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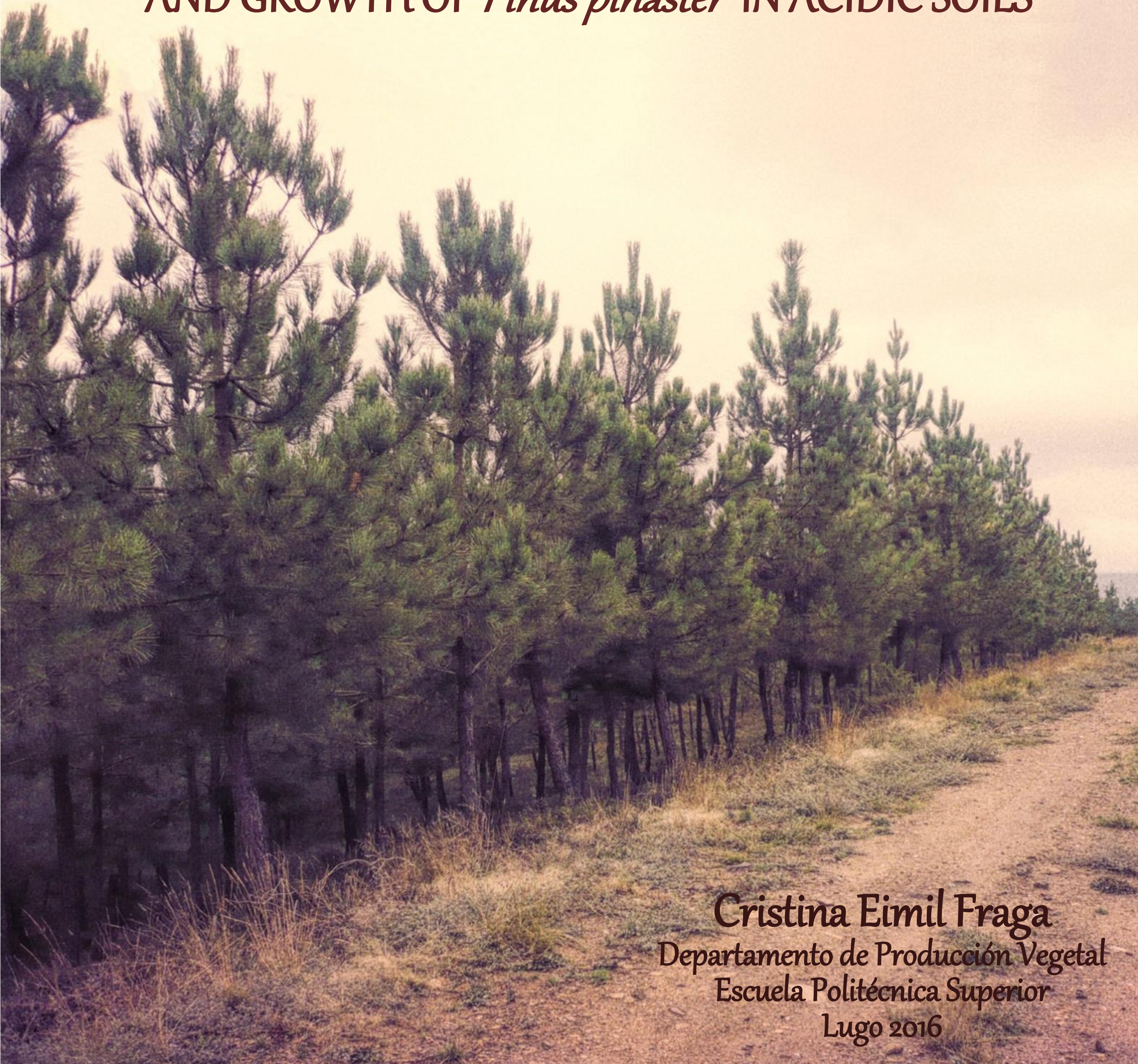
DOCTORAL THESIS

ANALYSIS OF EDAPHIC AND ECOPHYSIOLOGICAL PARAMETERS IN RELATION TO NUTRIENT LEVELS AND GROWTH OF *Pinus pinaster* IN ACIDIC SOILS



Cristina Eimil Fraga
Departamento de Producción Vegetal
Escuela Politécnica Superior
Lugo 2016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Os doctores D. Roque Rodríguez Soalliro, D. Federico Sánchez Rodríguez e Dna. Esperanza Álvarez Rodríguez, como Director/res da tese titulada: Analysis of edaphic and ecophysiological parameters in relation to nutrient levels and growth of *Pinus pinaster* in acidic soils

Pola presente **DECLARAN:**

Que a tese presentada por Dona Cristina Eimil Fraga é idónea para ser presentada, de acordo co artigo 41 do *Regulamento de Estudos de Doutoramento,* pola modalidade de compendio de artigos, nos que o doutorando tivo participación no peso da investigación e a súa contribución foi decisiva para levar a cabo este traballo.
E que está en coñecemento dos coautores, todos eles doutores, participantes nos artigos, que ningún dos traballos reunidos nesta tese serán presentados por ningún deles noutra Tese de Doutoramento, o que asinan baixo a sua responsabilidade.

En Lugo, a 25 de abril de 2016.

Os directores:

Dr. D. Roque Rodríguez Soalleiro Dr. D. Federico Sánchez Rodríguez

Dra. Dna. Esperanza Álvarez Rodríguez


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A mi familia


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RESUMEN

El principal objetivo de esta tesis doctoral fue mejorar la comprensión de la relación entre parámetros ecofisiológicos y edáficos que determinan el crecimiento de *Pinus pinaster* y su capacidad para adaptarse a distintos ambientes, con el fin de facilitar la toma de decisiones a la hora de producir madera y biomasa y otros productos forestales. Para ello, se abordaron cinco estudios concretos. Se estudiaron las relaciones entre las propiedades del suelo, nutrientes foliares y el crecimiento en 128 parcelas de *Pinus pinaster* establecidas sobre diferentes tipos de roca (rocas graníticas, sedimentos, areniscas y cuarcitas, pizarras y filitas, mica esquistos, esquistos biotíticos, gneis y migmatitas). Se encontró una buena adaptación de *Pinus pinaster* a suelos desarrollados sobre esquistos biotíticos, rocas graníticas, gneis y migmatitas, donde esta especie tiene los mayores crecimientos y, en general, niveles de nutrientes foliares más elevados, particularmente de K. Se desarrollaron dos modelos de regresión para predecir el índice de sitio. En un modelo completo que incluye todos los materiales geológicos, Ca y K foliares, profundidad del suelo y temperatura media anual, explicaron un 52% de la variación del índice de sitio. En otro modelo que incluye solo rocas graníticas, los parámetros anteriores, exceptuando el Ca foliar, explicaron un 53% de la variación del índice de sitio. En 31 parcelas se estudió el tamaño y las características de las acículas y los parámetros del sitio. Se observó que la longitud, ancho y grosor de las acículas están muy relacionados con las condiciones climáticas, el año de formación de las acículas y el N y Mg foliares. La clase de edad de las acículas fue el principal factor que afectó a la variación en el tamaño de las mismas. La superficie foliar específica proyectada fue positivamente afectada por los nutrientes foliares, especialmente K. La variabilidad en la vida útil de las acículas, la biomasa foliar y el índice de área foliar se analizaron en las 31 parcelas anteriores. La longevidad de las acículas se relaciona con el índice de sitio y el Mg y K foliares. La biomasa foliar y el índice de área foliar mostraron una correlación negativa con la edad de las acículas y positiva con el índice de sitio y los nutrientes foliares. Por su parte, la eficiencia en el crecimiento (ratio entre el crecimiento corriente en biomasa total y el índice de área foliar) aumentó con el K foliar y, especialmente con el incremento de la relación K:N. La influencia de la roca madre en el fraccionamiento, especiación y toxicidad del Al se estudió en 4 de las 31 parcelas anteriores, desarrolladas sobre esquistos biotíticos, mica esquistos, granitos y pizarras. Se observó que la parcela sobre esquisto biotítico presentó concentraciones más altas de Al oxalato y pirofosfato, tendiendo a formar complejos orgánico-alumínicos altamente estables. Sobre pizarra predominaron en la fase sólida del suelo las formas de Al más lábiles, más susceptibles de pasar a la fase líquida y ser absorbidas por la planta. Las especies de Al consideradas más tóxicas (Al^{3+} y Al-OH) fueron más altas en suelos sobre pizarra y mica esquisto, de acuerdo con la menor calidad de estación de estas parcelas. Todos los índices de toxicidad de Al aplicados indican un mayor riesgo en las parcelas desarrolladas sobre pizarra y mica esquisto, y no existirían problemas por este elemento en las desarrolladas sobre esquistos biotíticos. Los índices obtenidos a partir de la disolución del suelo, Al lábil y Al^{3+} + Al-OH, indican que no existe riesgo de toxicidad por Al en las parcelas sobre granito, lo que concuerda con las variables de productividad y biomasa, mientras que la aplicación del resto de los índices utilizados indicaría toxicidad de este elemento.

Palabras clave: roca madre, nutrición, crecimiento, edad acículas, dimensiones acículas, superficie foliar específica, longevidad acículas, biomasa, índice de área foliar, fraccionamiento de Al, especies de Al, índices de toxicidad de Al

RESUMO

O principal obxectivo desta tese doutoral foi mellorar a comprensión da relación entre parámetros ecofisiolóxicos e edáficos que determinan o crecemento de *Pinus pinaster* e a súa capacidade para adaptarse a distintos ambientes, co fin de facilitar a toma de decisións á hora de producir madeira e biomasa e outros produtos forestais. Para iso, abordáronse cinco estudos concretos. Estudáronse as relacións entre as propiedades do solo, nutrintes foliares e o crecemento en 128 parcelas de *Pinus pinaster* establecidas sobre diferentes tipos de rocha (rochas graníticas, sedimentos, areniscas e cuarcitas, lousas e filitas, mica xistos, xistos biotíticos, gneis e migmatitas). Atopouse unha boa adaptación de *Pinus pinaster* a solos desenrolados sobre xistos biotíticos, rochas graníticas, gneis e migmatitas, onde esta especie ten maiores crecementos e, en xeral, niveis de nutrintes foliares máis elevados, particularmente K. Desenvolvéronse dous modelos de regresión para predicir o índice de sitio. Nun modelo completo que inclúe todos os materiais xeolóxicos, Ca e K foliares, profundidade do solo e temperatura media anual, explicaron un 52% da variación do índice de sitio. Noutro modelo que inclúe só rochas graníticas, os parámetros anteriores, exceptuando o Ca foliar, explicaron un 53% da variación do índice sitio. En 31 parcelas estudouse o tamaño e as características das agullas e os parámetros do sitio. Observouse que a lonxitude, ancho e grosor das agullas está moi relacionado coas condicións climáticas, o ano de formación das agullas e o N e Mg foliares. A clase de idade das agullas foi o principal factor que afectou á variación no tamaño das mesmas. A superficie foliar específica proxectada foi positivamente afectada polos nutrintes foliares, especialmente o K. A variabilidade na vida útil das agullas, o índice de biomasa foliar e a área foliar analizáronse nas 31 parcelas anteriores. A lonxevidade das agullas relaciónase co índice de sitio e o Mg e K foliares. A biomasa foliar e o índice de área foliar mostraron unha correlación negativa coa idade das agullas e positiva co índice de sitio e os nutrintes foliares. Pola súa parte, a eficiencia no crecemento (ratio entre o crecemento corrente en biomasa total e o índice de área foliar) aumentou co K foliar e especialmente co incremento da relación K:N. A influenza da rocha nai no fraccionamento, especiación e toxicidade do Al estudouse en 4 das 31 parcelas anteriores, desenroladas sobre xistos biotíticos, mica xistos, granitos e lousa. Observouse que a parcela desenrolada sobre xistos biotíticos presentou concentracións máis altas de Al oxalato e pirofosfato, tendendo a formar complexos orgánico-alumínicos altamente estables. Sobre lousa predominaron na fase sólida do solo as formas de Al máis lábiles, máis susceptibles de pasar á fase líquida e ser absorbidas pola planta. As especies de Al consideradas máis tóxicas (Al^{3+} e Al-OH) foron máis altas en solos sobre lousa e mica xisto, de acordo coa menor calidade de estación destas parcelas. Todos os índices de toxicidade de Al aplicados indican un maior risco nas parcelas desenroladas sobre lousa e mica xisto, e non existirían problemas por este elemento nas desenroladas sobre xistos biotíticos. Os índices obtidos a partir da disolución do solo, Al lábil e Al^{3+} + Al-OH, indican que non existe risco de toxicidade por Al nas parcelas sobre granito, o que concorda coas variables de produtividade e biomasa, mentres que a aplicación do resto de índices empregados indicaría toxicidade deste elemento.

Palabras chave: rocha nai, nutrición, crecemento, idade agullas, dimensións agullas, superficie foliar específica, lonxevidade agullas, biomasa, índice de área foliar, fraccionamiento de Al, especies de Al, índices de toxicidade de Al

ABSTRACT

The main aim of this doctoral research was to improve the understanding of the relationships between the ecophysiological and edaphic parameters that determine the growth of *Pinus pinaster* and its ability to adapt to different environments, in order to facilitate the decision-making involved in wood and biomass production and other forest products. For this purpose, five specific studies were carried out. The relationships between soil properties, foliar nutrients and growth were studied in 128 plots of *Pinus pinaster* established in soil over different types of bedrock (granitic rocks, sediments, sandstone and quartzite, slates and phyllites, mica schist, biotitic schist, gneiss and migmatites). Good adaptation of *Pinus pinaster* was observed in soils developed over biotitic schist, granitic rocks, gneiss and migmatites, in which growth of the species was highest and foliar nutrients, particularly K, were also generally higher than in the other types of soil. Two regression models were developed for predicting site index. In a complete model considering all geological materials, foliar Ca and K, soil depth and average annual temperature explained around 52% of the variability in site index. In another model considering granitic rocks, all of the previous parameters, except foliar Ca, explained 53% of the variability in site index. Needle size, leaf traits and site parameters were studied in 31 plots. Needle length, width and thickness were closely related to climate conditions, year of formation and also foliar concentrations of N and Mg. Needle age class is the main factor leading to variation in needle dimensions. The specific leaf area was positively affected by concentrations of foliar nutrients, particularly K. The variability in needle lifespan, foliar biomass and leaf area index was analysed in the 31 plots. Needle longevity was closely related to site index and foliar concentrations of Mg and K. Foliage biomass and leaf area index were negatively correlated with needle age and positively correlated with site index and foliar nutrients. Growth efficiency (the annual above-ground biomass increment per unit leaf area) increased as foliar K and particularly the K:N ratio increased. The influence of the parent rock on Al fractionation, speciation and toxicity was studied in 4 of 31 plots developed over biotitic schist, mica schist, granite and slate. In the soil over biotitic schist, the concentrations of oxalate and pyrophosphate Al were higher than in other soils and tended to form highly stable organic–aluminium complexes. In the soil developed from slate, the more labile forms of Al predominated and were more liable to move to the liquid phase and be absorbed by the plant. The highest concentrations of the Al forms considered most toxic (Al^{3+} and Al-OH) were found in the soils over slate and mica schist, in accordance with the lower site index in these plots. All toxicity indices considered indicated a higher risk of Al toxicity in the plots developed over slate and mica schist, but no risk of Al toxicity in the plots on biotitic schist. The indices obtained considering labile Al and Al^{3+} + Al-OH in the soil solution indicated no risk of Al toxicity in plots over granite, according to productivity and biomass variables. Application of the other indices indicated risk of toxicity by this element.

Keywords: bedrock, nutrition, growth, needle age, needle size, specific leaf area, needle longevity, biomass, leaf area index, Al fractionation, Al species, Al toxicity indices

Chapter 1

Introduction and objectives


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1. GENERAL INTRODUCTION AND OBJECTIVES

1.1. Natural and man-made spread of forest stands

Maritime pine (*Pinus pinaster Ait.*) is thought to have extended throughout southwestern Europe during the Quaternary and its abundance in the landscape has changed in parallel to the vegetation fluctuations associated with climatic conditions, as revealed by pollen analysis (Ramil-Rego and Aira, 1993). At the beginning of the Holocene, after the cold and dry phase denominated Younger Dryas (11.000-10.000 years BP), that caused an important reduction in forest area and an increase of temperature, an initial expansion of Pinus-Betula was produced (10,000–9500 BP). This was followed almost immediately by *Quercus robur* (9500–8600 BP), and by *Corylus* (8600–8000 BP) expansion in the more oceanic zone, reaching the forest its maximum expansion towards 8500–6000 BP, except areas at high elevation or exposed to oceanic winds (Ramil-Rego et al., 1998).

In Galicia (NW Spain), *Pinus pinaster* samples have been found in Atlantic and Subboreal sediments in different locations in northern Lugo, both near the coast and in the Subboreal-Subatlantic transition in interior areas (Ramil-Rego, 1992; Ramil-Rego and Aira, 1994). The species almost disappeared by the Subatlantic period, because of the increase in the presence of broadleaf species in the landscape (Guitián Rivera, 1996), although it was still present in some sites where pollen studies have been conducted.

Since the Holocene and in particular from the Atlantic period onwards, anthropogenic influence can be considered as the main factor affecting the deforestation processes (Ramil-Rego and Aira, 1993; Rico Boquete, 1995).

The distribution area of the species increased through afforestation, which began on a small scale in the 18th century. At this time, planting of “pinabete” close to the seashore was already recommended by the marine forest visitors because of its many advantages: ease of cultivation, higher production than other trees, possibility of early thinning for poles at age 6 or 8 years, additional thinning for ship masts at age 16 or 18 years and possibility of obtaining resin before final cutting at 24 or 28 years (García de Longoria, 1798). These first afforestations were performed in areas of Lower Miño and High Limia, in northern Portugal (Guitián Rivera, 1996).

During the first half of the 19th century, the pine was introduced slowly, and afforestation with this species did not become important until the last third of the 19th century. The seeds used were probably obtained from northern Portugal (Ruiz Zorrilla, 1981) and used by farmers who had recently acquired properties and who planted pine nuts often mixed with cereal or gorse. The demand for wood, the reduction in prices of agricultural products and the increased price of timber led to pine afforestation being a good option in the short to medium term (Rico Boquete, 2014). On the basis of pine productivity information and wood trade statistics from Galicia harbour records, it has been estimated that the area of this species may have increased to 90000 ha by 1930 (Rico Boquete, 2014).

Pines played an important role in the General Plan for the Reforestation of Spain in 1939, and maritime pine was one of the species most commonly used in the afforestation programme. The plan was implemented over three decades, and the area covered by the species increased to 400000 ha by 1971 (MAGRAMA, 1979), with pine extending from coastal to inner areas and eventually throughout the whole of Galicia. The afforestation activities, carried out within the framework of the forest consortia led to important rural conflicts derived from the fact that the traditional private collective ownerships of many forests were not recognised by the government authorities. The lands were considered as public and taken under a compulsory use to be covered by trees. This was contrary to the traditional use of the land as pasture land and production of "esquilmes". As a result of this initiative, more than 9% of the Galician territory was reforested within 35 years, with *Pinus pinaster* being the most commonly used species in more than half of the afforested area. With regard to the planting results, the outcome was variable as planting was sometimes carried out in site-limited conditions or with inadequate seed. In the 1950s, pine stands covered some 250000 hectares of land in Galicia, and the sawmilling industry represented the third top source of wealth after crop farming and cattle farming.

