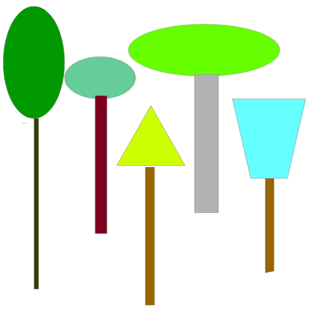
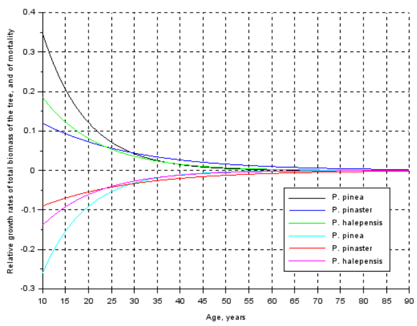
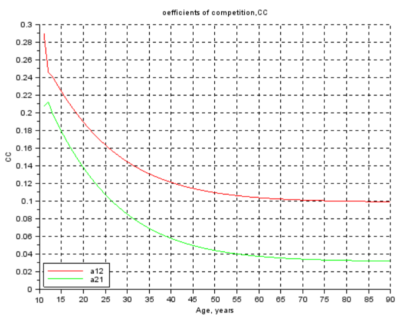
Overyielding in Mixed Forests Revisited

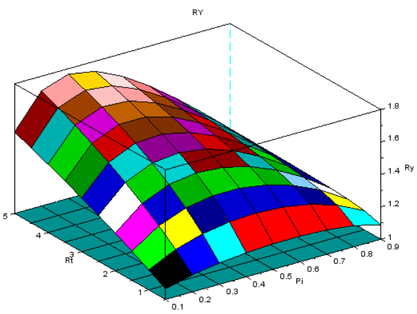
A Theoretical and Simulative Inquiry

Luís Soares Barreto









Costa de Caparica
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A table with all my texts available in the library of the Instituto Superior de Agronomia, is located in the following URL:

https://www.repository.utl.pt/handle/10400.5/196/simplesearch?filterquery=Barreto%2C+Lu%C3%ADs+Soares&filtername=author&filtertype=equals

Seventeen papers I published in *Silva Lusitana*, from 2001 to 2013, are available in thhe following URL:

http://www.scielo.mec.pt/cgi-bin/wxis.exe/iah/

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Overyielding in Mixed Forests Revisited

A Theoretical and Simulative Inquiry

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Abstract. The author uses his theory for mixed stands, and his model BACO2 for tree competition to clarify the global yield, and allometry of self-thinned even-aged mixed stands with two species. He analyses the effects of the competitive hierarchy, initial proportions of the species, and the relative size of the trees of the two competitors. He extends the results to self-thinned uneven-aged mixed stands. A mechanism to explain the emergence of over yielding is proposed. He apples his theoretical results to the analyse of real cases of overyielding available in the literature, with success. He also simulates the emergence of overyielding in self-thinned even-aged mixed stands with two e European species of trees.
Key words: overyielding; mixed forests; competitive hierarchy; global stand biomass; relative rates of variation

Sumário. O autor recorre à sua teoria para os povoamentos mistos e ao seu modelo BACO2 para clarificar a produção e alometria globais de povoamentos auto-desbastados mistos regulares com duas espécies. Analisa o efeito da hierarquia competitiva, proporções iniciais das duas populações e do tamanho relativo das árvores das suas árvores. Estende os resultados obtidos aos povoamentos auto-desbastados mistos irregulares. É proposto um mecanismo para explicar a emergência de sobreprodução. Aplica os seus resultados teóricos à análise da casos reais de sobreprodução disponíveis na literatura, com sucesso. Simula também a emergência da sobre-produção em povoamentos auto-desbastados mistos regulares com duas espécies europeias.
Palavras-chave: sobreprodução; florestas mistas; biomassa global; hierarquia competitiva; taxas relativas de variação

Introduction

The occurrence of overyielding in mixed forests had been theoretically, and empirically studied by several researchers (Barreto, 2012; Jactel et al., 2018; references herein). The present contribution is an attempt to increase, and refine the understanding I already attained, about overyielding in mixed stands.

First, I will approach the forests of Mediterranean pines. The results obtained are used to analyse, and conceptualize the occurrence of overyielding. After, I will approach empirical cases of mixed stands, and I will show that the previous results are consistent with the evidence exhibited in these analysed stands. Finally, I simulate the emergence of overyielding in other mixed stands with two European tree species.

To elaborate this paper, I used software Scilab (https://www.scilab.org).

Theoretical Background, and Methodology

This paper is underpinned by my theory for mixed forests and associated models BACO2, and BACO3 for competition (Barreto, 2010: chapters 14-19; 2011: chapters 14-19). As these two books are freely available in the site of the library of the Instituto Superior de Agronomia (see references) I will not explain the theory. Nevertheless, I present here two important results of the theory.

The approaching of mixed stands not underpinned by a sound conceptual, and mathematical model for tree competition does not look like a very fruitful endeavor, in my humble opinion. This is trivial scientific method. “No theory, no science”.

Let represent the characteristic relative mortality rate, or the rate of mortality per capita by or relative mortality rate **rmr** (Barreto, 2011: equation 4.61), and define the relative size of the trees of two species as:

$$Rt=\frac{Final\ biomass\ of\ the\ mean\ tree\ of\ the\ dominant\ species}{Final\ biomass\ of\ the\ mean\ tree\ of\ the\ dominated\ species}$$

My inquiry in mixed stands arrived to the two following laws, referred to self-thinned mixed even-aged stands (**SEMS**):

L1. The dynamics of the densities of the populations of a SMES are affected a) by the rmr of the species, and b) by the initial proportions of the trees of each species, relative to the total number of trees.

L2. The yield of timber or total biomass of a SMES is influenced a) by the rmr of the species, b) by the initial proportions of the trees of each species, relative to the total number of trees, and c) by the relative size of the mean trees of the competitors.

Given two species, A, B, if it is observed **$|rmr_A| > |rmr_B|$**, then in the competitive hierarchy between the two species, A is the dominant species, and B the dominated one (A>B).

To simulate the SEMS of two, and three Mediterranean pines I used model BACO2 introduced in chapter 14 of Barreto (2010, 2011). To calculate the coefficients of competition I applied equations 16.2a, 16.2b displayed in Barreto (2010; 2011), associated to model BACO3.

The metric for overyielding is **RY** defined as the ratio of the total biomass of the mixed stand divided by the sum of the biomasses of equivalent pure stands of the same species. The symbol for the initial proportion of the trees of the dominant species is P**i**. Overyielding occurs when RY>1.

I also use the three following symbols: **OY** for overyielding; **rgrf** for the relative growth rate of the total biomass of the forest or all trees of a given species; **rgrt** for the relative growth rate of the total biomass of the tree of a given species.

Overyielding in Forests of Mediterranean Pines

Vila et al. (2007) verified the occurrence of OY in mixed Mediterranean forests. These observations in Mediterranean forests, and the simulated verification of its occurrence in mixed forests of *Pinus pinaster*, and *Pinus halepensis* (Barreto, 2010, figure 18.5; Barreto, 2011, figure 18.6; Barreto, 2012, figure 6), and in mixed forests with the three main Mediterranean pines: *Pinus pinea, Pinus pinaster*, and *Pinus halepensis* (Barreto, 2010, figure 18.10; Barreto, 2011, figure 18.11) are in the origin of this section.

The Characterization of the Species

The Mediterranean pines here considered are *Pinus pinea* (**Ppe**), *Pinus pinaster* (**Ppa**), and *Pinus halepensis* (**Pha**), characterised in table 1. These pines coexist in natural mixed stands, where the following hierarchies are observed in SEMS:

Till age 25 years: *P. pinea*> *P. halepensis* > *P. pinaster*

From 25 to 30 years: *P. pinea* > *P. pinaster* > *P. halepensis*

From 30 to 38 years: *P. pinaster* > *P. pinea* > *P. halepensis*

After 38 years: *P. pinaster* > *P. halepensis* > *P. pinea*

Table 1. Characterization of the three Mediterranean pines. c= coefficient of competition in the Gompertz equation; R_{-2}= (density at age 10)/(final density) in self-thinned even-aged pure stands; LHS=life-history strategy; GI= growth index; RI=regeneration index; SI=survival index; L=longevity, years.; A=acronym. See chapters 8, and 9 in Barreto (2010,2011) for the explanation of the concepts here used

Species	c	R_{-2}	LHS	GI	RI	SI	L	A
Pinus halepensis	0.082	5.4260	r-3	1.535	0.0328	0.9682	180	Pha
Pinus pinaster	0.050	6.0191	r-3	0.743	0.1376	0.8623	100	Ppa
Pinus pinea	0.105	11.9152	K-2	16.343	0.0127	0.9873	250	Ppe

For more detailed information about the dynamic characteristics of the species, see also table 4.1 in Barreto (2011).

In figure 1, I illustrate de dynamics of the absolute values of the rmr of these three Mediterranean pines.

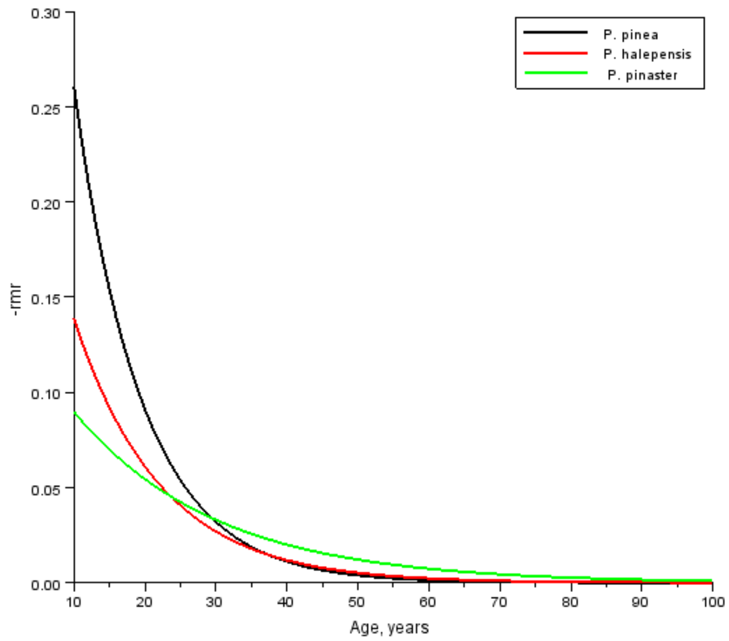

Figure 1. Representation of the absolute values of the relative mortality rates of the three pines

The Simulation of Overyielding

Now, I will introduce four graphics simulated with model BACO2, that illustrate the ocurrence of OY (RY) in mixed stands with the three Mediterranean pines. In these graphics the effects of the relative size of the trees (Rt) and the proportion of the dominant specie (Pi) are evident.in All graphics of OY, the age of simulation is 90 years, this is, I estimate the emergence of OY in the SEMS at age 90 years. In Barreto (2011:subsection 18.4.5) I approach the effect of age on the emergence of OY.

We used the asymptotic total biomasses of each population in pure, and mixed stand to evaluate the relative performances of each population, and the whole stand.

Figure 3 shows a situation of underyielding (RY<1). Underyielding can emerge in nature, as verified by Drössler et al. (2018).

From figure 3 we can also formulate a conjecture: underyielding occurs in sites of poor quality for the dominant species.

