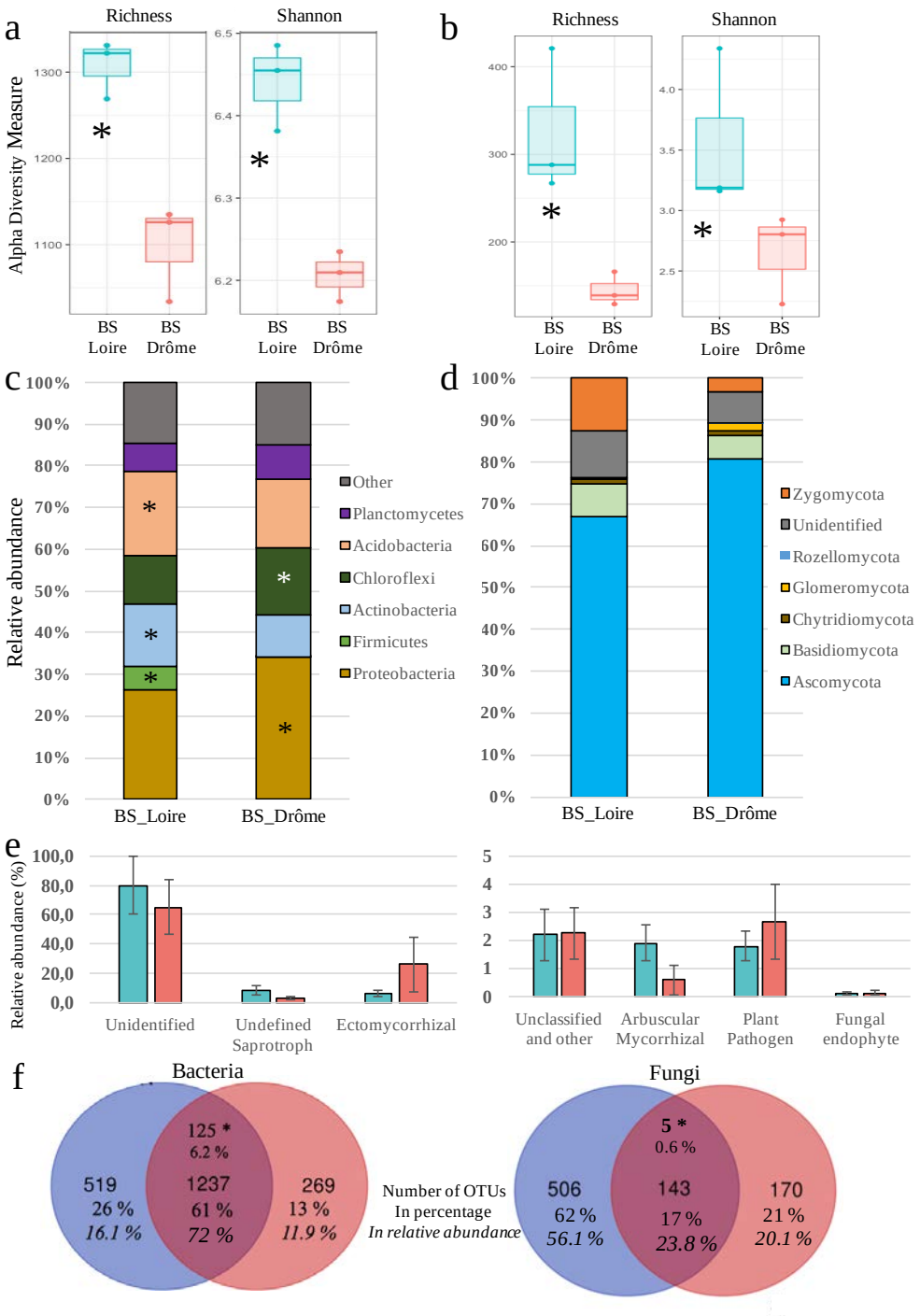

Figure 30 - Composition and structure of sediment microbiome. Alpha diversity (Richness and Shannon index) of the bacterial (a) and fungal (b) communities detected in BS samples collected in Loire (red) and Drôme (blue). The asterisks denote significant difference in each alpha diversity measure between Loire and Drôme BS (ANOVA, P<0.05). Distribution of most dominant bacterial (> 5 % in relative abundance) (c) and fungal (d) phyla detected in BS samples from Drôme and Loire. The asterisks denote significant difference in relative abundance of each bacterial and fungal phyla between Loire and Drôme BS (ANOVA, P<0.05). Venn diagrams of the bacterial and fungal OTUs only detected in BS samples from Drôme and Loire or shared by both (http://bioinformatics.psb.ugent.be). The number in bold represents the number of OTUs whose relative abundance is significantly different between the two types of sediments. This value is converted in percentage in bold and in relative abundance of total OTUs in brackets. The asterisks denote significant difference in relative abundance of each bacterial and fungal OTUs between Loire and Drôme sediments (ANOVA, P<0.05) (e). Relative abundance of fungal guilds detected in the Loire (in red) and in Drôme (in blue) sediments (f).

Analysis of the compartment effect (BS vs R and R vs E) in each treatment (seedling origin, sediment and climate)

For each treatment (i.e., LLL, Loire seedlings cultivated in the Loire sediment and under Loire climate; LDL, Loire seedlings cultivated in the Drôme sediment under Loire climate; LDD, Loire seedlings cultivated in the Drôme sediment and under Drôme climate; LLD, Loire seedlings cultivated in the Loire sediment and under Drôme climate; DDD, Drôme seedlings cultivated in the Drôme sediment and under Drôme climate; DLL, Drôme seedlings cultivated in the Loire sediment and under Loire climate; DLD, Drôme seedlings cultivated in the Loire sediment and under Drôme climate; DDL, Drôme seedlings cultivated in the Drôme sediment and under Loire climate) analyses were performed to determine whether i) the rhizosphere microbiome differed from the BS microbiome and ii) the rhizosphere microbiome differed from the endosphere microbiome.

The NMDS and PERMANOVA analyses revealed for most of the treatments that the bacterial community structure varied significantly ($P<0.05$) between BS and R compartments (*i.e.*, the rhizosphere effect) and between R and E compartments (*i.e.*, the host root filtering effect) whatever the sediments and climate conditions (*i.e.*, Loire and Drôme) (Table 2). A single exception was observed (BS=R) for the LDL treatment ($P=0.246$, Table 2). Concerning the fungal community structure, no difference was observed between R and BS, while the R and E compartments (*i.e.*, the host root filtering effect) significantly differed ($P<0.05$) (Table 2).

The comparisons done on the taxonomic composition revealed significant differences between the different compartments (BS vs R and R vs E) in the native conditions (*i.e.*, DDD and LLL) for both bacteria and fungi. For the LLL treatment, a significant gradient of enrichment was observed from BS to E for several bacterial phyla such as Actinobacteria, Bacteroidetes and Verrucomicrobia (BS<R<E, $P<0.05$). Proteobacteria appeared only enriched in R compared to BS. For the DDD treatment, a significant gradient of enrichment was also observed from BS to E for the Bacteroidetes phylum. Chloroflexi appeared more abundant in R than in BS and E, while Actinobacteria were significantly enriched in E (Figure 32 a). Among the dominant bacterial genera detected in our study, several appeared enriched in rhizosphere (R>BS; *Niastella*, *Ohtaekwangia* and *Steroidobacter*) and/or in the endosphere (E>R; *Streptomyces*, *Actinoplanes*, *Niastella* and *Steroidobacter*) (Table S6).

