



Young scientist contract (PhD) offered by INRA within the doctoral school RP2E (Université de Lorraine) Call for applications - April 2017

Inra and the Doctoral School RP2E offer during 2017 a "Contrat Jeune Scientifique" (Young Scientist Contract) for 3 years (duration for completion of a PhD). Research will take place at Nancy (France). Candidates may choose among the five topics offered this year:

Topic 1

Interactions between biogeochemical cycles of the main elements in forest ecosystems

Topic 2

Microrefugia facing climate change: bioclimatic modeling of steep-sided valleys in northeastern France.

Topic 3

The key role of biomechanics for shaping tree stems

Topic 4

How do environmental and ontogenic factors modulate the distribution of growth along tree stems?

Topic 5

Forest biomass and carbon accounting in the French forests: Identification and modelling of inter-specific, management-driven and environmental- patterns in wood density from new records of the French national forest inventory

The topics and contact persons for specific information are detailed in the text.

Applications

Applicants to this contract should send the application files including:

1. A detailed CV with all details about obtained degrees, fulfilled training and results;
2. A motivation letter (2 pp) indicating the selected topic, a description of the skills of the candidate with respect to the topic and the plans of the candidate for his/her future career;
3. Two recommendation letters provided by professors or researchers who supervised the candidate during his/her training.
4. Whenever possible, a copy of the degrees obtained up to now.

You should hold a Master's degree in life sciences or environmental sciences with an excellent grade list. You should demonstrate an interest in transdisciplinary research. You are expected to be creative and open-minded and to have the ability to establish and maintain good interpersonal relationships. Knowledge of French language is not a prerequisite. You should demonstrate a good level of spoken and written English, and the thesis may be written in English.

The research will mostly take place at the Inra campus, Champenoux (30 min by bus) or at the Faculté des Sciences et Techniques, Université de Lorraine, Nancy. The research groups are all members of the "Laboratoire d'Excellence" ARBRE (<http://mycor.nancy.inra.fr/ARBRE/>), and the project will be run under the auspices of the PIA2 Initiative ISITE "Lorraine Université d'Excellence" (<http://lue.univ-lorraine.fr/fr/>). In these groups, you will benefit from the support of advanced technical platforms devoted to genomics, stable isotopes, electronic and confocal microscopy, wood science, etc... You will be member of a large-scale research community of about 350 persons working in forest and wood sciences (see <http://www.nancy.inra.fr/>).

Nancy is a medium-sized city (350000 inhabitants including suburbs) located in North-Eastern France. The city is very attractive in terms of gastronomy, cultural activities, architecture (ranging from the UNESCO classified Place Stanislas (18th century) to the so-called 'Ecole de Nancy' style),....The countryside is very peaceful with lakes and many forests, close proximity to the Vosges mountains (for skiing, trekking, mountain biking...), to Belgium, Luxembourg and Germany. There is very easy access to Paris (1h30 to Paris with the high speed TGV train) and to other destinations in France and the continent (30 min from National Airport Nancy-Metz, 1h15 from Luxembourg International Airport).

Applications files should be sent to the administration of the Doctoral School (christine.fivet@univ-lorraine.fr) with a copy to the president of INRA Centre de de Recherches Grand Est-Nancy (presid-nancy@inra.fr) not later than Friday May 19th 2017. We recommend that you have a brief exchange with the scientist responsible for each topic before applying.

A selection committee will examine all applications and will select the candidates for an audition, based on skills and adequation to the selected topic. The final selection will follow the audition of the candidates (Mid June 2017). Each audition will be based on a 15 min presentation followed by 20 min questions. The audition may be organised with a video conferencing system.

For more information, please contact: presid-nancy@inra.fr or the scientist responsible for each topic.

RP2E website : <http://www.rp2e.univ-lorraine.fr>

INRA website: <http://www.nancy.inra.fr>

Research topic 1

Interaction between biogeochemical cycles of the main elements in forest ecosystems.

Research Units

UR 1138 Biogéochimie des Ecosystèmes Forestiers

Supervisors of the PhD thesis

Marie-Pierre Turpault, Research Director, Inra, marie-pierre.turpault@inra.fr

General aims and state of the art

Chemical element transfer in the atmosphere-vegetation-soil-regolith system is of key importance for economic activities as agronomical production, wood production..., and for the maintenance of environment quality (water and soil quality, biodiversity...) particularly in forest ecosystems. At each ecosystem layer (canopy, forest floor, in different soil horizons), different fluxes (rainwater, plant uptake, canopy exchange, organic matter mineralization, mineral dissolution...) control the element transfers. In this critical zone, biogeochemical cycles (Odum, 1951) are complex in forest ecosystems (Ranger and Turpault, 1999 ; Drever, 2005). This results from biotic and abiotic interactions between the numerous ecosystem components (tree, micro-organisms, organic matter, minerals and soil solution...), the exchanges with the atmosphere and material parent (geochemical cycle), and the translocation between different tissues into the trees (biochemical cycle).

Even if certain studies clearly show the interactions between cycles (for example, the interactions between water, C and N, Battaglia et al., 2004 ; or the interactions between nitrate-and mineral weathering, Mareschal et al., 2013), this research field is still little explored mainly because the experimental sites required to lead such studies are scarce. The BEF laboratory of the INRA built in 2011 such an experimental site in the North-Eastern France at Montiers in collaboration with the ANDRA.

We assume that all element cycles interact and that the understanding of these interactions will advance the knowledge on the biogeochemical functioning of forest ecosystems, including the response of ecosystems to different pressures. The aim of this thesis is (i) to monthly quantify the fluxes of principal elements, i.e., C, N, Si, Mg, K, Ca, P, Na as well as water at each ecosystem layer, (ii) to determine the interactions between the biogeochemical cycles in a beech forest, and (iii) to determine the environmental parameters which drive these interactions.

Specific research topic

Which are the interactions between C, N, Si, Mg, Na, Ca, K, P and water cycles? Which are the relations between elements for the various fluxes? Are these relations an indicator of specific sources/sinks or of nonstoichiometric mechanisms? Which are the main factors controlling these reactions?

The program includes four tasks :

- 1- Establishment of fluxes and stocks (elements speciation, sources and sinks) for each compartment of the ecosystem;
- 2- Determination of the stoichiometric ratios between elements in the solution at each layer of the ecosystem;
- 3- Validation/search for the main sources/sinks characterized by these ratios, from data on the solids (reactive sub-compartments of plants, litter in decomposition, various soil primary and secondary minerals) and identification of the main non-stoichiometric mechanisms ;
- 4- From intra- and inter-annual variations, establishment of the main factors of interaction between the cycles.

Novelty and relevance of the research project to the team

To our knowledge, this is the first time that such a complete and comprehensive of temperate forest ecosystem functioning study is done.

This project is original for multiple reasons: the monitoring device (one flux tower and three biogeochemical stations highly instrumented along a soil gradient); the large available database including data on stocks and fluxes in several compartments, i.e., soil (mineral, organic matter), solution, gas, tree growth and biomass; the approach is multi-element simultaneously; the long term monitoring (6 full years and still ongoing)

This study is in keeping with works done by the team and collaborators, i.e., water budget in forest ecosystem, distribution of biominerals in trees, fertility of forest soils, and microbial diversity in soils... The ambition of this project is to make the link between processes governing ecosystem functioning, and to assess the interactions between compartments and between cycles.

Innovation and impact for the society

The services provided by forests are numerous, i.e., water quantity and quality, carbon storage, wood production, recreation, landscape... In a context of global changes (climate changes, increase of biomass exportation, changes in atmospheric deposits), pressures on forests are growing. Understanding the interactions between the biogeochemical cycles (water, nutrients, carbon and other elements of the ecosystem) and the abiotic and biotic driving factors is an important issue to evaluate their evolution while facing these pressures. Until now, in spite of a very good knowledge on the individual cycles in the forest ecosystems (for example, carbon and nutrients) or on specific fluxes (mineralization, gaseous C exchange of C in the atmosphere, weathering, atmospheric deposits ...) in France (BEF, ECO&sol, EEF, ISPA in particular), little research was carried out on the interactions between all these cycles. We have the ambition to raise this challenge during this PhD project through the use of a site which has been specially built for this purpose and where the collected data and the knowledge accumulated on each individual cycle make possible this project.