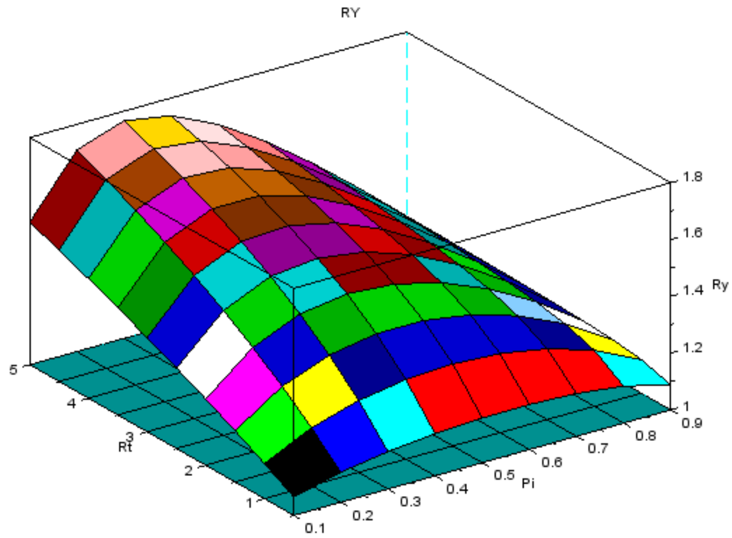

Figure 2. Simulated representation of the emergence of overyielding in mixed stands with *P. halepensis*, and *P. pinaster*

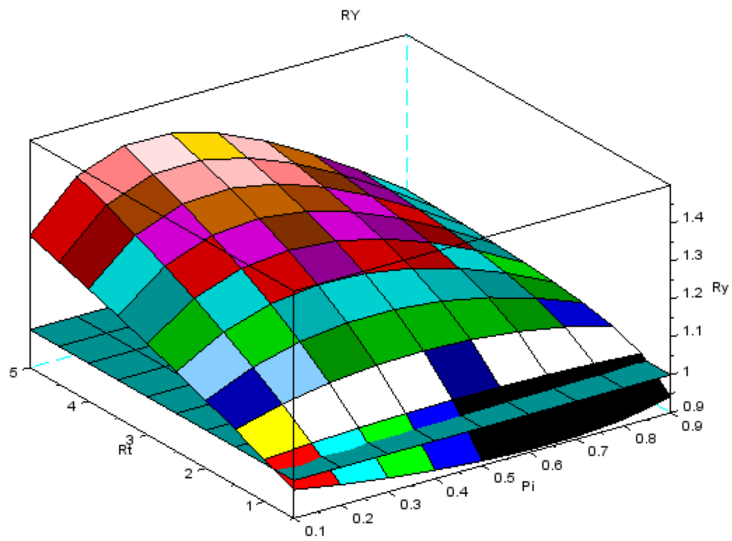

Figure 3. Simulated representation of the emergence of overyielding in mixed stands with *P. pinea*, and *P. halepensis.* Overyielding occurs only when Rt>1

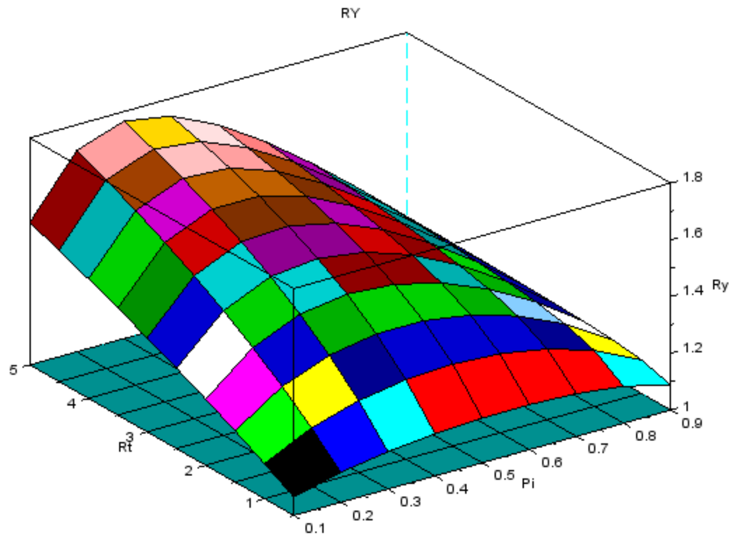

Figure 4. Simulated representation of the emergence of overyielding in mixed stands with *P. pinea*, and *P. pinaster.*

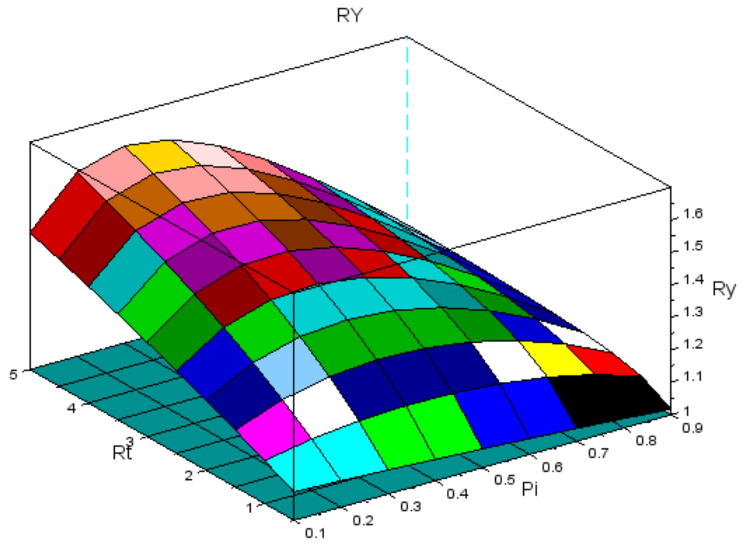

Figure 5. Simulated representation of the emergence of overyielding in mixed stands with *P. pinea*, *P. halepensis*, and *P. pinaster*

Analysing Overyielding in Forests with Mediterranean Pines

A General Explanation for Overyielding

An explanation at a stand level. The relative rates of variation of the forest variables are related to each other (Barreto, 2011: table 4.1, Section 6.3). It is expected that when a species is dominant, and transfer its mortality of self-thinning to the other competitors, the species is capable of take the maximum benefit from the available resource for its growth. This happens if the maximum relative rate of mortality occurs simultaneously with the highest values of the relative rate of growth of the total biomass of the dominant species. This is, the relative rates of mortality (negative values as they represent a loss of individuals) , and the relative rates of growth of total biomass of the species, when displayed in the same graph, must exhibit a high degree of symmetry. This is what happens as shown in figure 6. It is this symmetry that causes the OY in mixed stands of species that went through a process of coevolution. Shifts of dominance enhance both coexistence, and OY. See figure 7.

Shifts of dominance can also occur in mixed stands of species that did not coevolved, planted by men, and eventually OY can emerge. For an example see Lu et al. (2016).

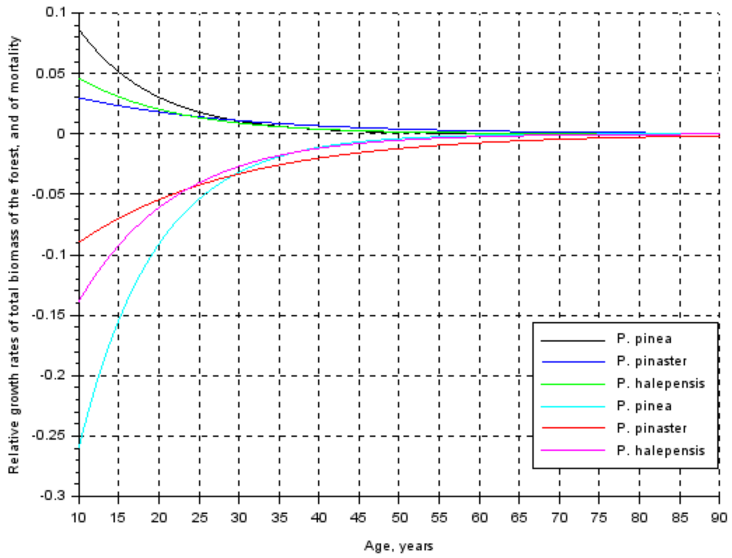

Figura 6. Graphic of the relative growth rates of total biomass of the forest, and relative rates of mortality of *Pinus pinea*, *Pinus pinaster*, and *Pinus halepensis*

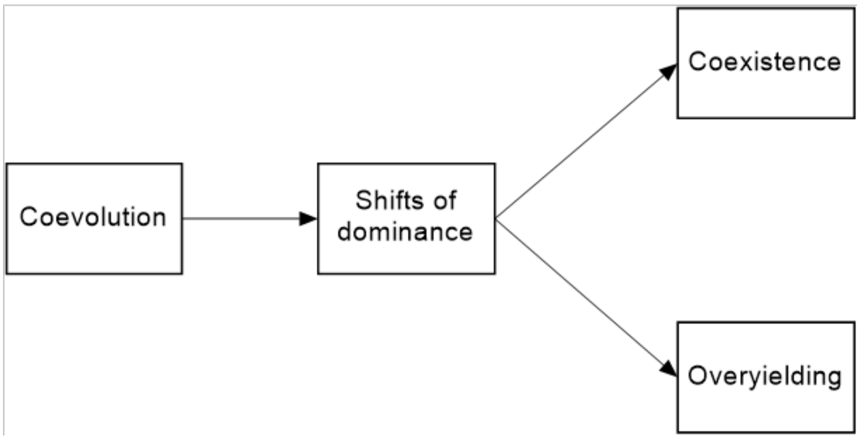

Figura 7. A diagrammatic representation of the effects of the occurrence of coevolution in mixed forests

At a local level, let me attempt a parallel explanation for OY in self-thinned uneven-aged mixed stands. Now, I deal with the relative growth rate of the total biomass of the **tree**. Comparing to the surrounding trees of the same age, and older trees, a given tree has the highest growth rate of its total biomass simultaneously with its highest competitive dominance relative to its neighbour trees of other species. The graphic in figure 8, comparable to the graphic in figure 6, sustains this statement. In the same conditions of access to limiting resources (e.g., light), this dominant tree is spared by self-thinning, and survive. Thus, in a small spot of trees, the tree that has higher probability of survival is the one whose total biomass growth has the highest contribution to the total biomass of the forest.

This explanation can be extended to self-thinned even-aged mixed stands. In this situation, all competing trees in the small spot have the same age.

There is empirical evidence of the role of neighbourhood interactions in the emergence of OY in mixed forests in Fichtner et al. (2018).

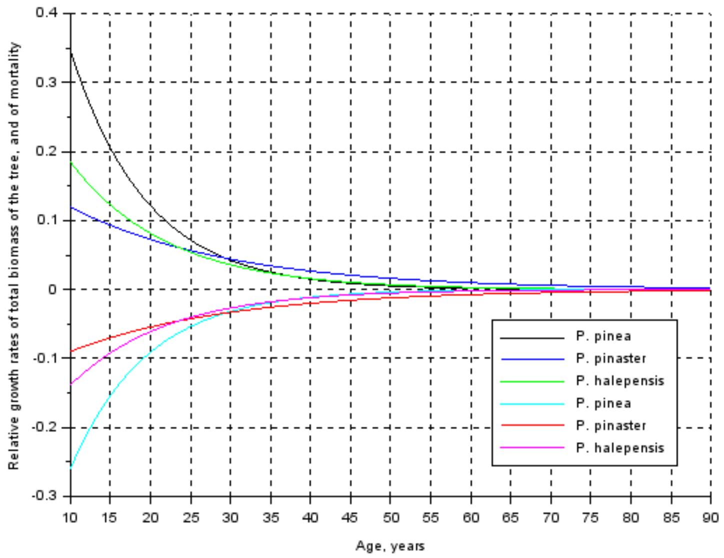

Figura 8. Graphic of the relative growth rates of total biomass of the tree, and relative rates of mortality of *Pinus pinea*, *Pinus pinaster*, and *Pinus halepensis*

The Interpretation of Figures 2 to 5

In Barreto (2010; 2011:subsection 18.4.6; 2012) I already advanced an interpretation of the simulations displayed in figures 2 to 5. Let me retrieve it.