The main reason for establishing pine plantations at that time was that maritime pine was considered a non site demanding species, able to grow well in poorest areas of the mountains in inland Galicia. It was therefore recommended as the species of choice for the drier and most unprotected land (Ceballos and Ximénez de Embún, 1939; Rico Boquete, 1995). After this ambitious afforestation plan, the forest administration activity was limited to replanting pine stands that had been burned (e.g. ICONA (Instituto para la Conservación de la Naturaleza, 1971-1995) during the period 1971-1983).

After the devolution process, the forest administration was transferred to the regional government of Galicia in 1985. European Council (EC) regulations (EC, 1992; EC, 1999) concerning rural development encouraged afforestation of agricultural land in Spain. The main objective was to develop forests, considering their triple functions: production, environmental conservation and social conservation. In Galicia, regulations were applied by successive orders that regulated the concession of subsidies from 1993 onwards. Globally, *Pinus pinaster* was the species most commonly planted within this programme and the resulting increase in forest stands, often established on land that had not been cultivated for a long time, was remarkable. Spanish decree 250/1993 (Xunta de Galicia, 1993) established that agricultural areas targeted for planting must have been in agricultural use the past decade. Clearly the land planted during this period, particularly with pine, differed from those planted by the Forest Authorities 40 years previously, precisely because of agricultural use and generally better soil characteristics (López-Varela et al., 2008). The main set of plots considered in this study represent this type of afforested agricultural land.

From 2006 onwards, calls for grants from the regional government changed the target from afforestation of agricultural land to reforestation of forest land. This has led to a slight change in the type of sites reforested, characterized by steeper slopes and poorer soils. By 2012, a total of 11384 ha of land had been reforested with maritime pine under this scheme, representing 56% of the total reforestation carried out with grants in forest land in the period (2006 to 2012) (Garrido, pers. comm.).

1.2. A multiple-use forest

Promotion of pine led, as early as in the last third of the 19th century, to the flourishing of economic activities linked to the main product obtained from the stands, the timber. The expansion of maritime pine plantations that took place between 1857 and 1920 led to establishment of a sawmill industry. The annual growth rates enabled production of boards in rotations of 25 to 40 years, as well as slabs destined for the manufacture of packaging. In addition, the small round wood was marketed as poles for use in mines and construction. The period 1931-1934 witnessed an increase in national and international markets for wooden packaging boxes. In 1960, 80% of wood cut in Galicia was *Pinus pinaster* (Rico Boquete, 2014).

Galician maritime pine has clearly visible annual rings, with white-yellowish sapwood and reddish heartwood, which is the dominant part of the section at ages older than 20 years. Core wood, also called juvenile wood, is formed up until almost 12 years and is represented by an inner cylinder. The basic density is 408 kg m^{-3} (Riesco-Muñoz and Barrio-Anta, 2010), the total volumetric shrinkage is 14.5%, and the timber is classified as of medium hardness. Characterization of timber strength allowed the use of sawed timber classified as ME-2 (structural sawed timber class 2) as resistant class C18, and class ME-1 as C24. The aforementioned properties enable use of maritime pine timber in a variety of applications, provided that the round timber defects are not limiting. The most common defects include knots, resin pockets, curvature, juvenile wood or compression wood, many of which can be prevented by applying appropriate silviculture practices (Riesco-Muñoz et al., 2014).

Although maritime pine timber has been used in rural construction, naval carpentry, and to produce mine poles, packaging, boxes and even as combustion fuel for pitch production, other products have been or still are important: the bark was used for tanning, cones for firewood and pine nuts to feed livestock.

Collection of mushrooms for commercial purposes and for personal consumption is now an important activity in maritime pine forests, which provide some of the best habitats for mushroom harvesting. Commercially important mushrooms of excellent quality that frequently occur in *Pinus pinaster* plantations include *Lactarius deliciosus*, *L. semisanguifluus*, *L. sanguifluus*, *Boletus edulis*, *B. aereus*, *B. pinophilus*, *Cantharellus cibarius, Hydnum repandum, Tricholoma equestre, Tricholoma portentosum, Russula cyanoxantha* and *Russula virescens*. Other species of good quality present in these plantations, although of less commercial value in Spain, include *Boletus erythropus*, *Cantharellus tubaeformis*, *Cantharellus lutescens*, *Tricholoma* *terreum*, *Xerocomus badius* and *Suillus luteus* (Fernández de Ana Magán and Rodríguez Fernández, 2000).

Fungal communities change and develop over time, so that *Laccaria*, *Suillus* and *Amanita* dominate in young stands, whereas some commercial species such as *Lactarius*, *Russula* and *Cantharellus* become important in stands of intermediate age (11-20 years). The much sought-after edulis group is more abundant in pine stands older than 30 years, but the productivity decreases in more mature stands. The yield of *Boletus edulis* in *Pinus pinaster* stands is approximately 0-29.5 kg ha^{-1} year^{-1} and the total yield of edible mushrooms is between 45 and 200 kg ha^{-1} year^{-1} (Nieto and Carbone, 2009; Fernández-Toirán et al., 2006).

Although yields of edible and commercial mushrooms vary greatly from year to year, an average yield of 20-50 kg ha^{-1} may be expected in maritime pine stands, indicating economic value. The recent expansion of commercial mushroom harvesting, both in terms of number of species and fresh weight, has led to harvest regulations being implemented in Castilla y León and also recently in Galicia (Martínez et al., 2003).

The exploitation of resin was extremely important in Spain for several decades. The First National Survey (1965-74) reported that 25.5 million pine trees were tapped for resin, this represented 10.5% of the trees larger than 17.5 cm dbh. The maximum production of crude resin was 40000 t in Spain in 1961, corresponding to 270000 ha of tapped forests (Serrada, 2004). Average yields per tree were very variable, ranging from less than 1 kg tree^{-1}, which were not tapped, to 6 kg tree^{-1} (average value for the whole forest). In the most productive forests, individual tree yields of 10 kg tree^{-1} were frequent, and maximum values were registered in exceptional trees of 30 kg tree^{-1}.

Many stands of *Pinus pinaster* have been affected by resin harvesting in the past (Schweingruber, 1993) and the quality of their timber depends on the tapping method used. Moreover, the estimated reduction in growth of *Pinus pinaster* due to resin tapping in Spain is around 25–33 % (Rodríguez et al., 2008; Génova et al., 2014).

In Galicia, resin was only harvested in pine forests in Baixo Miño and south of Ourense in the 1970s, and pine trees with open “faces” (tapping wounds) could be observed in the 1990s. The area was considered less productive than the sandy banks of Central Spain. Extraction of pine resin has recently been initiated in the south of Pontevedra, mainly in communal forests. The first production figures, which should be considered with caution, indicate values higher than 2 kg tree^{-1} and season. It is important that the methods used to harvest resin should not damage the timber, the main product in these forests and that the effects of harvesting on woodland vigour and abundance of *Monochamus galloprovincialis* (pinewood nematode vector) should be assessed. Management of woodland density can also be affected by resin harvesting (Martínez Chamorro, 2016).

The multifunctional character of maritime pine forests is nowadays of key importance in their management, with important aspects such as wildlife conservation and recreation being taken into consideration.

1.3. Development of the pine forest industry

Primary processing of *Pinus pinaster* basically involves sawn timber production in small facilities. However, the more concentrated pulp and wood-based board industries became important during the 1960s. Sawmilling activity peaked in the 1960s. At this time, 80% of the wood felled in Galicia was derived from maritime pine stands (Rico Boquete, 2014). Conifer species comprised 82% of the total production of sawn timber and maritime pine comprised 62% of all conifer production. In 2001, the annual production of industrial round wood of *Pinus pinaster* in Galicia was 1.9 million m^3, corresponding to 37% of total round wood produced in this region annually (MAGRAMA, 2001).

According to the available data, 19 companies processed more than 20000 m^3 of pine round wood with bark (37% of total consumption). Another 38 medium-large-sized companies processed between 10000 and 20000 m^3 of timber with bark (24% of the consumption). The remaining portion (clearly larger in number) corresponds to small sawmills, mostly family business with small production capacity. In recent years, there has been a drastic reduction in the number of sawmills, which were evaluated as 469 in 2004 and 363 in 2010 as a result of the external competition and the low average productivity of the sector.

Pinus pinaster sawn timber was mostly used to produce planks and boards for construction and carpentry (78%), small boards for pallet manufacture, packaging and boxes (19%), construction elements (2%) and 1% other uses. The best quality timber was used for carpentry and furniture-making (Sanz et al., 2006).

The pulp and wood-based panel industries became established between the end of the 1950s and the beginning of the 1960s, with the production of the first chipboards and hardboards. Pine was only used for pulp production until the 1970s. At that time, there was a strong expansion of the panel industry, which progressed through the 1980s with the installation of the first medium-density fibreboard (MDF) industrial production lines. In Galicia alone, it was estimated that around 13500 people may have been employed indirectly in this type of industry (Sanz et al., 2006).

This industrial sector has been able to maintain efficiency levels and to innovate, although the construction crisis that arose in 2009 directly affected production levels and thus also timber prices. The range of products includes chipboard, MDF, hardboard and plywood. There is currently a trend for vertical integration of value-added processing such as melamine surfacing, veneering and postforming or production of wood-based products such as laminate flooring (Sanz et al., 2006).

Since the outset, growth of this industry has been backed by consumption of maritime pine wood grown in Galicia. However, consumption overtook supply and coniferous wood had to be imported. Thus, in 1999, 0.5 million m^3 of coniferous wood had to be imported to complement supply.

In Galicia, secondary wood processing is carried out by about 2400 companies involved in carpentry and joinery as well as in manufacturing of wooden objects. Of the total employment created by the wood processing industry in Galicia, estimated to be about 17000 jobs, most involve carpentry and furniture-making (10000). The most commonly used materials are chipboard and MDF. Solid timber comes in second place (30% of total consumption). Some 88% of the solid wood is imported from abroad and 6% from other areas of Spain. Only 6% of solid timber used in Galicia is obtained from local sources (Sanz et al., 2006).

Finally, most of the best quality maritime pine, used for furniture-making, is sent to other regions of Spain such as Valencia, Andalucía and Cataluña. Recently, some initiatives of pellets production from industrial by products and pine logs were developed, which increases the demand for wood of this specie.

1.4. Development of *Pinus pinaster* wood resources

The Atlantic pine forests of *Pinus pinaster* are of great productive and ecological importance in northwestern Spain. The fourth National Forest Inventory (NFI4) (MAGRAMA, 2011) indicates that the species covers 15.35% of the forest area in Galicia (Figure 1), with volume over bark of 39.3 M m^3 in pure stands, reaching up to 58.4 M m^3 if mixed stands are taken into account. This indicates an increase of 19% in the standing volume relative to National Forest Inventory (NFI) 3 (MAGRAMA, 2002) (Table 1). The species is of great importance in the forest landscape of Galicia and it is present in most strata of NFI 4, covering a total area of 217281 ha in pure stands (MAGRAMA, 2011).

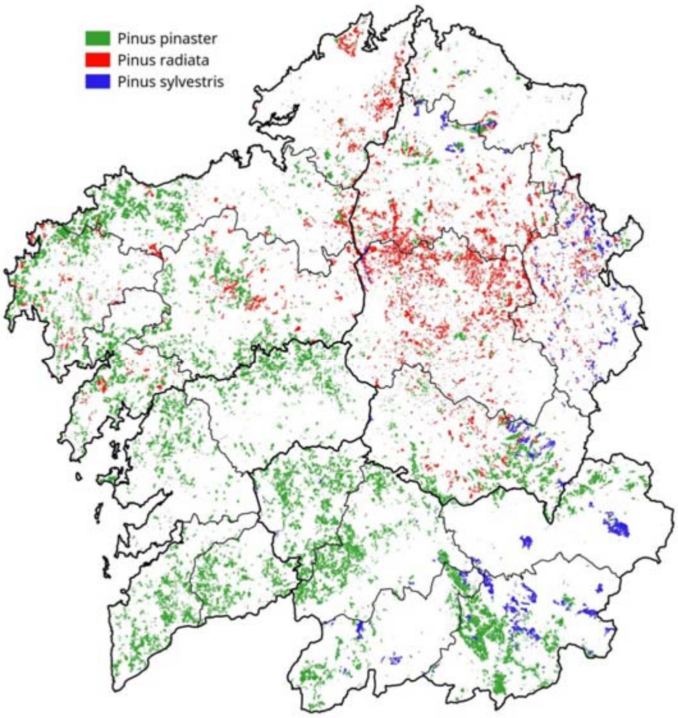

Figure 1. Distribution of *Pinus pinaster*, *Pinus radiata* and *Pinus sylvestris* in Galicia. *Source: UXFS*

Table 1. Development of maritime pine growing stocks in Galoicia. NFI: National Forest Inventory

	NFI 1	NFI 2	NFI 3	NFI 4
Volume over bark (M m^3)	43.0	45.4	49.1	58.4

The distribution of the total growing stock in different forest districts is shown in Figure 2. Sizeable accumulations can be seen in the province of Pontevedra and central parts of the province of A Coruña. The presence of large growing stocks in southern Lugo and northwestern Ourense are also highlighted.

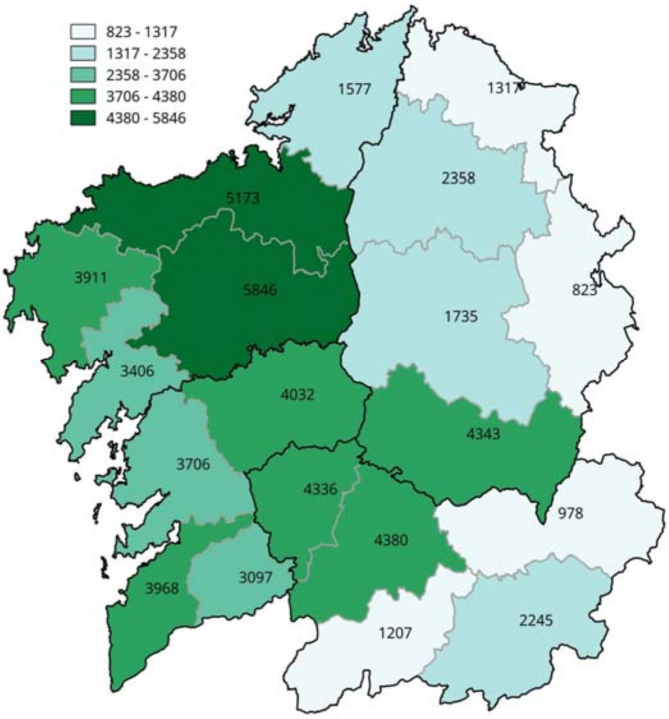

Figure 2. Distribution of volume over bark (thousands m^3) of *Pinus pinaster* in the different forest districts. *Source: UXFS*

The development of growing stock in terms of diameter distribution for *Pinus pinaster* in Galicia, obtained from the NFI of Spain is shown in Figure 3. The most marked difference was observed between NFI 2 (MAGRAMA, 1993) and NFI 3. In the 30 cm diameter class, there was a drastic reduction in growing stock, from approximately 19 million m^3 in NFI 2 to 5 million m^3 in NFI 3. The growing stocks were slightly higher in NFI 4 than in NFI 3. The last inventory (NFI 4) revealed an increase in growing stock in diameter class 70 cm, confirming maritime pine stocks as the second most elderly trees in Galicia (MAGRAMA, 2011). This indicates a process of ageing of the stands, which may be of concern in relation to the future availability of timber resources if reforestation programmes or active management of naturally regenerated stands are not envisaged. In fact, the use of the maritime pine in reforestation programmes has decreased in favour of other faster growing but more nutrient demanding species, such as *Pinus radiata* and *Eucalyptus globulus* (Sánchez-Rodríguez et al., 2002; Merino et al., 2003).

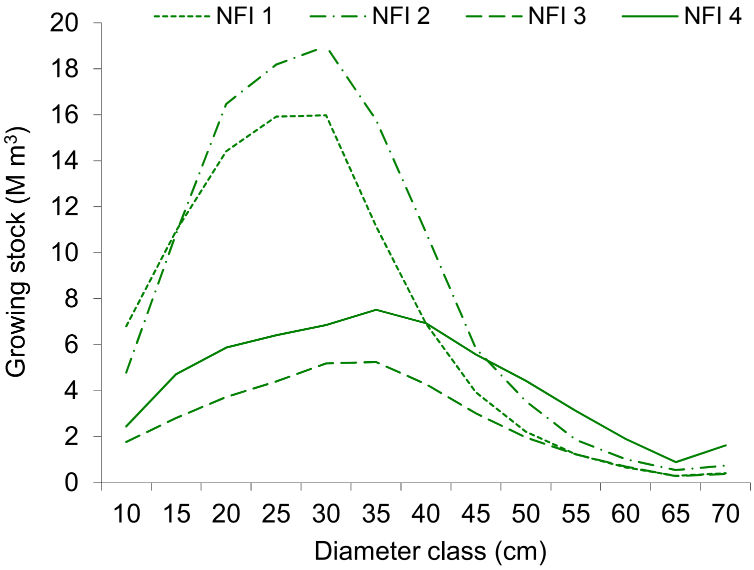

Figure 3. Development of growing stock in terms of diameter classes for maritime pine in Galicia

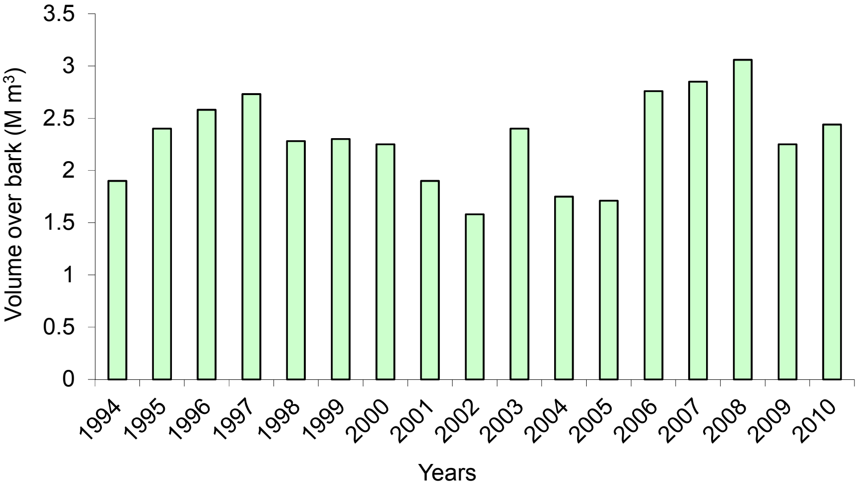

Figure 4. Development of harvested volume over bark (M m^3 $year^{-1}$) for *Pinus pinaster* in Galicia

Figure 4 shows the wood production of *Pinus pinaster* in Galicia between 1994 and 2010. The average volume over bark in the last 17 years was 2.3 M m^3, reaching a maximum of 3 M m^3 in 2008. In Galicia, it is estimated that the volume over bark felled in 2014 was 2.8 M m^3. The industrial destination was as follows: 1.76 M m^3 for the sawing and veneer industry, 0.65 M m^3 for the board industry, 225000 m^3 for biomass and firewood, and 5000 m^3 was transferred to other Autonomous Communities and 160000 m^3 exported outside of Spain. There are three types of *Pinus pinaster* producers: private forest owners sold 71% of the wood cut (1.99 M m^3 with bark), communal forests sold 22 % (0.62 M m^3) and the forest service department of the Consellería do Medio Rural sold the rest (0.19 M m^3) (Asociación Forestal de Galicia, 2015).

