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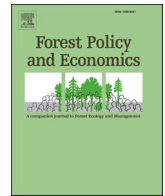
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# Innovation in forest tree genetics: A comparative economic analysis in the European context

Aline Fugerey-Scarbel<sup>a</sup>, Xavier Irz<sup>b</sup>, Stéphane Lemarié<sup>a,\*</sup>

<sup>a</sup> Univ. Grenoble Alpes, INRAE, CNRS, Grenoble INP, GAEL, 38000 Grenoble, France

<sup>b</sup> University of Helsinki, Finland

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## ABSTRACT

In the context of global environmental change, European forests are expected to fulfil a broad range of functions, including the supply of raw materials to the bioeconomy, biodiversity preservation, and the provision of ecological services. Given fast progress in applied genetics, the selection and diffusion of genetically improved forest reproductive material (FRM) has a role to play towards the achievement of some of those goals. We therefore investigate European forest tree breeding conceived as an innovative activity on the basis of four case studies (eucalyptus in Portugal, maritime pine in France, and Norway spruce in Sweden and Finland), using a conceptual framework combining the innovation system approach and the economics of innovation. The genetic progress achieved for each of those species has been steady since the beginning of tree breeding activities. Despite that, we identify both systemic issues and market failures that hinder FRM genetic innovation and make the prospects of a forest tree breeding revolution unlikely. While the innovation systems in the studied countries are structurally sound, we identify several functional deficiencies. We also identify incentive problems limiting both supply and demand of genetically improved FRM. On the demand side, forest owners value improved FRM only moderately because of long lags between plantation and harvest, imperfect knowledge of the potential gains from adoption of genetically improved FRM, and risk aversion. On the supply side, returns to investments in genetic improvement are heavily constrained by the slowness of the breeding process, capacity constraints related to FRM production, limited demand-pull and regulatory uncertainty. Those incentive problems are partially overcome in situations where the industry is vertically integrated, from FRM production to wood processing, as observed in the case of eucalyptus in Portugal or Norway spruce in Sweden. In the other cases, public support for breeding programmes is paramount.

## 1. Introduction

Climate change creates challenges for forests and the stakeholders influencing their management, from forest owners to the forest industry and policy makers. Although contexts vary globally, it is clear that forest disturbances are sensitive to climate and that ongoing climate change raises multiple abiotic risks (e.g., fire, drought, wind, snow and ice) and biotic risks (insect pests and pathogens) (Seidl et al., 2017; Venäläinen et al., 2020), with potentially adverse effects on forest health, productivity, ecosystem services and economic activity. At the same time, the need to rapidly decrease net carbon emissions in order to reduce the risk of catastrophic climate change has given renewed importance to forests and their management. Forests have a key role to play in future carbon cycling (Reich, 2011), as they have the potential to take up and store

large quantities of carbon, although that potential depends crucially on how forests are managed.

From the large potential of carbon capture in forests and their soils as well as the anticipated enhanced vulnerability of forests to climate change follows the need to raise the resilience and productivity of forests globally. One relatively unexplored option in pursuit of that goal is forest tree breeding and related deployment of forest reproductive material (FRM). Breeding consists in creating new material cumulating favourable genes from different parents. This activity is recursive and consists in making successive cycles, each cycle starting with forest tree mating, followed by the evaluation and selection among the offspring. Conventional tree breeding is not new but the efficiency of all breeding programmes is hampered by the long time interval of a typical breeding cycle, which may last several years to decades, and the late expression of

\* Corresponding author.

E-mail address: [stephane.lemarie@inrae.fr](mailto:stephane.lemarie@inrae.fr) (S. Lemarié).

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important traits such as wood properties (Grattapaglia, 2014). Those elements imply high costs and uncertainty of tree breeding programmes, but scientific progress also offers considerable room for improvement. As an example, the potential shortening of tree breeding cycles by early selection based on genetic markers was recognized by forest geneticists in the early 1990s (e.g., Neale and Williams, 1991). However, to date the promises of genomic breeding have not been realised, which is explained in part by scientific and technical issues (Grattapaglia, 2017).

Against this background, this article analyses the innovation system for forest tree genetic innovation in Europe, which covers the activities related to genetic selection, the multiplication of improved seeds and seedlings and the extension services for the use of the improved varieties. The analysis relies on several case studies: maritime pine in France, eucalyptus in Portugal and Norway spruce in Finland and Sweden. In each of these cases, the creation and deployment of several generations of improved forest trees has been achieved (see appendix A for more details). Those case studies are built from secondary data, scientific and gray literature, as well as a series of interviews. By focusing on the organization of existing tree breeding systems, we first show that a rather complete innovation system for the creation and deployment of improved varieties exists for all the combinations of tree species and countries that we have studied. However, we identify several functional deficiencies related to the lack of entrepreneurship, knowledge flow, advocacy coalitions and market formation. We then analyse the private incentives to adopt innovations on the demand side (by forest owners), and to create and deploy improved FRM on the supply side. We find that several demand-side constraints explain why the valuation of genetic improvement by forest owners is limited. On the supply side, we show that, despite the long duration of the breeding cycle and lack of demand-pull, private incentives to invest in breeding are sometimes strong enough for private firms to support breeding activities directly or indirectly, as observed in the case of eucalyptus in Portugal and Norway spruce in Sweden. Overall, our research enables us to put to light the bottlenecks that may prevent the benefits from tree breeding from being realised, and offer some solutions for the removal of those bottlenecks. By placing our study in the context of the existing literature, we also demonstrate that analysing forest tree breeding through the prism of innovation theory is largely novel and has the potential of identifying salient entry points for improvement in the sector.

We proceed in four steps. The next section develops a conceptual framework supporting the analysis of innovation processes, combining two different approaches from the literature, namely the innovation system approach and the economics of innovation. The third section explains the empirical material and methods. The fourth section presents the results, which are discussed in section 5, while section 6 offers conclusions.

## 2. Conceptual framework and previous applications

### 2.1. The economics of innovation

The economic theory of innovation treats research and development (R&D) activities as investments in the production of knowledge with immediate costs and uncertain benefits in the form of increased productivity that will only materialize in the future. The rise in productivity may originate from various sources, including new or improved outputs, new, better or cheaper inputs, more responsiveness to changing circumstances or better combinations of inputs and outputs (Alston et al., 1995). As with any other form of capital, knowledge increases through investment, depreciates over time, and generates a flow of services that form an input in the production function.

In this framework, the normative assessment of innovation systems starts from the possibility of market failures, or situations where private costs and benefits from R&D differ from their social counterparts. The key concern is that because of this divergence, R&D and innovation

opportunities that would be socially desirable may not be exploited by private agents (Alston and Pardey, 1999), leading to suboptimal outcomes, and opening the door to government intervention.

The primary source of market failure results from the public good nature of the output of research, knowledge, which in its purest form is both non-rival and non-excludable (Stiglitz, 1999). Non-excludability means that appropriation of all benefits from investments in R&D is not possible due to knowledge spillovers. Non-rivalry implies that full appropriation of those benefits would not be socially desirable anyway. In the real world, the output of R&D is only a partial public good and institutions/regulations (e.g., patents) have been developed in order to define and protect intellectual property rights (IPRs). However, the situation varies tremendously across sectors due to inherent differences in technologies as well as other specificities (Cohen, 2010). In this article, we address this question empirically for the case of the tree breeding sector.

The non-rivalry of knowledge created by R&D investment also implies that knowledge development represents a fixed cost for the firm since, once produced, the marginal cost of its use is zero. However, the dynamics of competition in a perfectly competitive sector means that firms do not make excess profits and are therefore unable to recoup this type of fixed cost. It follows that R&D investments will be low unless imperfect competition creates opportunities for market rents, as proposed by Schumpeter (1942) and nuanced more recently by Aghion et al. (2005). This is likely to represent a more significant issue in commodity markets (Potts and Kastle, 2017), including those for natural resources. In addition, given that the extracted rent is also a function of the size of the market, this implies that R&D efforts are generally low in markets with weak demand or markets where the consumer has a limited valuation of the innovation (Acemoglu and Linn, 2004).

In addition to the public good nature of knowledge and technology, there are other potential sources of market failures in R&D investments. The process of innovation remains fundamentally uncertain at the level of the individual firm, creating disincentives to invest in R&D particularly in situations where credit and insurance markets are incomplete and the firm is small, limiting the possibilities of diversification. The length of the planning horizon due to long lags between investment and rewards may also result in sub-optimal levels of investment in research and innovation. At another level, research-led innovation may be hindered by informational asymmetries. The producers of innovations typically have access to more and better information than the end user of the innovation, resulting in a potential “lemon problem” (Akerlof, 1970) where the market only provides technologies, goods and services of relatively low quality, with limited innovation and quality differentiation.

Altogether, this classical approach to the economics of innovation considers that the innovation problem is essentially an allocation problem resulting from market failures and characterized by infra-optimal investments in R&D. The specific nature of scientific knowledge and technology reduces the incentives to allocate scarce resources towards R&D and the discovery of new business opportunities. From this diagnosis and the implicit assumption that governments can fix market failures follows government-led solutions involving the strengthening of IPRs, Pigovian subsidies or direct public provision of R&D efforts (Potts and Kastle, 2017). In the agricultural sector, for instance, those ideas have been instrumental in the development of a public science push model in which much agricultural research is carried out by public research institutes, universities and international organizations (e.g., CGIAR - formerly the Consultative Group on International Agricultural Research).