In my model for plant competition, the dominant species transfers part of its mortality to the dominated population. Thus, when the value of Rt is high, self-thinning acts close to a low thinning, and given the higher growth rate of the dominant competitor OY can emerge. For a given initial proportions of the two species, there is a critical value of Rt, Rt_c, such that if Rt> Rt_c than OY happens. In natural stands, for a given mixture, Rt_c depends on the ratio of the of the relative growth (or mortality) rates of the two competing species, and the quality of the site. In nature, for certain mixtures, the conditions necessary for the satisfaction of Rt> Rt_c may never occur, and these stands do not exhibit OY.

In mixed stands artificially created by man, when shifts of dominance occur, and simultaneously Rt> Rt_c is verified, overyielding emerges.

The greater is Pi, the fraction of the dominant species, the greater is the number of trees that originate a more intense self-thinning, and there are few trees of the dominated species to support the transference of mortality. The occurrence of the maximum value of RY is the result of equilibrium between the effects of Rt, and Pi. The equilibrium depends on the characteristic of the competitors, this is, on the dynamics of the competitive hierarchy.

The Emergence of Facultative Mutualism

The only interaction among populations that can explain OY is mutualism, as already shown in Barreto (1999). Mixed stands where OY occur can show only mutualism ([+ +]) or mutualism followed by asymmetric competition ([+ +] [+ -]). In the second case, the duration of the mutualistic phase depends on the degree of dominance, and the initial proportions of the number of tres of the species.

To scrutinize the kind of interactions that occur, I will use my model BACO2 (Barreto, 2011: chapters 14, 15) to simulate the dynamics of the stand, and after model BACO3 to calculate the coefficients of the interaction. The coefficients are given by equations 16.2, in Barreto (2011:211-212).

I will start with mixed stands of Ppa+Pha. Ppa acts as a dominant species, and $\mathbf{a_{12}}$ measures the effect of species 2 on species 1 (the dominant); $\mathbf{a_{21}}$ measures the effect of species 1 on species 2.

In figura 9, we only see the occurrence of both interactions when the initial density of the dominant species (Ppa) is very high. Also, the differences of the values of the coefficients of competition are larger with the increasing of the initial density of Ppa.

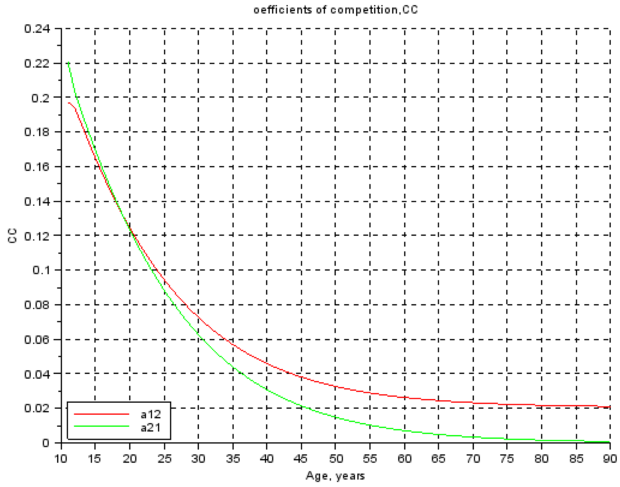

Figure 9.A. SEMS with Ppa+Pha, initially with 2000 trees of Ppa, and 8000 trees of Pha. Only mutualism occurs. At age 90 years, the mixed stand has 6% more trees than the sum of the densities of the two pure stand

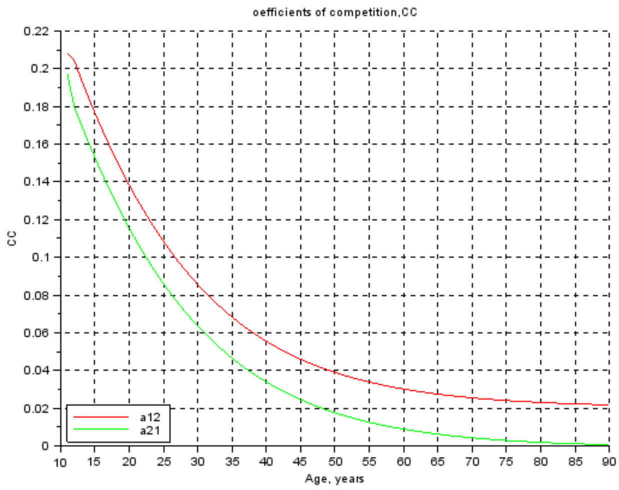

Figure 9.B. SEMS with Ppa+Pha, initially with 5000 trees of each species. Only mutualism occurs. At age 90 years, the mixed stand has 11% more trees than the sum of the densities of the two pure stand

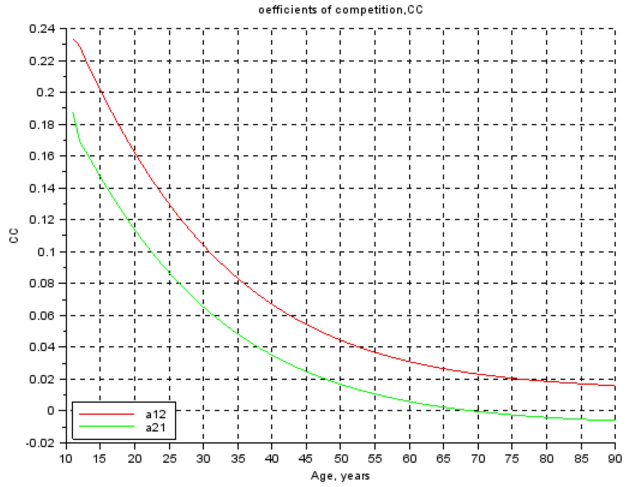

Figure 9.C. SEMS with Ppa+Pha, initially with 8000 trees of Ppa, and 2000 trees of Pha. The large initial size of the dominant species cause the emergence of asymmetric competition that starts at age 70 (a_{21}<0). At age 90 years, the mixed stand has 9% more trees than the sum of the densities of the two pure stand

Now, I will analyse the SEMS with Ppe+Pha. The results of the simulations are in figure 10. Now we have an interaction of two species with different LHS (table 1), and Ppa has more competitive ability. In figure 10, in all three graphics both mutualism, and asymmetric competition occur. The greater is the initial proportion of the dominant species (Ppe) the shorter is the mutualistic phase.

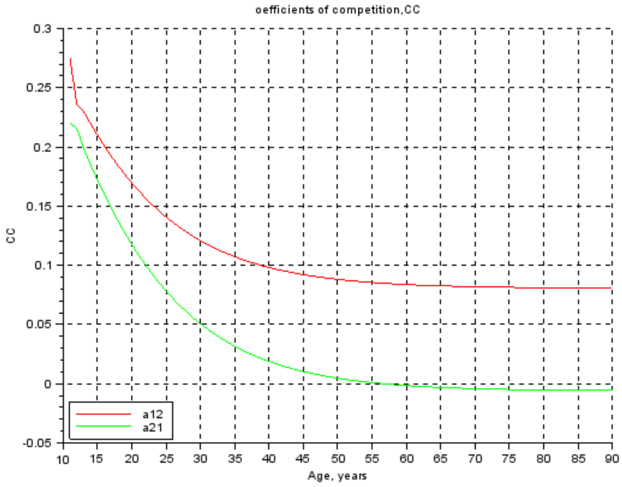

Figure 10.A. SEMS with Ppe+Pha, initially with 2000 trees of Ppa, and 8000 trees of Pha. Both mutualism, and asymmetric competition occur. At age 90 years, the mixed stand has 2% more trees than the sum of the densities of the two pure stand

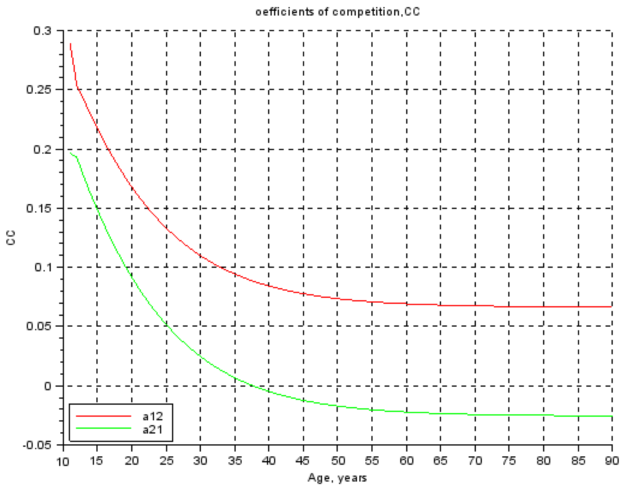

Figure 10.B. SEMS with Ppe+Pha, initially with 5000 trees of Ppa, and 5000 trees of Pha. Both mutualism, and asymmetric competition occur. At age 90 years, the mixed stand has 3% more trees than the sum of the densities of the two pure stand

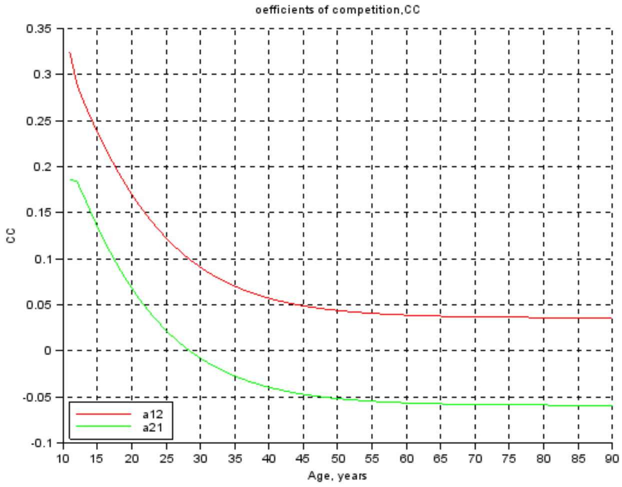

Figure 10.C. SEMS with Ppe+Pha, initially with 8000 trees of Ppe, and 2000 trees of Pha. Both mutualism, and asymmetric competition occur. At age 90 years, the mixed stand has 2% more trees than the sum of the densities of the two pure stand

Let me display the graphics with the coefficients for the SEMS Ppe+Ppa. Ppe is the dominant species (a_{12}>a_{21}).