1.5. Current interest in the availability of wood

The lack of optimal forest management regimes for *Pinus pinaster* stands has greatly limited both productivity and the possibility of obtaining quality wood. It is still quite common to find stands where silvicultural treatments, such as thinning, pruning and cleaning have not been carried out.

For many years, the market advisers recommended orienting management of *Pinus pinaster* forests towards production of large diameter pine, to yield timber for use in the sawing or veneer industries. Rotation periods of 30 to 40 years are used to ensure that tree diameters of 35 and 40 cm are reached at final cutting. It is therefore necessary to carry out several thinning operations to maintain relatively low densities. Wood obtained from thinning can be used by the pulp and wood-based board industries and in sawmilling.

There is currently a high demand for solid timber of relatively large diameter; however, there is also demand for new products derived from small timber, mainly forest biomass for bioenergy and engineered wood. Data from Aquitaine in SW France shows that the difference in price between large logs and small timber is constraining, because of the reduction in timber resources as a result of the storms that occurred in 1999 and 2009 and the increase in demand for timber from cogeneration power plants and the pulp and board industries (Martinez de Arano and Lesgourgues, 2014). Pine timber markets in SW France are known to have a strong effect on timber prices and demand in northern Spain. *Pinus pinaster* plantations in Galicia should therefore be increased to address the needs of the productive sector, through promotion of naturally regenerated and planted stands. Natural regeneration has been already applied to many stands in Galicia and Portugal, and it is known that this type of management leads to dense young stands suitable for thinning to produce biomass for energy purposes. It is also important to promote grants for establishing plantations and to encourage and active forest management, such as actions to support the natural regeneration of *Pinus pinaster*.

The definition of new silvicultural methods can improve the management of small non-industrial forests and communal forests, thus possibly achieving effective use of natural regeneration. These silvicultural models would be used by managers of both types of forests to respond to the demand for raw material to produce bioenergy and new wood products. Bio-economic models can also be used as an instrument whereby it will be possible to define forest management instruments in order to respond to the socio-economic objectives and restrictions of forest owners and managers of communal forests. These models can be used to decide which regeneration method should be promoted in each case: plantation of genetically improved plants or promotion and tending of naturally regenerated stands.

The fragmentation of forest properties and the abandonment of many forests, with the consequent lack of active management are all weaknesses in the forest chain related to maritime pine (Rodríguez-Vicente and Marey-Pérez, 2009). Another difficulty for owners is the age at which trees are usually cut, which reduces the economic profits. In this context, it is important to define silvicultural schemes that enable production of intermediate benefits for forest owners, and which serve to improve stand conditions and shorten rotations. Some schemes have been proposed by the regional government of Galicia (Xunta de Galicia, 2014). Recent projects developed under the umbrella of SUDOE (Southwest European Space Territorial Cooperation Programme) have attempted to test silvicultural models that optimize the production of wood and biomass for energy purposes This is the case of the SILVAPLUS project, which involves the installation of a network of plots with strip management of pinewood with the goal of timber production or direct biomass production in the south of Galicia and north of Portugal (Figure 5).

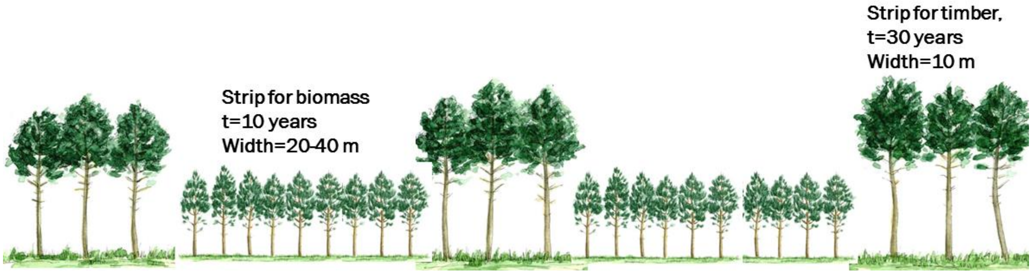

Figure 5. Scheme for timber and biomass production.

1.6. Threats to maritime pine stands

Promotion of active forest management is affected by the different threats to which *Pinus pinaster* is subjected, such as health problems, forest fires and windstorms.

1.6.1. Health problems and the nematode threat

Among the various forest health problems that exist, many native pests and diseases affect maritime pine, although the damage does not represent a major threat to the productivity at a regional scale. Pine processionary moth and scolytid beetles, particularly *Ips sexdentatus*, cause reduced growth of trees and their presence has led to the need for extensive felling in both the Iberian Peninsula and Aquitaine. The fungi *Armillaria spp.* and *Heterobasidion annosum* cause white putrefaction of the roots, whereas *Peridermium pini* may produce damage in needles, branches and trunk (Fernández de Ana Magán, 2005).

Nowadays, one of the most important threats to pine is pine wilt disease (PWD) caused by the pine wood nematode (PWN) *Bursaphelenchus xylophilus*. This species is associated with stressed, dead or decaying conifers in its original distribution area in North America and is considered a quarantine organism as it causes serious damage to pines worldwide, outside its native area. In Europe, PWN was first detected in Portugal (Mota et al., 1999), and evidence that the insect vector is *Monochamus galloprovincialis* in this country (Sousa et al., 2002) has stimulated studies on its further distribution and other potential vector insects in Europe, including Spain (Zas et al., 2014). The risk of spread of pine wood nematode into Spain from

Portugal is clear, as a result of both natural spread and the movement of timber between the two countries. In 2008, PWN was identified in Extremadura, and preventative measures have been implemented on the basis of an official contingency programme led by the Spanish Ministry of Environmental Affairs in agreement with the European Union. As a consequence of systematic sampling along the Portuguese border and within Spain, *B. xylophilus* was morphologically and molecularly identified at As Neves (Pontevedra, Galicia) in 2010. Affected specimens showed typical symptoms associated with pine wilt, including needle discoloration and death of branches. Maritime pine is particularly sensitive to the effects of PWN (Abelleira et al., 2013).

Protocols for the elimination of PWD epidemics involve preventative silvicultural control of PWN-infected pines with no wilt symptoms. Such control entails clear-cutting and the physical removal of logs and branches. In 2006, a phytosanitary strip 3 km wide and devoid of *Pinus pinaster* was established in Portugal to prevent spread of PWD epidemics (Rodrigues, 2008; Mota and Vieira, 2008). If silvicultural control is applied in newly infested areas, suppression of PWD epidemics could be envisaged.

Eradication measures recommended by EPPO (2012) on detection of a focal point of infection include the immediate cutting and destruction of affected trees, together with the forest harvesting residues, and delimiting an area of radius 5 km around the affected trees to detect possible additional outbreaks. For localized infection, clear cutting in a surrounding area of radius between 0.5 and 3 km is recommended. For example, in the outbreak in Extremadura, an area of radius 3 km was proposed for eradication of the disease (Junta de Extremadura, 2009). The Galician resolution (Xunta de Galicia, 2010) establishes an area of radius 1.5 km as the eradication zone.

The removal of forest harvesting residues may be produced by burning or crushing, following the decisions of the European and Mediterranean Plant Protection Organization (EPPO, 2012) to reduce slash to pieces of less than 3 cm.

This material should be marketed, mainly for potential use by the biomass industry. PWN is considered eradicated if infected trees are not found in the demarcated area in a period of three years.

Monochamus sawyer beetles can also cause extensive damage to freshly cut pine timber. The general measures used to control populations of these beetles are very similar to those recommended for preventing bark beetle: removal of wood piles before the flight period, restrictions on the size of forest harvesting residues left on site, maintenance of good hygiene in the forest, elimination of dying trees, and appropriate control of forest fires, which is one of the factors that has led to the increase in *Monochamus* populations.

1.6.2. Forests fires

Fire is sometimes an essential part of land management and forest regeneration as it can have beneficial effects on reproductive capacity. However, fire usually becomes a problem when it spreads out of control in forests used for a particular purpose, as for example timber production. Wildfires are increasingly causing damage to forests, leading to the destruction of forest vegetation and biomass, considerable soil erosion by wind and water, and air pollution. Maritime pine is the forest species most affected by fire in the Iberian Peninsula, especially in Galicia (MMA, 2006). The main causes of the proliferation of forest fires in Galicia include the lack of active forest management, the abundance of unproductive small land plots, the use of fire as an agricultural tool, and the existence of large areas with high forest fuel loads and continuous structures (Chas Amil, 2007; Fernández-Alonso et al., 2013). Forest fires in the region caused the loss of 1758 ha of *Pinus pinaster* plantations in 2013; some of this land (627 ha) was young woodland without commercial use, and the remainder (1131 ha) was mature woodland of commercial use (MAGRAMA, 2015).

Most forest fires that occurred in Galicia in 2006 (more than 90%) were caused by man (Chas Amil, 2007).

For trees of the genus *Pinus*, fire is often considered a positive factor, because most pines can resist the effects (Fernandes and Rigolot, 2007). However, maritime pine forests are considered fire-prone ecosystems (Agee, 1998), partly due to their frequently dense understory, favoured by a light canopy, which facilitates considerable fuel loads and high intensity fire (Fernandes and Rigolot, 2007).

The severity and intensity of fire are related to the type of fuel present in the stand, and the fuel loads depend on silvicultural treatments. The lack of management and silviculture plus the abundance of fuel lead to situations of greater risk. Active management of stands and the application of preventive silviculture measures would allow structures with low fuel and good options for firefighting. Different treatments can be used to reduce the fuel loads: manual or mechanical brushing, prescribed burning, chemical treatment of understory and grazing. Shrubs can be crushed, chipped, removed from the stand, cut and strip piled, burned or harvested to biomass (Agee and Skinner, 2005).

1.6.3. Windstorms

Windthrow is also an important threat to maritime pine stands, particularly in Atlantic areas exposed to winter gales and occasional severe storms, which can lead to large loss of timber. Although wind speed is the most important factor contributing to windthrow, other factors such as topography, soil conditions, silvicultural treatment and stand structure are also important in determining the resistance of forest stands to wind loading. In Aquitaine, the storms that occurred in 1999 and 2009 were particularly violent. Winds of speeds higher than 170 km h^{-1} devastated the region and caused estimated losses of 26.1 M m^3 of timber in 1999 (Cucchi and Bert, 2003), while in 2009, the storm "Klaus" felled 40 M m^3 of standing timber (Martinez de Arano and Lesgourgues, 2014). Galicia has been less seriously affected by such threats, although "Klaus" felled at least 1.5 M m^3 of timber in 2009. Several studies have shown that the slenderness coefficient (considered as tree or stand index) is highly correlated with stem bending, windsnap and windthrow. Becquey and Riou-Nivert (1987) plotted this coefficient against stand dominant height to define three stability zones for stands (stable, not very stable and unstable). For stand heights between 20 and 30 m, mean slenderness coefficient (SC) values above 90 indicate unstable stands, while the mean SC value for stable stands is below 60. Thus, the risk increases with stand age, and forest managers should ensure that early thinning is applied, particularly in productive sites in which height growth is more important (Castedo et al., 2009).

1.7. Site properties and growth models

When maritime pine reforestation and active management are envisaged, sound plans considering the real dependence of growth on site properties should be constructed. Although past and recent studies have addressed the relationships between site index and site parameters (Pacheco-Marques, 1991; Álvarez-Álvarez et al., 2011), the real influence of soil properties on stand characteristics and biomass growth are still not well understood.

Growth and dynamics of pure and mixed stands have been studied in maritime pine on the basis of information from individual tree growth or stand growth, leading to the development of management tools based exclusively on empirical, statistically based models (Arias Rodil, 2015). However, there is a lack of data that enable the design of preventive silviculture measures or silvicultural treatments for mixed production of wood and biomass. Stand development must therefore be determined using models based on the real processes of net production of biomass and its allocation to biomass compartments in the forest system. The application of process-based models requires knowledge about a number of relevant forest parameters, many of them related to leaf area and leaf biomass.

Study of needle morphology is of interest because the information obtained has diverse applications such as the direct estimation of leaf area or leaf area index (LAI). Leaf area is a key trait in plant growth and an important indicator of plant strategies, and it is widely used in plant ecology, agronomy and forestry (Poorter et al., 2009). The mass of leaves, reflected in leaf area, determines energy interception, which influences the rate of photosynthesis, while root mass and distribution are major factors in water use and nutrient uptake (Landsberg and Sands, 2011).

LAI is directly associated with the ability of the canopy to absorb light and produce photosynthates and is therefore a key parameter for estimating plantation productivity (Vose and Allen, 1988; Innes et al., 2005). LAI is also the primary biophysical parameter used in forest productivity modelling and carbon sequestration studies, and it is commonly used by forest managers to quantify canopy responses to silvicultural treatments (Landsberg and Gower, 1997, Gower et al., 1999). In various process models used to estimate primary net production (Landsberg and Waring, 1997), leaf area index is included as an input variable that can be estimated from the foliar biomass and leaf area.

Information about foliar nutrition, litterfall rates, leaf area, leaf biomass, LAI and fuel structure in pine forests is therefore necessary for parameterization and application of these models to realistic silvicultural proposals. These process-based tools can determine possible answers to the incidence of disease, conditions of greater severity of fire or other risks to which the stands are subjected with an appropriate edaphic and ecophysiological basis.

Leaf longevity is one of traits influencing pine crown architecture and leaf display that may contribute to the competitive success of pines. The longevity depends on resource availability and environmental conditions, as well as their interactions and their relationships with morphological and physiological traits (Schoettle and Fahey, 1994).

The variation in growth efficiency (GE), defined as the ratio between the increase in biomass and LAI, is a useful metric for describing tree and stand growth processes and can contribute to variation in production. The climatic and soil factors that affect the availability of water and nutrients also affect GE (Fox et al., 2007; DeRose and Seymour, 2009).

The nature of bedrock is the main factor affecting soil properties, particularly in homogeneous climate zones (Hartmann and Moosdorf, 2012). The role of the parent material as an explanatory factor for vegetation cover and tree growth has recently been recognized and highlighted (Cocco et al., 2013; Hahm et al., 2014).

In Galicia, the bedrock is a very important factor in the distribution and properties of soils. Many of the soils are shallow because the rock is scarcely alterable (quartzite, non-tectonized granite, some slates), whereas deeper soils (> 1 m) occur over basic rocks (gabbro, amphibolites) and schists (Ordenes Complex). The rock also influences the texture of the soil, coarse fractions predominate in soils developed over hard rocks, which are less able to store water. This leads to more drought-related problems for vegetation during the summer than in soils formed over readily alterable rocks, which are of finer texture. The chemical limitations of Galician soils are related to the nature of the original material, and the effect of leaching is promoted by high rainfall and good drainage. Thus the more soluble minerals (halides) and minerals of intermediate solubility (carbonates) are easily removed from the drainage water. The more mobile elements such as Ca, Mg, Na and K (basic cations) are also leached, causing a decrease in pH and an increase in the presence of Al in soils (Macias et al., 1986). This process occurs faster in soils derived from acidic rocks, but also affects soils developed on basic rocks over time. In conclusion, the major deficiencies observed in the Galician soils in terms of chemical fertility are strong acidity (i.e. low pH), low cation exchange capacity, high content of Al in exchange positions, fixation of P, S and Mo and the slow mineralization rate of organic N. Soil developed over granitic rocks can fix K via clays, while soils developed on basic rocks are deficient in this nutrient because it is not present in the primary minerals. In these sites, Al is highly soluble and occupies most of the negative surface charges present in colloids, saturating the exchange complex (set of negative charges), often by more than 60% (Alvarez et al., 1992; 2002).

Therefore, aluminium is a particularly important element affecting soil chemistry in Galician soil. In addition to occupying the negative charges of colloids and their toxicity, it is involved in other aspects related to fertility: reaction with organic matter (delayed organic matter mineralization and recycling of nutrients to the plant), the buffer effect on the soil (maintaining the pH between 4 and 5, so that Galician soil has a high ability to resist acidification processes) and precipitation with P to form compounds of low solubility (Macías, 1986).

Approximately 40% of the world’s arable soils are acidic and may be subject to the effects of aluminium (Al) toxicity (Haug and Foy, 1984). This element is considered the main factor limiting the fertility of most acid soils and impedes plant development at pH less than 5 or even under 5.5 in kaolinitic soils (Foy, 1984). The symptoms of Al toxicity are not easily identifiable. Thus, in plants the foliar symptoms resemble those of P or Ca deficiency (Foy et al., 1978). Calcium uptake and transport have been strongly affected by Al toxicity (Panda et al., 2009). The major Al toxicity symptom observed in plants is inhibition of root growth (Delhaize and Ryan, 1995; Panda et al., 2009).

Studies covering a complete set of plots considering the bedrock as a basis for classification of soil are scarce. Moreover, determination of fertility levels and fertility indices do not consider Al forms in the soil, many of which have clearly toxic effects on the trees and directly affect the nutritional status.

Some authors have recommended several indices for evaluating Al toxicity: edaphic indices use parameters associated with the soil exchange complex and parameters determined in the soil solution and foliar and root indices use various different elements (Cronan and Grigal, 1995; Boudot et al., 1994, 2000).

The presence of different forms of Al in the solid phase may be influenced by different factors related to soil formation. Given the importance of the Al fractions, different extractants such as acid ammonium oxalate and sodium pyrophosphate (pH 10) are commonly used to quantify the Al fractions in soil (Paterson et al., 1993).

1.8. Objectives

The overall aim of this doctoral research was to improve the understanding of the relationships between the ecophysiological and edaphic parameters that determine the growth of *Pinus pinaster* and its ability to adapt to different environments, in order to facilitate the decision-making involved in wood and biomass production.

The specific objectives were as follows:

Chapter 3: To investigate differences in the concentrations of available nutrients in soil, foliar levels of nutrients and site index in 128 plots established on soils developed from a wide range of types of bedrock in Galicia.

- To propose site index models based on type of bedrock.
- To determine nutritional deficiencies in relation to bedrock.

Chapter 4: To establish some of the sources of variation in maritime pine foliar parameters, focusing on the effects of site, needle age class and nutritional status in 31 plots. - To assess and rank the sources of variation of basic needle dimensions, including age classes, in a set of plots covering a range of site characteristics in maritime pine plantations just before canopy closure.

- To explore how needle length and mass are related to site parameters in different age classes.
- To determine the stand level properties of needles, such as specific leaf area and needle tissue density, and relate these to nutrient status, area-based N concentration, site index, basal area per plot and elevation.

Chapter 5: To investigate how nutrients affect the productivity of 31 maritime pine plantations and whether they directly influence needle longevity, foliar biomass and leaf area.

- To determine the average needle lifespan, needle biomass and leaf area index in a network of plots before canopy closure.
- To relate the aforementioned variables to site index, growth efficiency and mean shrub height.

Chapter 6: To investigate the influence of parent material on the chemical properties of acidic soils under *Pinus pinaster*, especially in Al fractions in the soil solid phase and the total concentration of Al in solution, and to determine soil chemical parameters that affect the presence of different Al forms.