### 2.2. Innovation systems

The empirical observation that in agriculture and other sectors, increases in the supply of knowledge and technologies do not necessarily translate into innovation and sectoral growth has forced a re-

examination of the “innovation problem” and its solutions outlined above (World Bank, 2006). The linear model of innovation based on the premise that basic science leads to applied science, innovation and growth has proved too simplistic, leading to more attention being paid to the role of diverse actors and their interactions in innovation processes. In a first step, alternative models of innovation have been proposed, as illustrated by the demand-pull model that considers that technological innovation is stimulated by market demand rather than scientific discovery (Lane and Godin, 2013). However, more fundamental rethinking of innovation also took place by recasting the innovation problem as one of entrepreneurial discovery taking place in markets rather than knowledge creation in laboratories (Potts and Kastle, 2017).

The idea of innovation as involving complex systems of disruptive and discontinuous events resulting from the actions of networks of actors ultimately resulted in the mid-1990s in a new paradigm falling under the broad umbrella of “innovation systems” (Tidd, 2006). Those are defined as “all important economic, social, political, organisational, and other factors that influence the development, diffusion, and use of innovations” (Edquist, 1997, p. 14, cited in Purkus et al., 2018). The basic elements of an innovation system typically subject to empirical scrutiny are the actors, networks/interactions as well as institutions (Klerkx et al., 2012). However, the traditional approach to the analysis of innovation systems has been criticized for an excessive focus on structures in a largely static framework, resulting in a revised empirical approach emphasizing the dynamic processes underlying innovation, or “functions” of the innovation system (Hekkert et al., 2007).

### 2.3. Review of existing applications in the agricultural and forest sectors

To our knowledge forest tree breeding and the deployment of improved FRM conceived as an innovation process have not been the subject of previous empirical investigation, but important insights can be derived by broadening the scope of the literature review to include breeding activities in agriculture as well as generic innovation in the forest sector.

The market failure perspective on innovation has been studied extensively in agriculture, in particular through the analysis of rates of return to R&D investment in the sector, as reviewed recently by Rao et al. (2019). Their meta-analysis establishes very high returns to agricultural R&D investments, indicative of significant under-investment. Evidence pertaining specifically to breeding innovations in agriculture is limited but suggests that this general conclusion also applies to that sub-sector (Von Witzke et al., 2004).

The state of innovation research in forestry and forest-based industries has recently been summarized by Weiss et al. (2020), who reviewed a total of 230 studies identified through a systematic search. Forest tree breeding or FRM deployment does not appear in the topical focus of the reviewed articles (see Fig. 3 of the review). The vast majority of studies published to date applied qualitative approaches to models of innovation diffusion and innovation systems, while little attention has been paid to measuring the efficiency of innovation processes. It is worth noting that the literature review does not mention explicitly any market failure nor any of the concrete elements of the “allocation problem” outlined above. This absence of application of classical innovation economics to the forest sector contrasts with its popularity in other natural resource sectors such as agriculture (Potts and Kastle, 2017). However, some case studies have investigated the costs and benefits of genetic improvement programmes. As an example, Chamberland et al. (2020) compared different approaches to varietal improvement and deployment for white spruce in Quebec to conclude to the higher financial performance of scenarios involving genomic-based schemes, compared with traditional schemes. In another example, Jansson et al. (2017) concluded their review of the genetic and economic gains from forest tree breeding programmes in Scandinavia and Finland by stating that such programmes typically resulted in a positive benefit-cost

balance when using conventional discount rates in the 2% to 4% range.

The more common application of the innovation system approach to the forest sector has allowed the identification of systemic deficiencies preventing or slowing down innovation. Multiple lacks of interactions among stakeholders have been highlighted, in particular between researchers and practitioners (Stone et al., 2011), with public agencies (Aboal et al., 2018) or along the value chain (Weiss et al., 2017). The literature also focuses on other structural and functional characteristics of innovation systems in forest-based value chains, including the intensity and quality of knowledge exchange, resource mobilization (i.e., funding), missing public or private actors, innovation support policies, coordinating institutions (e.g., associations) or openness to other sectors (Weiss et al., 2020).

### 2.4. Research gap, objectives and conceptual framework

Altogether, although the analysis of innovation in the forest sector is not new, we identify important gaps, including: 1- The lack of application of the innovation system perspective to the specific issue of forest tree breeding and FRM deployment; 2- The near absence of application of the traditional economic analysis of innovation to the forest sector; and 3- A relative lack of cross-country analyses of innovation in the forest sector, allowing to put national contexts into a broader perspective, as underlined by Weiss et al. (2020). Thus, analysing forest tree breeding and FRM deployment through the prism of innovation theory is largely novel and has the potential of identifying salient entry points for improvement in the sector.

We frame our investigation by combining several approaches outlined above with the aim of deriving broad insights into the workings of a sector that has not been previously investigated. Our first specific objective is to diagnose potential systemic failures that currently hinder innovation in the forest tree breeding sector. For that purpose, we start by presenting the tree breeding innovation system by adopting what Klerkx et al. (2012) refer to as an “infrastructural view”. Although largely static, this approach allows us to lay out the main components of the system, such as the actors, their activities and the key public policies related to the studied innovation. This static analysis is then complemented by a more dynamic one focusing on the functions of innovation systems as proposed by Hekkert et al. (2007). Those functions include knowledge development, entrepreneurial activities, knowledge diffusion through networks, guidance of the search, resources mobilization, market formation and the creation of legitimacy. Our second objective is to analyse incentive issues highlighted in the economics of innovation, and that could be related to functional deficiencies identified before. Our analysis will address successively failures related to demand and supply sides.

## 3. Empirical methodology and background information

Breeding activities as well as FRM production and deployment are specific to species and, most of the time, also countries. As a consequence, the case studies correspond to combinations of tree species and European countries. For each case, the tree species represents a significant area in the country and at least one breeding programme exists in this country. The four cases correspond to three different zones of Europe: Portugal (southern), France (central), and Sweden and Finland (Northern). These cases were also chosen to capture various organizational and institutional contexts.

We present here the methodology used for collecting data and general background information. Background information covers, for each of the cases studied, the context of forest production and wood transformation. The innovation system related to FRM research and production will be analysed in detail in the results section.

**Table 1**  
Number of interviews per case studied and type of organization.

Tree species	Country	Eucalyptus	Maritime pine	Norway spruce
		Portugal	France	Finland and Sweden
Upstream	Breeding organizations	2	3	2
	Seed producers and nurseries	2	6	2
Forestry	Confederations of associations, cooperatives, farmers and forest owners	3	3	2
Wood processing	Industry associations	1	1	1
Transversal	Professional organizations	1	1	0
	Regulatory organizations	1	1	4

**Table 2**  
Key figures of the forest sector for each case studied.<sup>a</sup>

	Maritime pine – France	Norway spruce - Sweden	Norway spruce - Finland	Eucalyptus – Portugal
Total area	1.03 Mha	6.4 Mha	Polyculture - spruce is the dominant species on 5 Mha	845,000 ha
Number of forest owners	250,000 in Nouvelle Aquitaine	> 300,000	500,000	400,000
Ownership structure (percentage of the area)	Private forest owners: 87%	Private forest owners: 50% State: 20% Companies: 25%	Private forest owners: 58% State: 37% Companies: 5%	Private forest owners: 83% Companies: 17%
Age of logging	about 40 years	60–70 years in the South / 100–120 years in the North	From 50 to 100 years - more generally about 60–70 years	1 rotation: 10–12 years - generally 3 rotations for a stand
Thinnings	3 to 4 between 10 and 30 years	1 or 2	2 to 3 at 25–30 years and 40–45 years	None
Productivity	about 12 m <sup>3</sup> /ha/year	3–8 m <sup>3</sup> /ha/year	2–6 m <sup>3</sup> /ha/year	6–10 m <sup>3</sup> /ha/year
Income Streams from silviculture	Gross margin: 200–250€/ha/year	Revenues: 205€/ha/year	Revenues: About 250€/ha/year	Gross margin: about 260€/ha/year
Replanting costs	about 1000€/ha	930€/ha	1500€/ha	1800–2000€/ha
Wood price	about 40€/m <sup>3</sup>	45€/m <sup>3</sup> (for logs) and 30€/m <sup>3</sup> for pulp	57.8€/m <sup>3</sup> for logs and 17.7€/m <sup>3</sup> for pulpwood	about 45€/m <sup>3</sup>
Wood volume	growing stock: 143 Mm <sup>3</sup> uptakes: 6.9 Mm <sup>3</sup> /year	growing stock: 1300 Mm <sup>3</sup> annual fellings: 40 Mm <sup>3</sup>	growing stock: 740 Mm <sup>3</sup> 31,6 Mm <sup>3</sup> drained annually	pulp&paper companies' supply in portuguese wood: 5.5 Mm <sup>3</sup> /year
Wood processing outlets	Lumber: about 60% Industrial wood (wood chips and paper pulp): 30% Chemical industry/ wood energy: 10%	Main outlets: sawlogs and pulpwood Residuals are used for bioenergy production and heating	Logs - structures, panels, furniture: 55% Pulp / paper: 40% Energy: 5%	Mainly pulp and paper

<sup>a</sup> A conversion rate of 0.093€/SEK is applied for Sweden (average rate over the five last years).

### 3.1. Data collection

To elaborate this analysis, we used bibliographic resources (websites, technical reports, scientific articles, etc.) and information gathered through semi-structured interviews with stakeholders related to each case study.