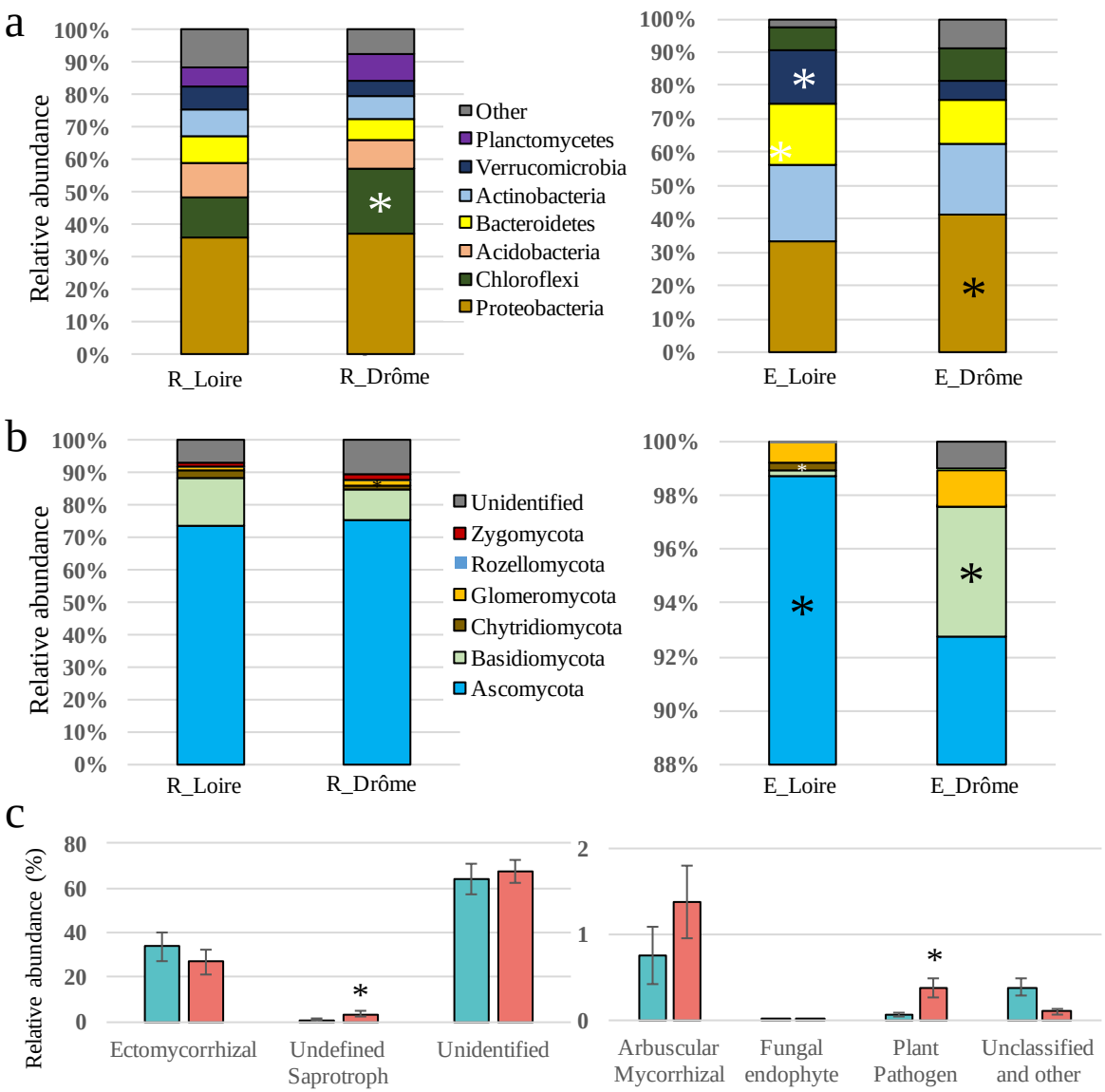

Figure 31 - Composition and structure of Populus nigra root microbiome. Distribution of most dominant bacterial (> 5 % in relative abundance) (a) and fungal (b) phyla detected in the rhizosphere (R) and in the endosphere (E) of the seedlings of Drôme and Loire progenies cultivated in their native conditions of sediments and climate (i.e, DDD and LLL treatment). The asterisks denote significant difference in relative abundance of each microbial phyla detected in the R or E compartments between the seedlings of the DDD or the LLL treatment (ANOVA, P<0.05). Relative abundance of fungal guilds detected in the endosphere of the seedlings of the Loire (in red) and the Drôme (in blue) cultivated in their native conditions (c). The asterisks denote significant difference in relative abundance of each fungal guild between the DDD and LLL treatment (ANOVA, P<0.05).

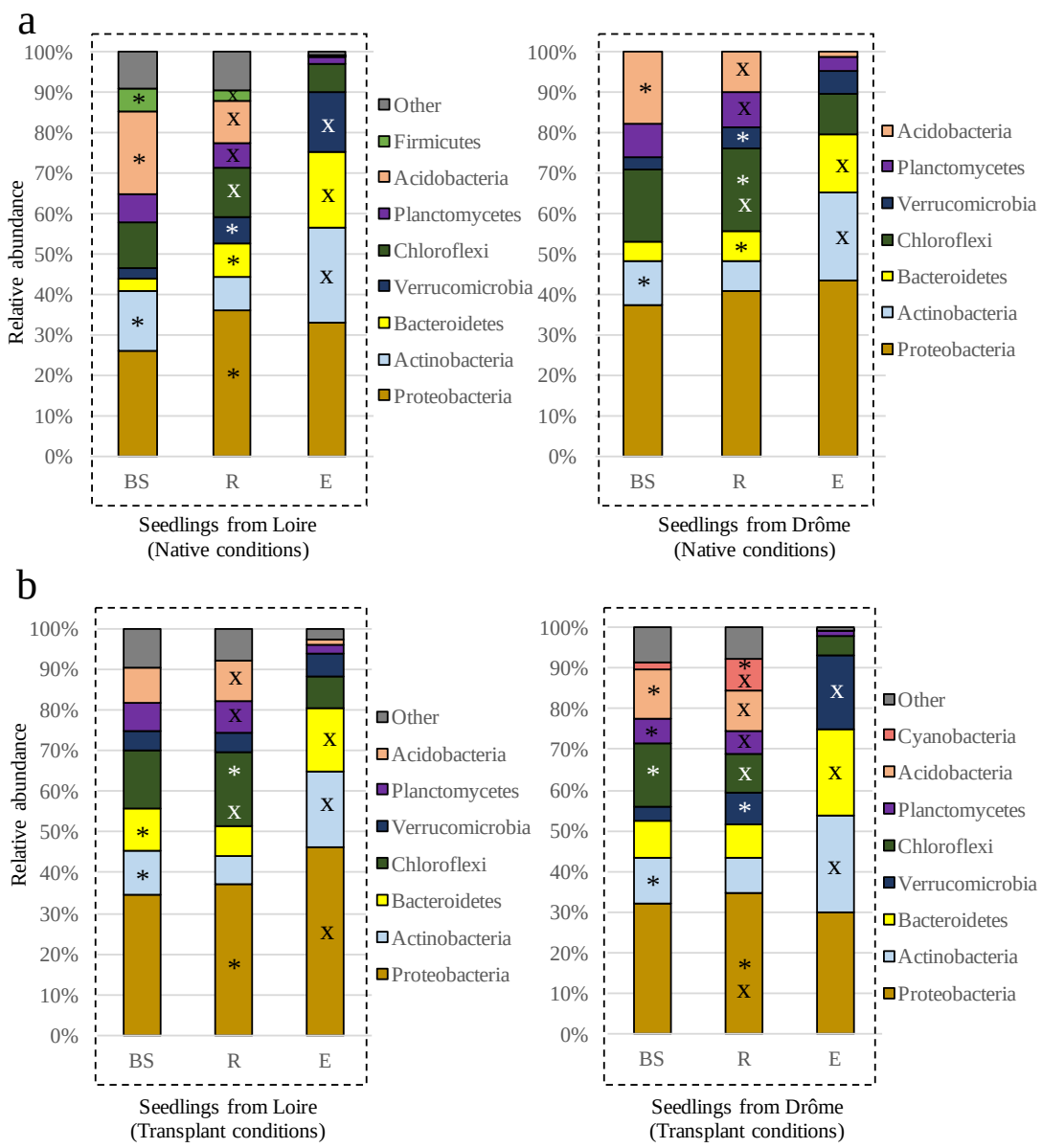

Figure 32 - Rhizosphere and root filtering effects in the native and transplant conditions. Distribution of most dominant bacterial phyla (> 2 % in relative abundance) detected in the bulk soil (BS) and in the rhizosphere (R) and the endosphere (E) of Populus nigra seedlings of the Loire and the Drôme cultivated in their native conditions (i.e., LLL and DDD treatments) (a) and in the transplant conditions (LDD and DLL treatments) (b). The asterisks denote significant difference in relative abundance of bacterial phyla between BS and R compartments (ANOVA, P<0.05). The crosses denote significant difference in relative abundance of bacterial phyla between R and E compartments (ANOVA, P<0.05).