Available equipment / experimental support / associated research projects

Will be available for the candidate:

- 1- An experimental site instrumented with a flux tower and three biogeochemical stations on three various soil types (species, age, forestry practices being identical along this gradient). Uncertainties assessments from 3 repetitions (3 sub-stations by station) is fundamental for this study. Moreover a device of rainwater exclusion can be used, if necessary, to test assumptions.
- 2- The complete database of the site of Montiers (acquired in 2010 for the initial state of the site (soil, humus, flora, and stand characteristics), and since the end of 2011 for the follow-up which includes a) the soil and stand characteristics at the building of the biogeochemical stations (2011) and after 6 years of monitoring (stock of elements: chemical analyses of major and trace elements, element speciation), b) the monthly and annual monitoring of tree growth; seasonal monitoring of litterfalls; monitoring of the solutions at various layers of the ecosystem (monthly for quantities and major element concentrations, occasionally for trace elements and isotopes such as Sr, Nd, B), and monitoring of climate and forest-atmosphere exchanges via the flux tower.
- 3- Experimentations on litter degradation and mineral weathering set up since 2013 on the three soil types.
- 4- Models of stand growth established for the various soil types of the Montiers site (beech, maple; thesis A. Genet, BEF) and of hydric fluxes (thesis G. Kirchen, BEF ; Kirchen et al., 2017)
- 5- Data on (i) the average cycles (C, water, nutrients) and fluxes (atmospheric exchanges/contributions, drainage, immobilization in trees, litterfall...) on a multi-annual scale by two PhD students (L Heid, EEF; G Kirchen, BEF), (ii) the cycle of B and its isotopes (P. Roux, BEF-Univ. Strasbourg), (iii) data on taxonomic and microbial functional diversity (INABACT project, S. Uroz, O. Nicolich and Y. Colin, IAM; Nicolitch et al., 2016), and (iv) data on the speciation of the elements in the perennial and annual tree compartments (post-Doc. of Célia Krieger, BEF, Krieger et al., 2017).

Skills that the doctoral fellow will gain during the contract

The PhD student will acquire competences in biogeochemistry, but also in soil science, ecology, ecophysiology and in data processing which he will be able to put forward for his professional future.

Because this project is very innovative, at least three to four publications regarding concept, comparisons of cycles and fluxes, sources/sinks and control factors... should be published in excellent journals.

Publications of the research group on the topic (max. 5)

- KRIEGER C., CALVARUSO C., MORLOT C., UROZ S., SALSI L., TURPAULT M.P. 2017. Identification, distribution and quantification of biominerals in a deciduous forest, *Geobiology*, 15, 296-310.
- KIRCHEN G., CALVARUSO C., GRANIER A., REDON P-O., VAN DER HEIJDEN G., BREDA N., TURPAULT M-P 2017. Local soil type variability controls the water budget and stand productivity in a beech forest. *Forest Ecology Management*, 390, 89-103.
- NICOLITCH O., COLIN, Y., TURPAULT, M-P., UROZ, S. 2016. Soil type determines the distribution of nutrient mobilizing bacterial communities in the rhizosphere of beech trees *Soil Biology & Biochemistry*
- LEQUY E., CALVARUSO C., CONIL S., TURPAULT M.-P. 2014. Atmospheric particulate deposition influence by tree canopy in beech forests in the north of France. *Science of the Total Environment*. 487, 206-215.
- MARESCHAL L., TURPAULT M. P., BONNAUD P., RANGER J., 2013. Relationship between the weathering of clay minerals and the nitrification rate: a rapid tree species effect. *Biogeochemistry*, 112, 293-309.

Research topic 2

Microrefugia facing climate change: bioclimatic modeling of steep-sided valleys in northeastern France.

Research Unit

UMR-1137 Ecologie et Ecophysiologie Forestières (EEF) (Centre Inra de Nancy-Lorraine, Université de Lorraine)

Supervisors of the PhD thesis

Jean Luc DUPOUEY, Directeur de Recherches, Inra, UMR UMR-1137 Ecologie et Ecophysiologie Forestières ; dupouey@nancy.inra.fr;

Sandrine CHAUCHARD, Maitre de Conférences, Université de Lorraine, UMR UMR-1137 Ecologie et Ecophysiologie Forestières ; sandrine.chauchard@univ-lorraine.fr;

Vincent BADEAU, Ingénieur de recherches Inra, UMR UMR-1137 Ecologie et Ecophysiologie Forestières ; vincent.badeau@nancy.inra.fr.

General aims and state of the art

The Jurassic limestone plateaus in Northeast France (from Longwy (north) to Dijon (south)) are deeply carved by several wide river valleys (e.g. Moselle, Marne, Meuse, Armençon, Yonne) but also by numerous steep-sided valleys. These peculiar landforms, often parts of wide and homogeneous forest areas, have long been identified as specific and rare habitats, of high environmental value (Le Tacon & Timbal, 1972; Bugnon et al., 1974; Rameau & Timbal, 1979). According to the variability of their orientation, length, width, depth, hydrography and sinuosity these steep-sided valleys are characterised by a diversity of small-scale microclimates (Scherrer and Körner 2011) which differ greatly from the regional climate and the surrounding plateau, with greater thermal and moisture amplitudes (at a daily or annual time step; Le Tacon & Timbal 1972). If the south-facing slopes are much warmer and characterized by a sub-mediterranean climate, north-facing slopes and thalwegs are colder, wetter and characterized by a sub-montane climate. Consequently, each steep-sided valley of the Jurassic limestone plateau exhibits large variation of climate at fine-scale (below 100m scale) «Cold valleys» constitute thus a microrefugia - e.g. *small areas with local favourable environmental features in which small populations can survive outside their core distribution area* (Rull, 2009) - for both cold-adapted and thermophilous species.

Presence of these restricted microclimate leads to the occurrence of specific plant species (thermophilous species on south-facing slope e.g. *Quercus pubescens*, cold-adapted species in the thalweg and on the north-facing slope, e.g. *Aconitum lycoctonum* or *Cardamine heptaphylla*) and habitats (Bugnon & Rameau 1974, Noirfalise 1960, Timbal 1977). Species and habitats of "cold valleys" are in sharp decline for several reasons: presence of forest tracks in the thalwegs, changing hydrology due to management, substitution of native deciduous forest species by coniferous plantations, strong logging on steep slopes leading to soil erosion or at the other extreme decrease of forest management leading to a canopy closure and the disappearance of the heliophilous species (such as the very rare *Cypripedium calceolus*, for example). Climate change poses a new threat to these ecosystems but it has never been evaluated. Since the coldadapted plant species located in the north-facing slopes and thalwegs of the "cold valleys" are already located at their lower altitudinal range, a temperature increase could have strong negative impacts on their distribution and then lead to change in species distribution and then communities composition. On the opposite, thermophilous species located in the south-facing slopes should benefit from temperature increase and their range should expand. Then, in a context of anthropogenic warming, "cold valleys", as microrefugia might i) continue or not to provide suitable habitat for some cold-adapted species, ii) provide suitable habitat for new threatened species (mesic species) and mitigate the extend of the biotic extinction (Rull, 2009) and iii) play a role in subsequent range expansion notably for thermophilous species located in the south-facing slope (Hylander et al, 2015). "Cold valleys" should contribute to mitigate climate change effect as their microclimates are decoupled from

the regional climate. Their present and future roles depend on the degree and the persistence of decoupling. Indeed, portion of the sites with strong decoupling to regional conditions have a greater potential to persist through time (Dobrowski, 2010). Microrefugia, notably warm-stage microrefugia, have been the subject of recent studies and syntheses in mountain environment, notably in the Alps (Patsiou et al. 2014, Gentili et al 2015) but none was conducted in lowlands whereas climate change velocity should be much higher in flat landscapes (Loarie et al. 2009). Moreover, sites that support microrefugia most often differed for cold and warm stage (Dobrowski 2010). "Cold valleys" offer both kinds of microrefugia in close vicinity: warm-stage microrefugia for cold-adapted species in the thalweg and the north-facing slopes, and cold-stage microrefugia for thermophilous species on the south-facing slopes. Thus, "cold valleys" offer the opportunity to study the different roles of microrefugia in a lowland landscape: i.e. conservation of cold-adapted species and source for range expansion of thermophilous species.