Chapter 7: To evaluate the influence of type of bedrock on Al fractionation and speciation in the soil solution.

- To evaluate the risk of Al toxicity in soils developed from different geological materials, by using various toxicity indices.
- To evaluate growth and biomass parameters of *Pinus pinaster* growing in acidic soils in relation to the different Al toxicity indices used.

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Chapter 2

Plot networks


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2. PLOT NETWORKS

The details of the material and methods used are included in each chapter. In this section, additional information about the plots used in the studies is given to clarify the origin of the data.

2.1. The main plot network

Most of the studies were carried out in 31 Pinus pinaster plots installed in 2006 by TRAGSA in collaboration with UXFS (USC) (Figure 1). At that moment, the main study aims were to evaluate the early growth of plantations established in former agricultural or abandoned communal land, the proportion of plantations with stability-related problems, and the relationship between stability and morphological parameters of the roots. Funding for these studies was supplied by the Regional Government of Galicia (CG419 2003/2005). The sampling considered the database of forest grants awarded in 1995 and 1996. The plots were chosen from this database to represent the geography of the region. In the current doctoral research, this net of plots was remeasured and needle sampled was performed to deal with additional objectives. The studies carried out in these plots are described in Chapters 3, 4 and 5.

Planting stock in these plantations predominantly comprised containerized seedlings of local Atlantic provenances, aged one or two years. At plantation establishment (which was funded by public grants), initial spacing ranged from 741 to 2000 plants ha^{-1}. The stands were not precommercialy thinned, and the density determined in the inventories was therefore due to natural mortality between planting and canopy closure. The average mortality was 14.8%.

Rectangular plots of size 30x20 m were established and all the trees were measured twice at an interval of two years (2007 and 2009). The principal dendrometric parameters for the second inventory are reported in Chapters 2 and 3. Additional variables related to height, including the relative spacing (Hart (1928); Becking (1954)), are shown in Table 1. The precipitation and temperature data were obtained from thermopluviometric stations close to each plot. The mean precipitation was calculated for each season (winter, spring, summer and autumn). The minimum temperature is the mean minimum air temperature in the coldest months and maximum temperature is the mean maximum air temperature in the hottest months (Table 2).

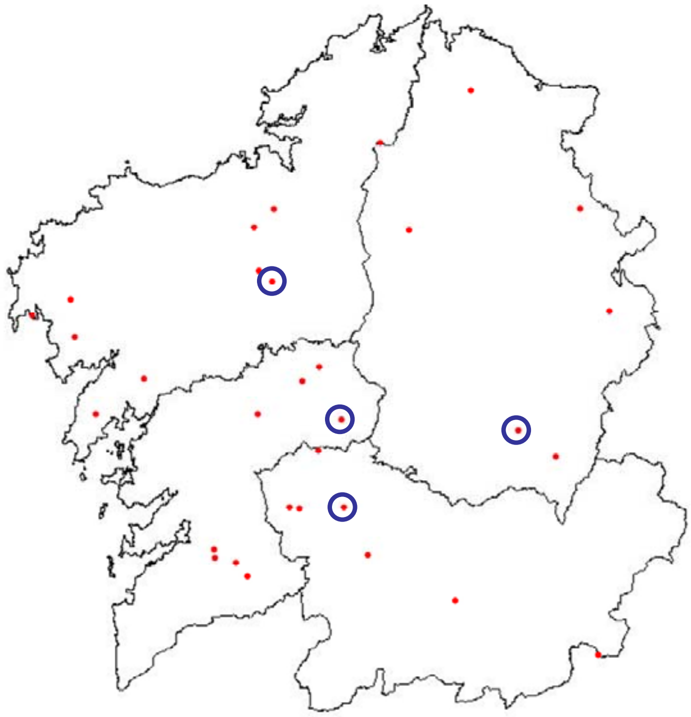

Figure 1. Location of the 31 *Pinus pinaster* plots used in the study. The blue circles represent a subgroup of plots used in the aluminium-related studies.

Table 1. Descriptive statistics for height-related variables in the 31 study plots

Variable	Average	Minimum	Maximum	Standard deviation
Height (m)	6,80	3,49	11,08	2,34
Crown height (m)	2,22	0,29	5,52	1,41
Dominant height (m)	7,95	4,28	12,45	2,40
Slenderness coefficient	57,92	45,27	78,82	8,31
Relative spacing (%)	43,63	25,28	72,71	14,34

Table 2. Descriptive statistics for the climatic variables in the 31 study plots

Variable	Average	Minimum	Maximum	Standard deviation
Annual precipitation (mm)	1392,10	728,0	2287,0	418,15
Winter precipitation (mm)	537,39	186,2	923,3	192,48
Spring precipitation (mm)	314,96	182,0	550,2	100,81
Summer Precipitation (mm)	119,40	66,3	178,2	31,63
Autumn Precipitation (mm)	420,40	194,3	635,1	112,75
Annual Temperature (ºC)	12,11	10,0	16,1	1,27
Minimum Temperature (ºC)	2,47	-1,30	8,60	1,97
Maximum Temperature (ºC)	25,15	20,0	29,2	2,06

A subset of 4 plots, included in the 31 plots and marked in Figure 1, was used for detailed study of the aluminium fractions and toxicity risk in acidic soils as reported in Chapters 6 and 7. These experimental plots were chosen to represent different types of parent material (slate, biotitic schist, mica schist and granite).

In all 31 plots, soil pits were used to identify soil horizons, and the soils were classified according to the World Reference Base for soil resources (WRB, 2006). Table 3 shows the basic information about the sites and the types of soils classified in each plot. Independently of the parent material, most of studied soils were classified as Haplic Umbrisols (58% of the plots), followed by Umbric Leptosols (32%) and Haplic Regosols (10%). A range of horizon distributions was found among the soils classified as Umbrisols, which were also characterised by a broad range of soil depths. Regosols were mainly present in sites where unconsolidated material accumulated as a result of changes in slope.

Table 3. Information about the plots and FAO classification

Plot	Substrate	pH H_2O	Organic matter	Soil depth (cm)	Slope (%)	Elevation (m)	FAO Classification
1	Biotitic schist	5.25	8.15	0.6	0	83	Haplic Umbrisol
2	Biotitic schist	4.70	16.87	0.4	1	443	Haplic Umbrisol
3	Gneiss	3.65	28.33	0.4	38	535	Haplic Umbrisol
4	Granite	4.47	34.25	0.4	21	520	Haplic Regosol
5	Phyllite/Slate	4.69	20.02	0.2	11	450	Umbric Leptosol
6	Biotitic schist	4.94	10.78	0.4	0	325	Haplic Umbrisol
7	Phyllite/Slate	4.46	14.78	0.2	56	643	Umbric Leptosol
8	Gneiss	4.56	11.86	0.2	11	690	Umbric Leptosol
9	Granite	4.61	31.81	0.3	25	510	Haplic Umbrisol
10	Phyllite/Slate	4.43	17.79	0.25	45	655	Umbric Leptosol
11	Migmatite	4.74	18.62	0.43	25	110	Haplic Umbrisol
12	Granite	4.05	21.72	0.35	25	840	Haplic Umbrisol
13	Phyllite/Slate	4.58	9.71	0.25	17	875	Umbric Leptosol
14	Phyllite/Slate	4.75	12.64	0.4	14	480	Haplic Umbrisol
15	Phyllite/Slate	4.02	20.52	0.2	34	643	Umbric Leptosol
16	Mica schist	4.35	12.52	0.3	9	645	Haplic Umbrisol
17	Mica schist	4.62	7.79	0.3	9	503	Haplic Umbrisol
18	Mica schist	5.06	11.46	0.15	36	370	Umbric Leptosol
19	Phyllite/Slate	5.03	12.34	0.4	35	690	Haplic Umbrisol
20	Biotitic schist	4.52	11.07	0.45	0	290	Haplic Umbrisol
21	Phyllite/Slate	4.36	24.31	0.25	10.5	558	Umbric Leptosol
22	Mica schist	4.33	18.96	0.3	15	773	Haplic Umbrisol
23	Granite	4.73	17.41	0.6	17	660	Haplic Umbrisol
24	Mica schist	4.84	8.59	0.2	15	447	Umbric Leptosol
25	Migmatite	4.95	8.93	0.6	25	160	Haplic Umbrisol
26	Gneiss	3.83	16.34	0.35	13	383	Haplic Regosol
27	Granite	4.41	12.90	0.15	6	475	Umbric Leptosol
28	Granite	4.64	12.50	0.5	15	200	Haplic Regosol
29	Granite	4.66	14.14	0.5	8	500	Haplic Umbrisol
30	Granite	4.38	12.55	0.5	43	340	Haplic Umbrisol
31	Granite	4.43	6.93	0.6	10.5	340	Haplic Umbrisol

2.2. The Bará and Toval plots

In the study described in Chapter 3, additional plots were considered in order to evaluate the influence of parent material. The study was carried out in the previously mentioned 31 plots and in a network of 97 plots established in 1974 and 1975 (Figure 2). The latter plots were part of a study by Bará and Toval (1983) and the information about the plots was extracted from a book written by these authors, with the exception of lithological information, which was obtained in the present study for all 128 plots.

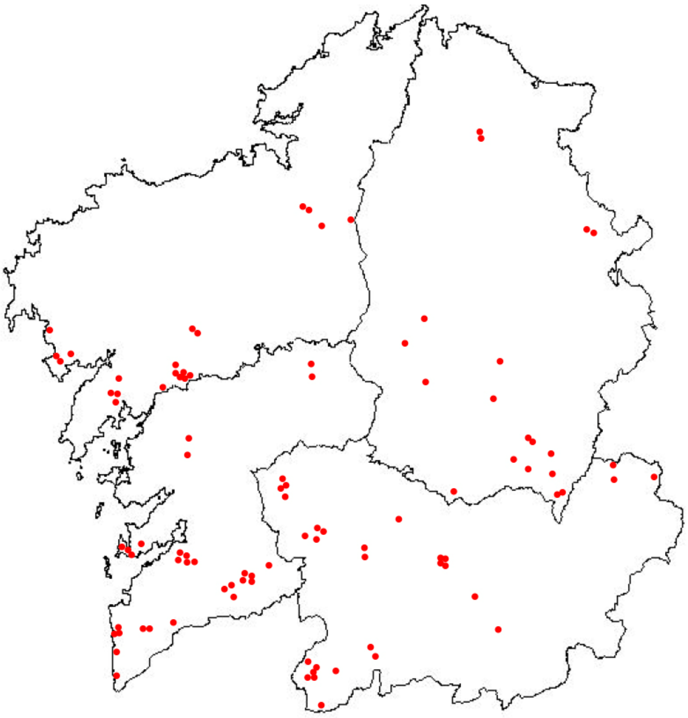

Figure 2. Location of the 97 *Pinus pinaster* plots included in the study (Bará and Toval, 1983)

Although there is no additional information about the soil types in this network of plots, the information provided in the original publication (Bará and Toval, 1983) allowed tentative classification of the soils. The variation in soil types was higher than in the first set of plots. Umbrisols were the most frequent type of soils (87%), probably represented by four subtypes: Cambic, Humic and Haplic Umbrisols. Leptosols were less frequent in these plots, as only 3 were classified as such since the other plots have an A horizon of more than 25 cm deep. Regosols would also be present, although number is difficult to estimate given the lack of complete soil profile information. We cannot rule out the possible presence of a small number of Cambisols and Arenosols in these 97 plots.

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Chapter 3

Bedrock, nutrition and growth

This work is included in the publication:

Eimil-Fraga, C., Rodríguez-Soalleiro, R., Sánchez-Rodríguez, F., Pérez-Cruzado, C., Alvarez-Rodríguez, E., 2014. Significance of bedrock as a site factor determining nutritional status and growth of maritime pine. Forest Ecology and Management. 331, 19-24.

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Chapter 4

Needle traits and stand parameters

This work is included in the publication:

Eimil-Fraga, C., Sánchez-Rodríguez, F., Álvarez-Rodríguez, E., Rodríguez-Soalleiro, R., 2015. Relationships between needle traits, needle age and site and stand parameters in *Pinus pinaster*. Trees. 29, 1103–1113.

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Chapter 5

Needle lifespan and foliar biomass

This work is included in the publication:

Eimil-Fraga, C., Sánchez-Rodríguez, F., Álvarez-Rodríguez, E., Rodríguez-Soalleiro, R., 2015. Variability in needle lifespan and foliar biomass along a gradient of soil fertility in maritime pine plantations on acid soils rich in organic matter. Forest Ecology and Management. 343, 34-41.

http://www.sciencedirect.com/science/article/pii/S0378112715000493


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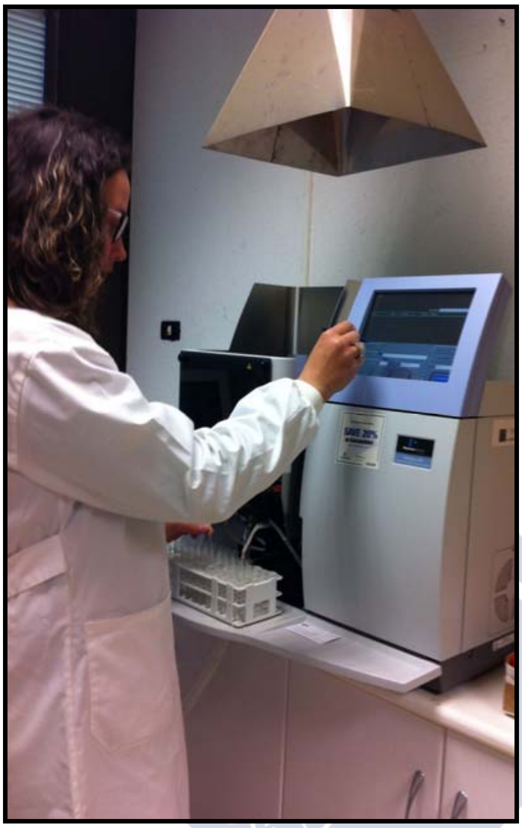
Chapter 6

Aluminium fractions in solid phase



This work is included in the publication:

Eimil-Fraga, C., Álvarez-Rodríguez, E., Rodríguez-Soalleiro, R., Fernández-Sanjurjo, M.J., 2015. Influence of parent material on the aluminium fractions in acidic soils under *Pinus pinaster* in Galicia (NW Spain). Geoderma. 255-256, 50-57.

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Chapter 7

Aluminium toxicity risk

This work is included in:

Eimil-Fraga, C., Fernández-Sanjurjo, M.J., Rodríguez-Soalleiro, R., Álvarez-Rodríguez, E. 2016. Aluminium toxicity risk for *Pinus pinaster* in acid soils (Galicia, NW Spain). Land Degradation and Development. Accepted


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ABSTRACT

The influence of bedrock on aluminium toxicity and aluminium speciation in the soil solution was studied in four *Pinus pinaster* plots. Growth and biomass parameters in the acidic soils were also evaluated in relation to different Al toxicity indices. The plots were developed over slate, biotitic schist, mica schist and granite. Samples of rhizospheric and non-rhizopheric soil, one-year-old needles and roots were collected in each study plot. Total Al, reactive Al, acid-soluble Al, non-labile and labile Al and Al species (Al^{3+}, Al-OH, Al-F and $Al\text{-}SO_4$) were determined in soil solution. Reactive Al dominated over the acid-soluble Al and the non-labile Al predominated over the labile Al in all soils, but particularly over mica schist. In the biotitic schist soil, the Al forms and total Al were lower, whereas concentrations were always higher over mica schist. The Al forms considered most toxic were Al^{3+} and Al-OH, and its concentrations were highest over slate and mica schist. Al toxicity indices in soil, needle and roots showed a risk of toxicity in mica schist, slate and granite. The stand site indices over slate and mica schist were lower, consistently with the high labile Al and Al^{3+} + Al-OH in soil solution. Despite the high stand site index over granite, the growth efficiency was low, accordingly to very low ratios Ca/Al in needles or fine roots. This confirmed the adaptation of maritime pine to granitic substrates.

Keywords: parent materials, acid soils, aluminium species, aluminium toxicity indices, growth efficiency

1. INTRODUCTION

Acidic soils are common in temperate and humid regions of the world where cation leaching has occurred over long periods and the parent material may also be acidic. The region of Galicia (NW Spain) is a good site for studying naturally acidic soils where pine forest plantations are common. In these soils, an intense cation leaching has occurred during weathering of the parent material, generating active aluminium species (García-Rodeja and Macías, 1984). In addition to these natural processes, anthropogenic effects derived from industrial, agricultural and mining activities can also produce more rapid soils acidification (Decock et al., 2015). These activities can lead to degradation of the soil by acidification, with consequent Al mobilization and problems related to heavy metal pollution (Roy and McDonald, 2015; Sacristán et al., 2015). This can affect biodiversity and the essential functions that soil performs in relation to humankind and the environment, such as support of primary production via organic matter and nutrient cycling, climate control via regulation of C and N fluxes, control of pests and diseases, and filtering of pollutants (Keesstra et al., 2012; Brevick et al., 2015).

In very acidic soils, the Al is readily bioavailable and Al toxicity is an important growth-limiting factor for plants (Poschenrieder et al., 2008). Knowledge about Al speciation in the soil solution is essential because this determines the toxicity of Al to plants (Waters and Webster, 2013). It is generally thought that Al^{3+} and monomeric hydroxyaluminium complexes are the most toxic Al species (Kinraide, 1991; Arunakumara et al., 2013). The phytotoxic form, Al^{3+}, predominates only under very acidic conditions. The degree of Al toxicity depends on other factors apart from pH, including the predominant clay minerals, organic matter content, concentrations of other cations, anions and total salts, and the type of plant species present (Rout et al., 2001).

To improve the production and functions of soils affected by chemical degradation, we can either add amendments that increase the pH and immobilize Al and heavy metals (Mahmoud and Abd El-Kader, 2015), apply phytoremediation treatments (Paz-Ferreiro et al., 2014) or select species adapted to the particular conditions. The latter option would be the most appropriate in relation to forestry (Gandullo and Sánchez-Palomares). In their natural range, pines appear to be particularly well adapted to marginal habitats in which several interrelated factors enable the trees to compete successfully with other types of vegetation. Understanding how pines can adapt to high levels of Al in soil may be of interest in identifying species that can grow rapidly in acidic conditions, to provide both timber and/or protection against erosion. Acidic soil environments are very limiting to a large number of species, and loss of plant diversity would lead to greater vulnerability of the soil to erosive processes (Berendse et al., 2015).

The appearance of symptoms of Al toxicity in plants is not closely correlated with the Al concentration in either the solid phase or the soil solution. Cronan and Grigal (1995) recommended several indices for evaluating Al toxicity: base saturation in the exchange complex; Ca/labile Al molar ratio in the soil solution; and Ca/Al molar ratio in leaf and root. Boudot et al. (1994, 2000) proposed indices that take into account the presence of non-toxic Al species.

The aims of the present study were i) to evaluate the influence of type of bedrock on Al fractionation and speciation in the soil solution, ii) to evaluate the risk of Al toxicity in soils developed from different geological materials, by using various toxicity indices, and iii) to evaluate growth and biomass parameters of *Pinus pinaster* growing in acidic soils in relation to the different Al toxicity indices used. Active growth and accumulation of tree biomass could be used to indicate the ability of the species to restore highly acidified areas.