For the fungi, the stronger modifications of composition were observed between the R and the E compartments, and in a lower extent, between the BS and the R. For instance, *Cladosporium* (plant pathogen), *Tetracladium* (saprotroph) and *Corallomycetella* (saprotroph) were significantly more abundant in the R compared to the BS, while *Geopora* (EcM) was significantly more abundant in the E compared to the R (Table S7). These observations were confirmed by the distribution of the fungal guilds identified by Funguild analyses across the three studied compartments. The EcM fungi were significantly more abundant in the endosphere (E) of the Loire and Drôme seedlings cultivated in their native conditions (34.3 ± 7.1 % in E_{Loire}, 28.9 ± 5.2 % in $E_{Drôme}$).

Significant modifications were also observed when only one parameter varied (*i.e.*, sediment [LDL and DLD] or climate [LLD and DDL]). When the seedlings were cultivated in another sediment (LDL and DLD) than their native sediment, several significant differences were observed at the phylum and genus levels (Figure 35, Table S6, Table S7). Notably, Proteobacteria presented a significantly higher relative abundance in E than in the other compartments whatever the origin of the seedlings (ANOVA, $P<0.05$). Verrucomicrobia tended to be increased in the root compartments (BS<R<E), especially in the DLD treatment. When the seedlings were cultivated in another climate (LLD and DDL) than their native climate, several significant differences were observed at the phylum and genus levels between compartments (Figure 35). Notably, Actinobacteria and Bacteroidetes, were enriched in E compared to the other compartment in LLD and DDL. Verrucomicrobia and Proteobacteria were only enriched in the endosphere of the LLD treatment. For the fungi, no difference was observed at the phylum and only few genera appeared affected such as *Geopora* (BS<R<E), and *Alternaria*, *Corallomycetella*, *Cladosporium* (R >BS=E) (Figure 35).

In the complete transplant conditions (i.e., LDD and DLL; climate + sediment), we observed that Proteobacteria, Chloroflexi and Cyanobacteria were enriched in the R of the Loire and Drôme seedlings (R>BS), while Proteobacteria, Bacteroidetes, Actinobacteria and Verrucomicrobia were significantly enriched in the E (E>R) (Figure 32 b). Several genera appeared more abundant in the endosphere (*Niastella, Streptomyces, Cellvibrio, Actinoplanes*) compared to the other compartments, while *Allorhizobium* was only significantly enriched in the rhizosphere (Table S6). For the fungi, no difference was observed at the phylum compared to the native conditions (Table S7). The funguild analyses revealed that EcM fungi significantly dominated the endosphere (E_{Loire} =32.7 ± 3.5 % vs R_{Loire} =15.7 ± 2.1 %; $E_{Drôme}$ 22.6 ± 4.0 % vs $R_{Drôme}$ 9.2 ± 1.9 %).

Comparative analysis of the compartments between the native conditions and transplant conditions

For each transplantation treatment (i.e., LLD, LDD, LDL, DLL, DDL and DLD), analyses were performed to determine whether i) the sediment origin, ii) the climate and iii) the sediment and the climate affected the composition of the rhizosphere and/or the endosphere microbiomes compared to native conditions (i. e., LLL and DDD). The NMDS and PERMANOVA analyses done directly on the OTUs revealed that the fungal and bacterial community structures varied significantly ($P<0.05$) in the two studied compartments (*i.e.*, R or E) between the seedlings cultivated in their native conditions and the seedlings cultivated in the transplant conditions of sediment and/or climate. Exceptions were observed in the endosphere for fungal communities for the LLD and DDL treatments ([E_{LLD}=E_{LLL}; P=0.377]; [E_{DDL}=E_{DDD}; P= 0.052]) (Table 3).

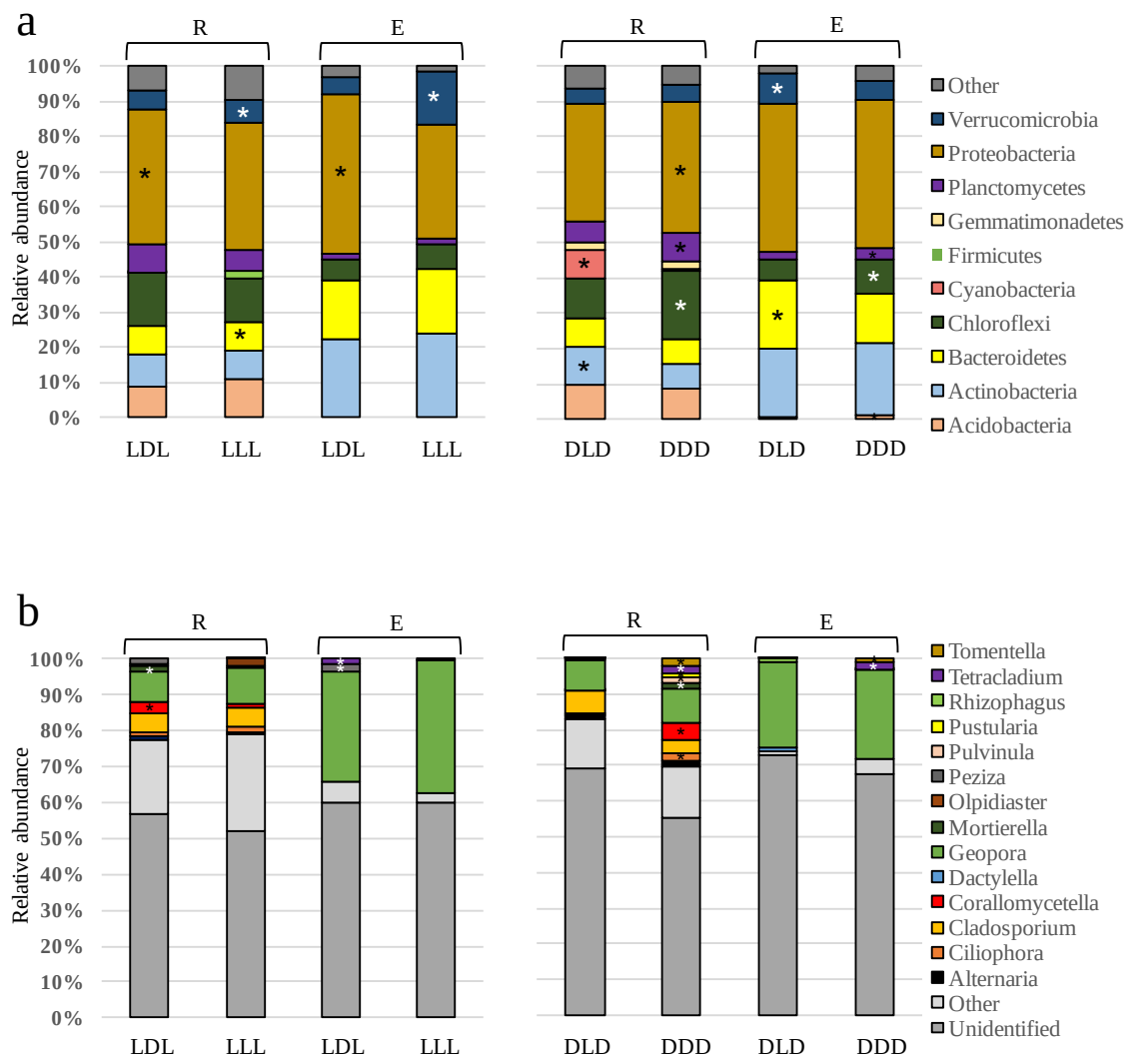

Figure 33 - Impact of sediment origin on the Populus nigra root microbiome. Distribution of most dominant bacterial phyla (> 1 % in relative abundance) (b) and fungal genera (> 1% in relative abundance) (c) detected in the rhizosphere (R) and in the endosphere (E) of Populus nigra seedlings of the Loire and the Drôme cultivated in their native sediment conditions (i.e., LLL and DDD treatments) and in the other type of sediments (i.e., LDL and DLD treatments). The asterisks denote significant difference in relative abundance of each bacterial phyla and fungal genera between the two conditions of seedlings culture (ANOVA, P<0.05).

The taxonomic composition of the microbial communities colonizing the R or the E compartments varied significantly between the native conditions (*i.e*., LLL and DDD) and the transplant conditions of sediment (i.e, LDL and DLD) and of climate (i.e, LLD and DDL) for both bacteria and fungi (ANOVA; P<0.05).