Specific research questions

Although the flora of "cold valleys" has been surveyed in the past, a synthesis of this documentation, often published in grey literature, is needed to consolidate our knowledge on the vegetation, soil and climate of these peculiar environments. This will help, on one hand, building a relevant knowledge basis to model the present (and then through times) distribution of these habitats and their specialized species and, on the other hand, identifying and protecting the most typical sites. This synthesis could help managers of protected areas, as Natura 2000 sites, to identify conservation values of site and prioritize conservation actions in an anthropogenic warming context.

Due to the high level of decoupling of the local and micro-climates of such "cold valleys" compared to the regional climate, they represent ideal and appropriate case studies for challenging and refining species and community distribution models that use climate and high-resolution topoclimatic predictors. Commonly used species or community distribution models that use only general climate parameters as predictors often show poor accuracy. Several studies have shown the relevance of using high-resolution topographic predictors to refine species distribution models (Lassueur et al. 2006, Pradervand et al. 2013, Leempoel et al. 2015). In particular, cold valleys could help in addressing the following questions: (1) are high-resolution topo-climatic predictors sufficient to detect the presence of such topographic features and to adequately predict the distribution of specialized species or vegetation units? (2) can new-developed predictors (slope, aspect, solar radiation, particular topographic features), selected to be proxies for processes occurring in cold valleys, improve the predictions of distribution models?

The main objectives of the project are:

- i) Improving our knowledge on location of "cold valleys" in order to help protect the most typical plant species and communities;
- ii) Characterising the vegetation and the local and micro climate of "cold valleys" as a function of their topographic attributes;
- iii) Understanding mechanistically the climatic basis of "cold valleys" with climate sensors to ultimately refine topo-climate predictors used in species and community distribution models;
- iv) Evaluating the temporal dynamics of climate and vegetation of cold valleys with the combination of databases, empirical models and *in situ* measurements by sensors. Novelty and relevance to the research project of the team:

Novelty and relevance of the research project to the team

UMR-EEF, notably Vincent Badeau, has been involved for many years in research projects related to the distribution of forest species at the national and European scales (e.g. GICC-Carbofor, ANR-Climator, ANR-QDiv, FP7-Trees4Future) and has a strong expertise in the field of climate databases (baseline and future scenarios) and the processing of these data. UMR-EEF has involved in research project centered on habitat and species conservation. This thesis represents a unique opportunity to refining species and community distribution models, notably to integrate new topo-climatic predictors (as predictors of temperature inversion and cold air pooling). The novelty lies in using both high-resolution topographic predictors and high-temporal resolution and modeled temperature/moisture from sensor to refine species distribution models. In this thesis, Christophe Randin (Lausanne

University) will be solicited notably for its competence in fine scale modeling of bioclimatic constraints in complex topographic contexts. Others Nancy teams (notably LERFOB) will be also solicited to its species niche and climate modeling competences (model including soil water holding capacity).

Innovation and impact for the society

This thesis will enhance our knowledge on "cold valleys" (notably their spatial distribution), enhance knowledge of vegetation-microclimate relationship, and, more generally, on the way species can or cannot move and survive in the long term in landscapes under climate change. It will help improve the adequacy of our decisions concerning the identification and the protection of the specific habitats which could act as refugia in the near future and therefore have a high environmental value. Several public agencies in France are directly interested in the results of this project: DREALs, Conservatory of natural sites, General council, Forest National Office.

Available equipment / experimental support / associated research projects

Floristic informations on species occurrences (Lorraine's and Burgundy's limestone plateaus) have been previously collected: 416 floristic inventories (mainly collected in the 1970s, 1980s) were compiled from ancient literature and SOPHY database and classified to offer habitat/communities characterization. The knowledge of such a list of species should allow a more efficient search for relevant ancient vegetation surveys in other, complementary databases (e.g. National Forest Institute database, regional databases). The teams have access to and expertise on the main environmental and forest vegetation databases at the French and European levels.

The availability and intensity of sunlight (solar radiation) can be calculated with computational routines developed by the team for ArcMap or R, using the digital terrain model of the IGN at a 25m resolution. Topographical features can estimate the cold air pooling, e.g. topographic amplification factor and local concavities/convexities of the terrain, as used by the Lausanne University team. The team owns about 30 temperatures/humidity sensors that will be used for field measures.

Skills that the doctoral fellow will gain during the contract

Integrative modelling starting from the cambium, to the whole tree within a stand;

Biomechanical modelling needs to combine different kinds of models dealing with structural mechanics, tree growth, mechanobiology especially about perception and responses;

3D morphometry from different sources (X-Ray, T-Lidar);

Forestry experiment (definition and management of protocoles);

General knowledge about forestry, tree development and grading of roundwood.

Five publications of the research group on the topic

Badeau, V., Dupouey, J.-L., Cluzeau, C., Drappier, J. (2007). Aires potentielles de répartition des essences forestières d'ici 2100. *Rendez-vous Techniques de l'ONF* (3), 62-66.

Cheib, A., Badeau, V., Boe, J., Chuine, I., Delire, C., Dufrière, E., ... & Thuiller, W. (2012). Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty. *Ecology letters*, 15(6), 533-544.

Engler, R., Randin, C. F., Vittoz, P., Czaka, T., Beniston, M., Zimmermann, N. E., & Guisan, A. (2009). Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? *Ecography*, 32(1), 34-45.

Patsiou, T.S., Conti, E., Theodoridis, S., Randin, C.F. (In revision) Quantifying the discrepancy between regional climate and climate in the micro-habitats of an arcto-tertiary relictual alpine species. *Progress in Physical Geography*.

Randin, C. F., Jaccard, H., Vittoz, P., Yoccoz, N. G., & Guisan, A. (2009). Land use improves spatial predictions of mountain plant abundance but not presence-absence. *Journal of Vegetation Science*, 20(6), 996-1008.

Research topic 3

The key role of biomechanics for shaping tree stems

Research Unit

UMR Inra/AgroParisTech 1092 Laboratoire d'Etude de la Ressources Forêt-Bois (LERFoB) F54280 Champenoux

Supervisors of the PhD thesis

Thiéry Constant (Chargé de recherches Inra) (thiéry.constant@inra.fr) and Mériem Fournier, head of AgroParisTech-Nancy (meriem.fournier@agroparistech.fr)

General context

Thigmomorphogenesis is a process allowing the adaptation of trees to their mechanical environment, and in particular to mechanical stresses due to wind, through the increase of the allocation to secondary growth. This results in a very effective stiffening of the wood axes, added to the fact that thigmomorphogenesis has also an effect on wood properties synthesized by the qualifier flexure wood (Telewski 1986). Since the discovery of this mechanism (Knight 1803) our knowledge about its importance has largely improved and we now know that it is of large importance. During 2015, an experiment began in a beech stand near Nancy, with the objective of disentangling the influence of the mechanical environment from those of other factors in the reaction to stand thinning (Bonnesoeur 2016). The comparison of the annual radial increments of control trees vs. thinned trees whose half is guyed, revealed that 45% of the 2015 radial increment compared to controls is due to the fact that trees are free to sway; this level reached 68% during 2016 where the period of growth was particularly long. LERFoB is convinced of the importance of mechanobiology in forest ecology and forest stand growth and this experiment participated to the effort for developing experiments beyond small scale experiments in green house studies.