2. MATERIAL AND METHODS

2.1. Experimental

The plots were established in *Pinus pinaster* plantations and were chosen to include soils in NW Spain derived from four different parent materials: slate, biotitic schist, mica schist and granite. The main properties, the fractionation of Al in the solid phase of the soils as well as climatic information about the sites were reported in a previous study (Eimil-Fraga et al., 2015a). The stands measured 20x30 m and the age ranged between 11 and 13 years. Site index (SI) was calculated as the dominant height of the stand, in metres, at a reference age of 20 years (Gónzalez et al., 2005), equation (1).

$$
\begin{gathered}
\mathrm{SI} = \mathrm{H}_1 \left(1 - \exp\left(- z * 20\right)\right) / \left(1 - \exp\left(- z * t_1\right)\right)^{\left(1.4202 + 0.0801 * \mathrm{I}\right)} \\
z = \left(0.1352 + 0.0276 * \mathrm{I}\right) * \left(\mathrm{H}_1 / t_1\right)^{\left(0.9831 + 0.0940 * \mathrm{I}\right)} * t_1^{\left(- 0.2108 - 0.0929 * \mathrm{I}\right)}
\end{gathered}
\qquad (1)
$$

where SI is the site index of the stand, t_1 and H_1 are the age and dominant height measured in each plot, and I is a variable that assumes values of 0 for the inner ecoregion and 1 for the coastal ecoregion.

The stand basal area (m^2 ha^{-1}) was also calculated for each plot. Biomass was estimated using the models proposed by Hevia-Cabal (2012) for stands of *Pinus pinaster* of the same age in northern Spain. The leaf area index (LAI, m^2 m^{-2}) was determined by multiplying the total needle biomass by projected specific leaf area. The growth efficiency (kg m^{-2} $year^{-1}$) was estimated as the annual above-ground biomass increment per unit leaf area (LAI) (Eimil-Fraga et al., 2015b). The annual biomass increment was calculated from the difference in biomass estimated from the current inventory and in an inventory performed 2 years before.

In each plot, three samples of rhizospheric and three samples of non rhizospheric soil were obtained (see Eimil-Fraga et al., 2015a). Rhizospheric and non rhizospheric soil samples were separated following the method of Chung and Zasoski (1994), modified by Sanjurjo et al. (2003). In the field, the soil at a distance of about 20 cm from each stem was loosened to a depth of 20 cm to enable collection of roots and rhizosphere samples. The root segments were dissected and immediately after being cut they were gently separated from the soil and vigorously shaken. Three dominant trees were selected at randomly in each plot. From each of these trees, a well-illuminated branch of the upper third of the crown was removed and one-year-old needles were collected for elemental analysis. The root and needle samples were oven-dried for 48 h at 65 ºC, ground to a fine powder, and digested with nitric acid in a microwave oven, determining Ca, Mg and Al by atomic absorption spectrophotometry. The roots were classified in fine roots (diameter <1.5 mm) and medium roots (diameter between 1.5 and 3 mm).

The soil samples were dried at 40°C and passed through a 2 mm sieve. The following measurements were made on the solid fraction: pH in water and in 0.1 M KCl (soil:solution ratio, 1:2.5) (Guitián and Carballas, 1976); total C and N, with a LECO CNS-2000 autoanalyzer; effective cation exchange capacity (eCEC), as the sum of Ca, Mg, Na, K, and Al (Kamprath, 1970) displaced by 1 M NH4Cl (Peech et al., 1947) and determined by atomic absorption (Ca, Mg, and Al) and atomic emission (Na and K) spectrophotometry (Perkin Elmer AAnalyst 200, USA). Al saturation was calculated as the ratio between Al in the exchange complex and the effective cationic exchange capacity and expressed as a percentage (Kamprath, 1970). The concentration of P was measured by the Olsen method (Olsen and

Sommers, 1982). The main characteristics of the solid phase of the soil in the plots are shown in Table 1. The soils were acidic, rich in organic matter, of alic character (percent of exchangeable Al>60%) and contained low-moderate levels of Ca and Mg.

Table 1. Average values (and standard deviations) of general parameters of the soil solid phase in relation to parent material

	Slate	**Biotitic schist**	**Mica schist**	**Granite**
pH H_2O	4.78 (0.29)	5.36 (0.13)	4.95 (0.22)	4.85 (0.19)
C (g kg^{-1})	111.3 (17.82)	63.9 (7.29)	75.4 (24.77)	65.3 (16.32)
N (g kg^{-1})	5.4 (0.102)	5.0 (0.040)	4.4 (0.12)	4.3 (0.10)
C/N	20.71 (1.26)	12.74 (0.58)	16.74 (1.12)	15.31 (0.39)
eCEC (cmol(+) kg^{-1})	12.20 (2.46)	5.73 (0.39)	8.91 (2.91)	6.88 (1.02)
% Al	87.22 (3.32)	72.99 (5.77)	82.72 (4.36)	90.31 (2.01)

The soil solution was estimated by aqueous extracts (soil:solution ratio, 1:10). The extracts were filtered (0.45 μm) and analyzed to determine the following parameters: pH; electrical conductivity (EC); Ca and Mg concentrations (by flame atomic absorption spectrophotometry); Na and K (by flame atomic emission spectrophotometry); and sulphate by turbidimetry (Bardseley and Lancaster, 1960). Total fluoride was measured with an ion selective electrode after addition of a total ionic strength adjuster and buffer (TISAB IV; Orion, 1976). The dissolved organic matter (DOM) was determined by UV-visible spectroscopy.

Total dissolved Al, determined after acidification of samples to pH 1 for 1 h and heating them to boiling point, was separated into reactive Al and acid-soluble Al fractions, according to Driscoll (1984) and Álvarez et al. (1992). Acid-soluble Al comprises colloids, polymers and/or organo-aluminum complexes. Reactive Al, determined by slight acidification and without heating, was separated into labile monomeric and non-labile monomeric Al, by passing the solution through an ion exchange column with Amberlite 120 resin containing both H^+ and Na^+, so that the effluent pH was similar to that of the samples being analyzed. Non-labile Al, which passed through the column, mainly consisted of organic monomeric Al. Labile Al retained by the column consisted of inorganic monomeric Al. Total Al, reactive Al and non-labile Al were determined by visible spectrophotometry, with pyrocatechol violet (Dougan and Wilson, 1974). Acid-soluble Al was calculated as the difference between total Al and reactive Al. Labile Al was calculated as the difference between reactive Al and non-labile Al. Speciation of the labile Al into $Al^{3+,}$ Al-OH, Al-F, and $Al\text{-}SO_4$ was carried out with the aid of the SOLMINEQ computer program (Kharaka et al., 1989).

2.2. Aluminium toxicity indices

Different indices were calculated from the data in order to assess the Al toxicity. Two of the indices were calculated with the exchangeable cations: percent base saturation of the exchange complex (% base saturation) and BC/Al_{exc} molar ratio (BC=Ca+Mg+K and Al_{exc} is exchangeable Al). Four indices determined from parameters of the soil solution were used: labile Al; the sum of Al^{3+} and Al-OH concentrations; the Ca/labile Al molar ratio and the Aluminium Toxicity Index (ATI) (Boudot et al. 1994, 2000), equation (2).

$$\mathrm{ATI} = \frac{9\mathrm{Al}^{3+} + 4\mathrm{AlOH}^{2+} + \mathrm{Al(OH)_2}^{+} + 9\mathrm{Al(OH)_4}^{-} + \mathrm{Al(SO)_4}^{+}}{4\mathrm{Ca}^{2+} + 4\mathrm{Mg}^{2+} + 0.02\mathrm{K}^{+} + 0.02\mathrm{Na}^{+}} \qquad (2)$$

The following indices from root tissues were used: Ca and Al concentrations, Ca/Al molar ratio and the Ca+Mg/Al molar ratio. The following indices from leaf tissues were calculated: Ca and Al concentrations and the Ca/Al molar ratio.

The results were compared with critical values proposed by various authors for each index (Truman et al., 1986; Cronan et al., 1989; Sverdrup et al., 1992; Boudot et al., 1994, 2000; Cronan and Grigal, 1995; Blaser et al., 2008), indicating the point at which an unacceptable risk of forest damage is reached, either as a result of direct toxicity or of antagonism between nutrients.

2.3. Statistical analysis

The data were analysed to determine mean values and ranges of variation. Mean classification was performed by using the Duncan's test to examine all possible differences in relation to parent material. Pearson's correlation coefficients were calculated to assess the relationships between variables. Non linear and linear regressions were applied, using the variables most closely correlated with forms of labile Al. Several procedures in the SAS statistical package (SAS Institute, 2004) were used to analyse the data. BIAS (average deviations in respect to the mean) and RMSE (root mean square error) were used to evaluate the bias and precision of regression equations.

3. RESULTS AND DISCUSSION

3.1. General characteristics of the soil solution

As the ANOVA did not indicate any significant differences between rhizospheric and non-rhizospheric soils for any of the variables studied, the samples were considered together. The mean values and standard deviation of properties determined in soil solutions in relation to parent material (slate, biotitic schist, mica schist and granite) are shown in Table 2. The ANOVA revealed that the parent material had a significant effect on all variables studied, except SO_4^{2-} (Table 2). The pH in the soil solution values ranged between 4.74 and 5.68. This pH varied in a similar way as observed in the solid phase (Eimil-Fraga et al., 2015a) and the mean value was significantly higher in the soils over biotitic schist than in the other soils (Table 2). The low pH is consistent with the lithology and the temperate-humid climate of the study area (Álvarez et al., 1992). The EC values varied between 19.8 and 47.1 µS cm^{-1}, and they were significantly higher in the soil developed over slate than in that over granite. These values indicate very dilute solutions, which is consistent with the acidity of the rocks and the intense cation leaching in these ancient open systems.

3.2. Al fractionation and speciation in the soil solution

The total Al present in the soil solution ranged between 17.2 and 64.2 µmol L^{-1} and was significantly higher in the plot over mica schist than in the soils developed over granite and biotitic schist (Table 2). Similar concentrations of total Al have been reported in other forest soils in Galicia with presence of pines: 40.7-115.9 µmol L^{-1} for pure *P. sylvestris* and mixed *P. pinaster* and *P. sylvestris*, respectively (Fernández-Sanjurjo et al., 1998) and 33 µmol L^{-1} (Arbestain et al., 2004) and 41.9 µmol L^{-1} (Álvarez et al., 2005) for *P. radiata*. Nonetheless, the values obtained in the present study are high. A detailed comparison shows that values are higher in maritime pine than in Scots pine and radiata pine, thus indicating that maritime pine has a higher capacity to resist Al toxicity. The total Al values in soil solution are consistent with those reported by Collignon et al. (2012) and Boudot et al. (2000) for different kinds of soils and forest species. Other authors reported very high values, close to 150 µmol L^{-1} for *Fagus sylvatica* and *Picea abies* in granitic soils in the Czech Republic (Tejnecký et al., 2010), clearly derived from acidification through acid rain (Drabek et al., 2005).

Table 2. Average values (and standard deviations) of parameters obtained in the soil solution of soils developed over different parent material. The respective p values for the ANOVA are also shown. Different letters indicate significant differences using the Duncan's test

	p value	Slate	Biotitic schist	Mica schist	Granite
pH (soil solution)	0.0001	5.00 (0.41) b	5.68 (0.16) a	5.09 (0.31) b	4.74 (0.17) b
EC (dS m^{-1})	0.0057	47.1 (19.8) a	33.1 (6.80) ab	33.9 (8.67) ab	19.8 (3.88) b
Ca (mg L^{-1})	0.0169	0.31 (0.16) ab	0.45 (0.25) a	0.54 (0.26) a	0.15 (0.024) b
Mg (mg L^{-1})	0.0002	0.32 (0.18) b	0.37 (0.12) b	0.82 (0.37) a	0.16 (0.041) b
Na (mg L^{-1})	<0.0001	2.34 (0.40) a	2.53 (0.68) a	1.49 (0.16) b	1.28 (0.16) b
K (mg L^{-1})	0.0119	2.38 (1.35) a	2.91 (0.83) a	1.98 (0.46) ab	1.16 (0.23) b
F^- (mg L^{-1})	<0.0001	0.031 (0.0073) a	0.025 (0.0018) b	0.017 (0.0024) c	0.015 (0.00079) c
SO_4^{2-} (mg L^{-1})	0.3909	9.64 (2.31) a	11.29 (2.15) a	9.44 (2.12) a	9.64 (1.64) a
DOM (mg L^{-1})	0.0175	6.02 (2.40) a	2.81 (0.88) b	7.69 (3.84) a	5.02 (1.43) ab
Total Al (µmol L^{-1})	0.0006	51.2 (15.7) ab	17.2 (5.88) c	64.2 (26.5) a	38.3 (10.2) b
Reactive Al (µmol L^{-1})	0.0003	38.2 (11.9) ab	11.5 (4.12) c	46.1 (17.5) a	28.3 (8.77) b

EC: electrical conductivity and DOM: dissolved organic matter

Regarding the fractionation and speciation of Al, significant differences were observed in relation to soil parent material. The reactive Al fraction (range between 11.5 and 46.1 µmol L^{-1}) generally dominated over the acid-soluble Al (range between 5.76 and 18.16), and the concentrations of both were highest in the soil developed over mica schist (Table 2 and Figure 1a). The non-labile Al (organic monomers) predominated over the labile Al (inorganic monomers) in all the parent materials, but particularly for mica schist (Figure 1a), representing more than 52% of the reactive Al. The highest concentration of non-labile Al (26.9 µmol L^{-1}) was found over mica schist, which was significantly higher than in the soil over granite (14.5 µmol L^{-1}) and biotitic schist (5.99 µmol L^{-1}). Labile Al ranged between 5.46 and 19.1 µmol L^{-1}, and it was significantly lower in the soil developed over biotitic schist (Figure 1a). The acid-soluble Al and non-labile Al are greatly determined by the DOM content of these soils, yielding positive and highly significant correlations between DOM and non-labile Al ($\rho=0.97$, $p<0.0001$) (Figure 2a) and between DOM and acid-soluble Al ($\rho=0.86$, $p<0.0001$) (Figure 2b).

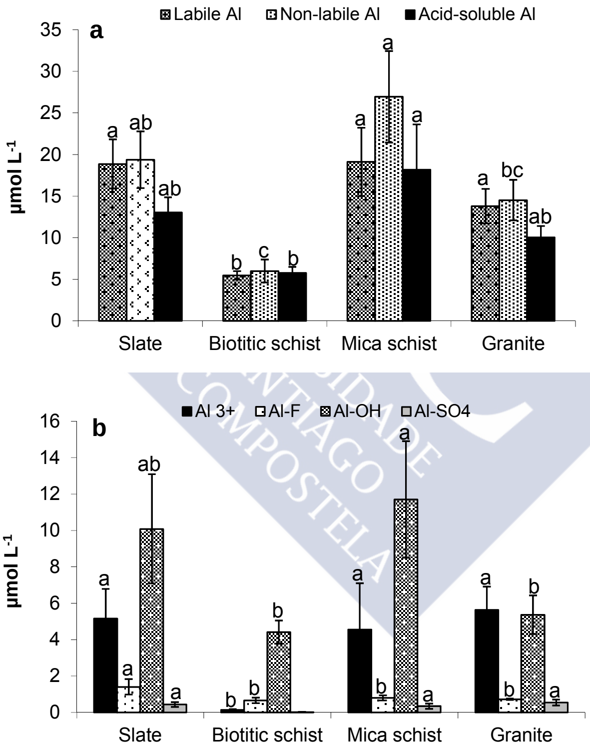

Figure 1. Mean values (and standard deviations shown as error bars) for fractionation of the Al (a) and labile-Al species (b) present in the soil solution. Letters correspond to the groups of parent materials according to Duncan's test.

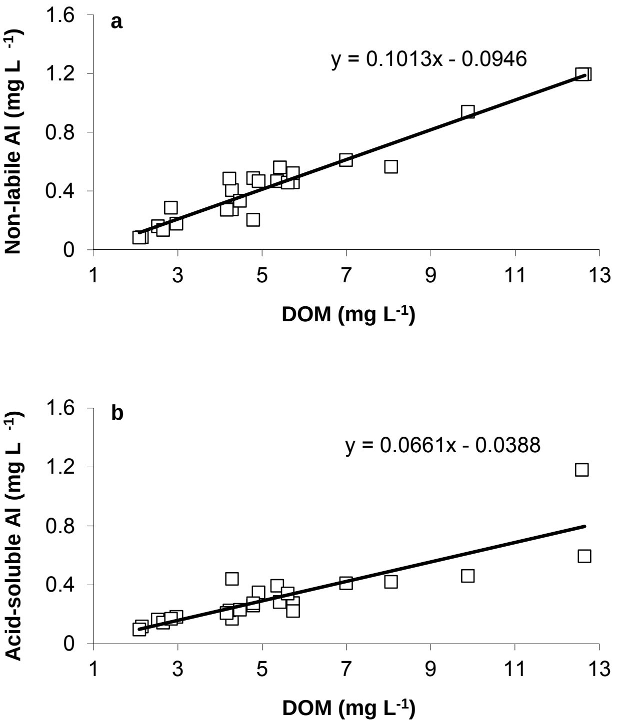

Figure 2. Correlation between a) DOM (dissolved organic matter) and non labile Al, and b) DOM and acid-soluble Al in all soil samples. ρ is Pearson's correlation coefficient and the line represents the linear trend in the data.

The distribution of labile Al in species is shown in Figure 1b. The concentration of Al-OH complexes ranged between 4.41 and 11.7 µmol L^{-1}. Although they were generally abundant in soils developed from all parent materials, they were significantly more abundant in those developed over mica schist than in the other soils (Figure 1b). Linear regression analysis revealed that pH explained 93% of variance in the ratio Al-OH/labile Al, with a positive effect (Table 3). This equation reaches values of Al-OH percentage close to zero when the pH is below 3.9, predominating Al^{3+} in this situation. The levels of Al^{3+}, considered as the most phytotoxic species (Kinraide, 1991; Arunakumara et al., 2013), ranged between 0.14 and 5.64 µmol L^{-1}. The amount of Al^{3+} was significantly higher in soils developed from granites, slate and mica schist (Figure 1b). The non linear regression analysis also indicated that pH explained 98% of variance in the ratio

Al^{3+}/labile Al, with a negative effect on the regression (Table 3). The highest concentrations of Al^{3+} were obtained in soils of pH < 5.0 (Figure 3a) with labile Al concentrations > 7 µmol L^{-1} (Figure 3b). The concentrations of Al-F complexes were significantly higher in plot over slate (Figure 1b). The pH, SO_4^{2-} and F^- explained most of the variance in the ratio Al-F/labile Al (41%), with SO_4^{2-} entering the equation as a negative variable (Table 3). Concentration of Al-F for low values of pH and F^- is close to zero. Finally, the concentrations of Al-SO_4 complexes were very low in soils developed from all parent materials, and they were significantly lower in soils over biotitic schist than in the other soils (Figure 1b). The non linear regression analysis showed that pH, SO_4^{2-} and F^- explained 98% of the variance in the Al-SO_4/labile Al ratio (Table 3). Several studies have demonstrated that SO_4^{2-} in solution reduces Al toxicity, as Al-SO_4 complexes are less toxic than free Al (Alva et al., 1991; Gallon et al., 2004). All parameter estimates affecting predictive variables were significant at p<0.15, and the models showed low bias and RMSE.