Very few studies (if any) exist, to our knowledge, describing the organization of research activities and the diffusion of improved varieties in forest tree sectors. We therefore conducted 36 semi-structured interviews with different stakeholders between January and October 2020 (see Table 1 for details). Most of the interviews, which lasted an average of one hour and a half, were conducted by telephone or videoconference. The need for a broad comprehension of the sector advocated for a specific interview guideline for each interviewee on the missions and activities of his/her organization and its links to the other stakeholders. The guideline covers the presentation of the interviewee, the description of the activities of his or her organization and his or her personal opinion on the issues and prospects for the sector for the species and country of interest. Thus, our interviewees were asked to describe the functioning of the sector in their field of activity (research in varietal improvement, dissemination of improved varieties, forestry, wood processing) by presenting the actors involved and their respective missions, their perceptions of the issues specific to their activities, the regulations and their justification, as well as the link with the other

actors in the sector. Appendix B provides the detail of one interview guideline addressed to a cooperative in Portugal. These interviews were systematically recorded in agreement with the interviewees. A detailed report of each interview was drafted and sent to each of our interlocutors for review and validation. Four reports have been elaborated from each of the case studied. These reports synthesize the features collected in the bibliography and during the interviews.

Our investigation had two parallel objectives: compiling factual elements on the organization of the sector and more subjective elements on the stakeholders' strategies and visions. The first objective was met on the basis of bibliographic resources and interviews. Each interviewee having an expertise on one specific part of the sector, the data collected were not comparable and no coding was necessary. The numerous sources of information corresponding to this first objective are not detailed in the following result section but they are provided in the case study reports that are available from the authors upon request. On the second objective, we gathered opinions on specific themes related to barriers and levers to innovation in the sectors studied. These elements were coded in the detailed reports to allow us to analyse the convergences and divergences of stakeholder's opinions, following a thematic coding as proposed by Miles and Huberman (1994). The results corresponding to this second objective are identified in the next section by making explicit references to the interviews and providing some verbatim quotations.

### 3.2. Background information on forest tree production and transformation

Table 2 synthesizes some key figures for each of the cases studied. Each species covers from 0.8 to 6.4 Mha per country studied<sup>1</sup> and represents the most – or one of the most – important forest species in each country. In all cases, the stands are mainly owned by a very large number of small forest owners who manage very small areas, their forest activity being generally secondary. In the case of maritime pine in France, and more specifically in the main growing area (Massif des Landes de Gascogne which is part of Aquitaine), the average area grown by independent owners is 38 ha, which is larger compared to the other cases.

On the side of these independent forest owners, in Portugal and Sweden, private forest industry companies also grow a significant part of the productive forest land (17% for Portugal and 25% for Sweden). At last, forest can also be owned by the state, which is the case in Scandinavian countries for a significant proportion of the forest, and in France where the public entity ONF (Office National des Forêts) owns and manages, for maritime pine, the narrow strip of coastal forests located along the Atlantic ocean. In this last case, maritime pine is used mainly for the environmental management of coastal dunes.

Except for eucalyptus, the forest production cycle is very long and lasts several decades. For eucalyptus, growers can harvest after 12 years and keep the same stand during three rotations. Thinnings are made for maritime pine and Norway spruce but they do not generate significant net revenues. The revenues come mainly from the wood harvest, with levels that are quite similar among the cases (between 200 and 250€/ha/year). Replanting cost ranges from 1000 to 2000€/ha and wood price ranges between 40 and 60€/m<sup>3</sup>. Hence, the main difference between these different cases is related to the duration of the production cycle, which is particularly short for eucalyptus.

A large proportion of private forest owners subcontract the management of their forests to service providers. The services cover soil preparation, stand installation, forest management (thinning for example), harvest and tree logging. Indeed, these operations require specific and expensive equipment that can hardly be afforded by small forest owners. Service providers are generally small business units. They play an important role for stand installation in Portugal (contractors), in France (ETF – Entrepreneurs de Travaux Forestiers) and in Sweden and Finland. In France, big cooperatives like Alliance Forêt Bois or UniSylva are also major actors who provide forest management services. In Sweden and Finland, large forest industry companies have procurement units offering all aspects of forest management and local associations of forest owners provide forest planning and management services.

The wood produced by forests can be used for multiple purposes. In Portugal, eucalyptus is mainly processed as pulp and, from pulp, into paper and cardboard. The transformation process is operating in mills. The main pulp and paper companies are The Navigator and Altri. Pulp production is the core of their business, but they have vertically integrated forest production as well as FRM related activities. The other forest industry companies, which are not vertically integrated, are Renova, DS Smith and Goma Camps. For maritime pine in France, the same stand and the same tree can supply various outlets depending on the parts of the trees (thinning wood with low diameter, trunks with large diameter, bark...). The main outlets are lumber (factory and shop lumber, structural lumber, furniture, wooden floor...), industrial wood (wood chips and paper pulp), chemical industry and wood energy. The case of Norway spruce in Nordic countries is somewhat intermediate between those of eucalyptus in Portugal and maritime pine in France.

<sup>1</sup> See appendix C for a map of the geographical distribution of maritime pine stands. A map for eucalyptus in Portugal is available in Deus et al. (2022). In the case of Norway spruce in Finland and Sweden, the stands are distributed throughout the countries except in Lapland.

55% of the outlets in wood volume corresponds to the production of structures, panels, furniture, etc. Spruce also has long lean and straight fibers which makes it an ideal raw material for the forest industry companies (40% of the outlets). It is also a source of biomass for the production of renewable energy (5%). There are five large forest industry companies in Sweden (i.e., the “big five”): Sveaskog, Holmen Skog, Stora Enso, SCA and Södras. Some of those are multinationals. These companies are vertically integrated as they own forest land, orchards, and tree nurseries in addition to their core wood processing facilities. Some large industry companies also process Norway spruce wood in Finland (e.g. UPM, Stora Enso, Metsä Group – which is a cooperative).

Forest production may be affected by specific events. Portugal is regularly affected by wildfire and the presence of eucalyptus forests is often mentioned as a prominent cause. As a consequence, since 2018, eucalyptus growing has been highly constrained by a restrictive legislation which prohibits any increase in eucalyptus area, and has an explicit aim to decrease that area. Planting eucalyptus stands on new areas is forbidden, and the replanting has to be approved after submitting a project.<sup>2</sup> Forest owners have to decrease their plantation area by 10% until the regional area reaches a certain limit. In France, maritime pine production was affected by two major storms in 1999 and 2009 which destroyed more than one third of the production. Replantation on these surfaces has been subsidized but this created a demand shock for FRM. Finally, in Nordic countries substantial forest damages are caused by a variety of factors, including storms, excessive snow loads, freezing and fungi (e.g., annosum root rot).

## 4. Results

### 4.1. A structurally sound system of innovation in forest tree genetics

We first characterise the innovation supporting infrastructure by describing the main actors and their interactions, together with the infrastructures governing their behaviours, such as regulations (Klerkx et al., 2012). In each case study, tree breeding started several decades ago and generated several generations of innovations (see appendix A for more details). We here present the innovation system that leads to the development of new FRM, their deployment and adoption. The tree genetic innovation system covers multiple complementary activities, intermediary markets where the products or services related to these activities can be sold and, at last, a regulatory framework that provides guarantees on FRM quality. The activities of this innovation system cover tree breeding leading to new tree varieties, the production of improved FRM, and various extension activities enabling the forest grower to choose adequate FRM and silviculture practices.

The breeding activity consists in creating new varieties with interesting characteristics on various criteria. For each species, the breeding program started in the 50–60’s by the selection of particularly interesting trees (called “Plus trees”) in wild stands. Since then, several breeding cycles have been carried out recursively. As for the breeding of any other species, each cycle consists of two successive steps: (i) the cross-fertilization of parental trees that have been selected at the previous cycle, each cross generating offspring that are candidates for selection, and (ii) the evaluation of the performance of the candidates and

<sup>2</sup> This issue is a major concern for the eucalyptus sector. Six of the ten interviewees mentioned this point, reporting that the general public considers eucalyptus plantations as responsible for the dramatic propagation of forest fires, and considering the regulation as an important constraint for the eucalyptus sector. The link between the species and fire propagation is rather controversial. Two interviewees explained that scientific studies show that eucalyptus does not propagate fire more easily than other tree species, and that the main determinant of fire propagation is the poor management of the eucalyptus stands by small forest owners.

**Table 3**  
Actors involved in FRM production.

	Maritime pine – France	Norway spruce - Sweden	Norway spruce - Finland	Eucalyptus – Portugal
Seed orchards	Consortium between seed companies (ONF or Vilmorin) and nurseries	Big five forest companies: Sveaskog, Holmen Skog, Stora Enso, SCA and Södras	Tapio Silva Oy and Siemen Forelia (partly owned by the Finnish State)	Altri and Navigator
Seedling production from seeds	Independent nurseries (e.g. Foréélite, Planfor, Le Plant Landais, Naudet)	Big five forest companies (85–90%)	Numerous independent nurseries	- Subsidiaries of Altri and Navigator - Independent nurseries (50%)
Clone production		Not possible		Mainly Navigator

the selection of the best ones. New improved FRM can be created at each cycle on the basis of some of the selected trees. Tree breeding requires specific skills in genetics, physiology and statistics. The evaluation of the performance needs to be carried out within the producing region of the selected species. Within each country we observe generally one and possibly two breeding programs for a given tree species. For maritime pine, two breeding programs were launched initially by two public institutions (INRA and FCBA) and, since 1995, they have been jointly funded and coordinated within a specific structure (GIS “Pin Maritime du Future”). For Norway spruce, there is one breeding program in both Finland and Sweden, carried out by public institutions. In Finland, LUKE (Natural Research Institute Finland) is publicly funded while the breeding program in Sweden is funded half publicly and half privately. At last, for eucalyptus in Portugal, two breeding programs are carried out by the two main pulp and paper companies: Altri and The Navigator Group.