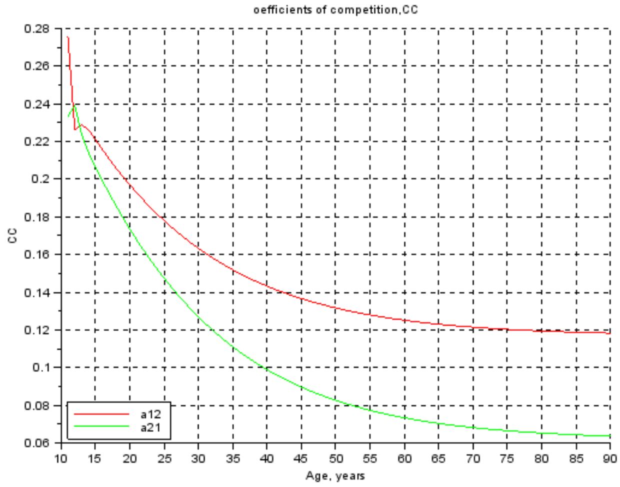

Figure 11.A. SEMS with Ppe+Ppa, initially with 2000 trees of Ppe, and 8000 trees of Ppa. Both mutualism, and asymmetric competition occur. At age 90 years, the mixed stand has 23% more trees than the sum of the densities of the two pure stand

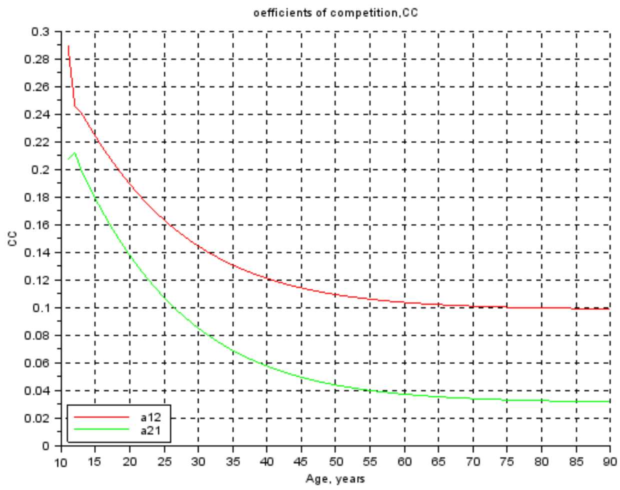

Figure 11.B. SEMS with Ppe+Ppa, initially with 5000 trees of Ppa, and 5000 trees of Ppa. Both mutualism, and asymmetric competition occur. At age 90 years, the mixed stand has 30% more trees than the sum of the densities of the two pure stand

Now, strictly speaking only about density (ignoring the size of the trees) we can verify that the SEMS with larger OY are the ones with *P. pinea*, and *P. pinaster*. In table 2, I summarize the emergence of the two interactions in the 9 simulations we did.

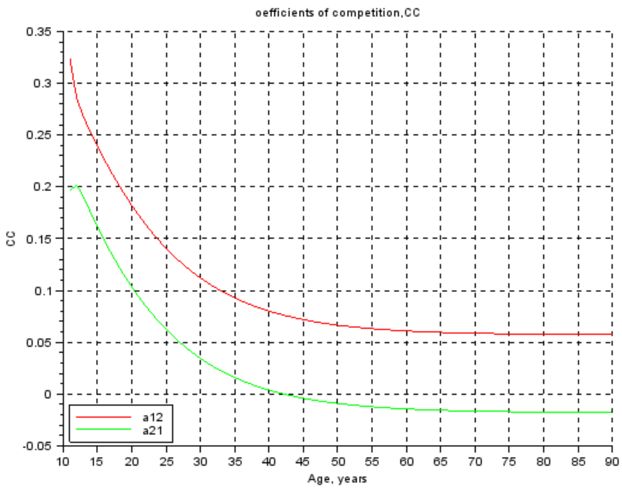

Figure 11.C. SEMS with Ppe+Ppa, initially with 8000 trees of Ppe, and 2000 trees of Ppa. Both mutualism, and asymmetric competition occur. At age 90 years, the mixed stand has 20% more trees than the sum of the densities of the two pure stand

Table 2. Compilation of the patterns of interactions that emerged in the simulations performed

SEMS	Initial densities		
	2000/8000	5000/5000	8000/2000
Ppa+Pha	[+ +]	[+ +]	[+ +] [+ -]
Ppe+Pha	[+ +] [+ -]	[+ +] [+ -]	[+ +] [+ -]
Ppa+Ppe	[+ +]	[+ +]	[+ +] [+ -]
Competitive hierarchy: Ppe>Ppa>Pha			

Next, I will approach six mixed stands with two species, exhibiting OY, described in the literature.

The SEMS with *Pinus sylvestris*, and *Pinus pinaster*

The four SEMS I will analyse have two species, as previously. The species are characterized in table 3.

The first SEMS I approach has trees of *Pinus sylvestris* (K-1), and *Pinus pinaster* (r-3). This type of mixed forest was studied by Riofrío, Río, and Bravo (2017), in Spain. Psy is the dominant species as evinced in figure 12.

Table 3. Characterization of the species we now consider. c= coefficient of competition in the Gompertz equation; R_{-2}= (density at age 10)/(final density) in self-thinned even-aged pure stands; LHS=life-history strategy; GI= growth index; RI=regeneration index; SI=survival index; L=longevity, years.; A=acronym. See chapters 8, and 9 in Barreto (2010,2011) for the explanation of the concepts here used

Species	c	R_{-2}	LHS	GI	RI	SI	L	A
Pinus sylvestris	0.03	34.25863	K-1	2.276	0.0102	0.9897	450	Psy
Picea abies	0.042	210.0399	K-2	22.014	0.0001	0.9999	300	Pab
Quercus robur	0.041	125.963	K-2	16.279	0.0003	0.9997	500	Qro
Fagus sylvatica	0.043	946.7456	K-3 (?)	132.550	0	1	300	Fsy
Betula pendula	0.035	20.04781	r-2	1.0490	0.0767	0.9232	120	Bpe
Pseudotsuga menziesii	0.046	82.19568	K-1	10.205	0.0008	0.9991	700	Pme

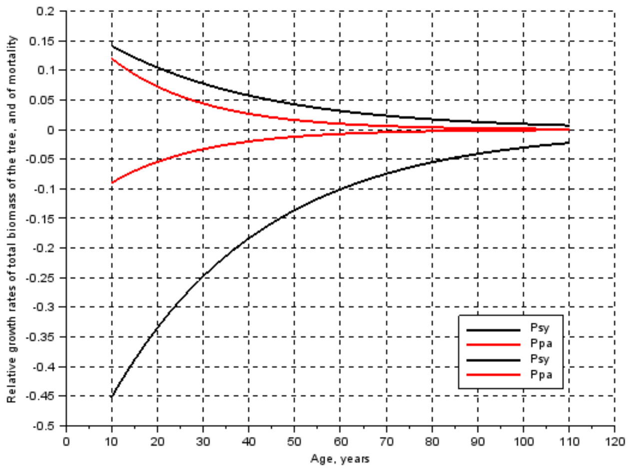

Figure 12. The dynamics of the rmr, and rgrt of Psy, and Ppa

In figure 13, I display the relation among RY, Rt, and Pi. OY occurs for values of Rt greater than about 1.5.

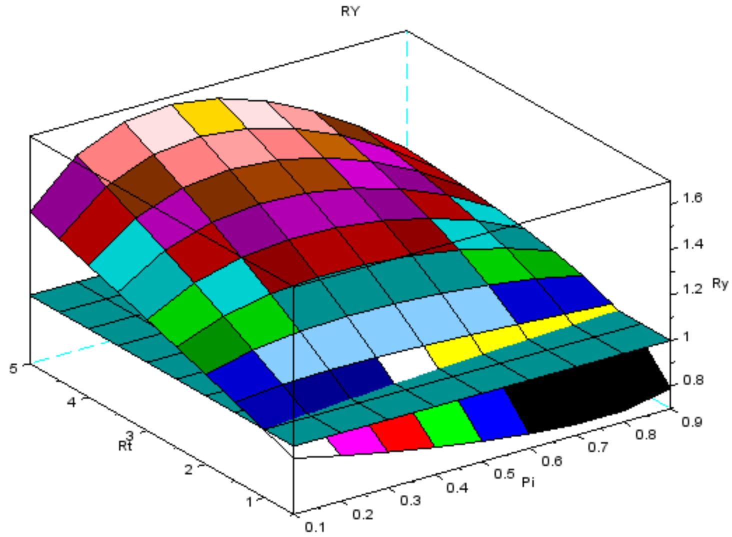

Figure 13. Simulated representation of the emergence of overyielding (RY>1) in mixed stands with *P. sylvestris*, and *P. pinaster*, at age 90 years

In figure 14, I scrutinize the dynamics of the interactions between the two populations. In the three combinations of initial density the sequence is [+ +] [+ -]. The greater is the initial proportion of the dominant species (Psy) the shorter is the mutualistic phase. The same general pattern that occurred in SEMS Ppe+Pha. This is the pattern when the dominance is strong.

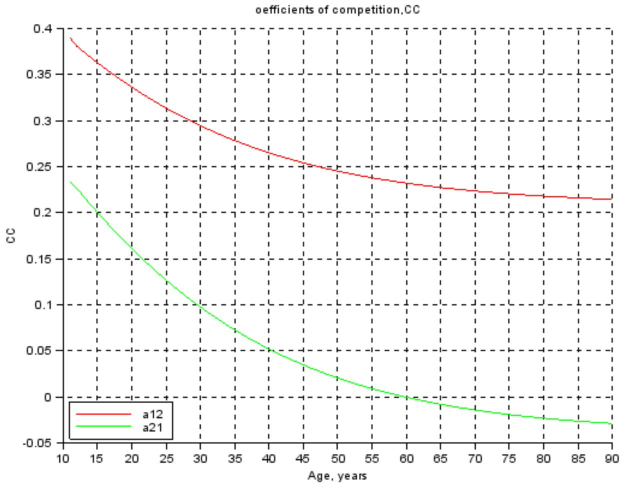

Figure 14.A. SEMS with Psy+Ppa, initially with 2000 trees of Psy, and 8000 trees of Ppa. Both mutualism, and asymmetric competition occur

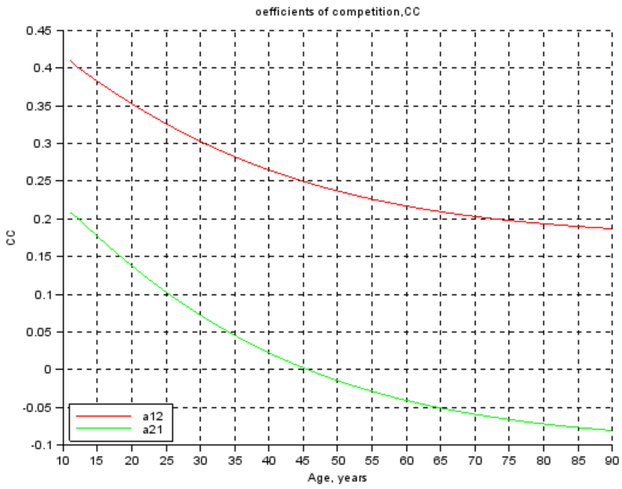

Figure 14.B. SEMS with Psy+Ppa, initially with 5000 trees of Psy, and 5000 trees of Ppa. Both mutualism, and asymmetric competition occur

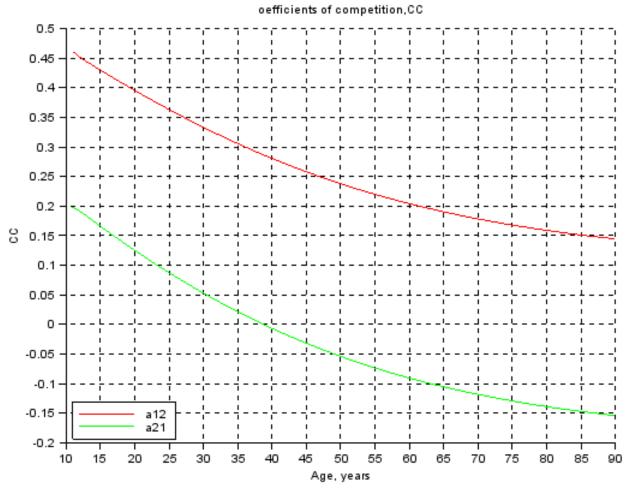

Figure 14.C. SEMS with Psy+Ppa, initially with 8000 trees of Psy, and 2000 trees of Ppa. Both mutualism, and asymmetric competition occur

The SEMS with *Pice abies*, and *Pinus sylvestris*

Drössler et al. (2018) approached the analysis of mixed forests with Pab+Psy. In this section I will apply my theory for SEMS to this type of mixed forests. Let me start by the establishment of the competitive hierarchy, in figure 15. Pab is the dominant species.