Table 3. Regression between forms of labile Al and parameters of soil solution

Regression	R^2	BIAS	RMSE
$Al^{3+} = \left(1794.2 * e^{-1.80 * pH}\right) * \text{labile Al}$	0.9803	-0.0048	0.042
$Al-OH = \left(-1.81 + 0.47 * pH\right) * \text{labile Al}$	0.9253	-0.0083	0.062
$Al-F = \left(-0.10 + 0.058 * pH - 0.007 * SO_4^{2-} - 0.00086 * 1/F^-\right) * \text{labile Al}$	0.4149	-0.0044	0.036
$Al-SO_4 = \left(95.5 * e^{-1.82 * pH + 0.087 * SO_4^{2-} - 1..94 * F^-}\right) * \text{labile Al}$	0.9786	-0.00028	0.0038

Al^{3+}, Al-OH, Al-F, Al-SO_4 and labile Al (µmol L^{-1}); SO_4^{2-} and F^- (mg L^{-1}). BIAS is the average deviation relative to the mean and RMSE is the root mean square error

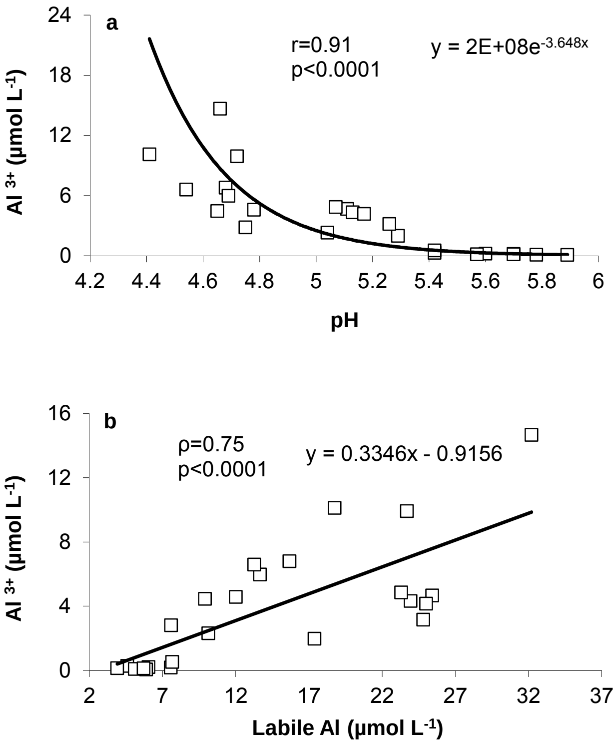

Figure 3. Correlation between Al^{3+} and a) pH, and b) labile Al in all soil samples. ρ is Pearson's correlation coefficient, r is Spearman correlation coefficient. The line represents the exponential trend (left) and the linear trend (right) in the data.

In this study, the average concentration of Al^{3+} was 3.87 µmol L^{-1} but varied widely depending on bedrock. The average value is lower than the value of 6.13 µmol L^{-1} found for soils developed over granodiorites, slates and limestones and under *Pinus radiata* stands in the same region (Álvarez et al., 2005). Values as high as 19.3 µmol L^{-1} were reported for mixed maritime pine and Scots pine stands over slates (Fernández-Sanjurjo et al., 1998), which is higher than the 5.16 µmol L^{-1} found in this study for the same bedrock. A value of 3.2 µmol L^{-1} was reported for *Pinus radiata* growing in granitic soils (Arbestain et al., 2004), which is lower than the 5.64 µmol L^{-1} found in this study. The same authors reported a value of 0.1 µmol L^{-1} for amphibolite, a very similar value to the 0.14 µmol L^{-1} found in this study for biotitic schist. Higher concentrations of Al^{3+} have been reported in other studies of areas formerly affected by acid rain (Drabek et al., 2005; Tejnecký et al., 2010).

Some of these comparisons are difficult to explain, as a lower value is expected over limestone. However, this can probably be explained by considering that the soil sampled by Alvarez et al. (2005) was deep, completely lacked a carbonate profile and occurred in a flat area. Regarding the species, the difference between maritime pine and radiata pine remains unclear after these comparisons, indicating the need for further research comparing these species growing under the same edapho-climatic conditions.

The concentrations of total Al, reactive Al, acid-soluble Al, non-labile Al and labile Al and particulary Al^{3+} were significantly lower in the soils over biotitic schist than in the other soils. This is also consistent with the higher pH values, with the highest contents of organoaluminic complex of high stability and with the scarcity of organoaluminic forms of low stability in the solid phase obtained previously by Eimil-Fraga et al. (2015a) in these same soils. The lower appearance of Al in solution in the soils over biotitic schist indicates that the Al is removed from the liquid phase to forms of high stability in the solid phase. On the contrary, the highest concentrations of Al in solution were obtained for soils developed from mica schist and slate, which have abundant Al forms of low stability in the solid phase, which therefore can enter easily in the liquid phase (Eimil-Fraga et al., 2015a).

3.3. Aluminium toxicity indices

3.3.1. Edaphic indices

All toxicity indices varied significantly depending on the parent material (Table 4). Different parameters associated with the soil exchange complex are used to determine the risk of Al toxicity. Thus Cronan and Grigal (1995) proposed the use of the percent base saturation for determining Al stress, with values of this parameter <15% indicating Al toxicity. In the present study, the percent base saturation varied between 9.4 and 27.0. The soils with the highest risk of Al toxicity were those developed over slate (11.5%) and granite (9.4%), whereas the soil developed over biotitic schist (27%) did not display any risk of Al toxicity (Table 4). Blaser et al. (2008) proposed use of the BC/Al_{exc} molar ratio, and considered a value of 0.2 as the threshold below which the risk for sensitive plants increases. In these plots, the lowest ratio was obtained for the soils over slate (0.07) and granite (0.08), and the highest ratio for soils over biotitic schist (0.25). The latter plot does not display any risk of Al toxicity according to this index (Table 4). Other authors use parameters determined in the soil solution to estimate the risk of Al toxicity. Truman et al. (1986) proposed the use of the labile Al concentration in solution, considering a value of 17 µmol L^{-1} for sensitive species such as *Pinus radiata* as a threshold limit. The labile Al ranged between 5.5 and 19.1 µmol L^{-1}. Considering a critical level of 17 µmol L^{-1}, we found risk of Al toxicity in the soils developed from slate and mica schist. The value of this index was significantly lower in plot over biotitic schist (p=0.0069) (Table 4). Most authors agree that Al^{3+} and Al-OH complexes are the most toxic Al species (Gallon et al., 2004). If the same critical level is used for the sum of Al^{3+} and Al-OH (17 µmol L^{-1}) (Álvarez et al., 2005), the soils developed from slate and mica schist (15.2 and 16.3 µmol L^{-1} respectively) were the closest to the critical level, whereas the values were significantly lower over biotitic schist (4.6 µmol L^{-1}) (p=0.0080) (Table 4).

Cronan and Grigal (1995) proposed the use of the Ca/labile Al molar ratio. According to these authors, for a Ca/labile Al ratio of 1 there is 50% risk of Al toxicity, if the ratio is 0.5 there is 75% risk, and if it is 0.2 the risk is between 95 and 100%. The Ca/labile Al molar ratio in soil solution varied between 0.30 and 2.05. The soils developed over slate and granite displayed a risk of between 75% and 95% of Al toxicity and the other soils did not show any risk (Table 4). The ratio was significantly higher in the plot over biotitic schist (p=0.0037). Similar results were obtained by applying the value of 0.5 proposed by Cronan et al. (1989) for this ratio in *Pinus taeda*, and we observed Al toxicity in the soils over slate and granite. The value of the Ca/Al ratio obtained for *P. pinaster* in granite and slate in this study (0.30) is comparable to the value of 0.45 reported for granitic soils with presence of *Pinus radiata* (Arbestain et al., 2004).

Table 4. Al toxicity index based on parameters determined in the soil, needles and roots. Different letters indicate significant differences (Duncan's test)

	Slate	Biotitic schist	Mica schist	Granite
Soil				
% base saturation	11.5 c	27.0 a	16.2 b	9.42 c
BC/Al$_{exc}$	0.08 b	0.25 a	0.14 b	0.07 b
Labile Al (µmol L^{-1})	18.9 a	5.46 b	19.1 a	13.8 a
Al^{3+} + Al-OH (µmol L^{-1})	15.2 a	4.56 b	16.3 a	11.0 ab
Ca/labile Al	0.49 b	2.05 a	1.05 b	0.30 b
ATI	1.02 b	0.39 c	0.43 c	2.08 a
Needles				
Ca/Al	3.46	5.06	4.71	1.61
Fine roots				
Ca/Al	0.064	0.13	0.092	0.064
Ca+Mg/Al	0.15	0.28	0.21	0.14
Medium roots				
Ca/Al	0.10	0.16	0.098	0.11
Ca+Mg/Al	0.21	0.38	0.27	0.24

% base saturation: < 15% risk of Al toxicity (Cronan and Grigal, 1995)
BC/Al$_{exc}$ (BC=Ca+Mg+K, Al$_{exc}$ is exchangeable Al): <0.2 correspond to risk of Al toxicity (Blaser et al., 2008)
Labile Al: >17 µmol L^{-1} risk of Al toxicity (Truman et al., 1986)
Al^{3+} + Al-OH: >17 µmol L^{-1} risk of Al toxicity (Álvarez et al., 2005)
Ca/labile Al: 1.0 correspond to 50% risk, 0.5 to75% risk and 0.2 to > 95 risk (Cronan and Grigal, 1995)
ATI: > 1 Al toxicity (Boudot et al., 1994, 2000)
Needle Ca/Al: 12.5 correspond to 50% risk and 6.2 to 75% risk (Cronan and Grigal, 1995)
Root Ca/Al: 0.2 correspond to 50% risk and 0.1 to 80% risk (Cronan and Grigal, 1995)
Root Ca+Mg/Al: <1.0 risk of Al toxicity (Sverdrup et al., 1992)

Another index based on parameter obtained in the soil solution is the called ATI proposed by Boudot et al. (1994). These authors take into account the differing toxicity of Al species and the beneficial effects of other cations. Values of this index higher than 1 indicate a toxicity risk. In the present study, the greatest risk of Al toxicity was found in soils over granite (ATI = 2.08) and to a lesser extent in the soils over slate (ATI = 1.02), being significantly higher than for the other types of parent materials (p<0.0001). Collignon et al. (2012) obtained values of ATI between 0.2 and 6.6 for plots of *Picea abies* and < 1.8 in *Fagus sylvatica* stands. Fernández-Sanjurjo et al. (1998) also used this index and observed an Al toxicity risk in some plots over slate with *P. pinaster*. However, Álvarez et al. (2005) did not find a toxicity risk in different plots over slate, granite and limestone with *Pinus radiata*, *Quercus robur* and *Eucalyptus nitens*.

3.3.2. Foliar and root indices

The values of the foliar Ca/Al molar ratios ranged between 1.61 and 5.06 (Table 4), with no significant differences in relation to parent material. According to Cronan and Grigal (1995), a Ca/Al molar ratio of less than 12.5 would indicate 50% risk of Al toxicity, whereas a ratio of less than 6.2 would indicate 75% risk of Al toxicity in forest ecosystems. In this study, the ratio was always less than 6.2, indicating at least 75% risk of Al toxicity (Table 4). The plot over granite presented the greatest Al toxicity risk according to this index and the plot over biotitic schist showed the lowest risk of Al toxicity. Truman et al. (1986) proposed a foliar Ca/Al ratio critical value of 1.8 for *Pinus radiata*, whereas Cronan et al. (1989) suggested a value of 2.3 for *Pinus taeda*. According to these values, the plot over granite displays a risk of Al toxicity.

The fine roots Ca/Al molar ratio varied between 0.064 and 0.13 mg g^{-1}, and for medium roots, between 0.098 and 0.16 mg g^{-1} (Table 4), with no significant differences between parent materials for fine and medium roots. Cronan and Grigal (1995) considered that a fine root Ca/Al molar ratio of 0.2 corresponds to 50% risk of Al stress and a ratio of 0.1, to 80% risk. In fine roots, the Al stress was higher than 80% for soils developed from all parent materials, except biotitic schist. Arbestain et al. (2004) and Álvarez et al. (2005) obtained higher values of Ca/Al ratio in roots of *P. radiata* in Galicia (0.23 and 0.5 to 0.9, respectively), and the risk of Al toxicity (<50%) was lower than in the present study. Applying the values proposed by Cronan and Grigal (1995) for fine roots to medium roots, the highest Al toxicity risk was obtained for the plot over mica schist (Table 4). Considering the threshold reported for *Pinus taeda* by Cronan et al. (1989) (0.32) and for *Pinus radiata* by Truman et al. (1986) (0.48), all plots displayed Al toxicity (Table 4).

In five forest sites in Switzerland, the Ca/Al molar ratio in fine roots *Picea abies* and *Pinus sp*. was between 0.8 and 3.6 (Brunner et al., 2002). Vanguelova et al. (2007) studied the fine root Ca/Al molar ratio in different forest species and obtained a range of 0.24 - 0.67 for *Pinus sylvestris*. The values of all of these ratios were higher than in the plots in the present study.

The values of Ca+Mg/Al molar ratio ranged between 0.14 and 0.28 for fine roots and 0.21 and 0.38 for medium roots. When this value is < 1.0, the root is damaged and the tree is under stress; for values <0.5 the root declines and mycorrhiza growth is retarded and for values <0.15, root tip growth stops almost completely, mycorrhiza growth declines, fine roots die and the tree is severely stressed. At this stage, the trees may still survive, but growth is significantly reduced (Sverdrup et al., 1992). In the present study, all values were <0.5, indicating root damage in all plots. The soils developed from slate and granite presented close values to 0.15 (Table 4), indicating a greater risk of Al toxicity in these plots.

3.4. Stand and leaf properties

Table 5 summarises the basic information on stand parameters related to growth and needle traits. The site index is closely related to basal area, providing information about stand productivity, which can be measured by the total biomass (Trichet et al., 2008). The values of site index, basal area and total biomass were highest in the plot developed from biotitic schist, which is consistent with the higher pH and lower Al toxicity risk estimated using edaphic parameters. Nevertheless, the plot over granite was the second most productive (Table 5), although the toxicity indices for needles and roots show high risk toxicity levels, according to threshold values reported in the literature. This can be explained either by the adaptation shown by this pine species to soils developed over such granitic substrates, which ensures high productivity provided that soil depth is sufficient (Bará and Toval, 1983), or by the possibility that the indices based on parameters obtained in needles and roots are not the most suitable for estimating the Al toxicity in this specie. Site index and productivity were lowest in the soils developed from slate and mica schist, which is more consistent with the toxicity indices for soil estimated using the concentration of labile Al in soil solution or the one summing up the two Al forms more able to produce toxicity (Al^{+3} + Al-OH).

Overall, the indices measuring the labile Al in soil solution or the most toxic Al species are those most directly related to productivity variables.

Table 5. Values of stand parameters in the plots under study

	Slate	Biotitic schist	Mica schist	Granite
Basal area (m^2 ha^{-1})	11.3	30.5	6.7	21.0
Site index (m)	13	18	8.5	15
Total biomass (t ha^{-1})	25.47	87.42	14.16	57.46
Needle biomass (t ha^{-1})	2.62	9.08	2.23	8.33
Leaf area index (m^2 m^{-2})	0.91	3.14	0.67	2.52
Growth efficiency (kg m^{-2} $year^{-1}$)	0.41	0.58	0.39	0.11

The values of total and needle biomass were also higher in the plots over biotitic schist and granite, as was the leaf area index. These results are again more consistent with the values of toxicity indices based on soil parameters (labile Al, and Al^{+3} + Al-OH) than with needle (Ca/Al) or root (Ca/Al, (Ca+Mg)/Al) based indices. The edaphic index obtained from soil solution therefore seems to be the most representative of the conditions enhancing both a high leaf area index and total biomass.

As regards the growth efficiency, the Al toxicity indices apparently most closely related are those expressed as Ca/Al ratios, both in needles and fine roots, as well as the soil indices including the base cations or percent base saturation. Thus, for example, for the plot over granite, the biomass productivity per unit foliar area is very low, which is clearly related to very low Ca/Al ratios in needles or fine roots. Nonetheless, this plot shows a higher value of foliar biomass than expected considering the high values of Al^{+3} + Al-OH.

The results of this study cannot be compared with other findings due to the lack of previous studies relating stand variables and Al toxicity indices. Although a decrease in forest growth is generally considered in modelling some toxicity ratios (Sverdrup et al., 1992), most experimental findings are derived from shoot and root elongation studies in seedlings grown in pots. As this study dealt with a small number of plots, a larger set of stands established as a chronosequence should be studied to clarify the present findings.

4. CONCLUSIONS

In the naturally-acidified soils under study, the parent material significantly influenced Al fractionation and speciation. The concentrations of all Al forms and species, particularly Al^{3+}, were lowest over biotitic schist, in accordance with the high pH. The opposite was observed in the soils developed over mica schist and slate. Overall, the edaphic Al toxicity indices obtained from soil solution were more closely related to productivity variables than the other indices used in this study. Thus, the site index, the total and needle biomass and leaf area index were higher in the plots over biotitic schist and granite, which is more consistent with toxicity indices based on soil solution parameters (labile Al; Al^{3+} + Al-OH) than with needle or root indices. The exception was the growth efficiency, which was related to Ca/Al ratios in needles or fine roots and exchangeable complex parameters. The soil developed on granite was the second most productive, after the soil on biotitic schist, despite the high risk of Al toxicity indicated by the foliar and root indices. The high productivity may confirm the adaptation of *P. pinaster* to this type of soil degraded by natural acidification or it may indicate that indices based on foliar and root parameters are not suitable for estimating Al toxicity.

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Chapter 8

General discussion


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8. GENERAL DISCUSSION

8.1. Discussion of the results

The results obtained in this doctoral research have helped to elucidate the mechanisms explaining the influence of edaphic variables and ecophysiological parameters on the growth of *Pinus pinaster*. The findings provide robust information that can be used to improve the selection of sites for forest plantations or for the management of existing stands, with the purpose of optimizing biomass, timber and other forest products. They are also important for enabling estimation of the resilience and plasticity of the species regarding natural or anthropogenic acidification processes currently affecting forest ecosystems.

Chapter 3 reports the findings of a study of the importance of the role of the bedrock, for which a wide range of types of bedrock were sampled: granitic rocks, gneiss, migmatites, biotitic schist, mica schist, phyllites and slates, quartzite and sandstone and quaternary sediments. Soil composition and properties are known to be strongly related to the chemistry and mineralogical composition of the bedrock. The chemical composition determines the elements that occur in the soil developed from the rock. Thus, if the rock contains low amounts of an essential element, the soil derived from the rock will also be deficient in this element (Macías, 1986). The soil properties and bedrock characteristics are therefore closely correlated and are due to the weathering conditions and to the composition and organization of the rock components. Soil depth is also known to be a result of rock weathering and therefore depends on the degree of fracturation, topography and intensity of erosion (Macías et al., 1982). Soil texture is also highly dependent on bedrock type and is directly related to the porosity and the permeability of the soil, as well as to the degradability of organic matter (Gandullo and Sánchez-Palomares, 1994).