For the bacteria, the LDL treatment, Proteobacteria were significantly more abundant in the two compartments (i.e, R and E) compared to their related native compartment (LLL) (P<0.05; Figure 33 a). For the DLD treatment, Cyanobacteria and Actinobacteria appeared only enriched in R (R_{DLD}>R_{DDD}), while Chloroflexi, Plantomycetes and Acidobacteria were significantly enriched in E (E_{DLD}>E_{DDD}) (P<0.05; Figure 33 a). For the LLD treatment, Cyanobacteria and Actinobacteria were significantly more abundant in the R, while Proteobacteria appeared significantly enriched in the E than in the LLL treatment (P<0.05; Figure 34 a). For the DDL treatment, Chloroflexi, Plantomycetes and Acidobacteria were significantly enriched in E compared to the native treatment (DDD) (P<0.05; Figure 34 a). Among the dominant bacterial genera detected in our study, several appeared enriched in rhizosphere (R) of the seedlings cultivated in the non-native sediment than in the native condition ((i.e., *Acidibacter*, *Allorhizobium, Azohydromonas Bacillus, Gaiella, Niastella, or Ohtaekwangia);* P<0.05; Table S8). Several dominant bacterial genera appeared also significantly enriched in the endosphere (E) of the seedlings cultivated in the non-native sediment (i.e., *Acidibacter, Allorhizobium, Actinocorallia, Actinoplanes, Azohydromonas*, *Bradyrhizobium, Cellvibrio, Lechevaliera, Ohtaekwangia*, *Rhodomicrobium, Steroidobacter*) (P<0.05; Table S8).

For the fungi, *Corallomycetella* (saprotroph) and *Mortierella* (endophytes) were significantly enriched in the R of the non-native treatments (LDL>LLL; DLD>DDD). *Tetracladium* (saprotroph) and *Tomentella* (EcM) were significantly enriched in the E of the LDL and the DLD treatments than in their related native treatments (P<0.05; Figure 33 b). *Tomentella* were significantly more abundant in the E of the seedlings of the DDL treatment compared to the DDD treatment (P<0.05; Figure 34 b). The funguild analyses revealed significant differences between the R compartments for the plant pathogens and of AM fungi (P<0.05; [Pathogen; R_{DDD} > R_{DLD}, R_{LLL} > R_{LDL}]; [AM fungi; R_{LLL} > R_{LDL}, R_{DDD} > R_{DLD}] (Figure 37).

In the complete transplant conditions (i.e., LDD and DLL), Chloroflexi and Planctomycetes appeared significantly enriched in the R compartment compared to the native treatments (i.e., LDD>DDD and DLL>LLL), while Proteobacteria, Planctomycetes and Acidobacteria were significantly enriched in the E of the LDD treatment compared to native treatment (LLL). For the DLL treatment, Verrucomicrobia and Bacteroidetes were significantly enriched in the R and E compartments compared to the native treatment (DDD; P<0.05; Figure 36 a). Several genera appeared more abundant in the rhizosphere and the endosphere of the seedlings of the LDD treatment compared to the native treatment (LLL; *Acidibacter* and *Steroidobacter*). For the DLL treatment, *Bacillus* and *Nodosilinea* appeared enriched in the rhizosphere (R_{DLL}>R_{DDD}), while *Ohtaekwangia* and *Streptomyces* were enriched the endosphere (E_{DLL}>E_{DDD}).

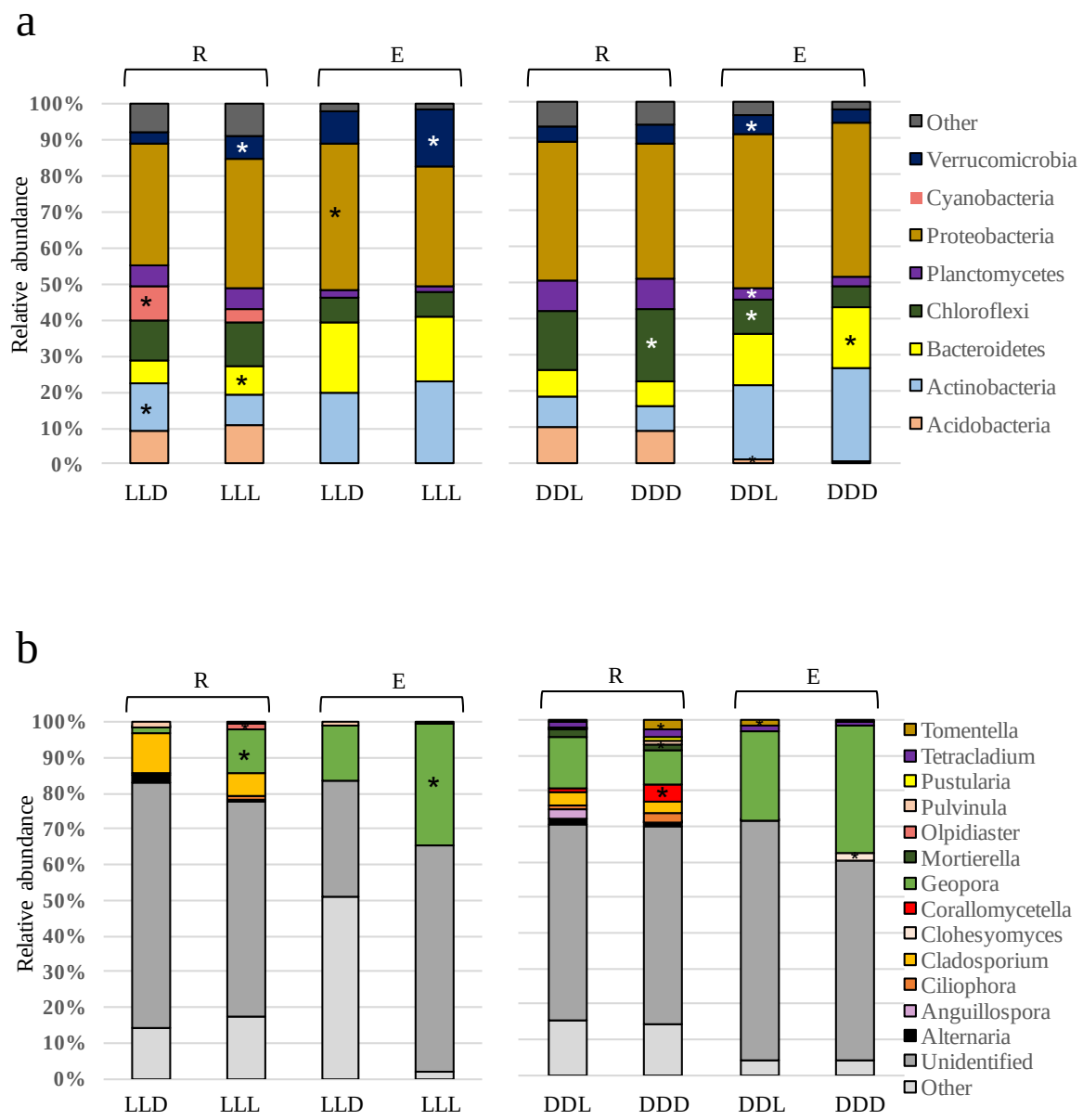

Figure 34 - Impact of climate on the Populus nigra root microbiome. Distribution of most dominant bacterial phyla (> 1 % in relative abundance) (a) and fungal genera (> 1 % in relative abundance) (b) detected in the rhizosphere (R) and in the endosphere (E) of Populus nigra seedlings of the Loire and the Drôme cultivated under their native climate (i.e., LLL and DDD treatments) and under the opposite climate (LLD and DDL treatments). The asterisks denote significant difference in relative abundance of each bacterial phyla and fungal genera between the two conditions of seedlings culture (ANOVA, P<0.05).