State of the art and novelty

This mechanism is enough important to be at the origin of a theory on the optimal scaling of trees to wind under the hypothesis of a uniform distribution of stresses (Metzger 1893, Dean, Long, 1986; Morgan, Cannell, 1994; Fournier et al., 2015 ; Moulia, Fournier, 1997) The latter has been long discussed and disproved recently (Minamino and Tateno, 2014), and even served as the basis for formulating a stand growth model. (Dean et al. 2002). One of the major recent advances of these works was the demonstration that the mechanical signal perceived by the plant was a deformation in the peripheral zone (Coutand and Moulia 2000) and that the secondary growth response depended on the integration of these deformations on the periphery in combination with sensitivity thresholds. These mechanisms of mechanoperception and response have been formalized using the S3m model, "Sum of Straining-Sensing Model" (Moulia et al., 2011, 2015)

For trees, another type of response to a mechanical signal is the negative gravitropism at the origin of the production of reaction wood. This biomechanical optimization of the shape of tree sections has been formalized in "theorems" and "axiom of the uniform stress distribution" by C. Mattheck, a German researcher specializing in the mechanical behavior of urban trees (Mattheck, Tesari, I. (2004) The mechanical self-optimization of trees (WIT Transactions on Ecology and the Environment, 73). Almeras and Fournier (2009, JT Biol) have formalized the biomechanical functionality of this growth differential from one side to the other in the process of straightening the trunks associated with their negative gravitropism. This mechanism is mainly attributed to the sedimentation of statoliths under the action of terrestrial gravity in specialized cells (CHauvet et al, 2016). This wood has often an anatomical structure different from that of normal wood and it is also frequently associated with a wider secondary growth in the same sector of the cross-section. Nevertheless, in particular situations, counterexamples exist where the presence of reaction wood is not associated with the widest zones of the annual growth rings (Wardrop et al. 1956, Sacre et al. 1959, Kroll et al. 1962, White et al. 1962, Hugues et al. 1965; Côté et al. 1969). Furthermore, Bastien et al. (2013), by studying the kinematics of the straightening motion, showed that the angle of inclination was not sufficient to explain

the movement, but that a proprioception of the curvature was necessary. They would support the hypothesis that the stimuli leading to the production of reaction wood and the increase of radial increments are not the same, even if they are often spatially concomitants. And this raises questions about the role that thigmomorphogenesis could play, knowing that the strains around a tilted stem are not identical over the entire periphery which is the reference configuration for the production of reaction wood.

From a physiological point of view, preferred pathways followed by carbohydrates from canopy to roots, can also be supposed to alter the peripheral distribution of radial growth, but to our knowledge this point of view is still an open question (Shi et al. 2015)

On the other hand, the tree biomechanics theories tend to establish links between local growth responses, for instance cambial activity, and the mechanical behaviour of the whole structure. They share this point of view with other theories, such as Pressler's law, derived from empirical observations, and the pipe model in an ecophysiological approach (Shinozaki et al., 1964a,b)). In particular, these laws stipulate that the area of the surface of an annual ring is constant below the crown and that explains why trunks over time lose their taper to acquire a more cylindrical shape. This constitutes a first mechanism of form regulation, but this does not explain the fact that the trees also gain in straightness. In this improvement of straightness, gravitropism plays a role, but the trunk geometry influences also the strain field at its periphery and could explain the fact that local curvatures disappear over time.

Moreover, these laws reflect average behaviour, and they are questioned for dominant trees where the surface of the ring can continue to increase below the crown base, and for suppressed trees may decrease below the crown, and eventually become zero. Due to their social status, these two categories of trees are more or less exposed respectively to mechanical stresses induced by wind, and the observed growth appears to be consistent with a thigmomorphogenetic reaction to the deformations that the trees would undergo.

Finally, it should be noted that during bending, local deformations tend to be higher at the base of the trunk, although this variation depends on the trunk geometry and the wood properties, but this pattern of variation presents some similarities to the change of surface of the wood rings creating the well known tapered shape. The same kind of reasoning can be held with regard to the buttresses which can be observed at the connection with the roots where very characteristic shapes can occur., with acting to increase the resistance to bending due to prevailing winds (Niklas. 2016),

These different arguments justify the motivation for going deeper in the understanding of the link existing between mechanical strains and differential growth to prospect a very significant role of thigmomorphogenesis in the structural development of trees, besides geometrical features such as curvature or inclination. Beyond this biological questioning, the consequences of this link address not only forest management but also roundwood quality in the context of the adaptation of trees to the changes of wind regimes associated to climatic changes.

Specific research question

The research question is to identify the role of biomechanics in the shaping of tree stems, introducing the different variables, inclination, strain, curvature, known to take part in the regulation of the cambial growth along the trunk.

A first objective will be to develop a theoretical biomechanical model to establish the links between strain field modelled from realistic geometrical models of trees, with inclination and curvature, under a simplified wind loading, and the variability of annual ring widths. The link between loading, trunk shape and strain field will be based on mechanical models, thanks to the Team's competences. The link between strain and annual ring widths will be inspired from the thigmomorphogenetical model S3m. The description of geometry will benefit of Team's know-hows in the analysis of T-LiDAR and X-Rays data.

The establishment of the model can be feed by two complementary approaches.

- A retrospective analysis of radial growth versus modelled strain fields : from a sampling of trees showing complex and representative shapes and coming from different silvicultural experiments. The aim is to observe how deviations of the stems due to curvature, apex death, fork pruning, diminish over time. X-ray

data are well suited to examine internal 3D structure, and to see how the concave side of a stem part is fulfilled over years. These observations will be faced to strain-field resulting from Finite Element Modelling to establish a first level of relationship.

- An experimental approach with controlled bendings : during a growing season artificial bending will be applied to saplings in the similar way than Bonnesoeur et al. 2016, adding the control of bending intensities to previous approach.

Novelty and relevance of the research project to the team

This project is dedicated to continue and reinforce the involvement of the team towards the understanding of the functional role of mechanobiology in tree growth in collaboration with the PIAF Unit in Clermont-Ferrand. One originality of the proposed work is to fulfill the gap between fundamental knowledge gained in physiology, ecology, and operational issues in close links with forest management and wood quality. After Vivien Bonnesoeur's PhD, which has transposed into a forest stand context, the concepts involved in the development of the S3m model, the objective is to continue on this line of research.

Despite its importance for the grading of roundwood and lumber yield, the trunk shape has been little studied in the past. This thesis will propose an original approach based on the different processes involved in the secondary growth which are all able to modify the shape of a woody axis, and will complement the phenomenological approaches aiming the modelling of growth, or shape characteristics, both developed in the team.

By looking at a best understanding of the biological processes affecting this characteristics, the objective of this work is to provide a better knowledge of the environmental factors affecting the quality of the wood production, which could influence silvicultural pathways.

This work will also contribute to enhance the available methodologies for extracting information from tools such as X-Ray CT Scanner or Terrestrial Lidar which could be transferred to other studies.

Available equipment/ experimental support/ associated research projects

This thesis will benefit of the work performed during the ANR Project FORWIND (2012-2016), including Vivien Bonnesoeur's PhD. The experience and the results gained during this project reinforce our conviction that mechanobiology is a relevant way for understanding and explaining the natural variability of woody axes' shape

This thesis will benefit of strong competences of the team in several domains :

- Forest experiment with control of the mechanical environment, including the measurement of strain
- Silvicultural trials allowing a variation of tree morphologies, including the "Vent-Éclair" experiment mentioned at the beginning of the proposal.
- Analysis of 3D structure described by CT-Scanner and T-LiDAR, for extracting the 3D characteristics, such as ring widths or longitudinal curvatures.

Skills that the doctoral student will gain during the contract:

Integrative modelling starting from the cambium, to the whole tree within a stand.

Biomechanical modelling needs to combine different kinds of models dealing with structural mechanics, tree growth, mechanobiology especially about perception and responses.

3D morphometry from different sources (X-Ray, T-Lidar)

Forestry experiment (definition and management of protocols)

General knowledge about forestry, tree development and grading of roundwood.

Publications of the research group on the topic (max. 5):

Research topic 4

How do environmental and ontogenic factors modulate the distribution of growth along tree stems?

Research Unit

UMR Inra/AgroParisTech 1092 Laboratoire d'Etude de la Ressources Forêt-Bois (LERFoB) F54280 Champenoux

Supervisors of the PhD thesis

Fleur Longuetaud, Chargée de recherches Inra (fleur.longuetaud@inra.fr) & Francis Colin, Chargé de recherches Inra (francis.colin@inra.fr)

General context

In the context of climate change, the issues related to forests are multiple, and the pressure on this resource is increasing. Estimating forest biomass and accounting carbon stored by forests are among the key priorities in the fight against climate change and the search for solutions to mitigate the effects of climate change. There are also questions about the resistance and resilience of forest species in the event of extreme climatic conditions, which are becoming increasingly intense and frequent, such as heat waves and associated droughts, for example. Today, it is necessary to be able to define adapted and innovative forest management strategies for the future that deal with the choice of species as well as how to manage the stands in order to fulfill the many ecological, economic and social issues related to the multifunctionality of forests. To meet these challenges and propose solutions, it is now necessary to take into account climatic inputs in our growth models and this is the main objective of this thesis.