FRM production involves the production of seedlings of improved material that can then be sold to forest owners for planting new stands. Two main technical channels of FRM production are possible: the cloning of the selected trees, but this operation is not always possible at moderate cost; and the production of seedlings from seeds harvested in a dedicated stand (seed orchards) installed with trees from the breeding program. The production of clones or seedlings from seed is made in nurseries. The installation, maintenance and harvesting of seed orchards can be independent from the nursery activity. Most of these activities are now carried out by private actors as indicated in Table 3. It should be noted, however, that for Norway spruce in Finland, Tapio Silva Oy and Siemen Forelia are joint-stock companies with a high level of involvement of the Finnish state. Also, for maritime pine in France, the installation of seed orchards was highly supported by the state in the past. Seed production, which requires rather long-term investments, is more concentrated than seedling production. In some cases, seed and seedling production are integrated and made either by big enough nurseries (maritime pine in France) or large forest industry companies (Norway spruce in Sweden and eucalyptus in Portugal). In this last case, these large companies are also investing in the breeding activities.

Seeds, clones and seedlings are FRM whose commercialisation is regulated by the European Directive 1999/105/EC on the marketing of forest reproductive material. The main objective of this regulation is to define traceability rules and quality standards to guarantee the origin and the quality of the FRM sold to forest owners. In other words, this regulation reduces information asymmetry between FRM producers and users. Different categories of FRM are defined, depending on the type of provenance and the level of information available on this material: source-identified, selected, qualified and tested.

Extension activities are important for the deployment of improved tree varieties by providing information on the performance of these varieties. These activities cover more broadly all advice related to legal,

fiscal and regulatory issues, as well as economic and technical topics, including the choice of the FRM. They combine, on the one hand, a back-office activity which consists of reference acquisition based for example on field tests comparing different FRM and, on the other hand, a front-office activity which covers multiple forms of exchange with forest owners leading to the diffusion of the information. Many players are involved in these activities and, as is common in agriculture, forest owners do not pay directly for this service. For eucalyptus, this advice is mainly given by forest owners’ associations, cooperatives and technicians from the industry. In the case of maritime pine, the main actors of the extension are public entities (CRPF), forest owners’ associations (SPFA) and cooperatives (e.g. Alliance Forêts Bois, UNISYLVA). In Sweden and Finland, forest owners’ associations also play a key role in diffusing technical and economic information to forest owners, together with the procurement arms of the main forest industry companies. Service providers specialised in tree production also provide advice to forest owners because they have generally knowledge of FRM material and silviculture practices.

Altogether, this overview establishes that the structure of the analysed tree breeding sectors is sound in the sense that it does not suffer from obvious infrastructural failure: all the markets, actors, economic activities, networks and regulations are in place to support the innovation process.

#### 4.2. Some functional deficiencies

The capacity of those systems to deliver all the functions necessary for the efficient production of innovation is much weaker, however. With reference to the seven functions of innovation systems proposed by Hekkert et al. (2007), henceforth denoted F1 to F7, the collected information suggests that current setups present several limitations.

There is no doubt that knowledge development (F2) for the breeding of the three species proceeds continuously, as evidenced by regular academic publications and conferences. The mobilization of resources (F6) for this R&D work occurs from both public and private sectors, depending on the species and country and as detailed further in section 4.4.

However, the current systems leave rather little room to entrepreneurial activities (F1), with limited influence of market forces in guiding the search (F4) for new technologies and FRM products. Hence, for the case studies in Finland, France and Sweden, public institutions and researchers strongly determine the direction of the innovation process, with market participants adopting a largely reactive role through contributions to various forms of consultations. The breeding of Eucalyptus in Portugal, which is largely the result of private initiatives, stands as an exception to which we will return in section 4.4.

The produced knowledge diffuses through formal and informal networks (F3) but only imperfectly, as revealed by our interviews.

**Table 4**  
FRM production, commercialisation and use of the studied species (source: own interviews).

	Maritime pine – France	Norway spruce – Sweden	Norway spruce – Finland	Eucalyptus – Portugal
FRM production capacity	- 300 ha of seed orchards currently in production - 124 selected stands on 13,211 ha	Mainly seed orchards, in 44 sites and on 470 ha	- 30 seed orchards: 348 ha - selected stands	- 8.2 ha of seed orchards (open-pollination) and 40 ha of propagation parks (controlled crosses): 48 ha - 330,000 clone plants (17 genotypes) - selected stands
Area replanted each year with FRM	30,000 ha	100,000 ha	50,000 ha	10,000 ha in 2018 (decrease)
Seedlings sales	36 millions/year - 96% of the annual planted area is installed by seedlings, of which 96% come from seed orchards	190 millions/year	100 millions/year - about 60% are improved but varies a lot	About 20 millions/year - 25% clones, 25% improved seedlings - 50% commercial seedlings
Replanting costs	about 1000€/ha	930€/ha	1500€/ha	1800-2000€/ha
Seedlings price	0.20€/seedling - 300€/ha	0.1–0.5€/seedling	0.20 €/seedling	- clones: 0.20–0.30€ - improved seedlings: 0.15–0.20€ - commercial seedlings: 0.10–0.20€

Interviews revealed that some forest owners “are completely unaware of genetics” (a forest cooperative in maritime pine), “often lack knowledge about tree breeding and its benefits” (public organization, Norway spruce), but this situation tends to evolve with the extension activities; “forest owners tend to be interested in and positive about the genetic improvement of trees, reflecting the efforts made by the forest industry to explain tree breeding and its merits” (nursery, Norway spruce). This is particularly true in the case of eucalyptus where “most of the forest producers understand the importance of using good plants, (...) [they] expect from improved materials better performance in pest resistance and growth” (a confederation, eucalyptus). This lack of knowledge diffusion can also be observed for new technologies. In the case of maritime pine, six of the interviewees indicated that they did not have sufficient knowledge to answer our questions on the impact of new technologies. A maritime pine seed producer argued: “we trust the researchers, we consider that they are much more competent to use the most adapted means (...) we are far from this part of the selection”. In the case of eucalyptus, two interviewees expressed clearly their ignorance of new technologies, but apart from those of breeders, the answers from respondents lacked precision on this topic, suggesting that their knowledge is limited. The respondents for the Norway spruce study seemed to be more aware of the technological opportunities, as five of them mentioned somatic embryogenesis as a promising new technology for tree vegetative propagation.

At another level, our empirical analysis did not detect meaningful advocacy coalitions promoting tree breeding as a promising solution to tackle the multiple challenges faced by European forests. Hence, current systems do not perform the function of enhancing the legitimacy (F7) of forest tree breeding.

Finally, we were unable to identify protective measures aimed at facilitating the development of market related to genetically-improved FRM, whether regulatory or fiscal, so that the market formation (F5) of current innovation systems appears very weak.

#### 4.3. Lack of demand-pull

Several of the functional deficiencies outlined above may be explained by the fact that demand for improved varieties of trees is limited, which reduces the incentives for entrepreneurs to search for new business opportunities (F1), create advocacy coalitions (F7) and establish niche markets (F5). The main idea relates to the fact that trees are perennial crops harvested after several decades. We illustrate this argument more particularly with the case of maritime pine in France, for which the production cycle lasts approximately 40 years, but the ideas are transposable to all countries and species under investigation.

First, the market size for new varieties to consider is defined by the

surface planted each year. However, as stands are established for a long period, this surface is only a small fraction of the total acreage for this forest tree. Maritime pine in France covers >1 Mha but only 30,000 ha are planted each year (about 1/30).

Second, for most tree species, the harvest is made at the end of the production cycle. Thinning may occur in between, but it only generates moderate profit. For maritime pine, it is generally considered that the sale of wood from thinning is just enough to cover the cost. Most of the traits that are improved for tree production are related to the yield and the quality of the wood. Hence, the benefit from using improved varieties is obtained after several decades while the cost of the seedling occurs in the first year. As a consequence, the benefit is highly discounted compared to the cost. For example, with a 4% discount rate, 1€ of benefit earned after 40 years is equivalent to 0.21€ of benefit earned the first year. In addition, the forest owner faces multiple risks during this long production cycle, as several problems may affect the plantation (storm, fire, pest, etc.) and wood prices can also fluctuate.<sup>3</sup> For these different reasons, the potential benefit of using improved varieties is highly discounted at the time when the farmer has to make his planting decision. Some approximate figures related to maritime pine can illustrate this argument. Average yield after 40 years is 320 m<sup>3</sup>/ha leading to a 12,800€/ha sale. A 1% yield gain generates an extra 128€/ha at harvest, but only 27€/ha after discounting and much less if risk is taken into account. Knowing that seedling cost is about 250€/ha for maritime pine, the valuation of improved seedling is rather limited. All these figures illustrate the “tyranny of discounting” also observed in other sectors (Lozhnikova et al., 2014).

The two arguments mentioned above depend a lot on the duration of the production cycle. In this aspect, eucalyptus is specific with a short cycle of 10–12 years between successive harvests. Note that eucalyptus can regenerate after harvesting so that plantation occurs only after 2 or 3 rotations (24 or 36 years). Hence the surface planted each year is very small compared to the total surface of eucalyptus, as for the other tree species. However, the effect of benefit discounting is smaller because of shorter rotations.

A third complementary argument corresponds to the perceived gain of the forest owners from using improved FRM in their specific context. Because of interaction between genotype and environment, the best improved FRM may be different from one plot to the other. With annual crops, this explains why a farmer generally does not use only one seed

<sup>3</sup> The forest owner can manage short-term price fluctuations by postponing harvest. However, more structural and long-lasting price fluctuations are a source of uncertainty.



product and prefers to experiment a new seed product on a limited area before using it more widely. This learning strategy is not possible with tree production because of the much longer duration of the production cycle. Hence, even if forest owners are informed by extension services about the potential performance of improved varieties, the perceived benefit they can get from this improved FRM on their specific land is more uncertain and lower. This is especially true for species with long production cycles. In the case of maritime pine, one interviewee explains that it is impossible to install the evaluation stands before the commercialization of the new variety, as it is necessary to wait for the seed orchards to be productive. Once seeds are collected on the seed orchards, they are used both for commercialisation and evaluation, but the first results of the evaluation are not available before 8 years, even though the variety has been deployed since then. This interviewee argued: *“several trials are needed to average the environmental effects of the area where the trial is installed. We have a correct evaluation of the variety (...) at the moment when we stop marketing it!”*. In the case of eucalyptus which has shorter production cycles, the evaluation in specific growing conditions is easier and can be shown to forest owners. One interviewee added that *“when the forest owners doubt about the improved eucalyptus materials, the nurseries give them some materials they can plant in their stands. Hence, the forest owners can see the difference by themselves”*.