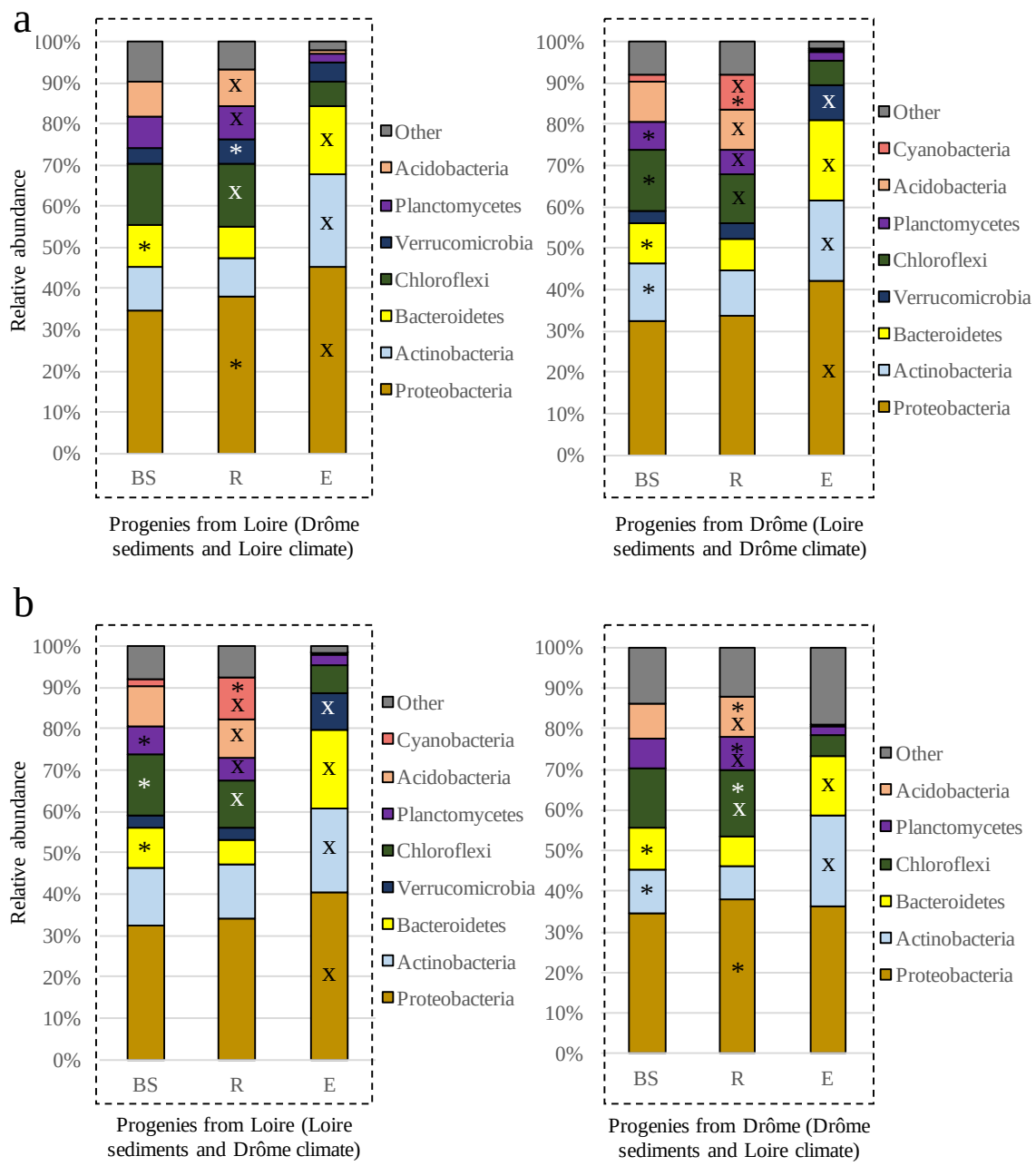

Figure 35 - Rhizosphere and root filtering effects in the non-native conditions of culture. Distribution of most dominant bacterial phyla (> 2 % in relative abundance) detected in the bulk soil (BS) and in the rhizosphere (R) and the endosphere (E) of Populus nigra seedlings of the Loire and the Drôme cultivated in the non-native sediments (i.e., LDL and DLD treatments) (a) and in the non-native climate (i.e, LLD and DDL treatments) (b). The asterisks denote significant difference in relative abundance of bacterial phyla between BS and R compartments (ANOVA, P<0.05). The crosses denote significant difference in relative abundance of bacterial phyla between R and E compartments (ANOVA, P<0.05).

For the fungi, no difference was observed at the phylum compared to the native conditions. *Tomentella* were significantly enriched in the R and E compartments of the LDD treatment compared to the native treatment (LLL). *Verrucladosporium* were significantly enriched in the R of the DLL treatment compared to the native treatment (DDD; P<0.05; Figure 36 b). The funguild analyses revealed that EcM fungi, the saprotrophs and the AM fungi were significantly enriched in the R of the native treatment (DDD > DDL) (Figure 37).

Focus on the microbiomes of the different progenies

The global analyses (NMDS and PERMANOVA) done on the OTUs revealed no significant shift in the fungal and bacterial community structures between the 3 progenies of each site (i.e., Loire and Drôme) when the different treatments were compared (Table 4).

However, detailed analyses done on the taxonomic composition revealed significant differences between the rhizosphere microbiomes of the different progenies (*i.e.,* Drôme or Loire), but no effect for the endosphere. In native condition, Chloroflexi appeared significantly enriched in the rhizosphere of D11 compared to the other Drôme progenies (ANOVA, P=0.003; D11 (22.6 ± 1.9 %) > D13 (17.4 ± 1.1 %)= D15 (19.2 ± 0.6 %)), while Actinobacteria appeared significantly enriched in the rhizosphere of L08 than in the other Loire progenies cultivated under Drôme climate (i.e, LLD treatment) (P=0.005; L08 (20.3 ± 5.1 %) > L06 (10.8 ± 1.7 %) = L04 (9.8 ± 1.3 %)). At the genus level, *Niastella* (member of Bacteroidetes) was the single genus significantly enriched in the rhizosphere of the D11 progeny in the DDL treatment (P=0.002; D11 (2.1± 0.3 %) >D13 (1.1 ± 0.2 %) = D15 (0.68±0.25 %)).

Concerning the fungal communities, no effect was observed at the phylum level. At the genus level, *Geopora* (one of the main genus detected in our study) appeared significantly enriched in the rhizosphere of the L08 progeny only in the LLL treatment (L08 (19.3 ± 10.1 %)>L06 (11.1 ± 4.6 %)> L04 (3.0 ± 1.5 %) (ANOVA; R_{L04}, P=0.002). The same genus appeared also significantly enriched in the rhizosphere of the D11 progeny in the DDD treatment (R_{D11}, P=0.003; D11 (15.6 ± 4.7 %) >D15 (9.1 ± 2.7 %)>D13 (5.1 ± 1.0 %)), in the D15 progeny in the DLD treatment (P=0.006; D15 (15.0 ± 3.9 %) > D13 (4.3 ± 2.4 %) = D11 (3.9 ± 3.2 %)) and in D15 in the DDL treatment (P=0.002; D15 (25.5 ± 10.7 %) > D13 (10.1 ± 2.3 %) = D11(11.1 ± 3.3 %)). The funguild analyses evidenced a significant enrichment of plant pathogens under the Drôme climate (*i.e*, LLD treatment) for the Loire progeny L08 progeny (P=0.04; L08 (23.5 ± 8.7 %) > L06 (9.6 ± 3.3 %) = L04 (4.7 ± 1.9 %)).