Modelling of the annual increments of radial growth and biomass, and in particular modelling their distributions along the stem, under the effects of ontogeny, forest management and climate, would make it possible to adapt silvicultural strategies to the needs and environmental conditions, and would help to address the many issues cited above.

State of the art and novelty

Radial growth of forest trees is often observed at the reference level of 1.30 m (breast height) for practical reasons. However, what is observed at this level is not representative of what is happening at other levels in the stem. For beech, Bouriaud et al. (2005) showed that during the dry years, radial growth was more reduced at breast height than higher in the stem. This higher sensitivity to climate at 1.30 m is interesting for dendrochronological studies but leads to an underestimation of the increments in volume and biomass for these particular years. Surprisingly, for the same species, opposite results were obtained by Latte et al. (2016), with a sensitivity to climate increasing with height in the tree, and thus, as in Bouriaud et al. (2005), significant divergences between observations at 1.30 m and higher.

Past studies have shown that the distribution of radial growth along the stem is influenced by several factors, including ontogeny and competitive status of trees (Figs 1, 2 and 3), and could also be modified by extreme events such as thinning or drought (Farrar, 1961; Tasissa and Burkhart 1997; Courbet 1999; Bouriaud et al., 2005). In addition, differences in cell organization (anatomical patterns) imply differences in tree functioning that may affect the shape of growth ring profiles and their sensitivity to the environment. For example, in the case of beech, it is possible to have growth ring completely absent at the base of the stems for some particular years, whereas this cannot occur in oak whose vessels are embolized each winter and which consequently has to produce a new ring for the reactivation of its hydraulic functioning (Barbaroux and Bréda, 2002).

At the annual level, the volume produced and distributed along the stem will be particularly studied. The Pressler's law which assumes a constant growth ring area along the stem, in a part of the stem located between the butt swell

and the crown base, is not valid in a number of cases (Saint-André et al., 1999; Hatsch, 1997 in Dhôte et al., 2000; Poudroux et al., 2001). In particular, this law does not apply to trees close to free-growing conditions (Le Goff and Ottorini, pers. comm.) or trees under severe stress. It would be necessary to further investigate the validity of this law (limits of validity, use in practice, possible alternatives).

Regarding wood density (we use here the term “wood density” both for speaking about “density” or “specific gravity” or “basic specific gravity”), its vertical variations have been very little studied. In studies to estimate forest biomass, it is usually the average densities of the species that are used, derived from large shared databases (e.g., Chave et al., 2009), and in the best case a density measured more locally but almost always at 1.30 m. Some studies including very recent works have highlighted the importance of taking into account the radial and vertical variations in wood density within the stem in order to obtain reliable estimates of biomass and carbon (Repola, 2006; Nogueira et al., 2008; Bastin et al., 2015; Wassenberg et al., 2015; Longuetaud et al., 2016, 2017). Past works have shown a strong relationship between wood density and ring width for some species (Zhang et al., 1993; Guilley et al., 2004) and less strong relationship for other species (Bouriaud et al., 2004). Is this relationship, when it exists at the 1.30 m level, valid at other height levels in the stem? Moreover, we know that there is a probable additional effect of climate directly on the wood density that cannot be taken into account indirectly, through the effect of the climate on the ring width (Bontemps et al., 2013).

A better understanding of the distribution of annual growth within the stem would allow us to improve existing growth simulators (e.g., SimCop under CAPSIS) and to add relevant climatic inputs to make our tools more robust and able to answer new questions related to climate change. To describe a stem profile, there are two families of models: (1) integrated models or stem profile equations, which directly give the diameter of the stem as a function of the height in the tree; (2) the incremental growth models, which first estimate the vertical profile of each annual ring (its surface or its width) and, by summing, enable to obtain the complete profile of the stem (Saint-André et al., 1999). For this work, the second family of models is more interesting since they simulate stem development by linking annual growth along the stem to functional characteristics (e.g., Mitchell 1975; Courbet, 1999). These models are more suitable to incorporate changes in environmental conditions in order to achieve, for example, simulations of forest growth in the context of climate change. Several models of ring area profiles have been developed in the past, whether based on ecophysiological processes (Deleuze and Houllier, 1995), or more statistical (Courbet, 1999; Courbet and Houllier, 2002), and they provide a basis for the development of a new model able to integrate the different factors.

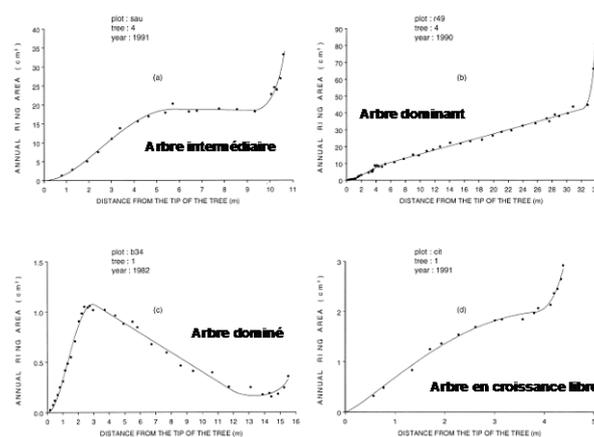


Fig. 1: From Courbet et al. (1999). Effects of the competitive status on the shape of ring area profiles: Top-left: Intermediate tree; Top-right: Dominant tree; Bottom-left: Suppressed tree; Bottom-right: Free-grown tree.

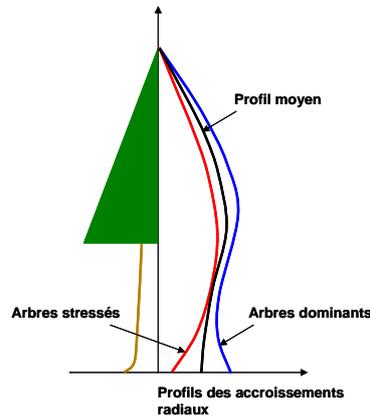


Fig. 2: Patterns of ring area profiles (Longuetaud, comm. pers.).

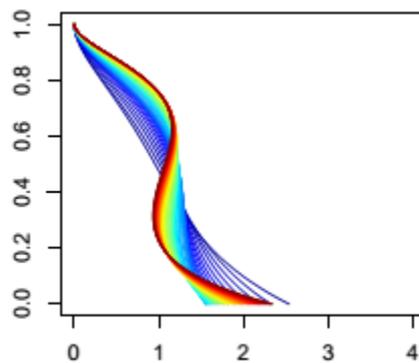


Fig. 3: Normalised ring area profiles showing the evolution of the growth distribution with ontogeny (blue: young stage; red: mature stage). This Figure was obtained through a model fit to data of a dominant Douglas fir tree from a control stand (Longuetaud et al., 2015).

Specific research question

The major research question of this thesis is to understand and then to model the distribution of radial growth along the stem under the influence of three factors: ontogeny, silviculture and climate.

Consequently, a number of other issues will be addressed in this work.

The representativeness of breast height measurements (ring width and wood density) and the possible consequences of a bias for biomass estimates will be analysed for estimations performed at different spatial scales (annual ring, stem, whole tree, stand, resource) and temporal scales (annual increment, sum over several years, tree life). To achieve this objective the volume of the ring, the distribution of the surface of the ring along the main stem, and the wood density will be all considered. It means to be able to attribute a realistic wood density to each ring based on the radial and vertical variations of density within the stem observed at macroscopic scale (Longuetaud et al., 2016) and complementary microdensitometric measurements at several heights. The effect of silviculture (competition, thinning) and climate (events leading to such stress level that the effects on the ring shape are visible) will be studied in interaction with tree age.

The link with the main functions of wood for the tree: support, storage and conduction will be researched, with considering that in certain situations, a tree can allocate in priority the produced biomass to either one of these functions (allometric approach vs. optimal partitioning theory, McCarthy and Enquist, 2007). Ideally, we will study species with contrasting anatomical patterns, e.g., beech (diffuse-porous wood), oak (ring-porous wood) and one or two coniferous species.