These different arguments can be applied to all tree species with some variation depending on the specificities of each species. Additional arguments are related to regulatory uncertainty and may vary depending on the country. In Portugal, the wildfires led to important restrictions on eucalyptus plantation. New areas of eucalyptus cannot be planted, and forest owners can only replant the surface that is cut if an authorization is granted. As long as this regulation is in place, the total surface of eucalyptus in Portugal can only decrease and the forest owner may decide to keep its plantation for a longer period. In France and many other European countries, there is a controversy about clear cutting. This practice is currently not regulated but there is uncertainty about possible restrictions in the future.

In summary, the markets for improved tree varieties are limited for the tree species considered here because of the limited area planted each year and the limited valuation of forest owners for improved varieties (Table 4). To give an illustration, the market for maritime pine seedlings, which is the largest among forest tree species in France, represents about 7.5 M€, while annual seed sales in France amount to >200 M€ for major crops such as wheat or corn. Most of these seedlings are produced from seeds coming from seed orchards, and seed cost represents about 25% of this figure.

On a different ground, the discounting and uncertainty of future gains explain why forest owners have limited incentives to adopt tree varieties adapted to specific use. One interviewee in the case of maritime pine reported that *“forestry advisors tell forest owners: ‘above all, grow reversible crops, don’t specialize too much because it is risky’”*. For example, the wood from maritime pine is commonly used primarily for lumber (construction or furniture) but the use for bioenergy increased during the last decade. Even if it was possible to develop new varieties with increased efficiency for bioenergy production, all the supply chain from seed producer to forest owner may have limited interest because of the uncertainty of the downstream industrial demand for this particular outlet after one or two decades. Hence, it is generally recognized that the heterogeneity of the FRM demand is mainly driven by adaptation to the producing conditions and there is no differentiation with respect to the final use of the wood.

At last, the demand is also limited because the markets are generally national so that international trade in FRM remains small, even if the

FRM regulatory framework is harmonized across Europe and a large number of countries worldwide. In some cases, this lack of trade can be explained by the adaptability to local production conditions, with an improved tree selected in one country likely to perform poorly in another. Trade can also be limited for sanitary reasons. For example, pine nematode has been a source of major damage in Portugal since 1999 and Spain since 2008. It is not yet present in France but it represents a major threat, so that FRM imports from these countries are prohibited. In a similar vein, policies aimed at preserving biodiversity, such as Norway’s Nature Diversity Act, create non-tariff barriers to trade. Finally, the previous arguments explaining the low valuation of forest producers for improved FRM apply to all countries. Hence, the potential benefit from exporting FRM is limited, while engaging in international trade imposes a minimum fixed cost, at least to contract with local actors.

#### 4.4. Private incentives on the supply side

The supply side covers the multiplication of FRM and the breeding for developing improved material. The two activities are important for innovation. Breeding defines the level of the innovation, while the multiplication of FRM is key to the diffusion of the innovation, the two activities then combining to produce the total impact of the innovation. For both activities, the long time interval for growing trees creates specific problems that reduce the private incentives to invest in these activities.

FRM production is constrained by production capacity, as adjusting capacity entails costs and requires time, hence creating inertia. Production capacity corresponds to hectares of orchards for producing seed or, in the specific case of eucalyptus clone production, the growing of mother plants. As an illustration, one hectare of maritime pine seed orchard costs 10,000€/ha for the set up and 2000€/ha/year for the management during the first ten years. The inertia for adjusting these capacities is related to the length of the period before the maturity of the tree, which is necessary for producing seeds (8 to 10 years for conifers). Because of this production capacity constraint and possibly specific problems like pests or bad weather that can affect yields, shortages have been reported by a large number of interviewees (9 in the case of maritime pine and eucalyptus and 7 in the case of Norway spruce). For example, the share of improved Norway spruce seedlings from nurseries has fluctuated between 20% and 75% in Finland over the past decade. In the case of eucalyptus, respondents indicated that the shortages tended to decrease because of the reduced demand linked to the new regulation limiting the possibility of replanting eucalyptus stands.

Seed shortage is typically more pronounced for the most recent improved material that embed the highest genetic gain. One reason is that the length of time during which a seed orchard is productive is generally longer compared to the interval between generations of new improved material. As investments in seed orchards are more easily covered when seed harvests are continued in existing orchards, seed producers have a low incentive to replace their old but still productive seed orchards by new and genetically superior ones. One interviewee added that *“investing in a seed orchard is both risky and expensive. Expensive because it requires a significant investment, and risky because production is not certain due to possible issues like storms and biotic problems”* (maritime pine - seed producer). Seed shortages are often overcome by collecting seeds in selected stands, i.e., forest stands which were not installed for seed production but whose characteristics are considered interesting for this purpose. Seed shortage problems could also be avoided by oversizing production capacity. However, such a strategy

requires high investment that cannot usually be covered by the sales of rather moderately-priced seeds.

Concerning breeding, the common wisdom in the agricultural economics literature corresponds to the situation observed for annual crops where we observe that breeding is carried out as a stand-alone activity by seed companies, who can cover their research cost by the sale of improved seeds. This scenario is never observed for tree breeding because of the long duration of the breeding cycle and the limited demand for improved material. Indeed, one breeding cycle lasts one or several decades, because multiple years are necessary to get mature trees ready for crossing and the performance of the candidates can only be evaluated with old enough trees. As a consequence, for the three species studied here, private seed or nursery companies can be involved in the multiplication of the improved material, but they do not fund breeding programmes on the basis of the expected markup from seed or seedling sales. Indeed, interviews indicate that a large part of the seed price is related to seed and seedling production cost, leaving limited margin for research funding<sup>4</sup>: “50% of the price of the seed corresponds to the maintenance and depreciation of the seed orchard, and the other 50% to the harvest and production of the seed” (maritime pine - nursery); “genetic improvement does not cost anything, it does not weigh much in the price” (maritime pine - seed producer); “I would like that the difference of price comes from the effort of breeding... but breeding is not a business” (eucalyptus - association); “we charge the cost of producing the grafts, not the cost of the breeding programme” (Norway spruce - breeder). Seed price differentiation is essentially linked to the productivity of seed orchards and harvest costs, and various interviewees report that prices are identical for improved and non-improved seeds, but this tends to evolve especially in the case of Norway spruce where interviewees observe some attempts by nurseries to differentiate prices.

However, we observe important breeding investments by forest industry companies in the case of eucalyptus in Portugal and Norway spruce in Sweden. In both cases, the companies are not only involved in wood transformation but also in tree production. In Portugal, Altri and Navigator, the two major pulp and paper companies manage 20% (0.17 Mha) of eucalyptus production. In Sweden, the major forest industry companies (Sveaskog, Holmen Skog, Stora Enso, SCA and Södras) manage 25% (6 Mha) of Norway spruce production. For eucalyptus, both Altri and Navigator manage their own breeding programmes. For Norway spruce, the companies fund half of the breeding program that is managed by Skogforsk. In both cases, interviews revealed that breeding was a long-term investment to guarantee the supply of wood as close as possible from the pulp and paper mills and other factories processing wood. Indeed, these plants represent major investments that require the regular supply of good quality wood in sufficient quantity. These constraints explain the investments in breeding as well as seed and seedling production. One breeder explained: “we do not aim to make the breeding activity profitable, it is rather a strategic activity. Our goal is to be able to improve the quality of growing stock in a continuous manner”. One other interviewee explained that “The big issue is to have sufficient raw materials for the mills that produce pulp and paper (...), this is why [eucalyptus breeders] want the Portuguese forest to be productive”. Six of our interviewees in Portugal recognize that breeders, integrated with pulp and paper companies, have a clear goal of increasing eucalyptus productivity, even more because the planted area cannot extend. It should be observed that, even if these companies are involved in tree production, most of the wood used in the mills comes from independent forest owners. Indeed, as the central aim of these companies is the supply of wood to mills, they are generally open to disseminate to independent forest owners both the genetic material and management practices they apply in their own forests. When this occurs, this diffusion is made at a moderate price, as the prime objective of these companies is not to make

profit out of seeds or seedlings but to increase the supply of wood to their mills. This statement is shared by five interviewees in the case of eucalyptus in Portugal: “We sell improved seeds to independent nurseries, without profit (...), in order to improve the availability of the better plants to portuguese forest” (a nursery belonging to a pulp and paper company), “the industry supplies the associations with the best plants (...), they make improved plants available, even giving them or selling them at a symbolic price” (association); “Since the regulation constrains a lot the eucalyptus plantations, there is a high stake in terms of increasing wood production by using improved materials (...). In this context, it is relevant that private nurseries can have access to improved seeds” (an association).

In summary, these case studies show that, despite the long duration of the breeding cycle and the limited market size for improved tree varieties, we can observe a private incentive to invest in breeding. However, the business model that drives this incentive is different from the classical business model that usually drives the incentives for breeding investment by major agricultural seed companies. Here, the investment is made by downstream companies that invest in all the upstream activities to secure the supply of their plants. One interviewee explains that, worldwide, the forest industry companies that invest in breeding are only those who are also involved in the production of wood on large areas. Hence, the breeding investment is part of a general investment of these companies in upstream activities.