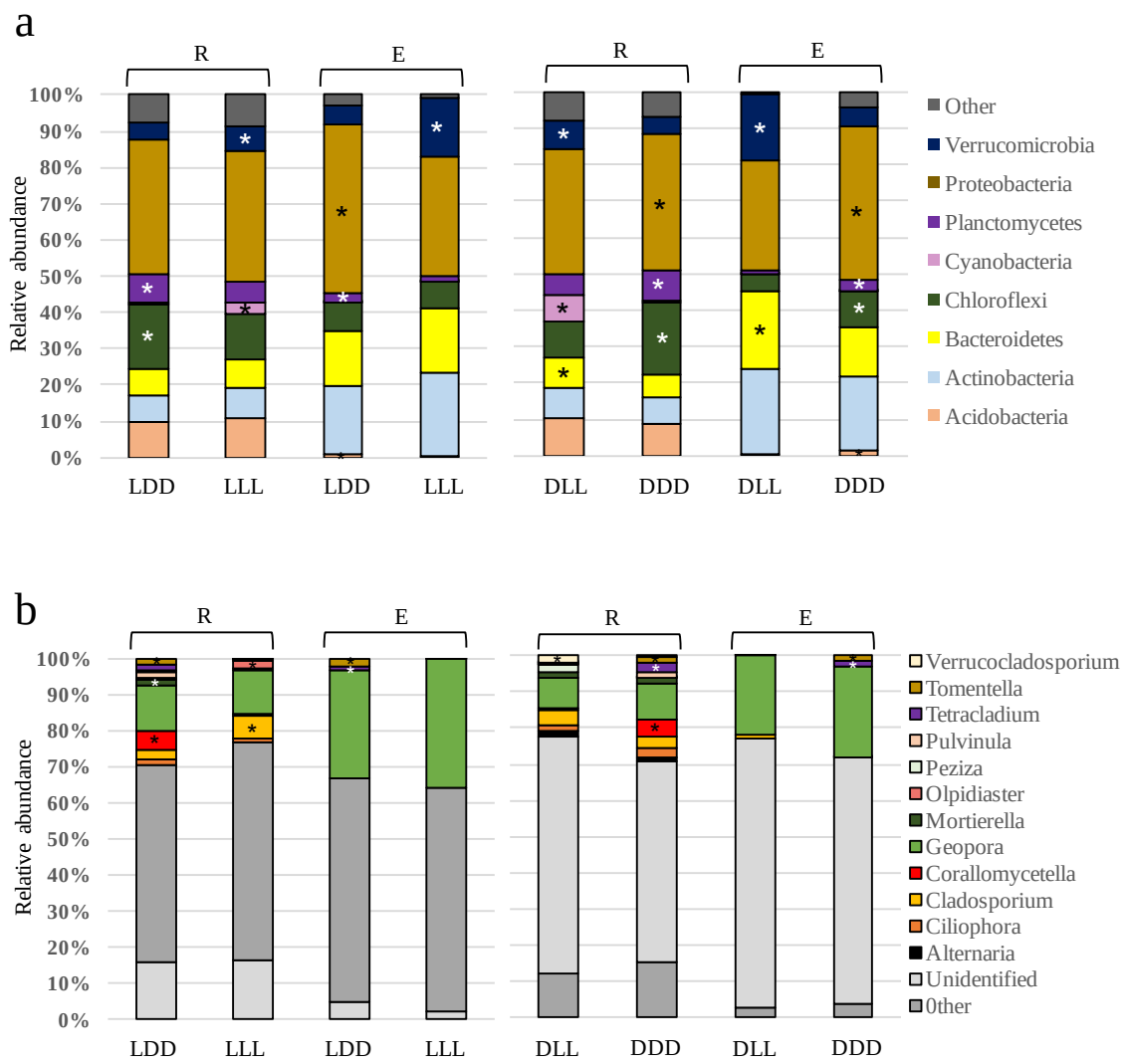

Figure 36 - Combined impact of sediment origin and climate on the Populus nigra root microbiome. Distribution of most dominant bacterial phyla (> 1 % in relative abundance) (a) and fungal genera (> 1 % in relative abundance) (b) detected in the rhizosphere (R) and in the endosphere (E) of Populus nigra seedlings of the Loire and the Drôme cultivated in their native sediment and under their native climate conditions (i.e., LLL and DDD treatments) and in transplant conditions (LDD and DLL treatments). The asterisks denote significant difference in relative abundance of each bacterial phyla and fungal genera between the two conditions of seedlings culture (ANOVA, P<0.05).

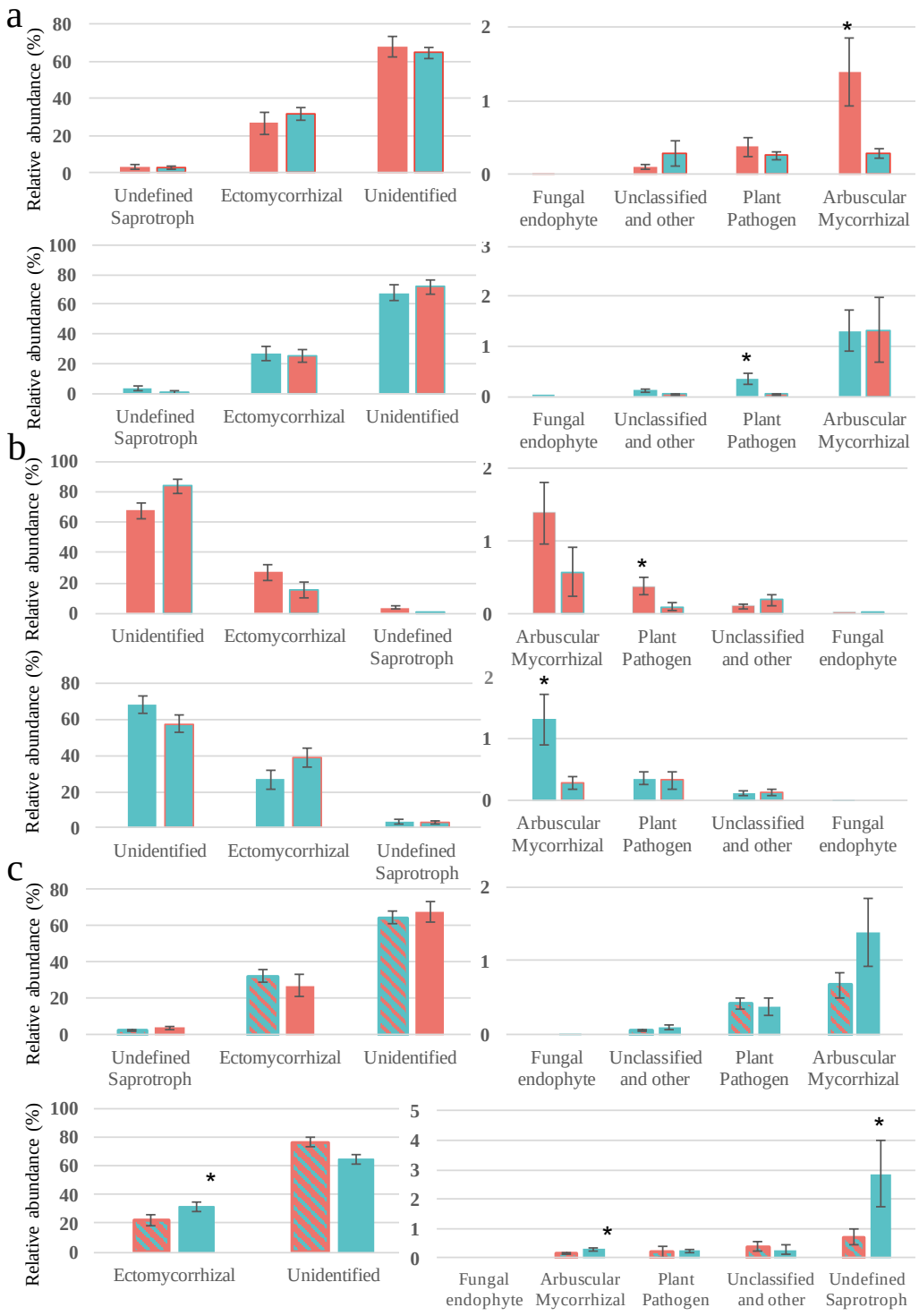

Figure 37 - Impact of the transplant conditions of sediment and climate on the relative abundance of fungal guilds detected in the endosphere of Populus nigra seedlings. Relative abundance of fungal guilds detected in the endosphere of Populus nigra cultivated in their native sediment (Loire in red and Drôme in blue) and in the other type of sediments (Loire sediments in red frame and Drôme sediment in blue frame) (a). Relative abundance of fungal guilds detected in the endosphere of Populus nigra cultivated under their native climate (Loire in red and Drôme in blue) and under the opposite climate (Loire sediments in red frame and Drôme sediment in blue frame) (b). Relative abundance of fungal guilds detected in the endosphere of Populus nigra cultivated in their native conditions of sediments and climate (Loire in red and Drôme in blue) and in the transplant conditions of sediments and climate (Loire sediments in red frame and Drôme sediment in blue frame) (c). The asterisks denote significant difference in relative abundance of each fungal guild between the two different tested conditions (ANOVA, P<0.05).

Discussion

In this study, we used a transplant mesocosm approach to decipher how the structure and composition of the root-associated microbiome of *Populus nigra* are influenced by the soil properties, the climate and the plant traits. To do it, we compared the offspring of two progenies of *P. nigra* collected in two contrasted climate regions (Loire vs Drôme) using their related sediments as soil matrix and source of microbial inoculum and grow them in their native or transplant conditions. The combination of our culture-independent approach on the surrounding bulk soil and the root-associated microbiome (ie., the endosphere and the rhizosphere) with the measure of aerial growth of the *P. nigra* progenies in the different conditions allowed us to demonstrate that the adaptation of *P. nigra* seedlings in non-native conditions of culture (i.e, sediments and climate) strongly correlates with the enrichment of specific microbial communities in the rhizosphere and the endosphere.