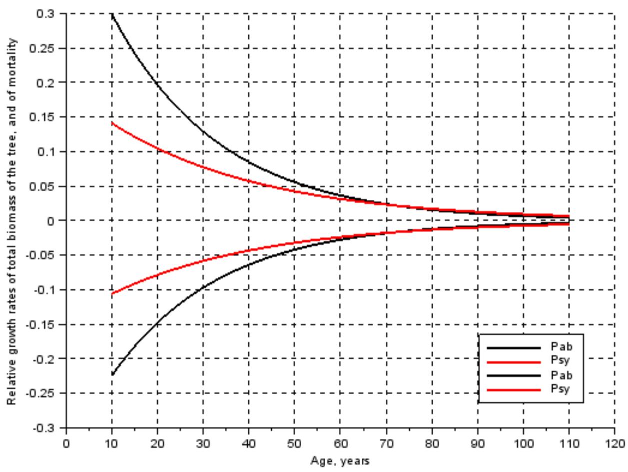

Figure 15. The dynamics of the rmr, and rgrt of Pab, and Psy

In figure 16 I display the landscape of the emergence of OY.

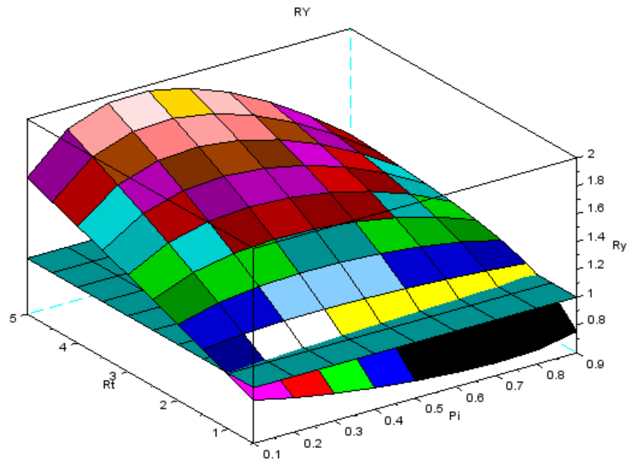

Figure 16. Simulated representation of the emergence of overyielding (RY>1) in mixed stands with Pab, and Psy, at age 90 years

As depicted by Drössler et al. (2018), both OY, and underyielding occur. These authors found overyielding in the range 0 to 30%. These values are within the range displayed in the figure.

In figure 17, I look for the interactions that occur.

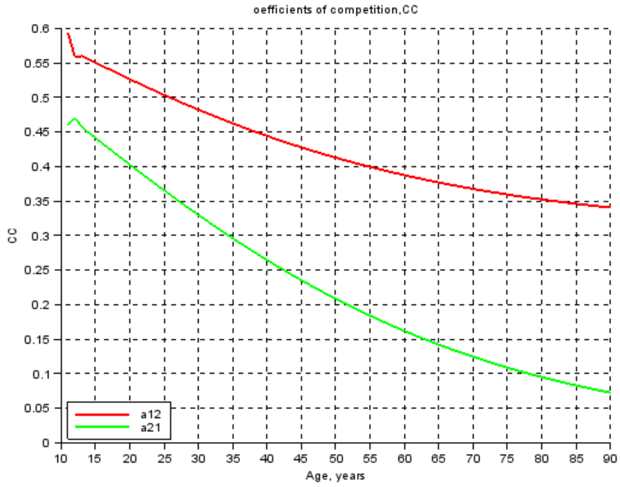

Figure 17.A. SEMS with Pab+Psy, initially with 2000 trees of Pab, and 8000 trees of Psy. Only mutualism occurs

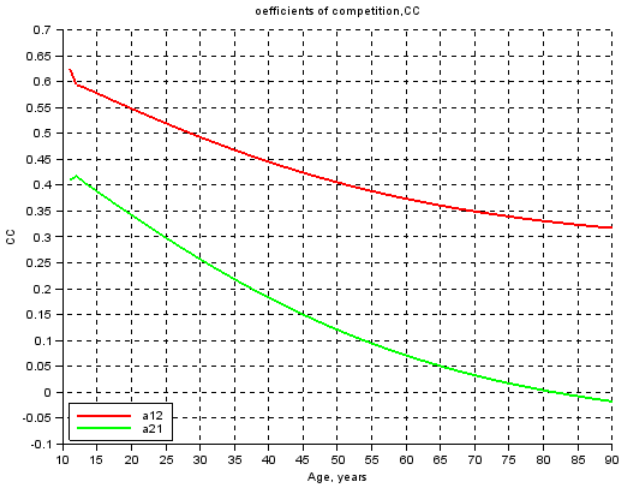

Figure 17.B. SEMS with Pab+Psy, initially with 5000 trees of Pab, and 5000 trees of Psy. Both mutualism, and asymmetric competition occur

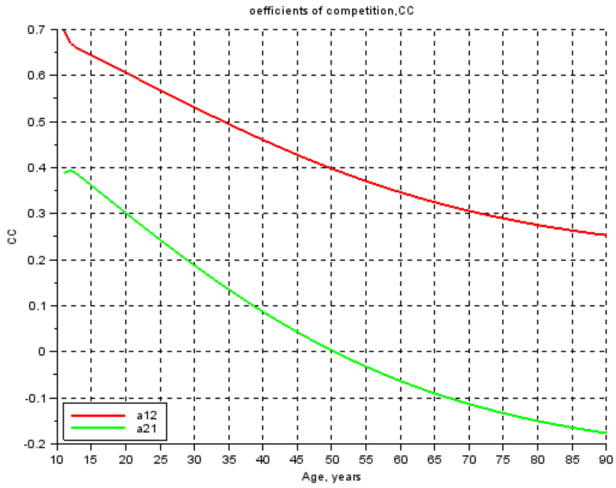

Figure 17.C. SEMS with Pab+Psy, initially with 8000 trees of Pab, and 2000 trees of Psy. Both mutualism, and asymmetric competition occur

As the dominance of Pab over Psy it is not very strong, when the initial density of Pab is low, only mutualism emerges.

The SEMS with *Quercus robur*, and *Pinus sylvestris*

Lu et al. (2016) analysed OY in four types of mixed forests, in Netherlands. They did not deal with stands strictly with only two species, but defined a criterium to consider a mixed with more than two species as only with two species. Although this situation, I decide to apply my theory for SEMS to the mixtures they studied.

Now, I approach SEMS with Qro+Psy. Let start as usual by the competitive hierarchy.

In figure 18 a shift of dominance occurs. Till age 69 years the hierarchy is Qro>Psy, after occur Psy>Qro. Globally, Qro acts as the dominant species.

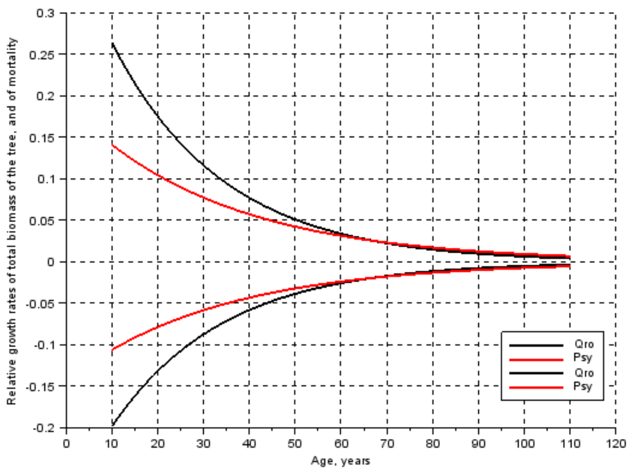

Figure 18. The dynamics of the rmr, and rgrt of Qro, and Psy

The stands in Netherlands are 30 years old. In figure 19, I simulate the emergence of OY at at 30 in this mixture. Lu et al. (2016) observed OY of 20.3% for Psy, and OY of 31.2% for Qro. These figures are compatible with the values of RY in figure 19.

As for the other SEMS already described, in figure 20 I display the correspondent graphic for age 90. Aging favours OY.

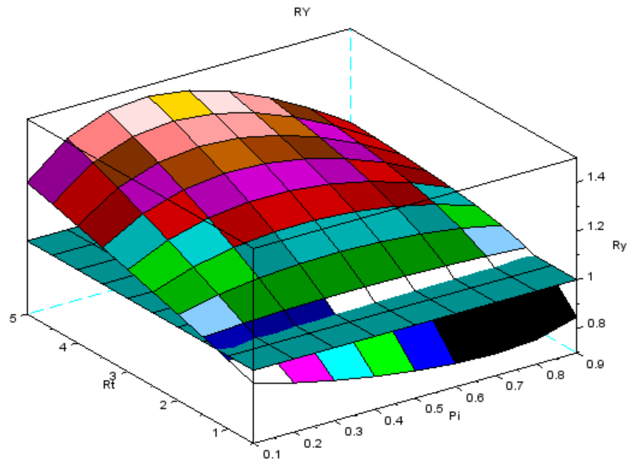

Figure 19. Simulated representation of the emergence of overyielding (RY>1) in mixed stands with Qro, and Psy, , at age 30 years

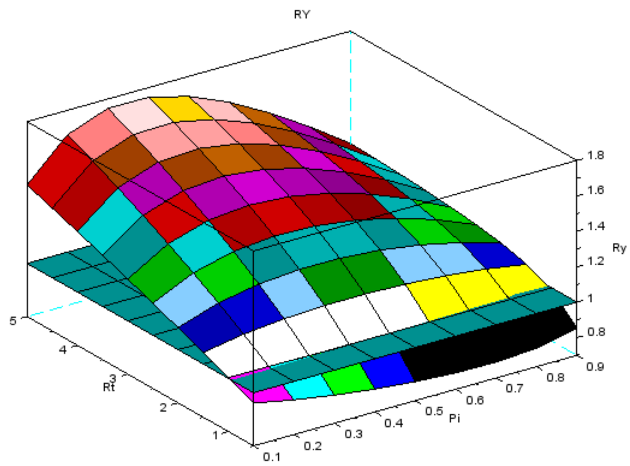

Figure 20. Simulated representation of the emergence of overyielding (RY>1) in mixed stands with Qro, and Psy, , at age 90 years

The coefficients of competition are displayed in figure 21. The behaviour of the coefficients are similar to what happens in the SEMS Pab+Psy.