This case with major private investment in tree breeding is rather exceptional. For most of the tree species, private investment for breeding is very limited, and breeding activities rely exclusively on public research organizations and public investment. For Norway spruce, the breeding activities rely on LUKE in Finland and Skogforsk in Sweden with the participation of private funds for half of the budget, as described above. For maritime pine, the breeding relies on two public organizations, INRAE and FCBA, coordinated within an ad-hoc structure (GIS Pin Maritime du Futur). To provide more precise figures, we estimate the investment in breeding for maritime pine over the period 2015–2020. The average investment was 693,000 €/year. The sources of funding were 95% public<sup>5</sup> and 5% private (seed producers or forest owners).

## 5. Discussion

Our analysis shows that even if the innovation system in place does not suffer from obvious infrastructural failure, several functional deficiencies can be observed, limiting the dynamics of the system. In this section we discuss three main factors that may change this situation in the coming years: (i) the introduction of new technologies as well as the entry of new players and start-ups in research, (ii) new mechanisms for private funding of research and (iii) the valorisation of forest ecosystem services.

New technologies (e.g., genomic selection, genome editing) create opportunities for improving the efficiency of breeding activities. For example, the application of genomic selection to dairy cattle breeding enables the selection of young bulls, hence shortening the duration of the breeding cycle (Xu et al., 2020). Forest tree breeding is heavily constrained by the duration of the breeding cycle and the cost of phenotyping so that new technologies may also have major advantages in this case. However, contrasted observations can be made concerning the potential impact of new technologies in the coming years. On the one hand, as already pointed out, the impact of new technologies was explicitly mentioned in all interviews, but very few interviewees showed a high interest and expertise in this area. The first reason for that is that the structural constraints on both the demand and supply sides (cf. section 4.3. and 4.4) reduce the potential benefit from the possible

<sup>4</sup> To illustrate this, the annual license fee paid by seed producers to public research for having access to new improved varieties is 35,000 €.

<sup>5</sup> Self-funding by the two public organizations covers 67% (of the total investment) and subsidies by the Region Nouvelle-Aquitaine, French State and the EU cover 27%.

increase in genetic gain. The second is related to efforts to preserve the naturalness of forest production by preventing the use of GMOs, as exemplified by the requirements of sustainable forest certification schemes (e.g., principle 10.4. in [Forest Stewardship Council, 2023](#)). This second reason is in line with the review by [Pelai et al. \(2020\)](#) who show that regulatory and legal mechanisms are more important barriers to biotechnology in the forest sector compared to agriculture in general. On the other hand, empirical evidence shows that several start-ups exploiting these new technologies are emerging. These start-ups are often providing research services for incumbents (e.g., Gondwana Genomics<sup>6</sup> based in Australia specialised in genomic selection, SweThree<sup>7</sup> in Sweden specialised in somatic embryogenesis and, more recently, genome editing). In some cases, start-ups are new entrants in the breeding activity with the objective to supply improved material (e.g., Living Carbon that recently commercialized GM poplar with photosynthesis enhancement trait to increase carbon sequestration<sup>8</sup>). New technologies may thus be introduced by new players and the rather conservative views of the incumbents we interviewed may evolve at some point if the new players' strategy is successful enough. However, we also know that start-up activity is highly risky with many failures so that those types of structural changes may only be transitory.

Tree breeding is very often publicly funded. However, private research funding can be an important factor to leverage tree breeding activities. Analysing the incentives for private research funding is thus important. One key result from our analysis is that the sale of improved seeds, which is the usual mechanism to create incentives for private research investment in the annual crop and vegetable markets, does not work in the forest tree sector. There is thus a lack of demand pull. For the time being, private research funding for tree breeding comes mainly from large multinational companies that integrate tree production. For those, investing in tree breeding is a way of securing the long-term supply of raw materials for large processing plants. Such investments only make sense if they are combined with investments in forest production, which requires large amounts of capital. A radical increase in these investments is rather unlikely. However, breeding activities may also be privately funded through alternative mechanism such as a levy on the product, also called End-Point Royalties, as is the case for some crops in Australia and Canada ([Gray, 2012](#)). In the case of France, 9.5 M€ is currently collected from forest harvesting<sup>9</sup> and the first processing stage. However, this fund is used to promote multiple activities related to the forest sector and a very low share goes back to breeding activities. Funding breeding activities on the basis of this mechanism would be interesting because it would avoid the problem caused by the long time lag between investment and economic impact: part of the current benefits from tree production would be used to fund current research to increase future benefits, instead of having expected future benefits justifying current research investments.

At last, the provision of ecosystem services by forest owners currently represents a positive externality that is under-supplied. The correction of some of those externalities could create additional incentives for a better management of forest stands and the adoption of improved FRM. For instance, compensation of owners for the carbon captured in their forests would increase the willingness to pay for fast growing FRM, or provide side income for FRM producers. In the Living Carbon example mentioned above, the company intends to raise revenue by selling carbon credits based on the carbon sequestrated in the improved trees that it sells. The interviewees barely mentioned this issue, showing that they consider that the main service provided by the

forest is wood production. Hence, we do not currently observe actors having a pro-active strategy with respect to the valorisation of ecosystem services. Part of that could be explained by the fact that markets for carbon credits in the land use sector remain in their infancy in a European context.<sup>10</sup> The other explanation could also be that the valorisation of ecosystem services may require a re-conception of forest management (e.g., use of different species, limitation of clear cutting) and a possible decrease in revenue from forest production. At this stage, new regulations are considered more a constraint and a source of uncertainty than an opportunity. In any case, our expectation is that the valorisation of ecosystem services requires significant evolution of the current innovation system.

## 6. Conclusion

In the context of global environmental change and increasingly frequent natural disturbances, European forests are expected to fulfil a broad range of functions into the foreseeable future, including the resilient and productive supply of raw materials to foster the development of the EU-bioeconomy, the maintenance of genetic biodiversity, and the provision of important ecological services (for example, carbon capture). Given fast progress in applied genetics, and the observation that crop breeding is being revolutionised by rapid DNA sequencing and genome editing ([Huang et al., 2016](#)), it is clear that the selection of genetically improved forest trees and related diffusion of FRM has a potential role to play towards the achievement of those goals. However, little is known about the organization of European forest tree breeding conceived as an innovative activity and, thus, about the capacity of the sector to translate new genetic knowledge into improved trees that are likely to be adopted by forest owners. In particular, a literature review reveals that forest tree breeding has not been previously analysed through the prism of innovation theory and that cross-country analyses, which are necessary to compare institutional settings and derive general conclusions, are particularly lacking.

To fill this gap, this study analysed forest tree breeding for maritime pine in France, eucalyptus in Portugal, and Norway spruce in Finland and Sweden. We use a conceptual framework that combines two perspectives. The first one is the innovation system perspective, with the objective to characterise the structure of this system with its public and private stakeholders, as well as its functions determining its dynamics. The second one is the economics of innovation perspective, that addresses innovation primarily as an allocation problem subject to potential market failures resulting from inappropriate incentives.

For all case studies, several generations of improved FRM have been introduced and adopted over the last decades. Our analysis shows that the innovation system in place does not suffer from obvious infra-structural failure: all the markets, actors, economic activities, networks and regulations are in place to support the innovation process. However, this innovation system suffers from functional deficiencies related to entrepreneurship, market formation, and guidance of the research. Using an economics of innovation perspective, we show that these deficiencies can be related to several structural elements both on the demand and supply side. On the demand side, the long duration of the production cycle and the limited information on the performance of improved FRM explain that the valuation of improved FRM is limited. On the supply side, the duration of the production cycle also explains both the capacity constraints for the production of FRM and the limited return on breeding research investments. In addition to these results that

<sup>6</sup> <https://gondwanagenomics.com.au>

<sup>7</sup> <https://swetree.com/>

<sup>8</sup> <https://www.livingcarbon.com/> and <https://www.nytimes.com/2023/02/16/science/genetically-modified-trees-living-carbon.html>

<sup>9</sup> For tree harvest, this levy is in a range from 0.15% to 0.5% of the value of the harvest (source: France Bois Forêt).

<sup>10</sup> An example is the company LapWall, a producer of wooden construction elements, which was approved as a provider of carbon sequestration in the Puro.earth marketplace that brokers carbon offsets, see <https://forest.fi/article/markets-for-voluntary-emissions-reductions-are-growing-plans-for-common-regulation-started-long-ago-but-negotiations-are-still-on-going/#00e9f1a3>, consulted 9.5.2023.

are specific to the forest sector, this analysis shows the interest of using these two complementary perspectives. Indeed, the innovation system framework enables to underline the richness of the innovation ecosystem and the multiple factors and activities that drive the innovations. The economics of innovation framework enables to analyse in more details the innovation incentives of the different actors that are part of the innovation system.

This work has limitations, which open several perspectives to consolidate the analysis of the activities related to forest tree breeding. Our analysis was based only on species in European countries that represent contrasted situations. Complementary cases with other species and/or other countries with different regulations and organization of forest tree production and processing would be very beneficial. The discussion section also raises new issues related to new technologies, research funding mechanisms and ecosystem services that may evolve in the coming years, thus requiring specific analysis in the near future. At last, our analysis was largely qualitative to make it possible to understand the organization of the tree breeding sector but also because it is often difficult to apply quantitative methods to analyse innovation systems as a whole. However, some quantitative analysis would be very useful to complement parts of our analysis. For example, our qualitative explanation of the lack of demand pull could be improved by designing surveys or experiments (such as discrete choice experiments) with forest growers to better characterise their willingness to pay for improved FRM.