Growth of *Populus nigra* is strongly depending on soil fertility but also on temperature

It is well established that plant growth is conditioned by the physico-chemical properties of the soil matrix (i.e., fertility, water content), the selection of beneficial microorganisms and the climate, but also by the genetic properties of the plants (Letey, 1958; Ryan, 2010; Martinez-Graza et al., 2016; Quan & Liang, 2017). In our study, the impact of the plant genetic was apparent as the three progenies considered per site showed significant differences in their growth (aerial part) when cultivated in their native conditions (Loire, L04<L08<L06; Drôme, D15<D13<D15, Figure 28). However, the level of growth and the progeny patterns appeared modified when cultivated in their non-native sediment. The Drôme progenies presented a higher growth in their native conditions of soil and climate than in the other treatments, while the Loire progenies presented a higher growth in the complete transplant treatment (i.e., Drôme climate x Drôme sediment). Based on the nutritive content of the two sediments considered and the temperatures measured on each site, such results were expected as the Drôme sediment is characterized by a higher fertility and warmer climate than the Loire sediment. This assumption was confirmed by the lower growth of the Drôme progenies in the Loire sediment (less fertile) and under a lower temperature than the one of the Drome region. Warmer temperature significantly enhanced the growth of deciduous trees such as beech, oak and ash as well as the soil fertility, especially C/N, and soil moisture (Levesque et al., 2016). This last factor was avoided in our study with the constant watering of the mesocosms. However, the differences in the progeny patterns between the native and transplant treatments suggest the existence of interactions between the different factors (genetic x soil x climate) and potentially the microbiome selected in *P. nigra* root system as previously suggested (Classen et al., 2015; Bonito et al., 2019). This hypothesis is in accordance with the work of Gungale et al. (2013) who showed that whatever the difference in soil fertility, pine trees (*Pinus cordata*) grew better in their introduced ranges (Swedish sites) compared to their native ranges (Canadian sites) thanks to the soil microbiome, especially fungi and bacteria.

Colonization of *Populus* nigra rhizosphere by fungi and bacteria is mainly driven by sediments origin and climate

The composition of the soil microbiome significantly shifted between Drôme and Loire sediments. This significant change could be linked to the important difference in physico-chemical properties observed between the two sediment types. It is likely an important driver of such differences, as previously demonstrated in other soils (Lauber et al., 2008; Fierer, 2017; Terrat et al., 2017; Nicolitch et al., 2019). By contrast, difference in average temperature between Drôme and Loire (2.6°C in average) did not seem to influence the microbiome of the sediments. Indeed, in our study, no significant difference in both microbial community structure and composition was observed between sediments placed under their native climate and those cultivated under the opposite climate. This result contrasts with the one obtained by Liang and colleagues who showed that soils transplanted to warmer regions caused more significant change in the microbial community composition and structure compared to the soil transplantation in colder region (Liang et al. 2015). These discrepancies may be explained by the fact that the experiment of Liang et al. was run on a longer period (several years) and with higher temperature gradients (up to 6°C). Nevertheless, the difference between temperature of Drôme and Loire could impact the physiology and notably the photosynthesis of the seedlings. Such correlation was already made in *Populus simonii* (Song et al., 2014) and other trees such as subtropical forest trees (Slot et al., 2017; Wu et al., 2018) and pine (Hari & Nöjd; 2009).

We hypothesized that the change in the composition of sediment microbiome was responsible for the change in the composition of microbial communities colonizing the rhizosphere. The rhizosphere corresponds to the area of sediment directly under influence of roots where host factors (e.g., physiology, root exudates and genotype) as well as environmental factors (e.g., soil properties and climate) shape microbial community composition and structure while microbial communities of the bulk soil, the area of the soil free of tree roots is only influenced by environmental factors. By comparing both bacterial and fungal communities between the bulk soil and the rhizosphere compartments, we demonstrated that bacterial and fungal community composition varied significantly between BS and R, no matter the treatment (i.e. soil, climate …). However, this well-known phenomenon so-called the rhizosphere effect (Hiltner, 1904; Hartmann et al., 2008) was different according to the treatment. The most important variations were observed between LLL and LDL treatment (soil effect) and between DDD and DDL treatment (climate effect). These important shifts when seedlings were transplanted in the non-native sediment could be linked to the difference in physico-chemical properties (Lauber et al., 2008; Fierer, 2017; Terrat et al., 2017; Nicolitch et al., 2019). In addition, these important shifts when climate was reversed could be due to modification of tree physiology (e.g., photosynthesis, transpiration, root exudation quality and quantity) which indirectly modify the composition of microbial communities of the rhizosphere (Lau et al., 2017; Mercado-Blanco et al., 2018; Compant et al., 2019). In different tree species, root exudation, notably of carbon, is significantly affected by increased temperature. Indeed, increased of the temperature was responsible of the increase of root exudation of organic carbon by a factor of 1.7 in *Robinia* (Uselman et al., 2000). In seedlings of *Populus tremuloides* exposed to colder soils, the concentration of non-structural carbon increased in roots (Karst et al., 2016). These different observations could suggest that the significant enrichment of Cyanobacteria and the

copiotrophic bacteria belonged to the *Cellvibrio* genus (Spring et al., 2015) in DLL, DLD and LLD treatments could be linked to a modification of root exudation. Further analyses will be required to test this hypothesis. Concerning fungal communities, the plant pathogen *Cladosporium* and the saprotrophes *Tetracladium* and *Corallomycetella* were significantly more abundant in the R compared to the BS in seedlings cultivated in transplant conditions of sediments and/or climate. This observation was in accordance with the modification of the relative distribution of plant pathogens and AM fungi in the rhizosphere of Drôme and Loire seedlings cultivated in non-native conditions of sediment or of climate compared to the native conditions. Because abiotic factors such as temperature can affect host susceptibility to pathogens (Sturrock et al., 2011), the increase of root colonization by potential fungal plant pathogens (e.g *Alternaria* and *Cladosporium*) observed in the Drôme seedlings cultivating under Loire climate could suggest that alteration of average temperature could increase the proliferation of fungal pathogens. By contrast, the relative abundance of the EcM fungi *Geopora* was significantly enriched in the rhizosphere of Drôme and Loire seedlings cultivated in Drôme sediment suggesting that only sediment origin affect the colonization of this fungus.

Taken together, these observations showed that the soil matrix and temperature could have a strong impact on bacterial and fungal community colonizing the rhizosphere of trees via the alteration of the reservoir of microorganisms and/or modifications of the quality and the quantity of tree root exudation.

Populus nigra endosphere colonization is independent of the soil origin and the climate

The microbial colonization of tree roots is a highly dynamic process in which bacterial and fungal communities, mainly originating from the soil reservoir, colonize the endosphere from the rhizosphere (root filtering effect, Bulgarelli et al., 2013). In *Populus*, the root filtering effect is well known (Gottel et al., 2011; Cregger et al., 2018) but the relative impact of soil origin and climate on the microbial communities which colonize the endosphere are poorly known. Detailed analysis of the microbial composition revealed that cultivating *P. nigra* seedlings of Drôme and Loire in their non-native conditions of sediment and/or climate significantly affected the composition of the microbial communities of the endosphere. Proteobacteria have been described as the predominant bacterial phylum present in root endophytic communities of *Populus tremula x alba* and *P. deltoides* (Gottel et al. 2011, Beckers et al., 2017). Surprisingly, this phylum was not significantly enriched in the endosphere of seedlings cultivated in their native conditions of sediments and climate although they were dominant members of both rhizospheric and endospheric compartments. However, we observed a significant enrichment of this phylum in the endosphere for each treatment except DLL and DDL. Four bacterial genera were particularly impacted by the transfer of the seedling on their non-native soil and climate: *Actinocorallia* (Actinobacteria), *Terrimonas (*Bacteroidetes*), Phytohabitans* (Actinobacteria) and *Rhodomicrobium (*Proteobacteria*)*. We could hypothesize that these specific bacterial endophytes are favoured by non-native culture conditions (i.e, soil origin and/or climate) in the rhizosphere and belonged to the small set of rhizosphere microbiome able to enter within the endosphere which represent a unique niche for these endophytes (Gottel et al., 2011; Beckers et al., 2017; Liu et al., 2017). By contrast, Verrucomicrobia were significantly enriched in the endosphere of Loire and Drôme seedlings only when cultivated in Loire sediments (i.e., LLL; DLD; LLD; DLL treatments). The relative abundance

of Verrucomicrobia was equal between Drôme and Loire sediments (BS_{Loire} = 2.7 ± 0.5 %, $BS_{Drôme}$ =2.8 ± 0.1 %) suggesting that the higher proportion of Verrucomicrobia colonizing *P. nigra* root was not linked to their dominance in the sediments of Loire. One could wonder if changes in the physiology of the seedlings when cultivated in Loire maybe responsible for this effect. Little is known about functional abilities of members of the Verrucomicrobia as very few representatives are cultivable up to now (Nunez de Rocha et al. 2011). However, Verrucomicrobia are expected to be oligotrophs whose growth depends on the nature of the carbon source in the rhizosphere (Aguirre von Woboser et al. 2018, Fierer et al. 2013). Such behaviour would fit with a potential change in the access to nutrients in the endosphere of roots grown in Loire.