Moreover, the validity or not of classical dendrometric laws (in particular Pressler's law but potentially others such as pipe model) will be studied, and depending on the results, finer and more stable formulations of these laws could be proposed.

We will try to answer questions such as: Why is the allocation modified under extreme environmental conditions for the tree? Do all species respond in the same way? What impact does this change in allocation have on the resistance and resilience of tree species?

Novelty and relevance of the research project to the team

The work that we have carried out in the frame of the EMERGE ANR project and the Modelfor project with Office National des Forêts (initially about questions concerning the shape of stems in this last project) enabled to highlight (and to confirm to some extent) that the tree response to some brutal climatic events was much stronger at the stem bottom than at the top. As another result, wood density was found to be higher at the bottom of tree stems. This thesis would allow us to complete this work and to progress in the understanding of the mechanisms involved in the allocation of biomass along the stem, notably by comparing species with supposed contrasted response due for instance to their anatomical pattern.

Moreover, in the context of climate change, we increasingly need to integrate climate into the forest growth simulators.

This work would contribute to this objective by allowing distributing more accurately biomass along the stem with considering three essential factors: ontogeny, silviculture and climate. It would be a significant improvement that would make our simulation tools more robust and efficient. In addition, they could be used to address new questions related to current issues about future forest management in the context of climate change, carbon storage and log quality.

Innovation and impact for the society

The range of targeted applications is very large.

Concerning biomass estimates, we will focus on the representativeness of breast height measurements. If breast height measurements of both annual ring width and wood density are found to not be representative of the whole stem, how to estimate the annual increments of volume or biomass? What are the errors related to this non-representativeness when biomass is estimated at the entire tree level and at large scale level (stand and resource; even if the change from the annual tree scale to the resource scale needs to be thought), as it is usually done?

From the point of view of species functioning, studying annual tree ring profiles should help to understand the tree response to intense stress (why this growth reduction at the stem bottom?), and especially should bring information about the resilience capacities after such event.

In addition, this work should lead to better assess the quality and homogeneity of the wood resource, as well for stem shape (stem taper) as for wood density. In France, wood quality of softwoods is a topical issue, especially for economic reasons, that requires research funding to answer questions about the best suitable stand managements in the context of climate change. This work should allow significant advances about the acquisition of stem shape during tree life under the influence of various factors.

The outputs of this work could be connected to the SimCop growth simulator developed at LERFoB for testing different silvicultural scenarios and answer research questions about carbon storage and quality of the produced stems.

Available equipment/ experimental support/ associated research projects:

Available equipment: microdensitometry (radiography, I-trax, Xyloscience platform); devices for ring width measurements (halle dendro.; IEC)

Experimental support/available data: old and very new databases (past Modelfor joint project with ONF) for Douglas fir and silver fir with measurements of tree ring widths at several heights along tree stems; contrasted thinning intensities; three age classes for Douglas fir; maps of wood density within stems; ring widths at several heights for oak and beech as well as wood density measurements are available at the lab. In the framework of the collaboration with François Courbet (INRA Avignon), it will be possible to use additional databases.

It would also be interesting to sample trees located at the limit of the distribution area of the species. The possibility to find such data through collaborations will be studied. Climatic data will be available through the tools developed by C. Piedallu et al. at AgroParisTech. These data will be connected to tree rings retrospectively with in addition the use of cross-dating techniques.

Associated research projects:

- ANR EMERGE project 2008-2013
- Modelfor joint project ONF-LERFoB 2012-2016
- Project about wood quality of Douglas fir in France « Changement climatique et sylviculture – Quel avenir pour le Douglas ? » (“Climatic change and silviculture – What future for Douglas fir?”); to be submitted for funding at MAAF (#FSFB) and FEDER Bourgogne
- PhD project about biomass estimates « Une valorisation optimisée de la biomasse forestière basée sur une connaissance de la variabilité de la densité du bois dans l’arbre et des volumes de nœuds, écorce, duramen et bois juvénile » (“An optimised valorisation of the forest biomass based on a knowledge of the variability of wood density in the tree and volumes of knots, bark, heartwood and juvenile wood”); to be submitted to ADEME and Région Grand Est

Skills that the doctoral student will gain during the contract:

Modelling; tree growth; growth dynamics; wood properties; biomass estimations; R programming; SimCop under CAPSIS use; development within the CAPSIS platform; scientific writing; oral presentation...

Depending on the skills and interests of the candidate, the scientific components needed to realise this work (e.g., forest dynamics, growth and yield, ecophysiology, dendrochronology) and their balance will be discussed and are likely to evolve.

Publications of the research group on the topic (max. 5):

- Bouriaud, O., Bréda, N., Dupouey, J. L. & Granier, A., 2005. Is ring width a reliable proxy for stem-biomass increment? A case study in European beech. *Canadian Journal of Forest Research*, 35(12), 2920-2933.
- Deleuze, C. & Houllier, F., 1995. Prediction of stem profile of *Picea abies* using a process-based tree growth model. *Tree physiology*, 15(2), 113-120.
- Longuetaud, F., Mothe, F., Fournier, M., Dlouha, J., Santenoise, P. & Deleuze, C., 2016. Within-stem maps of wood density and water content for characterization of species: a case study on three hardwood and two softwood species. *Annals of Forest Science*, 73(3), 601-614.
- Longuetaud, F., Mothe, F., Santenoise, P., Diop, N., Dlouha, J., Fournier, M. & Deleuze, C. Patterns of within-stem variations in wood specific gravity and water content for five temperate tree species. *Annals of Forest Science* (soumis).
- Mothe, F.; Longuetaud, F.; Seynave, I.; Rittié, D. & Deleuze, C., 2016. Annual growth distribution along stems of Douglas fir. IUFRO Working Parties 5.01.04 and 3.02.04 (WoodQc), 12-17 June 2016, Québec/Baie-St-Paul, Canada.

References

- Barbaroux, C. & Bréda, N., 2002. Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. *Tree physiology*, 22(17), 1201-1210.