#### Author statement

Use of AI and AI-assisted technologies: The authors have not used AI

#### Appendix A. Tree genetic innovations for the three case studies

Genetic improvement of Norway spruce and the diffusion of improved FRM has occurred at roughly the same pace in Finland and Sweden. In Finland, the seed orchards established in a first round in the 1960s and early 1970s are still the source of most improved FRM. However, new seed orchards of “generation 1.5” have been established since 2002, some of which are now starting to produce seeds.<sup>11</sup> The establishment of new 1.5 generation orchards is planned to continue until 2028, when second-generation material will become available. In Sweden a different terminology based on orchard rounds rather than generations is used. Two programmes of genetic improvements and FRM diffusion have progressed in parallel, leading to the Swedish 3rd round orchards, which is equivalent to the Finnish 1.5 generation orchards.

Haapanen (2020) has recently quantified the performance of genetically improved spruce in southern Finland, concluding that first-generation seed orchard progenies have a clear superiority over unimproved trees with a realised genetic gain of 8.4% in height growth, 9.0% in diameter growth, and 20.6% in stem volume growth. The respective genetic gains expected from 1.5-generation seed orchards are 12.8%, 13.5% and 36.9%. Although those figures cannot be directly interpreted as increases in productivity of genetically improved stands, they seem consistent with the estimate by Rosvall et al. (2001) of a 10 to 25% increase in per hectare volume growth attributable to the superior genetic quality of the spruce seeds originating from Swedish orchards (Haapanen, 2020).

In the case of maritime pine, four generations have been released since the beginning of the breeding program. The first generation (VF1 - Strength and Shape 1), released between the end of the 1980s and the end of the 1990s, led to an increase in performance of +15% on average for wood volume and straightness, in comparison with non-improved trees. This increase reached +30% with the second generation VF2, and + 40% with the third generation VF3 (Vidal, 2016). Furthermore, with this third generation, trees were selected for their resistance to pine rust. For the fourth generation VF4, the deployment is more dynamic, with a new improved FRM released every 3 years. The VF4-1 FRM, currently bred, is selected on growth, straightness, drought resistance and wood quality.

In the case of eucalyptus, the Altri genetic breeding program concluded its third breeding cycle, and the basis for a fourth cycle is now launched. On its side, the breeding subsidiary of Navigator is now running the fourth generation of breeding and is developing the fifth one. The selection is made simultaneously on growth and wood quality. Other characteristics such as stem straightness and tolerance to biotic or abiotic threats have been of secondary importance. The current improvement programs provide material with the capacity to increase forest productivity by 25 to 50%, and the best families now released show performances in volume/ha of +80% compared to original material from Australia (personal communication from Altri).

and AI-assisted technologies during the preparation of this work.

Author contributions: all three authors contributed equally to the different phases of the elaboration of this paper (Conceptualization, Methodology, Data collection, Data analysis and Writing of the different versions of the paper).

#### Declaration of Competing Interest

Stéphane Lemarié reports financial support was provided by European Commission. Stéphane Lemarié reports a relationship with ICF International Inc. that includes: consulting or advisory. Aline Fugeray-Scarbel reports a relationship with ICF International Inc. that includes: consulting or advisory.

#### Data availability

Data will be made available on request.

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<sup>11</sup> Compared to the generation 1 orchards, the generation 1.5 orchards are composed of a smaller set of plus trees (25–35 per orchard) identified by progeny testing to produce superior offspring (Haapanen, 2020).

**Appendix B. Example of interview guideline (cooperative involved in eucalyptus in Portugal)***- Cooperative's missions*

1. Can you introduce us your cooperative (how it is organised, what kind of members, what missions, ...)? What are your missions in your cooperative?
2. How many forest cooperatives are members of your cooperative? What share of the private forest owners do the forest cooperatives represent?
3. How do you represent the forest cooperatives when dealing with the different institutions and authorities? What are the main subjects that your cooperative defends?
4. What are the main stakes related to eucalyptus production in Portugal? Are there missions specific to eucalyptus in your cooperative? What share do eucalyptus' plantations activities represent among the cooperative members?

*- Links with the other stakeholders*

5. What are the differences between the missions of your cooperative and the missions of other organisms such as [name of other stakeholders with similar missions in the sector]?
6. What are the connections/relationships between your cooperative and these organisms?

*- Eucalyptus production in Portugal.**- The cooperatives and forest associations in Portugal*

7. What are the names of the main forest cooperatives in Portugal? What are the ones which deal with eucalyptus?
8. What share of the private forest owners joins these forest cooperatives? Do the forest cooperatives federate small private owners? Big forest owners?
9. What are the missions of the forest cooperatives? Supplying seeds, phytosanitary products, ...? Common farm equipment? Forest services? Advice to forest owners? Wood selling? Lobbying?
10. How many hectares of eucalyptus forest do the forest cooperatives manage? How many hectares of eucalyptus?
11. What are the most important forest associations and cooperatives in terms of number of employees or managed hectares in Portugal?

*- Forest cooperatives and eucalyptus plantation*

12. Broadly speaking, do you know how the different forest owners (small ones, big ones, companies) purchase the eucalyptus seedlings? Do they buy eucalyptus materials on their own or through forest cooperatives or forest associations?
13. Do the forest cooperatives buy eucalyptus seedlings and clones from the nurseries? How do they choose the nursery they work with? Are there contracts between cooperatives and nursery for seed purchase (on prices, on quantities, are there exclusivities)?
14. What kind of nurseries sell improved seedlings and improved clones (companies' nurseries? Independent nurseries?)? In terms of competition, can a forest cooperative buy eucalyptus materials from both independent private nurseries AND companies' nurseries?
15. Have forest owners and forest cooperatives an easy access to improved materials?
16. Who plant the forests of the cooperative's members?
17. Do you provide advice on varietal choice to foresters? If no, who takes in charge this advice? What are the names of these organisms?
18. What are the main expectations from the forest growers in regards to eucalyptus improved varieties?
19. Are there huge differences on the prices of the eucalyptus varieties? Are forest owners sensitive to these prices?
20. What is the position of the forest cooperatives in regards to eucalyptus improved materials? Do they ask for a larger diffusion/deployment of the eucalyptus materials?

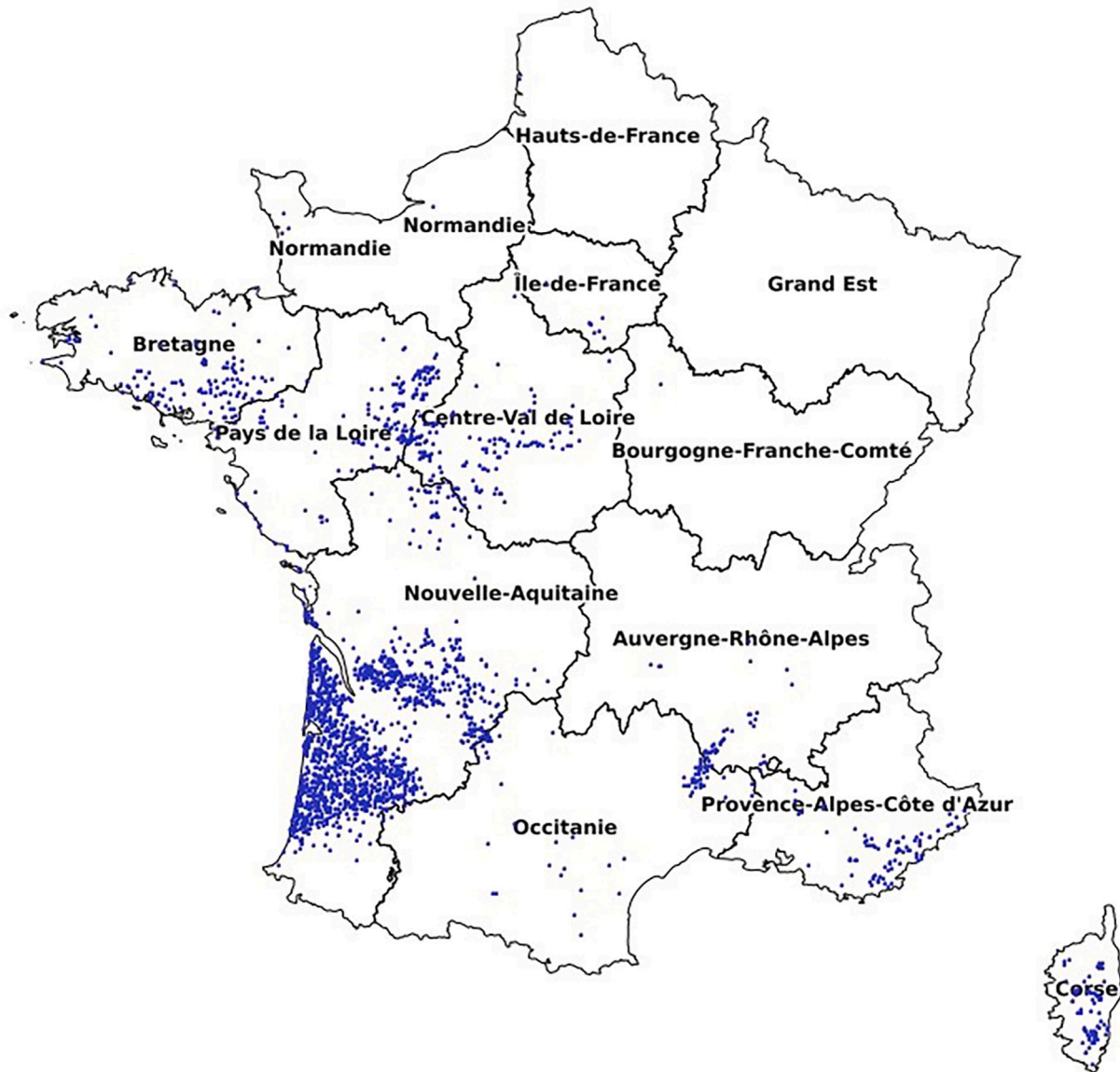
*- Some technical questions about eucalyptus production*

21. On what share of the new eucalyptus plantation are improved materials used?
22. Do forest owners plant with seeds?
23. When forest owners can't replant eucalyptus stands because of the legislation, what do they plant usually?
24. How do the forest owners value the quality of their wood? When selling the wood, can the forest owners value the eucalyptus varieties that they chose to plant?
25. When discounts are applied on the wood price due to quality defects, how do the intermediaries transmit it to forest owners?