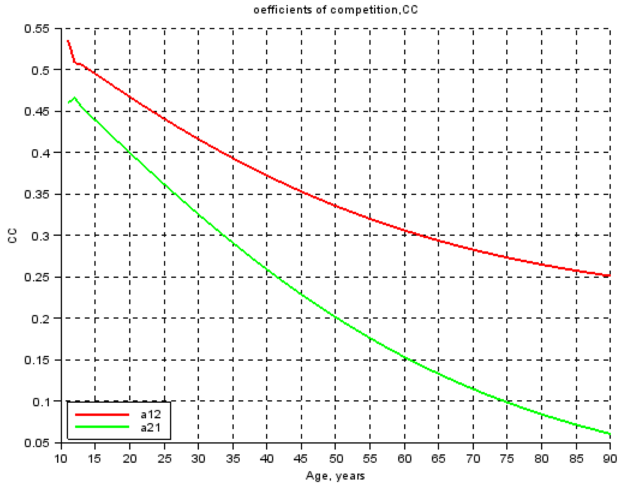

Figure 21.A. SEMS with Qro+Psy, initially with 2000 trees of Qro, and 8000 trees of Psy. Only mutualism occurs

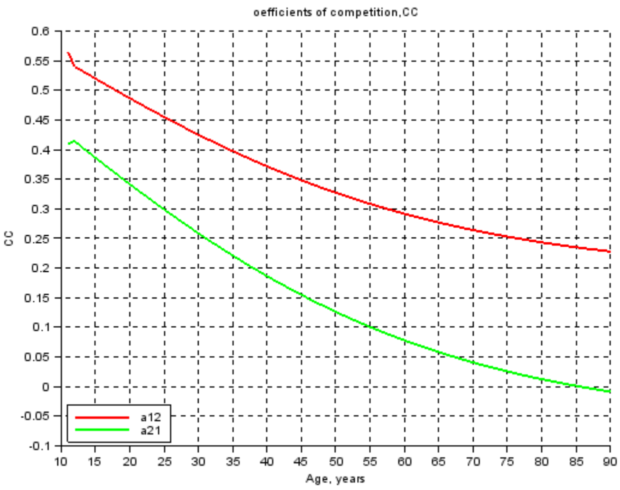

Figure 21.B. SEMS with Qro+Psy, initially with 5000 trees of Qro, and 5000 trees of Psy. Both mutualism, and asymmetric competition occur

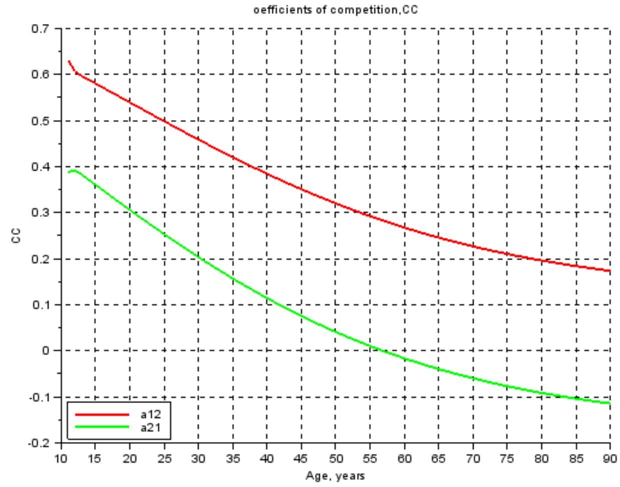

Figure 21.C. SEMS with Qro+Psy, initially with 8000 trees of Qro, and 2000 trees of Psy. Both mutualism, and asymmetric competition occur

The SEMS with *Fagus sylvatica*, and *Pseudotsuga menziesii*

Lu et al. (2016) analysed mixed stands with Fsy+Pme, with 17 years age. Let introduce the graphic of the rmr, and rgrt, of both species. Fsy is the dominant species.

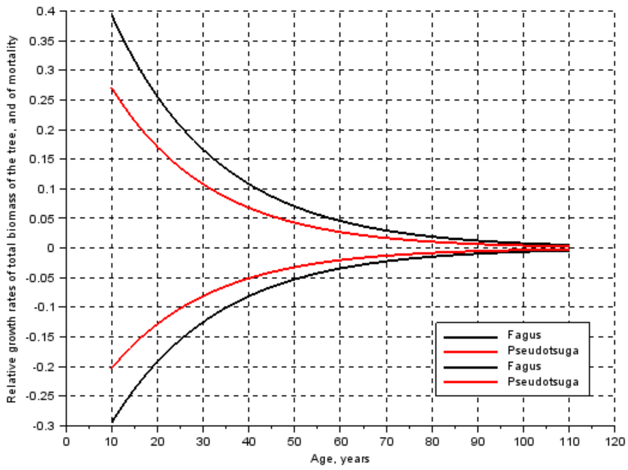

Figure 22. The dynamics of the rmr, and rgrt of Fsy, and Pme

In figures 23, and 24, I present the graphics of the emergence of OY, respectively, at ages 17, and 90 years.

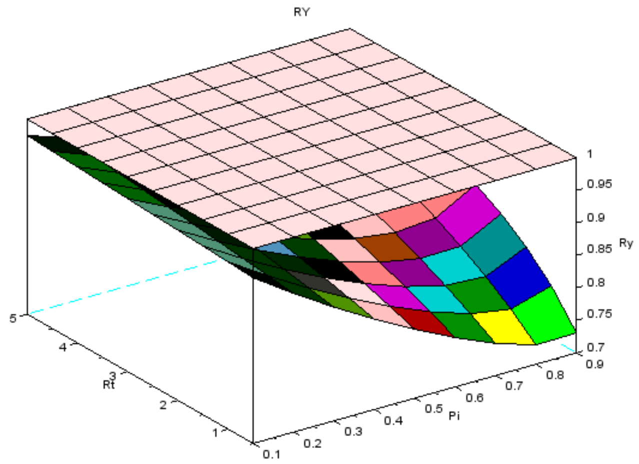

Figure 23. Simulated representation of the emergence of underyielding (RY<1) in mixed stands with Fsy, and Pme, at age 17 years

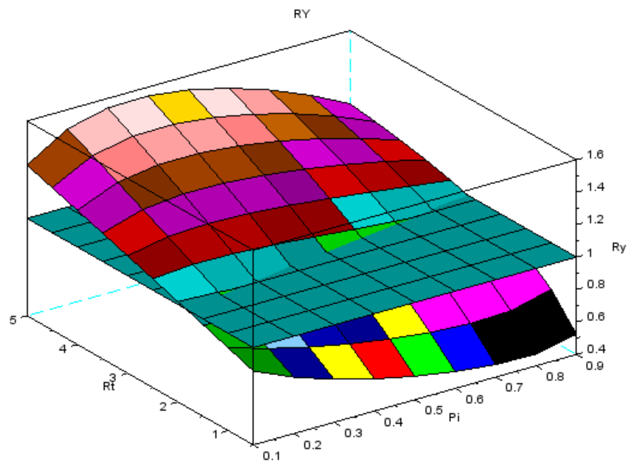

Figure 24. Simulated representation of the emergence of overyielding (RY>1) in mixed stands with Fsy, and Pme, at age 90 years

My simulations do not show OY, for so young stands as those with 17 years. As both species are K-strategists, and their longevities are very different I am not surprised with this occurrence.

In figure 25, I display the coefficients of competition.

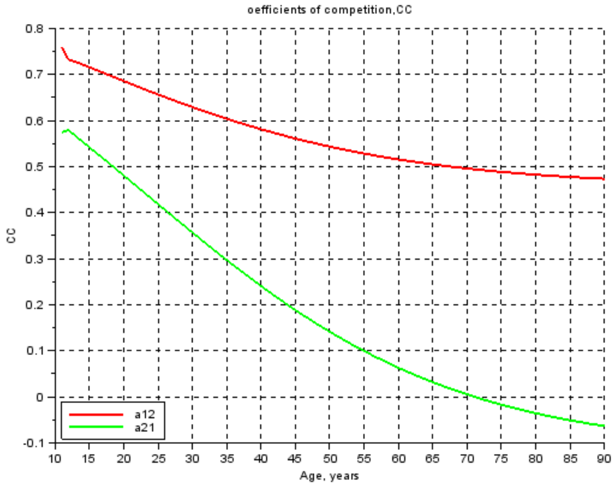

Figure 25.A. SEMS with Fsy+Pme, initially with 2000 trees of Fsy, and 8000 trees of Pme. Both mutualism, and asymmetric competition occur

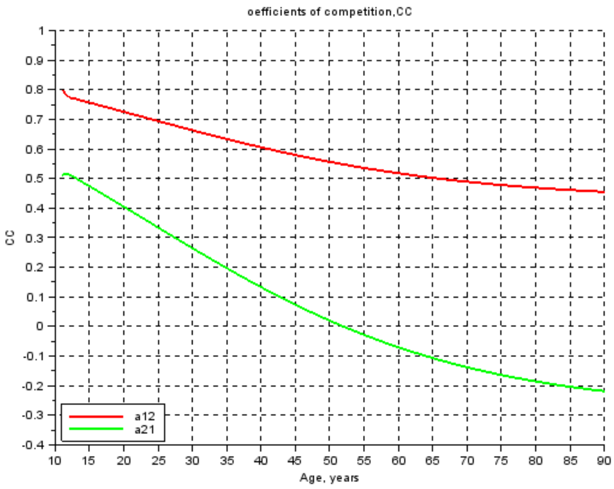

Figure 25.B. SEMS with Fsy+Pme, initially with 5000 trees of Fsy, and 5000 trees of Pme. Both mutualism, and asymmetric competition occur

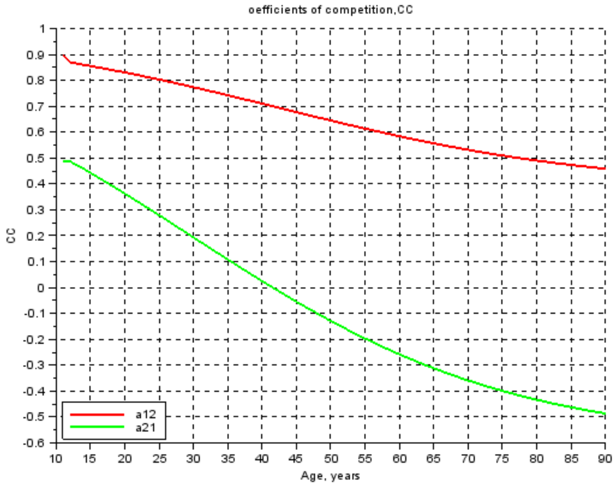

Figure 25.C. SEMS with Fsy+Pme, initially with 8000 trees of Fsy, and 2000 trees of Pme. Both mutualism, and asymmetric competition occur

The SEMS with *Fagus sylvatica*, and *Quercus robur*

Lu et al. (2016) analysed mixed stands with Fsy+Qro, with 18 years age. Let introduce the graphic of the rmr, and rgrt, of both species. Fsy is the dominant species.

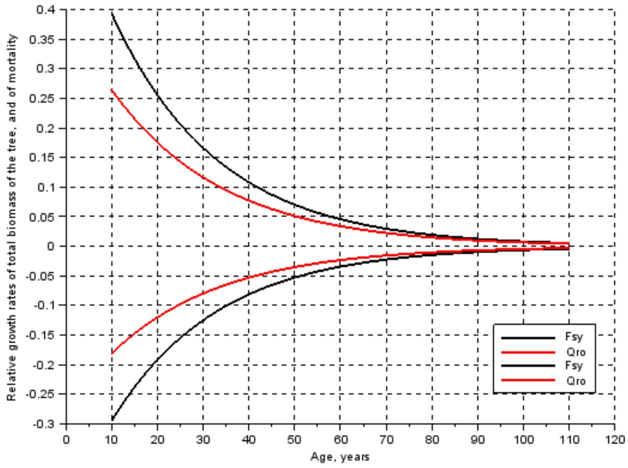

Figure 26. The dynamics of the rmr, and rgrt of Fsy, and Qro

In figures 27, and 28, I present the graphics of the emergence of OY, respectively, at ages 18, and 90 years.