- Bastin, J. F., Fayolle, A., Tarelkin, Y., Van den Bulcke, J., De Haulleville, T., Mortier, F., ... & De Cannière, C., 2015. Wood specific gravity variations and biomass of central african tree species: the simple choice of the outer wood. *PLoS one*, 10(11), e0142146.
- Bontemps, J. D., Gelhaye, P., Nepveu, G., & Hervé, J. C., 2013. When tree rings behave like foam: moderate historical decrease in the mean ring density of common beech paralleling a strong historical growth increase. *Annals of forest science*, 70(4), 329-343.
- Bouriaud, O., Bréda, N., Le Moguedec, G., & Nepveu, G., 2004. Modelling variability of wood density in beech as affected by ring age, radial growth and climate. *Trees*, 18(3), 264-276.
- Bouriaud, O., Breda, N., Dupouey, J.L., Granier, A., 2005. Is ring width a reliable proxy for stem-biomass increment? A case study in European beech. *Can. J. For. Res.-Rev. Can. Rech. For.* 35, 2920-2933.
- Chave J., Coomes D.A., Jansen S., Lewis S.L., Swenson N.G., Zanne A.E., 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12(4): 351-366.
- Courbet, F., 1999. A three-segmented model for the vertical distribution of annual ring area - Application to *Cedrus atlantica* Manetti. *Forest Ecology and Management* 119(1-3): 177-194.
- Courbet, F., & Houllier, F., 2002. Modelling the profile and internal structure of tree stem. Application to *Cedrus atlantica* (Manetti). *Annals of forest science*, 59(1), 63-80.
- Deleuze, C., & Houllier, F., 1995. Prediction of stem profile of *Picea abies* using a process-based tree growth model. *Tree physiology*, 15(2), 113-120.
- Dhôte, J.-F., Hatsch, E., Rittié, D., 2000. Forme de la tige, tarifs de cubage et ventilation de la production en volume chez le Chêne sessile. *Annals of Forest Science* 57, 121-142.
- Farrar, J. L., 1961. Longitudinal variation in the thickness of the annual ring. *The Forestry Chronicle* 37(4): 323-330.
- Guilley, E., Hervé, J. C., & Nepveu, G., 2004. The influence of site quality, silviculture and region on wood density mixed model in *Quercus petraea* Liebl. *Forest Ecology and Management*, 189(1), 111-121.
- Latte, N., Lebourgeois, F., & Claessens, H., 2016. Growth partitioning within beech trees (*Fagus sylvatica* L.) varies in response to summer heat waves and related droughts. *Trees*, 30(1), 189-201.
- Longuetaud, Fleur, et al. Patterns of within-stem variations in wood specific gravity and water content for five temperate tree species. *Annals of Forest Science* (soumis).
- Longuetaud, F., Mothe, F., Fournier, M., Dlouha, J., Santenoise, P., & Deleuze, C., 2016. Within-stem maps of wood density and water content for characterization of species: a case study on three hardwood and two softwood species. *Annals of Forest Science*, 73(3), 601-614.
- Longuetaud, F., Mothe, F., Rittié, D., 2015. Rapport Modelfor. Comprendre et modéliser le défilement des tiges de Douglas en France.
- McCarthy, M. C., Enquist, B. J., 2007. Consistency between an allometric approach and optimal partitioning theory in global patterns of plant biomass allocation. *Functional Ecology* 21(4): 713-720.
- Mothe, F.; Longuetaud, F.; Seynave, I.; Rittié, D. & Deleuze, C. Annual growth distribution along stems of Douglas fir. IUFRO Working Parties 5.01.04 and 3.02.04 (WoodQc), 12-17 June 2016, Québec/Baie-St-Paul, Canada, 2016.
- Nogueira, E. M., Fearnside, P. M., Nelson, B. W., Barbosa, R. I., & Keizer, E. W. H., 2008. Estimates of forest biomass in the Brazilian Amazon: New allometric equations and adjustments to biomass from wood-volume inventories. *Forest Ecology and Management*, 256(11), 1853-1867.
- Repola, J., 2006. Models for vertical wood density of Scots pine, Norway spruce and birch stems, and their application to determine average wood density. *Silva Fennica*, 40(4), 673.
- Saint-André, L., Leban, J., Houllier, F. and Daquitaine, R., 1999. Comparison between two stem taper equations, and validation on an independent sample. Case study of Norway spruce (*Picea abies* Karst.) in north-eastern France. *Annals of Forest Science* 56(2): 121-132.
- Tasissa, G. and Burkhart, H. E., 1997. Modeling thinning effects on ring width distribution in loblolly pine (*Pinus taeda*). *Canadian Journal of Forest Research* 27: 1291-1301.
- Wassenberg, M., Chiu, H. S., Guo, W., & Spiecker, H., 2015. Analysis of wood density profiles of tree stems: incorporating vertical variations to optimize wood sampling strategies for density and biomass estimations. *Trees*, 29(2), 551-561.
- Zhang, S. Y., Owoundi, R. E., Nepveu, G., Mothe, F., & Dhôte, J. F., 1993. Modelling wood density in European oak (*Quercus petraea* and *Quercus robur*) and simulating the silvicultural influence. *Canadian journal of forest research*, 23(12), 2587-2593.

Research topic 5

Forest biomass and carbon accounting in the French forests: Identification and modelling of inter-specific, management-driven and environmental- patterns in wood density from new records of the French national forest

Research Units

Inra, UR Biogéochimie des Ecosystèmes Forestiers, F 54280 Champenoux

IGN, Laboratoire de l'Inventaire Forestier, rue de l'Île de Corse, F 54000 Nancy.

Supervisors of the PhD thesis

Supervisor: Jean-Michel Leban, Inra, Research Director, Xylologist, BEF laboratory, 54280 Champenoux, jean-michel.leban@inra.fr ;

Cosupervisors: Jean-Christophe Hervé, IGN, Head of LIF research laboratory, Inventorist, 14 rue Girardet, 54000 Nancy; Jean-Daniel Bontemps, IGN, Research Director, Silvologist, LIF, 14 rue Girardet, 54000 Nancy.

Detailed scientific profiles including positioning and publications can be found at: sites.google.com/site/LabForestInventory.

General context

Over the last century and up to recently, European forests have faced unprecedented changes in their area, composition, growing stock and increment, all such factors that affect the nature and quantity of available wood resources, as well as their carbon sequestration potential. In France, the volume of the forest growing stock has doubled within the last 50 years. (Herve et al., 2016, FAO Global Forest Resource Assessment, 2015).

Concern for the climate mitigation potential of forests, for the role they are intended to play in the new "bio-economy" as well as for the current impacts on CC on biomass sequestration calls for comprehensive quantifications of wood biomass and forest carbon at scales ranging from national to European. In contrast to the important amount of "illustrative" studies typically performed on tree species taken in regional contexts over the past decades, new fundamental knowledge is required to provide inclusive coverage of the entire forested area, including coverage of the variety of tree species and forest management systems it is composed of.

State of the art and novelty

The research presented here focuses on forest biomass/carbon accounting in the French forests. The objective is to describe, analyze the sources of variations of, and model wood density in these forests by analyzing an original, and unprecedented database, built from a cooperative project between INRA and IGN launched in 2015. Wood density has hence been measured on the increment cores collected from the spatially systematic sampling design of the French National Forest Inventory during years 2016 and 2017, representing >30,000 tree cores/yr, over >7000 plots, and covering about 100 tree species, in all forest management systems whose attributes are further fully described through the NFI protocol.

Biomass stored in trees is mainly dependent on individual trees size and wood density. Destructive studies have demonstrated that wood density is the second most important predictor of tree biomass, after stem diameter, and before individual tree height (Chave et al., 2005). In addition, information on annual variations in wood density is required to complement that on growth variations, and assess how ongoing environmental changes affect the biomass/carbon sequestration of forests.

The objectives of this PhD project are:

- (i) to describe and quantify variations in wood density as driven by tree species, tree populations, and forest management systems, and infer the consequences of changes in the French forests attributes (composition, management, stocking) on their carbon sequestration potential,
- (ii) to model wood density as depending on tree, stand and environmental attributes in order to develop predictive tools able to be implemented on the French forest inventories (both past and future) and inform of state and trends in biomass/carbon stocks and flows as support information for forest policy.

Specific research question

The following questions can be listed:

- 1) what are the main effects and interaction of factors such as species, forest management and geographic location on the wood density variations? Subsequently, what is the growth-density trade-off among tree species found in the French forests? Do we identify regional patterns that would inform of possible genetic differentiation, in particular in coniferous tree species? Which among forest management and biological diversity predominates in variations in wood density? What are the consequences (identifiable drivers) for increasing forest mitigation potential?
- 2) Can we model and predict wood density accurately from tree and stand attributes as documented from the NFI protocol, and environmental information relevant to NFI plots?
- 3) Over the recent years, what are yearly variations in the wood density of the different species at the resource level? What is their environmental causality? Do we identify any significant footprint of climate on wood density that may influence wood quality and biomass sequestration potential currently, and in the future?

Novelty and relevance of the research project to the team

- For the first time ever wood density is measured on tree cores collected on a systematic sampling design applied to the whole French forested area. This ensures inclusive coverage of specific, ecological and management gradients,
- Turning the NFI a multi-purpose inventory is a major goal of IGN, and fostering capacities in biomass/carbon estimation as well as on wood quality assessment at the scale of forest resources is an essential step forward, at a time where only aboveground volume is routinely described by European NFIs, and the description of wood quality at this scale remains a challenge (Leban & Bontemps 2016, Bosela et al. 2016). Ongoing discussions on the European level on defining the forest baseline for carbon sequestration and follow-up budgets have stressed the importance of the NFI program to secure these estimates
- In an ecological perspective, intra- and inter-specific growth-density trade-offs can be measured and weighted. Whereas the inter-specific trade-off has been often inquired over succession gradients in ecology science, we are not aware of any quantification approach of intra-species density analysis that would inform of the quantitative role of stand management (density, species composition, stand structure) on this variability, and thus identify the most sensitive channels to biomass sequestration,
- This project is also a major step in fostering the scientific dialog between eco-physiological modelling and forest observations, as forest productivity as simulated by process-based models is expressed on a biomass scale. Therefore, by filling this centennial gap between physiology and forestry sciences, this project will allow provide large-scale and long-term forest growth series useable for calibration/validation of PB models. This is an important step for including process-based climate forcings into forest macro-dynamic models used in forest resource assessment and policies (Wernsdörfer et al. 2012)
- Measures on wood density are complementary to the tree increment database of the NFI, and as such it will allow develop management- and environment- dependent models, needed to predict wood density on future annual forest inventories, and monitor the carbon stocks and fluxes from the forests,