The results of the present study indicated that the type of bedrock significantly affected the following soil parameters: exchangeable Ca, total N, C/N ratio and soil depth. Regarding the foliar concentration of nutrients, the trees growing in plots developed on mica schist, phyllites and slates, quartzite and sandstone and sediments displayed deficiencies in more than one foliar nutrient, which is consistent with the lower site index of these plots. Nutrient levels and site index were highest in plots over biotitic schist, followed by granitic rocks, gneiss and migmatites. The findings of the study reported in Chapter 3 clearly showed that site index is closely related to soil depth, temperature, elevation and foliar K, Mg and Ca. In fact, two models (a complete model considering all geological materials and another for granitic rock) were developed in order to explain site index, with foliar K and Ca, soil depth and temperature as input variables.

These results provide additional insights into the influence of ecological parameters on maritime pine growth, particularly in relation to bedrock. Adaptation of this species to granitic soils is well known and has traditionally been attributed to its intolerance to compact soils and preference for coarse textured soils (Grau Corbí, 2003). Previous findings have not always been conclusive regarding the importance of the nature of the rock in relation to the productivity of the species. Bravo-Oviedo (2009) therefore compared diverse types of lithology and obtained very high site index for granites in sites located at moderate elevation and also high site index for soils developed on schists and slates at the same elevation. The soil depth and temperature explain the variance in site index in plots developed from feldspar sandstone, phyllite and conglomerate (Álvarez-Álvarez et al., 2011). Pacheco Marques (1991) evaluated the productivity of pine plantations on granite and schist, considering the input variables temperature, available K, total porosity and fine sand content. In a study carried out in Africa, Schafer (1988) proposed three models for predicting site index and four models for each of the geological classes present. These models used soil depth, radiation index and exchangeable Al as predictor variables. In Atlantic areas, with slight summer drought and highly desaturated acidic soils, the influence of bedrock nature may be more evident than in Mediterranean areas. Information on parent bedrock, available at a detailed spatial scale, may be used as a major basis for land classification, as recently confirmed in different studies. For example, for spruce in Sweden (Stendahl et al., 2002), the bedrock mineralogy explained 37-61% of the variation in site index. Other authors found that site index also depended on the soil parent rock for the same species in Poland (Socha, 2008). We conclude that knowledge about bedrock can facilitate evaluation of the site potential for maritime pine plantations, with a clear preference given to biotitic schist (and probably related bedrocks of basic composition), granitic rocks, gneiss and migmatites.

Other studies have considered how needle nutrient concentrations are related to site properties and growth limitations in this species (Bara and Toval, 1983; López Varela et al., 2009; Martins et al., 2009). Studies of nutrition concentrations in *Pinus pinaster* needleshave been carried out in France (Saur et al., 1992; Bonneau, 1995), Australia (Boardman et al., 1997) and to a lesser extent in Spain (Bará, 1998; Balboa Murias, 2005), and deficient levels have been proposed in some of these.

The availability of nutrients in soil solution and in the soil exchange complex is mainly derived from the abundance of organic matter and its decomposition rates in these highly leached soils formed over acidic parent material. In such conditions, the abundance of Al at exchange sites and its different species in the soil solution play an important role, because the Al can precipitate P, or can act as a cationic bridge to fix phosphates on the surface with negative charges. On the other hand, soluble organic matter removes Al from the exchange complex and soil solution, as highly stable Al organic matter complexes are usually formed in these soils. The reaction between Al and organic matter causes a decrease in the mineralization rate. In a recent study, the organic matter in soil under maritime pine stands was found to less active than in soil under other broadleaf species or pines, in parallel with higher Al saturation rates in the exchangeable complex (Carrasco, 2015).

In addition to nutrient levels, aluminium toxicity is an important growth-limiting factor for plants in acid soils (pH <5.0) in which the bioavailability of Al is high (Poschenrieder et al., 2008). Knowledge of Al fractionation and speciation in the soil solution is essential because this determines the toxicity of Al to plants (Waters & Webster, 2013). The influence of bedrock (slate, biotitic schist, mica schist and granite) on Al fractionation and speciation in the soil solution and on Al toxicity indices was therefore studied in four *Pinus pinaster* plots, and growth and biomass parameters were evaluated.

Studies of Al fractionation in the solid phase (Chapter 6) provided information about the importance of the formation of organo-aluminium complexes as a way of reducing Al saturation in the exchange complex (Álvarez et al., 1992, 2002; Adams et al., 2002). The parent material was found to have a non negligible influence on the abundance of each Al fraction. The more labile forms of Al (Al extracted by $CuCl_2$ and $LaCl_3$, exchangeable Al and total soluble Al) were present in soils developed over slate, which is consistent with higher values of C/N ratio and lower pH. By contrast, the soil over biotitic schist contained highly stable organic-aluminium complexes and the exchangeable Al and total Al in soil solution were lower than in the other soils, in accordance with low acidity and C/N ratio, thus explaining the previous results. In the latter plot, the organic matter removed the Al from the soil solution and from the exchangeable positions, forming highly stable complexes. The soil over slate was the most acidic and contained the least stable organic matter, thus favouring the formation of Al-organic matter complexes of moderate and low stability and higher concentrations of exchangeable Al and total Al in the soil solution. Intermediate behaviour was observed in soils developed over granite and mica schist. In a novel approach, multiple regressions were used to estimate the different forms of Al in the solid phase (Chapter 6). The input variables in these models were pH (measured in water and KCl), C, C/N ratio, N and effective cation exchange capacity, all of which are easy to measure. This enable estimation of the capacity of a soil to stabilize Al or even the treatments required to improve this capacity.

The fractionation and speciation of Al in soil solution (Chapter 7) showed higher values of Al total, reactive Al, acid-soluble Al, non-labile Al and labile Al in plots developed over mica schist, followed by the plots over slate. This is consistent with the abundance of aluminosilicates in these types of bedrock, confirming the strong influence that parent material has on chemistry and nutritional properties of soils in Galicia (Macías et al., 1982). The different species of labile Al estimated for the soil solution were Al^{+3}, Al-OH, Al-F and $Al\text{-}SO_4$. For soil and plants, Al toxicity indices derived from the different Al forms present in the soil enable evaluation of the toxicity risk by comparison with the wide variety of indexes proposed to date (Truman et al., 1986; Sverdrup et al., 1992; Cronan and Grigal, 1995; Boudot et al., 1994, 2000; Blaser et al., 2008). As reported in Chapter 7, these indices were calculated for four different parent materials: slate, biotitic schist, mica schist and granite. The findings indicate a high risk of toxicity at least in three of the four sites studied (soils over mica schist, slate and granite). For the toxicity index based on edaphic parameters, the best results regarding the relationship with growth were obtained for Al^{+3}+Al-OH in the soil solution, which confirms these as the most toxic forms (Álvarez et al., 2005). The concentration of labile Al in the soil solution was also closely related to the lower site indices reached in the plots on mica schist and slate. Some toxicity indices (such as the ATI) with a complex formulation that attempts to represent the toxic potential of each form of Al present in the soil solution (Boudot et al., 1994, 2000) did not produce good results at the sites tested, possibly because of renowned frugality of this species and its adaptation to these soils. Regarding toxicity indices evaluated in needles or roots, the results in the soil developed over granite indicated high toxicity. Nonetheless, accumulation of foliar biomass and a high level of leaf area index (LAI) were observed in this plot, either corroborating the well-known adaptation of the species to granite substrates (Bara and Toval, 1983) or the inability of the indices to identify toxicity. The results obtained enabled us to fit regression equations to estimate the species of labile Al with only three soil parameters: pH, F^- and SO_4^{-2}. As far as we know, these are the first predictive equations developed in this type of study, and they are of great interest for predicting toxicity risk for plants.

Although the direct relationships between site parameters and stand productivity has been clearly demonstrated in Chapter 3, it was also considered necessary to study the main drivers of the increased productivity. Needle traits were hypothesized to be important in explaining the real effects of site and nutritional status on aboveground biomass increment. Study of these parameters is described in Chapter 4, in which the different age classes present in the foliage were considered and foliar nutrients for each tree and age class were analyzed. The age class effect was the main factor to assess the variability in leaf dimensions, and the plot effect (variability between sites) was the second most important factor; the variability between trees was much less important. The findings showed that climatic conditions, site variables and foliar nutrients (N, Mg, Ca and K) affected the needle size (length, width and thickness) and specific leaf area. Indeed, the concentration of N plays an important role in the needle traits, and together with spring precipitation predicts the length of needles aged 1 year. Similar results were obtained in *Pinus radiata*, in a study in which the water availability was found to be the major factor affecting needle growth, with N availability having a secondary effect (Raison et al., 1992). The scarce significance of the relationship between foliar K and the needle length described in Chapter 4 may be due to the high mobility of K, which is readily translocated. Other authors have observed that foliar K concentration had only slight effects on needle length, thickness and width in *Pinus sylvestris* (Jokela et al., 1997). A functional relationship has also been observed between K supply, anatomical and biochemical leaf traits and photosynthesis in *Eucalyptus grandis* (Battie-Laclau et al., 2014).

Specific leaf area is known to be a key ecophysiological parameter influencing leaf physiology and photosynthesis (Nouvellon et al., 2010). The results reported in Chapter 4 clearly show that specific leaf area is related to site index and foliar K, Mg and N. These relationships support the hypothesis proposed by Niinemets and Kull (2003), i.e. that the strength of leaf structure vs. nutrient relationships varies depending on the availability of specific nutrients relative to other physiologically important factors. The relationship between leaf area and foliar K was also observed in other species (Battie-Laclau et al., 2013). Furthermore, specific leaf area is known to be related to allometric variables and can be accurately simulated at the tree level from diameter at breast height. The relationship between diameter at breast height and specific leaf area can further be used to estimate specific leaf area at the stand level (Nouvellon et al., 2010).

We conclude that in plots located at low elevations, with good site index and nutritional status of K and Mg, the specific leaf area was higher than in the other plots. Knowledge of needle size and the specific leaf area provided useful information about leaf traits and its relationship with site and stand parameters. The findings reported in Chapter 4 are consistent with those reported in Chapter 3, in which concentrations of foliar nutrients were also found to play an important role in understanding the high level of plasticity of maritime pine. Furthermore, studies of these ecophysiological parameters provide additional insights into the growth of maritime pine.

The study of the variability in needle lifespan, needle biomass and leaf area index enabled detailed evaluation of the performance of maritime pine on acid soils rich in organic matter. For this purpose, the nutritional status of the stands was first analyzed, showing that most of the plots displayed deficiencies in foliar concentration of P, K and N. The results obtained are shown in Chapter 5.

Foliage longevity and distribution in the crown are known to be critical for characterizing within crown radiation transfer and foliage efficiency for converting solar energy to woody biomass (Grace et al., 1987; Whitehead et al., 1990; Gholz et al., 1991). In addition, foliage longevity has ecological implications for carbon gain, nutrient use, growth efficiency and seasonal water use (Reich et al., 1992; Gholz et al., 1994).

Foliage development, abscission and longevity are recognised to influence decisions about the application of silvicultural treatments, including fertilization, weed control, pruning and thinning (Cown, 1977; Allen and Wentworth, 1993). This type of data is required for understanding process-based models driven by light interception of foliage (Landsberg and Waring, 1997; Coops et al., 1998; Sands et al., 2000). The findings reported in Chapter 5 indicate that most plots included four age classes of needles (maximum, five years). Survival decreased as the age of needle increased, with a strong decline between ages 2 and 3, indicating lower longevity than in Mediterranean provenances of the species (Mediavilla et al., 2011). Both site index and nutrient availability, specifically foliar K and Mg, had important effects on foliage development and longevity. Needle longevity and the K:N and Mg:N ratios were also closely related. A positive effect of K availability on leaf lifespan has also been observed in *Eucalyptus grandis* plantations (Battie-Laclau et al., 2013).

Leaf biomass is an important variable in models of ecophysiology processes because it reflects the capacity of a tree or stand to intercept radiation, reduce carbon dioxide, store carbohydrates, intercept rainfall, transpire water, and accumulate and store nutrients (Dougherty et al., 1995). In the study described in Chapter 5, significant relationships were observed between leaf biomass and site index, growth efficiency, foliar concentration (P, Ca, K, Fe and Cu) and soil exchangeable concentrations (K, Ca and Mg). In addition, the maximum values of needle biomass were representative of the site growth potential and the most limiting nutrients were closely related to needle biomass. Other studies have found that leaf biomass was related to climatic variables, resource availability (such as nutrients) and stand variables (such as basal area) (Vose and Allen, 1988; Hennessey et al., 1992; Dougherty et al., 1995).

Leaf area index (LAI) plays an important role as it is used as an input parameter in ecophysiological models. The results reported in Chapter 5 showed that LAI was higher in younger needles and decreased strongly as needle age increased; the same trend was also observed for needle biomass. Again LAI was closely related to site index, foliar concentrations of P, Ca, K, Fe and Cu and soil exchangeable K, Ca and Mg. The findings revealed that this parameter was very variable even for stands of the same age.

Growth efficiency, which has not been considered in previous studies for this species in Spain, was also important. In the study described in Chapter 5, growth efficiency was significantly related to needle longevity and K foliar concentration. This parameter provides useful information about tree and stand growth process, and the maximum values can be used as a surrogate for maximum photosynthesis efficiency.

The findings reported in Chapter 5, which are consistent with those reported in previous chapters, show that foliar nutrients, particularly K concentration, play an essential role in maritime pine growth and can be used to study site productivity, leaf traits, needle lifespan, biomass, leaf area index and growth efficiency.

The relationship between the site index and specific characteristics of the site, mainly soil properties and climate or stand nutrient status provide useful information for the planning involved in sustainable forest management. These relationships can be used to help select the most suitable species and predict forest growth. In a scenario of different types of risk to forest sustainability (pest and diseases, windthrow, climatic change, forest fires), land classification tools are particularly important.

8.2. Future lines of research

The results obtained provide new insights into the mechanisms of adaptation of species to acidic soils rich in organic matter. Such adaptation has certain limits, and rapid establishment and active growth of plantations is not expected in sites over slate or acidic schist, particularly at high elevations and on shallow soils. In this case, an almost steady state of plantation development would be maintained during many years prior to canopy closure, with a high risk of fire derived from the abundant shrubs.

Study of the effect of the toxicity index on growth efficiency is a possible future line of research. This parameter may be affected by the nutritional status of the forest, as we have shown in this study, by the ratio between aboveground and root biomass, or by the detoxification required by the trees, among other variables closely related to Al levels in the soil and forest. Some plots with good levels of needle biomass displayed very low levels of growth efficiency. Study of the Al fractions in solid phase, Al fractionation and speciation in the soil solution and its toxicity risk for maritime pine in a large number of plots is another possible line of research that would help to clarify the present findings. The difference between young and adult stands could also be investigated, to provide information about the resilience of this species towards high Al levels or to help establish thresholds Al levels for decaying processes in the forest stands. Recently reported findings show that the potential and actual mineralization of organic matter in soils under maritime pine is slower than for other tree species, which was attributed to a higher C/N ratio and a different composition of the soil organic matter (Carrasco, 2015). It would also be interesting to fractionate the organic matter to determine the influence of parent material on its reactivity and how the organic matter quality affects the fractionation and speciation of Al and productivity.

Many future lines of research can be proposed from the results obtained in this thesis in relation to needle traits. There is a lack of information that would enable the design of effective measurements of preventive silvicultural treatments for the mixed production of timber and biomass in a scenario of global climate change. Information about foliar nutrition, litterfall rates and fuel structure in pine forests is necessary to enable parameterization and application of ecophysiological models to realistic silvicultural proposals. Therefore, future studies could obtain information about litterfall and to estimate this parameter using traps installed in a chronosequence of plots. Detailed monitoring of nutrient retranslocation may also be important for establishing the biogeochemical cycle after canopy closure. Such studies could provide information for sound parameterization of the 3PG process model to Atlantic *Pinus pinaster* based on information obtained from different groups of plots. Inventory of shrub loads in the plots and development predictive models of shrub loads under pine forest depending on easy to measure silvicultural and seasonal variables would also be of interest.

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Chapter 9

Conclusions


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9. CONCLUSIONS

Nutritional status and growth of maritime pine as related to bedrock

- Differences in *Pinus pinaster* growth were found in relation to the type of bedrock, indicating the interest in basic geological information for land use classification and matching of forest species to site.
- The highest site index was associated with low elevation, high temperatures and deeper soils. The poorest growth and highest nutrient deficiencies were observed in the soils over slate and phyllite, sandstone and quartzite, mica schist and sediment, which explain the corresponding low site indexes.
- Foliar concentrations of K, Ca and Mg were the most closely related to site index, and the foliar K varied greatly depending on the bedrock.
- *Pinus pinaster* is better adapted to soils over biotitic schist, granitic rocks, gneiss and migmatite, where pines had higher growth and levels of foliar K.

Foliar parameters, nutrition and productivity

- Needle size was closely related to climate conditions, the year they are formed and foliar N and Mg. Needle age class was the main factor leading to variation in mean needle dimensions.
- The plot effect was the second most important factor and was representative of different site conditions related to the elevation, climate and nutritional conditions.
- Stands in Atlantic areas showed comparatively higher values of specific leaf area, which is directly related to site index. Specific leaf area was higher in sites with good nutritional status for K and Mg and was negatively correlated with the concentration of foliar N and the needle tissue density. Needle longevity was also related to site index and foliar concentrations of Mg and K.
- The foliage biomass decreased sharply as needle age increased and was positively related to site index and foliar nutrient concentrations. The nutrients most closely related to needle biomass and leaf area

index were soil total N, soil exchangeable K, Mg and Ca and foliar concentrations of K, Ca and P. Foliar N showed a dilution effect and nitrogen nutrition is not limiting in such sites. Growth efficiency increased as foliar K and the K:N ratio increase.

- Biomass, leaf area index and site index were higher in sites in which mean shrub height was lowest.

Fractionation, speciation and aluminium toxicity

- The soils over biotitic schist presented the highest concentrations of oxalate Al, pyrophosphate Al and highly stable complexes with organic matter. So, the organic matter removes the Al from the soil solution and from the exchangeable positions, to form strongly stable organic–aluminium complexes. Then, the concentrations of all Al forms and species in soil solution, particularly Al^{3+}, were lower.
- In the soils over slate, more labile forms of Al occurred, particularly Al extracted by $CuCl_2$, $LaCl_3$, NH_4Cl and water. The formation of these Al–organic matter complexes of moderate and low stability and the higher concentrations of exchangeable Al were in accordance with the highest concentrations of all Al forms and species in soil solution, particularly Al^{3+}.
- The site index, the total and needle biomass and leaf area index were higher in the plots over biotitic schist and granite, which is more consistent with toxicity indices based on soil solution parameters (labile Al; Al^{3+} + Al-OH) than with needle or root indices.
- The soil developed on granite presented high productivity, despite the high risk of Al toxicity estimated by the majority of indices (solid phase indices, Ca/Al lábil and ATI in soil solution, needles and root indices). The high productivity may confirm the adaptation of *Pinus pinaster* to this type of soil degraded by natural acidification or it may indicate that previous indices are not suitable for estimating Al toxicity, being more adequate labile Al and Al^{3+} + Al-OH in soil solution.