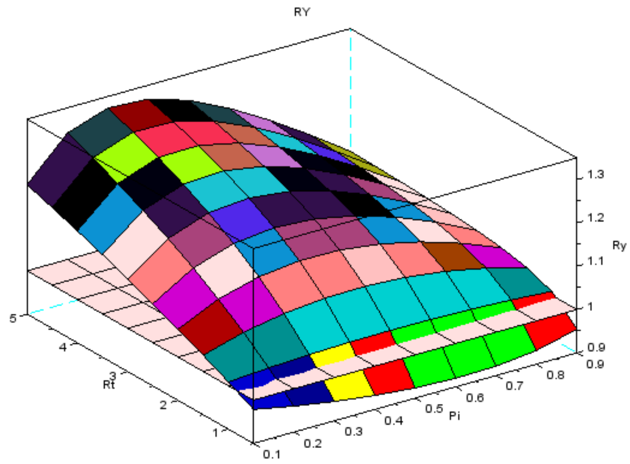

Figure 27. Simulated representation of the emergence of overyielding (RY>1) in mixed stands with Fsy, and Qro, at age 18 years

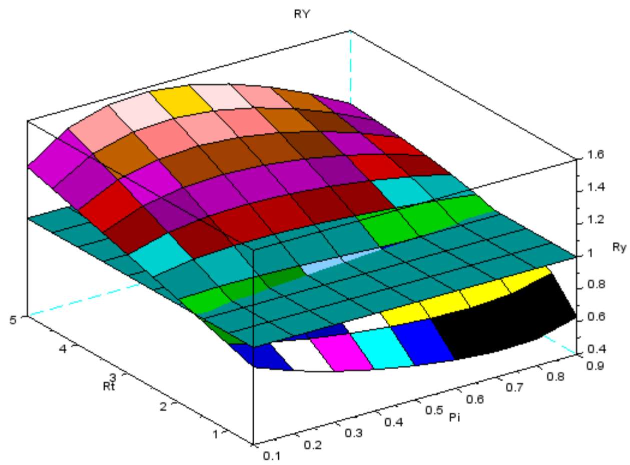

Figure 28. Simulated representation of the emergence of overyielding (RY>1) in mixed stands with Fsy, and Qro, at age 90 years

Lu et al. (2016) did not recognize significant OY in this mixture, and figure 27 admits this situation.

In figure 29, I present the coefficients of competition.

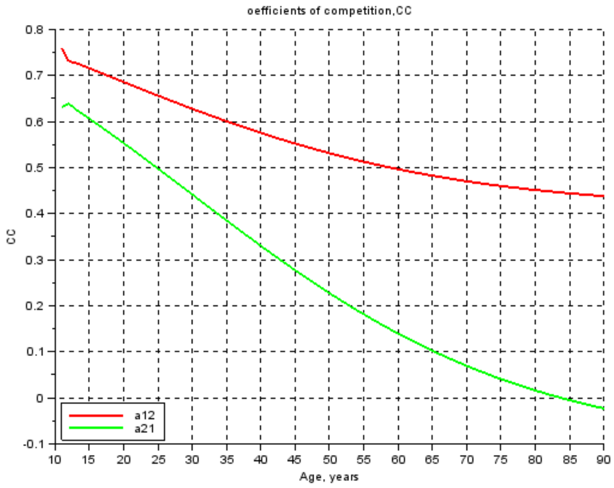

Figure 29.A. SEMS with Fsy+Qro, initially with 2000 trees of Fsy, and 8000 trees of Qro. Both mutualism, and asymmetric competition occur

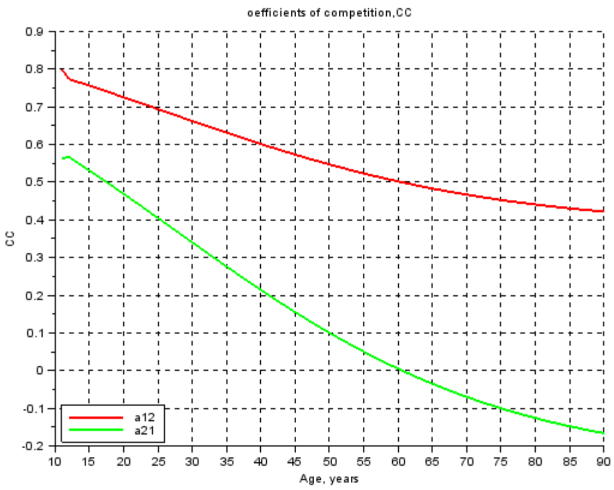

Figure 29.B. SEMS with Fsy+Qro, initially with 5000 trees of Fsy, and 5000 trees of Qro. Both mutualism, and asymmetric competition occur

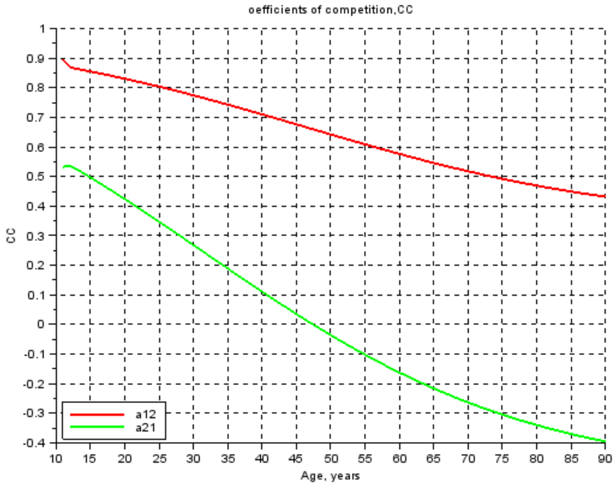

Figure 29.C. SEMS with Fsy+Qro, initially with 8000 trees of Fsy, and 2000 trees of Qro. Both mutualism, and asymmetric competition occur

The SEMS with *Quercus robur*, and *Betula pendula*

Lu et al. (2016) scrutinised mixed stands with Qro+Bpe, with 26 years age. In figure 30 I introduce the graphic of the rmr, and rgrt, of both species. Qro behaves as the dominant species, but there is a shift of dominance about age 65 years.

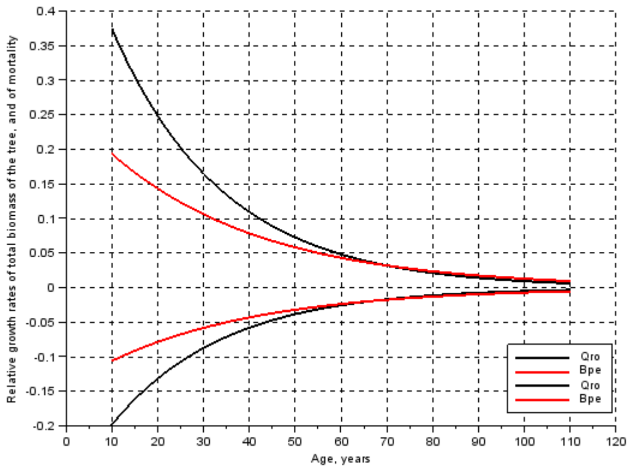

Figure 30. The dynamics of the rmr, and rgrt of Qro, and Bpe

In figures 31, and 32, I present the graphics of the emergence of OY, respectively, at ages 26, and 90 years.

Also, for this mixture, Lu et al. (2016) did not recognize significant OY, and figure 31 admits this situation.

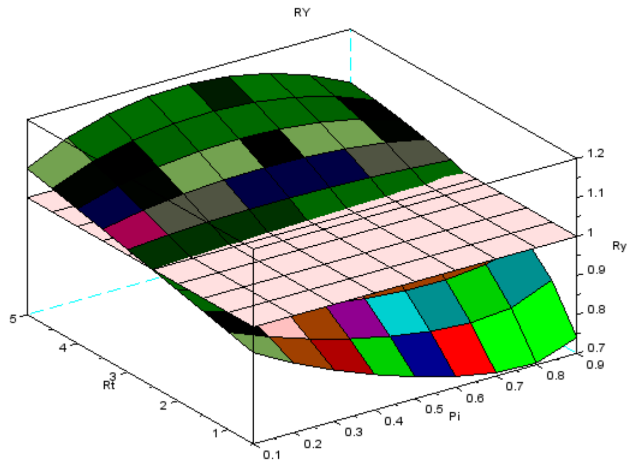

Figure 31. Simulated representation of the emergence of overyielding (RY>1) in mixed stands with Qro, and Bpe, at age 26 years

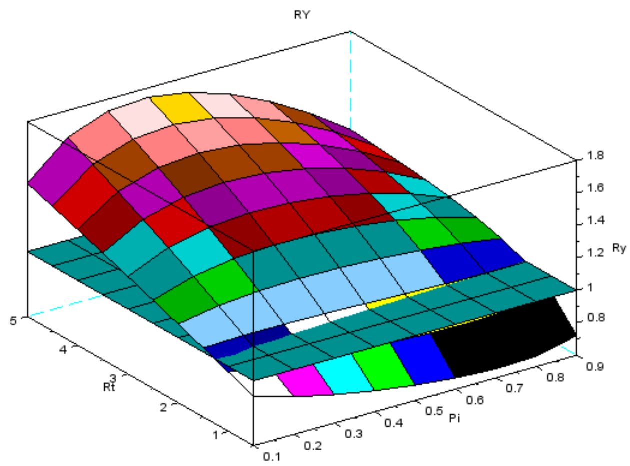

Figure 32. Simulated representation of the emergence of overyielding (RY>1) in mixed stands with Qro, and Bpe, at age 90 years

In figure 33, I display the coefficients of competition.

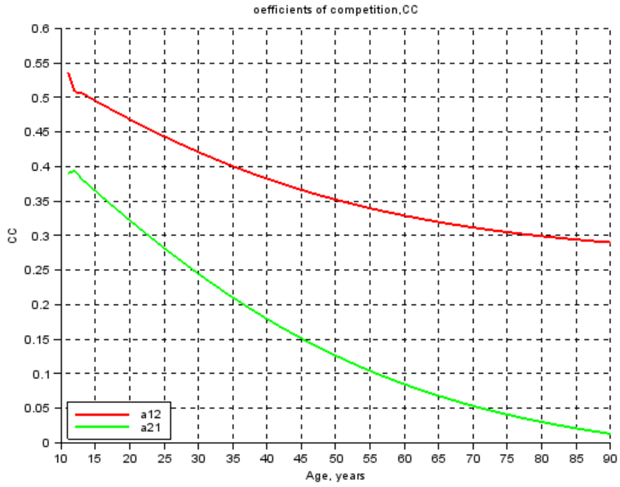

Figure 33.A. SEMS with Qro+Bpe, initially with 2000 trees of Qro, and 8000 trees of Bpe. Only mutualism occurs

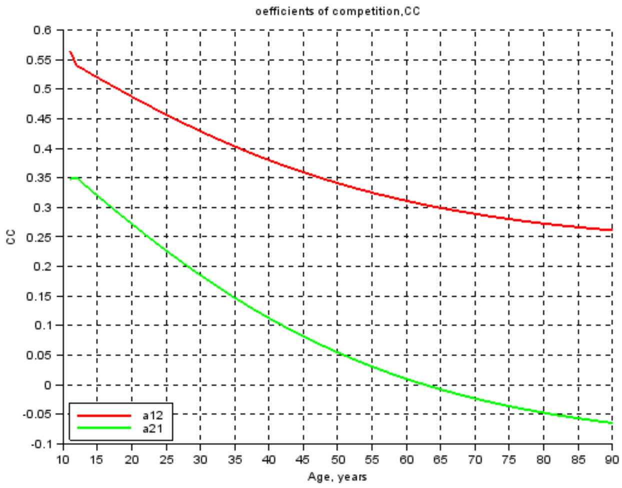

Figure 33.B. SEMS with Qro+Bpe, initially with 5000 trees of Qro, and 5000 trees of Bpe. Both mutualism, and asymmetric competition occur

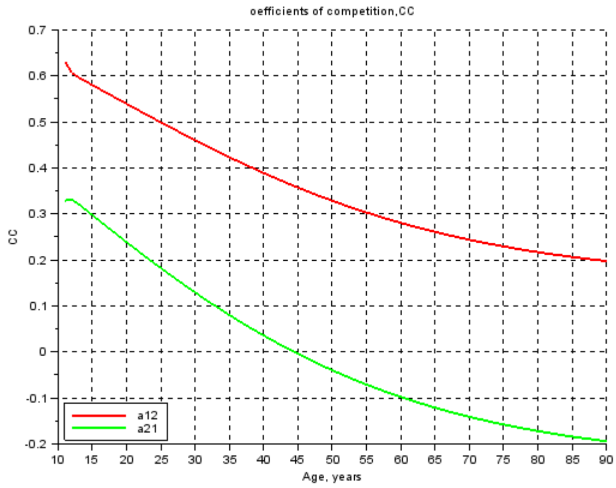

Figure 33.C. SEMS with Qro+Bpe, initially with 8000 trees of Qro, and 2000 trees of Bpe. Both mutualism, and asymmetric competition occur

Other mixed forests considered with interest in Europe are: Fsy+Psy, Fsy+Pab, Pab+ *Larix decidua, Pinus nigra*+Psy.