Regarding fungi, the EcM fungi *Geopora* dominated the fungal community of the endosphere. This fungus was also detected in the endosphere of other *Populus* species (Danielsen et al., 2012; Foulon et al., 2016; Durand et al., 2017; Gehring et al., 2017; Bonito et al., 2019). It was the only fungal genus significantly enriched in this compartment whatever the considered treatment (>25 % in relative abundance) and their relative abundance in the rhizosphere. As EcM fungi massively colonize the inner tissue of roots while the Hartig to exchange nutrients, such dominance in the endosphere is not unexpected. Long and colleagues proposed that the EcM *Geopora* could be defined as an important mutual partner for host tree resisting to the different environmental conditions (Long et al. 2016). More unexpected is the absence of effect of soil origin on the fungal community of the endosphere. Indeed, Bonito and colleagues found that the soil origin was the major determinant of fungal assembly in roots of *P. deltoides*. However, the EcM fungus *Geopora* was not detected in the roots of *Populus* studied in this work (Bonito et al., 2014). In addition, we could imagine that Loire sediments slow the colonization of EcM fungi *Geopora* in the rhizosphere of the *P. nigra* seedlings while roots favor this colonization whatever the origin of the seedlings.

These different observations suggest that the selection of bacterial endophytes has already taken place in the rhizosphere under the influence of the soil and the climate. By contrast, the colonization of *Populus* roots by the EcM *Geopora* is independent of the rhizosphere selection and the host tree.

Specific members of the rhizosphere of *Populus nigra* are affected by the progeny properties

Plant fitness is known to influence microbial community structure through the modification of plant signalling and the composition of root exudates (Lau et al., 2017; Mercado-Blanco et al., 2018; Compant et al., 2019). In our experimental conditions, a global analysis through a PERMANOVA did not permit to evidence significant differences in the microbial community structure between the different progenies of Drôme and Loire despite their different growth patterns. However, detailed analyses revealed that the relative abundance of several taxa was significantly affected in the rhizosphere but not in the endosphere. Notably, our analyses revealed significant effects of the sediment, or of the climate, but not by the combination of these two factors in the rhizosphere. For the bacteria, 16S rRNA sequences affiliated to the *Niastella* genus tended to be enriched in the rhizosphere of the D11 progeny cultivated in their native conditions (> 2 % in relative abundance) which is the progeny presenting the higher aerial growth. It was also significantly enriched in the rhizosphere of the D11 progeny cultivated under Loire climate compared to D13 and D15 progenies cultivated in the same conditions (DDL

treatment) which had a smaller size, suggesting a potential role of *Niastella* in the promotion of *P. nigra* growth. Interestingly, this genus was reported in the rhizosphere of plants such as maize (Visioli et al., 2018) and in the rhizosphere of various *Populus* species (Beckers et al., 2017; Bonito et al., 2019).

For the fungi, ITS sequences affiliated to the EcM fungus *Geopora* appeared significantly enriched in the rhizosphere of D11 progeny cultivated in their native conditions (DDD, 16 % in relative abundance) and in D15 progeny cultivated under Loire climate (DDL, 15 % in relative abundance). D11 seedlings showed the highest aerial part in the DDD treatment compared to D13 and D15. By contrast, D15 seedlings had the smallest aerial part in the DDL treatment compared to D11 and D13 seedlings of the same treatment and to D15 seedlings cultivated in the DDD treatment. Variations of the root-associated microbiome structure according to the plant genotype have been reported for several plants (*Boechera stricta*, maize; Wagner et al., 2016; Gomes et al., 2018) and different poplar species (Bonito et al., 2014; Lamit et al., 2016; Cregger et al., 2018; Bonito et al., 2019). In *Populus* roots, Bonito and colleagues found significant differences in fungal-root associated communities that could be attributed to the genotype but they could not associate the effect to specific OTUs, suggesting that the host effect occurred at the community level (Bonito et al., 2019). The dominance of *Geopora* in the root systems of *P. nigra* may explain the discrepancies with results obtained on *P. deltoides and P. trichocarpa* x *deltoides*. No specific enrichment of *Geopora* was detected in the endosphere of our seedlings suggesting that the modification of the growth of the aerial part is not due to a direct effect of the most dominant EcM fungus on the nutrition of the seedlings as previously shown for other trees (Quoreshi et al., 2008; Kipfer et al., 2012; Nylund & Wallander, 1989).

Taken together, these observations could partially explain the adaptation of young seedlings in new environmental conditions of sediments and temperature. Indeed, our results suggest that environmental factors (i.e, sediments and climate) could improve the root exudation and then, the colonization of the rhizosphere by specific taxa of plant-growth-promoting bacteria. However, we provide first evidences that specific fungal taxa such as EcM fungi was not responsible of the modification of the aerial part growth. Future works is needed to confirm these observations by taking into account other physiological parameters of *P. nigra* ssedlings as root growth.

Conclusion

Data from our experimentation in mesocosm provide new assessments on impacts of sediment origin, climate and *Populus nigra* progenies on fungal and bacterial communities from the bulk sediment to the root endosphere. For the same young black poplar belonging to the same progeny, the aerial growth pattern was unchanged or, on the contrary, modified by the different extrinsic parameter tested. The two sediment types showed differences in microbiome composition and structure related to the different physico-chemical properties observed in the two matrices. These differences were responsible of significant differences in the composition and structure of the rhizosphere and the root microbiome. In addition, climate was also correlated with these significant modifications

especially in the rhizosphere, the soil area richest in root exudates. Finally, the progeny effect was responsible of enrichment of specific microbiome members on the rhizosphere suggesting that modification of plant physiology by environmental factors was the key driver of the microbiome composition and structure.

Acknowledgments

We wish to thank Kenza Benkirane (INRAE Nancy) for her help in harvesting poplars.

Funding

LMP was supported by “Contrat Doctoral” from the French Ministère de l’éducation nationale et de la recherche. This work was funded by the Metaprogram ACCAF (project POPMICROCLIM) and the French National Research Agency through the Laboratory of Excellence ARBRE [ANR-11-LABX-0002-01].

IV. Conclusions

Les données de nos expériences menées en mésocosmes fournissent de nouvelles informations concernant les impacts de l'origine des sédiments, du climat et du génotype sur les communautés bactériennes et fongiques de la rhizosphère et de l'endosphère du peuplier noir (*Populus nigra* L.).

Pour chaque progénie de peuplier noir originaire de la Drôme ou de la Loire observée, le taux de croissance aérienne reste inchangé ou, au contraire, modifié par les différents paramètres extrinsèques testés (le type de sédiments et/ou le climat). Les sédiments de la Drôme et ceux de la Loire présentent des microbiotes différents en termes de composition et de structure des communautés microbiennes. Ces différences peuvent être corrélées aux différentes propriétés physico-chimiques des deux types de sédiments. De plus, ces différences de composition et de structure observées entre le microbiote des deux principaux réservoirs de micro-organismes entraînent une modification de la composition des communautés microbiennes sélectionnées dans la rhizosphère et l'endosphère des peupliers noirs de la Drôme et de la Loire. Le climat semble également être responsable de modifications importantes du microbiote, surtout dans la rhizosphère, la zone du sol la plus riche en exsudats racinaires. Enfin, l'effet progénie est à l'origine de l'enrichissement de certains taxa bactériens et fongiques dans la rhizosphère, ce qui suggère que la modification de la physiologie des plantes par les facteurs extrinsèques est le facteur clé de la composition et de la structure du microbiote racinaire.