*- Issues and prospects*

26. How do you think the organization of the breeding activities will evolve in the next decade and why? (For example: new actors, new partnerships...)
27. How could the new technologies such as genomic selection or somatic embryogenesis impact the organization of the breeding activities in the next decade?
28. Do you see any opportunities and threats towards breeding research activities and organization?
29. Do you see any possible changes in the deployment strategy of the improved varieties? New investments? New actors deploying the improved varieties?
30. Do you think that the FRM regulation will evolve in the next decade? If yes, how will it change and for what reasons?
31. What are the stakes concerning Eucalyptus sp. plantations and the wood sector in the next decade (and more in the long run)?

## Appendix C. Geographic distribution of maritime pine in France



Source: IGN – French national forest inventory, Raw data, Annual campaigns 2005 and following ones, <https://inventaire-forestier.ign.fr/data/IFN/>, Website consulted on May 16, 2023.

## References

- Aboal, D., Rovira, F., Veneri, F., 2018. Knowledge networks for innovation in the forestry sector: Multinational companies in Uruguay. *Forest Policy Econ.* 97, 9–20.
- Acemoglu, D., Linn, J., 2004. Market size in innovation: theory and evidence from the pharmaceutical industry. *Q. J. Econ.* 119 (3), 1049–1090.
- Aghion, P., Bloom, N., Blundell, R., Griffith, R., Howitt, P., 2005. Competition and innovation: an inverted-U relationship. *Q. J. Econ.* 120 (2), 701–728.
- Akerlof, G.A., 1970. The market for “lemons”: Quality uncertainty and the market mechanism. *Q. J. Econ.* 84 (3), 488–500.
- Alston, J.M., Pardey, P.G., 1999. The economics of agricultural R&D policy. In: Alston, J. M., Pardey, P.G., Smith, V.H. (Eds.), *Paying for Agricultural Productivity*. Intl Food Policy Res Inst., Washington D.C., USA.
- Alston, J.M., Norton, G.W., Pardey, P.G., 1995. *Science Under Scarcity: Principles and Practice for Agricultural Research Evaluation and Priority Setting*. Cornell University Press.
- Chamberland, V., Robichaud, F., Perron, M., Gélinas, N., Bousquet, J., Beaulieu, J., 2020. Conventional versus genomic selection for white spruce improvement: A comparison of costs and benefits of plantations on Quebec public lands. *Tree Genet. Genomes* 16, 17.
- Cohen, W.M., 2010. Fifty years of empirical studies of innovative activity and performance. In: Hall, B.H., Rosenberg, N. (Eds.), *Handbooks in Economics*, 1. Elsevier, pp. 129–213.
- Deus, E., Silva, J.S., Vicente, J.R., Catry, F.X., 2022. Eucalypt recruitment and invasion potential in protected areas of the Iberian peninsula under current and future climate conditions. *Forests* 13, 1199.
- Forest Stewardship Council, 2023. *Principles and Criteria for Forest Stewardship V 5.3*. <https://connect.fsc.org/document-centre/documents/resource/392>.
- Grattapaglia, D., 2014. Breeding forest trees by genomic selection: current progress and the way forward. *Genom. Plant Genetic Resour.* 651–682.
- Grattapaglia, D., 2017. Status and perspectives of genomic selection in forest tree breeding. In: *Genomic selection for crop improvement*. Springer, Cham, pp. 199–249.
- Gray, R., 2012. Intellectual property rights and the role of public and levy-funded research. In: *Improving Agricultural Knowledge and Innovation Systems*. Organisation for Economic Co-operation and Development, pp. 183–203.

- Haapanen, M., 2020. Performance of genetically improved Norway spruce in one-third rotation-aged progeny trials in southern Finland. *Scand. J. For. Res.* 35 (5–6), 221–226.
- Hekkert, M.P., Suurs, R.A., Negro, S.O., Kuhlmann, S., Smits, R.E., 2007. Functions of innovation systems: A new approach for analysing technological change. *Technol. Forecast. Soc. Chang.* 74 (4), 413–432.
- Huang, S., Weigel, D., Beachy, R.N., Li, J., 2016. A proposed regulatory framework for genome-edited crops. *Nat. Genet.* 48 (2), 109–111.
- Jansson, G., Hansen, J.K., Haapanen, M., Kvaalen, H., Steffenrem, A., 2017. The genetic and economic gains from forest tree breeding programmes in Scandinavia and Finland. *Scand. J. For. Res.* 32 (4), 273–286.
- Klerkx, L., van Mierlo, B., Leeuwis, C., 2012. Evolution of systems approaches to agricultural innovation: concepts, analysis and interventions. In: Darnhofer, I., Gibbon, D., Dedieu, B. (Eds.), *Farming Systems Research into the 21st Century: The New Dynamic*. Springer, Dordrecht.
- Lane, J.P., Godin, B., 2013. Pushes and Pulls: Hi (S) tory of the Demand Pull Model of Innovation. *Sci. Technol. Hum. Values* 38 (5).
- Lozhnikova, A.V., Akkerman, E.N., Muravyov, I.V., Kirpotin, S.N., 2014. The 'tyranny of discounting' in economic efficiency evaluation of capital investment projects susceptible to ecological and climatic changes. *Int. J. Environ. Stud.* 71 (5), 768–773.
- Miles, M.B., Huberman, A.M., 1994. *Qualitative Data Analysis: An Expanded Sourcebook*. Sage.
- Neale, D.B., Williams, C.G., 1991. Restriction-Fragment-Length-Polymorphism mapping in conifers and applications to forest genetics and tree improvement. *Can. J. For. Res.* 21, 545–554.
- Pelai, R., Hagerman, S.M., Kozak, R., 2020. Biotechnologies in agriculture and forestry: Governance insights from a comparative systematic review of barriers and recommendations. *Forest Policy Econ.* 117, 102191.
- Potts, J., Kastle, T., 2017. Economics of innovation in Australian agricultural economics and policy. *Econ. Anal. Policy* 54, 96–104.
- Purkus, A., Hagemann, N., Bedtke, N., Gawel, E., 2018. Towards a sustainable innovation system for the German wood-based bioeconomy: Implications for policy design. *J. Clean. Prod.* 172, 3955–3968.
- Rao, X., Hurley, T.M., Pardey, P.G., 2019. Are agricultural R&D returns declining and development dependent? *World Dev.* 122, 27–37.
- Reich, P.B., 2011. Taking stock of forest carbon. *Nat. Clim. Chang.* 1 (7), 346–347.
- Rosvall, O., Jansson, G., Andersson, B., Ericsson, T., Karlsson, B., Sonesson, J., Stener, L., 2001. Genetiska vinster i nuvarande och framtida fröplantager och klonblandningar [Summary: Genetic gains from present and future seed orchards and clone mixes]. *Redogörelse* (nr 1, Skogforsk. 35) 41p.
- Schumpeter, J.A., 1942. *Capitalism, socialism and democracy*. McGraw Hill, NY.
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Reyser, C.P., 2017. Forest disturbances under climate change. *Nat. Clim. Chang.* 7 (6), 395–402.
- Stiglitz, J.E., 1999. Knowledge as a global public good. In: *Global Public Goods: International Cooperation in the 21st Century*, 308, pp. 308–325.
- Stone, I.J., Benjamin, J.G., Leahy, J., 2011. Applying innovation theory to Maine's logging industry. *J. For.* 109 (8), 462–469.
- Tidd, J., 2006. *A Review of Innovation Models*, 16. Imperial College London.
- Venäläinen, A., Lehtonen, I., Laapas, M., Ruosteenoja, K., Tikkanen, O.P., Viiri, H., et al., 2020. Climate change induces multiple risks to boreal forests and forestry in Finland: A literature review. *Glob. Chang. Biol.* 26 (8), 4178–4196.
- Vidal, M., 2016. Optimisation des stratégies d'amélioration génétique du pin maritime grâce à l'utilisation de marqueurs moléculaires. In: *Sciences du Vivant [q-bio]*. Université de Bordeaux.
- Von Witzke, H., Jehlitschka, K., Kirschke, D., Lotze-Campen, H., Noleppa, S., 2004. Social rate of return to plant breeding research in Germany. *German J. Agricult. Econ.* 53, 206–210, 670-2016-45621.
- Weiss, G., Pelli, P., Orazio, C., Tykka, S., Zivojinovic, I., Ludvig, A., 2017. Forest industry clusters as innovation systems: analysing innovation support frameworks in five European regions. *Aust. J. Forest Sci.* 134 (2), 119–147.
- Weiss, G., Ludvig, A., Živojinović, I., 2020. Four decades of innovation research in forestry and the forest-based industries—A systematic literature review. *Forest Policy Econ.* 120, 102288.
- World Bank, 2006. *Enhancing agricultural innovation: How to go beyond the strengthening of research systems*. The World Bank.
- Xu, Y., Liu, X., Fu, J., Wang, H., Wang, J., Huang, C., et al., 2020. Enhancing genetic gain through genomic selection: from livestock to plants. *Plant Commun.* 1 (1), 100005.