- Last, this step is fundamental to evaluate the total carbon sequestration of forests including the soil compartment, as a joint project between IGN and INRA teams (B2IF),

Innovation and impact for the society

- The French NFI has been developed to provide accurate and regionalized statistics on the forests, as supportive information to forest policies and the forest sector, at regional to national scales. Therefore, any new metrics added to the inventory (namely biomass and carbon) is of immediate interest to these stakeholders,
- In terms of available wood resources, wood density assessment and modelling has two complementary implications, essential to the forest sector: 1) evaluating wood biomass is for example needed for quantification of energy wood in forest management systems of little value, 2) wood density is also essential to assess the quality of round woods, and this projects therefore forms a baseline for mapping wood quality over the territory as a support information to the forest sector. Including management conditions and species information into models will therefore provide novel accurate information on these stocks,
- Ongoing climate change impacts forests and their potential for biomass sequestration. The annual resolution of wood density measurements over a few years combined with the classical NFI information on growth, will allow meet this goal, by evaluating annual sequestration and map it over the French territory, as part of the CC-impact monitoring systems

References

- Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q. et al. (2005). Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, 145, 87–99
- Gegout JC, Coudun C, Bailly G, Jabiol B, (2005). EcoPlant: a forest site database linking floristic data with soil and climate variables. *Journal of Vegetation Science* 16 (2), 257-260
- Hervé JC, 2016. The French National Forest Inventory. Chapter 20, in *National Forests Inventories*, Vidal et al.(eds), 385-404
- Hervé JC, Bontemps JD, Leban JM, Saint-André L., Véga C., 2016. Evaluation des ressources forestières pour la bioéconomie: quels nouveaux besoins et comment y répondre ? Carrefour de l'Innovation agronomique, Nancy, 8 décembre 2016 (diapos en annexe).
<http://www.inra.fr/Entreprises-Monde-agricole/CIAG/Tous-les-magazines/Bioeconomie-foret-bois>
- Wernsdoerfer, H., Colin, A., Bontemps, et al., (2012). Large-scale dynamics of a heterogeneous forest resource are driven jointly by geographically varying growth conditions, tree species composition and stand structure. *Annals of Forest Science*, 69, 829–844.

Available equipment/ experimental support/ associated research projects

Experimental support

- The NFI sampling design (Hervé, 2016) leads to the ground sampling (phase 2) of >7000 plots/yr over a systematic sampling grid with an annual resolution of 10km. On these plots, information regarding stands (composition, structure, ownership), trees (status, size, growth, species) and the environment (floristic and soil surveys). All this IGN information is readily available to the project as well as derived products such as pH and C/N maps from the floristic surveys (Gegout et al. 2005), in addition to any auxiliary information that would be geo-referenced (e.g. climate, geological maps),
- For each sampled plot, pith-to-bark cores are extracted from two dominant trees for age assessment (sample A), and five-years increment cores are extracted from all the other trees measured on the plot (sample B). Wood density is measured on both samples (A and B) by the mean of the INRA X-ray tomograph.

Sample A is representative of wood density over tree life-history (age is known), and is therefore of primary interest to assess between-species variability in wood density and associated average growth-density trade-off. It is also of importance to evaluate the effect of forest systems (plantation, coppices, coppices with standards, high forests with mixed species, ...) on wood density; as such system patterns evolve slowly, typically over several decades, and weight the contribution of tree species/forest systems in these variations. On such a sample, spatial variations within

tree species at- fixed forest systems will also be explored to provide indications as to potential genetic differentiation between regional populations.

Sample B is representative of wood density over the past 5 years. On such a restricted temporal scale, tree attributes, stand density, structure and composition, can be assumed constant. This sample is therefore of primary interest to accurately model wood density as depending on tree, stand and environmental attributes, and use these models to estimate current forest biomass/carbon over the territory, as well as perform temporal comparisons by applying them on former NFI samples.

If additional experiments and measurements are needed, technical assistance is provided by qualified permanent staff from the INRA "XyloScience" platform for the physical measurements (shrinkage), calibration and microdensitometric measurements including the software development.

Associated research projects

In addition to this material, other projects are currently running that will support the present PhD:

- 1) The first one is "Grecofor-CC", a project funded by Labex "Arbre" (2016), and aiming at analyzing the yearly NFI growth information (for a sub-part of sample A, the ring-width of the five latest rings are measured on the field), the influence of tree and stand attributes, and isolating climatic signals in growth over the entire territory. This project is the first step toward a national monitoring system of CC impact onto forests.
- 2) The second project is "Expert-SFM", a project funded by Ademe and Region Lorraine (2015, one PhD associated). This project aims exploring the long-term variations in the area and growing stock of the French forests. By combining outputs from the current project and "Grecofor-CC", historical estimates of forest carbon over the national territory could be made available that would inform on the past and current trajectory of this carbon sink.
- 3) More largely, this project will also benefit from previous projects carried out in the team "Resources and wood quality" of former LERFoB laboratory, where ring density of different species in longitudinal samples has been explored on "illustrative" studies, including the effect of forest management and species wood structure, its temporal trends, and climatic determinism. This expertise combined with the one developed at LIF laboratory has no counterpart in France and forms the most substantial basis available to successfully carry out this project.

Skills that the doctoral student will gain during the contract:

- The doctoral fellow will profit from original insertion in both research (INRA) and decision-support (IGN) oriented institutes, providing expertise on both 1) what current policy issues in the forest sector are, and how to address them at a national scale by means of operative approaches of relevance to forest public and private stakeholders, 2) how to develop a research program from these policy issues, and implement research approaches (quantitative observation, modelling). This large scope may allow the PhD student to later evolve both in the engineering of forest resource sector, in applied research, or in more fundamental research,
- By essence, the doctoral fellow will learn about database handling/data mining and modelling skills that are typical of this era of intensive data acquisition, and can be valued also out of the research sector. He will also familiarize with technologies as different as forest inventory, X-ray densitometry,
- He will be supervised by scientists having expertise in both wood, forest and inventory science, and have collaborated over a significant period, which has strong added-value in a period where current policies try to foster links between the forest and industry sectors (an example is the "Plan National Forêt-Bois" national plan for forest and industry sectors, recently approved),
- Last, by gaining research-based training on biomass and carbon accounting, the doctoral fellow will develop an expertise on timely issues that may provide him/her with a young international expert's profile, able to draw attention from organizations such as ministries in charge of climate and energy policies, Forest Europe, FAO, EFI, etc.

Publications of the research group on the topic (max. 5):

- Leban, J.M., & **Bontemps, J.-D.**, 2016. Editorial: "Forest Inventories at the European level". *Annals of Forest Science*, 1–4. (Numéro thématique de *Annals of Forest Science* sur les inventaires forestiers européens)
- Pinto, PE, Bontemps, JD., Pierrat, JC., **Franceschini, T.**, Gégout, JC., Leban, J.M., 2016. Investigating the possible impact of atmospheric CO2 increase on *Araucaria araucana* wood density. *European Journal of Forest Research*, 135(2), 389–401.
- Bontemps JD, Hervé JC, Leban J.M., Dhôte JF (2011) Nitrogen footprint in a long-term observation of forest growth over the 20th century. *Trees* 25:237 – 251
- Franceschini T.**, Longuetaud F., Bontemps J.D., **Bouriaud O.**, Caritey BD, Leban J.M., 2013. Effect of ring width, cambial age, and climatic variables on the within-ring wood density profile of Norway spruce *Picea abies* (L.) Karst. *Trees Structure and Function* 27(4):913-925
- Franceschini, T.**, Bontemps, J. D., Perez, V., & Leban, J. M. (2013). Divergence in latewood density response of Norway spruce to temperature is not resolved by enlarged sets of climatic predictors and their non-linearities. *Agricultural and Forest Meteorology*, 180, 132–141.