Appendix

Abstract (Resumen)


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RESUMEN EXPANDIDO

Los pinares atlánticos de *Pinus pinaster* tienen una gran importancia productiva y ecológica en Galicia y la cornisa cantábrica. El cuarto inventario forestal nacional (IFN4) indica que la especie cubre el 15% de la superficie arbolada gallega, con unas existencias de 39,3 M m^3 con corteza en masas puras y 58,4 M m^3 teniendo en cuenta también masas mixtas. Tiene gran relevancia en el paisaje forestal gallego, al estar presente en la mayoría de los estratos del IFN4, siendo una importante especie de repoblación en el noroeste de España, al combinarse en ese ámbito la regeneración natural y artificial. Actualmente, *Pinus pinaster* es la especie que ocupa mayor superficie forestal arbolada en Galicia, con 217281 ha de masas monoespecíficas y 229417 ha en mezcla con *Eucalyptus spp.* y *Quercus robur*.

El principal producto que se obtiene en los rodales de *Pinus pinaster* es la madera. La falta de sistemas de gestión óptimos limita en gran medida la productividad y la posibilidad de obtener madera de buena calidad. En la actualidad existe una gran demanda de madera de diámetros relativamente grandes pero también se demandan nuevos productos derivados de madera de pequeñas dimensiones, principalmente madera técnica y biomasa forestal para bioenergía. La recogida de setas con fines comerciales o para consumo propio también es una actividad importante en estas plantaciones y las recientes experiencias de extracción de resina señalan otro aprovechamiento a tener en cuenta. El carácter multifuncional de las masas de *Pinus pinaster* tienen hoy en día una importancia clave en su gestión y este aspecto debería ser tomado en consideración.

Dada la importancia de la especie, el principal objetivo de esta tesis doctoral fue mejorar la comprensión de la relación entre parámetros ecofisiológicos y edáficos que determinan el crecimiento de *Pinus pinaster* y su capacidad para adaptarse a distintos ambientes con el fin de facilitar la toma de decisiones a la hora de producir madera y biomasa y otros productos forestales. Para alcanzar este objetivo se realizaron los siguientes estudios:

1. Importancia de la roca madre como un factor de sitio que determina el estado nutricional y el crecimiento de pino marítimo.
2. Relación entre las características de las acículas, edad de las acículas y parámetros de sito y de rodal en *Pinus pinaster*.

3. Variabilidad en la longevidad y biomasa foliar a lo largo de un gradiente de fertilidad del suelo en plantaciones de pino marítimo sobre suelos ácidos, ricos en materia orgánica.
4. Influencia del material de partida sobre el fraccionamiento del Al en suelos ácidos bajo *Pinus pinaster* en Galicia.
5. Riesgo de toxicidad de Al para *Pinus pinaster* en suelos ácidos.

La mayoría de los estudios se llevaron a cabo en 31 parcelas de *Pinus pinaster* instaladas por TRAGSA en colaboración con la UXFS (USC). Las parcelas eran de 20x30 m y se localizaron en plantaciones establecidas bajo el programa de reforestación de terrenos agrícolas abandonados. Estas parcelas fueron la base de los estudios 1, 2 y 3. Un subgrupo de 4 parcelas de las 31 anteriores fueron usadas para profundizar en el fraccionamiento del Al y el riesgo de toxicidad en suelos ácidos. Fueron escogidas para representar diferentes tipos de materiales de partida (pizarras, esquisto biotítico, mica esquisto y granito) y sirvieron de base para el estudio 4 y 5. Para el estudio 1 se consideró un mayor número de parcelas para evaluar la influencia del material de partida, añadiendo a la red de 31 parcelas ya comentadas un segundo grupo de 97 parcelas más, establecidas entre 1974 y 1975 por Bará y Toval (1983).

Se expone a continuación cada uno de los trabajos realizados, indicando los resultados y conclusiones obtenidos en cada uno de ellos.

1. Importancia de la roca madre como un factor del sitio que determina el estado nutricional y el crecimiento de pino marítimo

Las relaciones entre las propiedades del suelo, nutrientes foliares y el crecimiento se estudiaron en 128 parcelas de *Pinus pinaster* establecidas sobre diferentes tipos de roca en Galicia. Las parcelas se desarrollaron sobre los siguientes materiales de partida: rocas graníticas, sedimentos cuaternarios, cuarcitas y areniscas, pizarras y filitas, esquistos biotíticos, mica esquistos, gneis y migmatitas. El tipo de roca madre influyó significativamente en el Ca cambiable, N total y en la profundidad del suelo. La concentración de Ca cambiable fue más alta en suelos desarrollados sobre esquistos biotíticos. El N total fue más bajo en los sustratos de cuarcitas y areniscas, pizarras y filitas, sedimentos y mica esquistos, que presentaron una relación C/N más elevada. En cuanto a la profundidad del suelo, se observaron valores más altos en suelos sobre gneis, migmatitas, granitos y sedimentos. El tipo de roca también afectó significativamente al N, P, Ca, K y Mg foliares. Las concentraciones más altas de estos nutrientes fueron obtenidas en esquistos biotíticos, de hecho, en el caso del Ca no se encontraron diferencias significativas entre materiales cuando estas parcelas fueron excluidas del análisis. Para el N, Mg y K foliares se observó que los pinos presentaron mayores concentraciones sobre gneis, granitos, migmatitas y particularmente esquistos biotíticos. Considerando los niveles de deficiencia propuestos para esta especie, se observó que las parcelas sobre sedimentos, mica esquistos, cuarcitas y areniscas, pizarras y filitas y migmatitas mostraron deficiencias en más de un nutriente foliar. El estado nutricional fue más adecuado sobre gneis y particularmente sobre granitos, siendo las parcelas con más limitaciones las desarrolladas sobre cuarcitas y areniscas, y sobre sedimentos. Los resultados indican diferentes condiciones nutricionales en función del tipo de roca. El material de partida también se relacionó con la altitud, la temperatura y la pendiente, como resultado de la distribución de los materiales y la geomorfología. Se concluyó que los suelos desarrollados sobre esquistos biotíticos, gneis, migmatitas y rocas graníticas fueron los más favorables para el crecimiento de la especie. El menor crecimiento y las deficiencias nutricionales más graves se observaron en suelos desarrollados sobre sedimentos, mica esquistos, cuarcitas y areniscas y pizarras y filitas. Se desarrollaron dos modelos de regresión para predecir el índice de sitio: un modelo completo explicó 52% de la variación total en el índice de sitio y un modelo para rocas graníticas explicó 53% de la variación. Ambos indican la importancia de la profundidad del suelo, la altitud y K y Ca foliar como variables predictivas. Por lo tanto, *Pinus pinaster* está mejor adaptado a suelos desarrollados sobre gneis, migmatitas y granitos, caracterizados por ser moderadamente profundos y tener niveles más altos de K foliar. Estos también serán los materiales más adecuados para la promoción de la especie por plantaciones y para asegurar la gestión sostenible de las masas existentes.

2. Relación entre las características de las acículas, edad de las acículas y parámetros de sito y de rodal en *Pinus pinaster*

El tamaño y las características de la acículas y los parámetros del sitio fueron estudiados en 31 parcelas de *Pinus pinaster* en Galicia. En cada parcela se seleccionaron 3 árboles dominantes y de cada uno se seleccionó una rama bien iluminada del tercio superior de la copa. Todas las acículas se clasificaron de acuerdo a su clase de edad y los nutrientes foliares fueron analizados para cada árbol y clase de edad. Para las parcelas estudiadas, esta última varió entre 1 y 5. La edad de las acículas afectó significativamente a la longitud, el ancho y el grosor de las acículas, al área foliar (proyectada y total), a la superficie foliar específica (proyectada y total), a la densidad de las acículas, al N por unidad de área foliar, al peso medio seco y al contenido de humedad. En general, el porcentaje de varianza atribuible a la parcela y al árbol fue inferior que el de la clase de edad para todas las variables estudiadas. El análisis Boosted Regression Trees (BRT) mostró que el clima y las variables del sitio fueron fundamentales para explicar la variabilidad de las dimensiones de la hoja. En cuanto a los nutrientes, el N foliar fue el que más contribuyó a explicar las características de las acículas según el análisis BRT, comprobándose sin embargo que el efecto era positivo en unas variables y negativo en otras. El Mg foliar fue el segundo más importante y la menor contribución fue para el K. Un modelo de regresión fue desarrollado para predecir la longitud de las acículas de la clase de edad 1, indicando la importancia del clima y las condiciones nutricionales. Una importante proporción de la variación (25,2%) en la longitud para las clases de edad 1 y 2 se puede predecir únicamente con la precipitación de primavera. La superficie foliar específica proyectada fue positivamente afectada por los nutrientes foliares, especialmente K, y mostró un nivel bastante alto de plasticidad teniendo en cuenta que el pino marítimo es una especie exigente en luz. El análisis BRT también mostró una importante contribución del N foliar en esta variable. La superficie foliar específica proyectada de los rodales estudiados fue mayor que la de las procedencias de las zonas más secas. Además, esta variable fue mayor en las parcelas situadas en altitudes más bajas, con un buen índice de sitio y estado nutricional de K y Mg. La concentración de N foliar se correlacionó negativamente con la superficie foliar específica o el índice de sitio. En pino marítimo, el tamaño de las acículas está estrechamente relacionado con las condiciones climáticas, el año en que se forman y también con las concentraciones de N y Mg foliar. Los resultados muestran el importante rango de variación de los parámetros de la hoja en esta especie, que puede ser útil para la aplicación de modelos de crecimiento basados en procesos.

3. Variabilidad en la longevidad y biomasa foliar a lo largo de un gradiente de fertilidad del suelo en plantaciones de pino marítimo sobre suelos ácidos, ricos en materia orgánica

La variabilidad en la vida útil de las acículas, el índice de biomasa foliar y el área foliar se estudiaron en 31 parcelas de *Pinus pinaster* en Galicia, establecidas a lo largo de un gradiente de productividad del suelo en plantaciones de la misma edad (11-14 años). Los suelos bajo estudio fueron ácidos (pH 3,7 a 5,3) y muy ricos en materia orgánica (6,9 a 34,3%). En cada parcela se seleccionaron 3 árboles dominantes y de cada uno se seleccionó una rama bien iluminada del tercio superior de la copa. Todas las acículas fueron clasificadas de acuerdo a la clase de edad y se contabilizó la presencia/ausencia de acículas para evaluar la supervivencia. El área foliar específica y la biomasa de acículas se calcularon para cada parcela. Además, se midió la concentración foliar de nutrientes y se calculó el índice de sitio. Considerando los valores críticos propuestos en la literatura para acículas de pino marítimo, se observaron deficiencias en la concentración foliar de P, K y N. La edad máxima de las acículas fue de 5 años. La supervivencia de las acículas de más de 2 años disminuyó marcadamente. La longevidad de las acículas se vio afectada positivamente por el índice de sitio y los nutrientes foliares, en particular Mg y K, aunque la relación fue más clara con los ratios K:N y Mg:N. Esto sugiere que el pino marítimo responde a la baja fertilidad del suelo cuando disminuye la vida útil de las acículas a escala local. La biomasa de acículas y el índice de área foliar (LAI) fueron significativamente más altos en la edad 1 y 2 y disminuyeron cuando la edad de las acículas aumentó. Los valores de biomasa se relacionaron con el índice de sitio, la eficiencia en el crecimiento, la altura media del matorral y en menor medida con la superficie foliar específica. La biomasa de acículas también se relacionó con el P, Ca, K, Fe y Cu foliar y con el K, Ca y Mg cambiable. La tasa media de desfronde estimada fue similar a la considerada para especies de pino. El LAI fue muy variable y se relacionó con la productividad del sitio, con la altura media del matorral, con los nutrientes foliares (P, Ca, K, Fe y Cu) y con el K, Ca y Mg cambiable. La eficiencia del crecimiento fue también bastante variable y se relacionó con el K foliar y la longevidad de las acículas. La relación entre todas las variables asociadas con niveles altos de productividad y la altura media del matorral fue significativa y negativa, lo que indica una reducción en el riesgo de incendios. Los resultados muestran la importancia de los nutrientes en la determinación de la vida útil de las acículas y la variabilidad de la biomasa e índice de área foliar de los rodales.

4. Influencia del material de partida sobre el fraccionamiento del Al en suelos ácidos bajo *Pinus pinaster* en Galicia.

El estudio de la influencia de la roca madre en el fraccionamiento del Al en suelos ácidos que son ricos en materia orgánica, puede proporcionar información útil relacionada con la productividad de los bosques en las zonas de alta diversidad geológica. Se estudió cómo el material de partida afecta a varios parámetros químicos, centrándose principalmente en las formas de Al en la fracción sólida y el Al total en disolución en diferentes suelos ácidos en Galicia. Los suelos se desarrollaron sobre pizarra, esquistos biotítico, mica esquisto y granito y todos estaban bajo *Pinus pinaster*. En cada parcela de estudio se recogieron seis muestras de suelo, 3 muestras de suelo rizosférico y 3 muestras de suelo no rizosférico. El Al de la fase sólida fue extraído con las siguientes disoluciones: oxalato de amonio (Al_o), pirofosfato sódico (Al_p), cloruro de cobre (Al_{cu}), cloruro de lantano (Al_{la}) y cloruro de amonio (Al_{NH4}). Además, se estimó el Al que forma complejos altamente estables (Al_p-Al_{cu}), complejos de media estabilidad (Al_{cu}-Al_{la}) y complejos de baja estabilidad (Al_{la}-Al_{NH4}) con la materia orgánica. También se determinó el Al total (Al_t) en la fase líquida. No se encontraron diferencias significativas para ningún parámetro entre el suelo rizosférico y el no rizosférico. En todos los suelos, los complejos orgánico-aluminio predominaron sobre los compuestos inorgánicos de baja cristalinidad (Al_p siempre representó más del 96% de la Al_o). En general, el material de partida tuvo un efecto significativo sobre los parámetros químicos del suelo. En el suelo sobre esquisto biotítico, caracterizado por baja acidez (pH = 5,4) y evolución de la materia orgánica relativamente alta (C/N = 12,7), las concentraciones de Al_o y Al_p fueron más altas y tienden a formar complejos orgánico-aluminio altamente estables, mientras que las concentraciones de Al_{NH4} cambiable y Al_t fueron significativamente más bajas que en los otros suelos. Sin embargo, en los suelos desarrollados a partir de pizarra, la mayor acidez (pH = 4,7) y la evolución de la materia orgánica relativamente baja (C/N = 20,7) favorecieron la formación de complejos orgánico-aluminio de moderada y baja estabilidad y concentraciones más altas de Al intercambiable y Al total en solución. Las características de los suelos sobre granito y mica esquisto fueron intermedias. Se obtuvieron regresiones para estimar las diferentes formas de Al en la fase sólida. Las variables de entrada en los modelos fueron las siguientes: pH (agua y KCl) C, C/N ratio, N y la capacidad de intercambio catiónica efectiva, las cuales están relacionadas con la acidez y la evolución de la materia orgánica. El suelo sobre esquisto biotítico presentó el mejor índice de sitio, mientras que los suelos sobre mica esquisto y pizarra, que fueron menos profundos y en los que predominaron las formas de Al más lábiles, presentaron el índice de sitio más bajo.

5. Riesgo de toxicidad de Al para *Pinus pinaster* en suelos ácidos en Galicia

La influencia de la roca madre sobre la toxicidad del aluminio y la especiación de aluminio en la disolución del suelo se estudió en cuatro parcelas de *Pinus pinaster*. Los parámetros de crecimiento y de biomasa en suelos ácidos también se evaluaron en relación con diferentes índices de toxicidad de Al. Las parcelas utilizadas y el sistema de muestreo fueron los descritos en el apartado 4. En tres árboles de cada parcela también se recogieron muestras de acículas de un año de edad y muestras de raíces. El Al total, Al reactivo, Al soluble en ácido (complejos y/o coloides Al-materia orgánica), Al lábil (monómeros inorgánicos) y no lábil (monómeros orgánicos) se determinaron en la disolución del suelo. A continuación, se realizó la especiación del Al lábil en Al^{3+}, Al-OH, Al-F y $Al\text{-}SO_4$. En estos suelos acidificados por procesos naturales, el material de partida tuvo una influencia significativa en el fraccionamiento y especiación de Al. El Al reactivo predomina sobre el Al soluble en ácido y el Al no lábil predomina sobre el Al lábil en todos los suelos, pero sobre todo en mica esquisto. Las especies de Al consideradas más tóxicas, Al^{3+} y Al-OH, fueron más altas en suelos sobre pizarra y mica esquisto. Todos los índices de toxicidad de Al indicaron que no existe riesgo en la parcela desarrollada sobre esquistos biotíticos, mientras que sí podría haber problemas con este elemento en las desarrolladas sobre mica esquisto y pizarra. En las parcelas de granito aparecen problemas de toxicidad cuando se utilizan índices calculados a partir de parámetros determinados en la fase sólida del suelo, algunos obtenidos en la disolución del suelo (Ca/Al lábil, ATI) y los determinados en acículas y raíces, mientras que utilizando Al lábil, Al^{3+} + Al-OH obtenidos en disolución no existirían riesgos de toxicidad. Sin embargo, los suelos sobre pizarra y mica esquisto presentaron los menores índices de sitio de acuerdo con el más alto valor de Al lábil y Al^{3+} + Al-OH en la disolución del suelo y el mayor riesgo de toxicidad de Al estimado a través de los distintos índices. La parcela sobre esquisto biotítico fue la más productiva y la que arrojó una mayor biomasa total y mejores características de las acículas, en concordancia con las concentraciones más bajas de Al total en disolución y de las especies más tóxicas de Al (Al^{3+} + Al-OH), y con los menores riesgos de toxicidad por Al obtenidos con los distintos índices. La productividad, evaluada como índice de sitio, la biomasa total y de acículas y el índice de área foliar también fueron elevados sobre granito, lo que concuerda con los escasos riesgos de toxicidad de Al que indican los índices Al lábil y Al^{3+} + Al-OH de la disolución del suelo, pero no coincide con lo que indican los índices obtenidos a partir la fase solida del suelo, de acículas o de la raíz. Esta elevada productividad confirma la adaptación de *Pinus pinaster* a este tipo de suelos ácidos o indica que los índices de toxicidad de Al basados en parámetros obtenidos en la fase solida del suelo, acículas y raíz no son adecuados para la estimación de la toxicidad de Al. Sin embargo, la eficiencia en el crecimiento sobre granito fue baja, y este parámetro está más en concordancia con la bajo ratio Ca/Al obtenida en disolución de suelo, acículas y raíces finas.

The main aim of this doctoral research was to improve the understanding of the relationships between the ecophysiological and edaphic parameters that determine the growth of *Pinus pinaster* and its ability to adapt to different environments. The relationships between soil properties, foliar nutrients and growth were studied in plots of *Pinus pinaster* established in soil over different types of bedrock. Good adaptation of *Pinus pinaster* was observed in soils developed over biotitic schist, granitic rocks, gneiss and migmatites, in which growth of the species was highest. Foliar Ca and K, soil depth and average annual temperature explained around 52% of the variability in site index. Needle length, width and thickness were closely related to climate conditions, year of formation and also foliar concentrations of N and Mg. Foliage biomass and leaf area index were negatively correlated with needle age and positively correlated with site index and foliar nutrients. In the soil over biotitic schist, the concentrations of oxalate and pyrophosphate Al were higher than in other soils and tended to form highly stable organic–aluminium complexes. The toxicity indices considered indicated a higher risk of Al toxicity in the plots developed over slate and mica schist, but no risk of Al toxicity in the plots on biotitic schist.

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