I already simulated the emergence of OY in the two mixed stand with North-American species Pme+*Alnus rubra*, Pme+ *Picea sitchensis* in Barreto (2011:figures 18.7, 18.8).

In the next four sections I will simulate the emergence of OY in the four European mixed stands upper mentioned.

The characterization of *Larix decidua*, and *Pinus nigra* is presented in table 4.

Table 4. Characterization of the species we now consider. c= coefficient of competition in the Gompertz equation; R_{-2}= (density at age 10)/(final density) in self-thinned even-aged pure stands; LHS=life-history strategy; GI= growth index; RI=regeneration index; SI=survival index; L=longevity, years.; A=acronym. See chapters 8, and 9 in Barreto (2010,2011) for the explanation of the concepts here used

Species	c	R_{-2}	LHS	GI	RI	SI	L	A
Pinus nigra ssp. laricio	0.051	81.44081	K-2	15.982	0.0002	0.99 97	450	Pni
Larix decidua	0.043	40.09828	K-1	22.014	0.0001	0.9999	300	Lde

The SEMS with *Fagus sylvatica*, and *Pinus sylvestris*

As usual I start by displaying the graphic with rmr, and the rgrt of Fsy, and Psy, in figure 34.

In figure 35, I present the graphics of the emergence of OY, at age 90 years.

In figure 36, I display the graphics with the coefficients of competition.

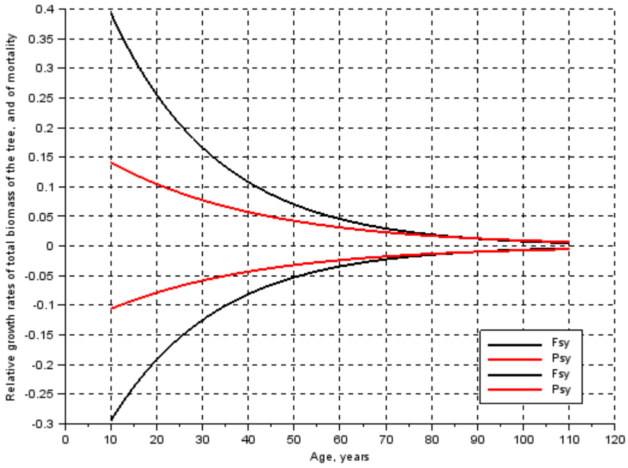

Figure 34. The dynamics of the rmr, and rgrt of Fsy, and Psy

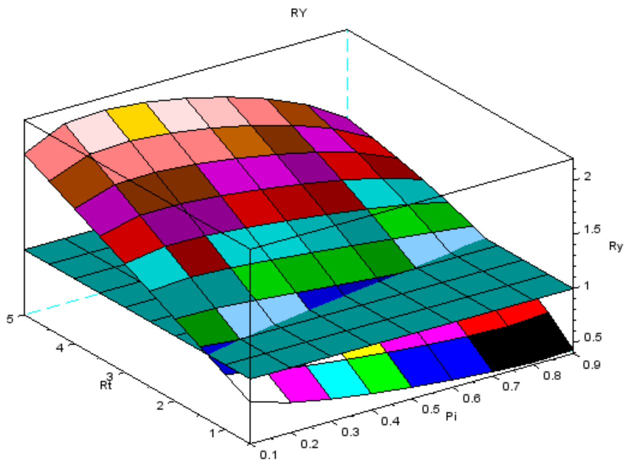

Figure 35. Simulated representation of the emergence of overyielding (RY>1) in mixed stands with Fsy, and Psy, at age 90 years

Figure 35 shows that the smaller is the proportion of Fsy (Pi), the smaller is the relative size of the tree of Fsy (Rt) required for the emergence of OY.

As usual, figure 36 shows that the higher is the initial proportion of the dominant species (Fsy) the shorter is the duration of mutualism.

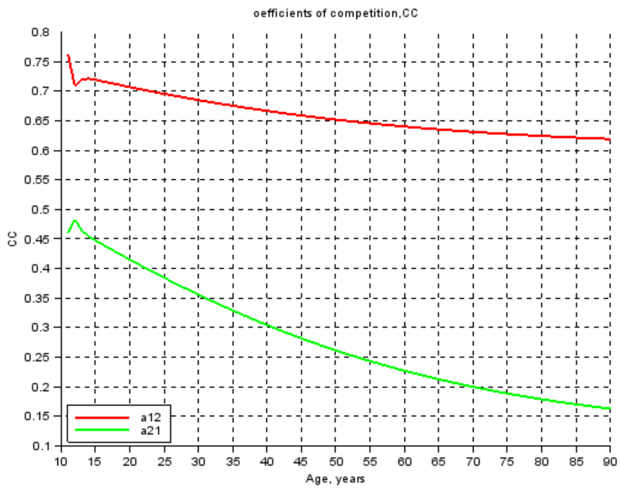

Figure 36.A. SEMS with Fsy+Psy, initially with 2000 trees of Fsy, and 8000 trees of Psy. Only mutualism occurs

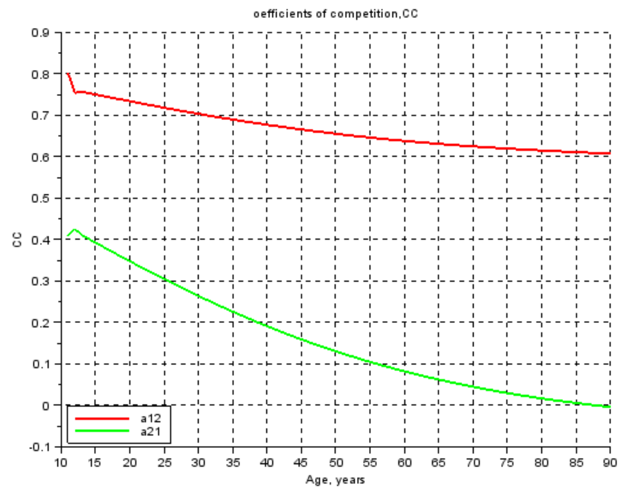

Figure 36.B. SEMS with Fsy+Psy, initially with 5000 trees of Fsy, and 5000 trees of Psy. Both mutualism, and asymmetric competition occur

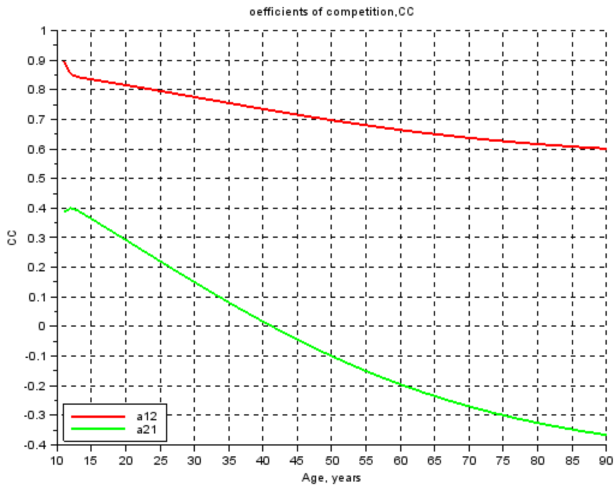

Figure 36.B. SEMS with Fsy+Psy, initially with 8000 trees of Fsy, and 2000 trees of Psy. Both mutualism, and asymmetric competition occur

The SEMS with *Fagus sylvatica*, and *Picea abies*

For the SEMS with Fsy+Pab, in figure 37, I display the graphic with rmr, and the rgrt.

I present the graphics of the emergence of OY, at age 90 years, in figure 38.

In figure 39, I display the graphics with the coefficients of competition. As both species have strong K strategies, in all three graphics both mutualism, and asymmetric competition occur. The greater is the initial proportion of Fsy, the shorter is th phase of mutualism, as expected.

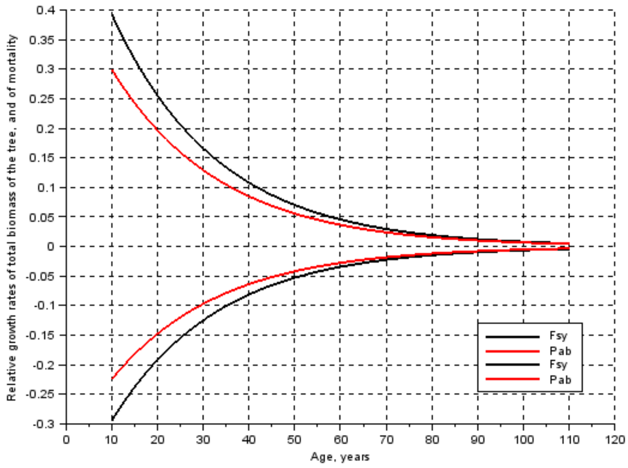

Figure 37. The dynamics of the rmr, and rgrt of Fsy, and Pab

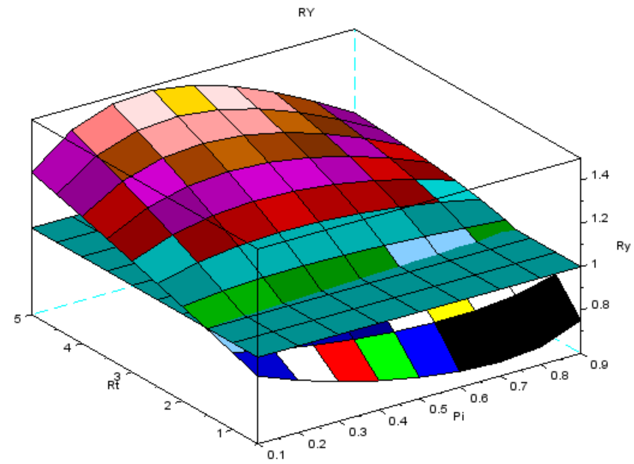

Figure 38. Simulated representation of the emergence of overyielding (RY>1) in mixed stands with Fsy, and Pab, at age 90 years

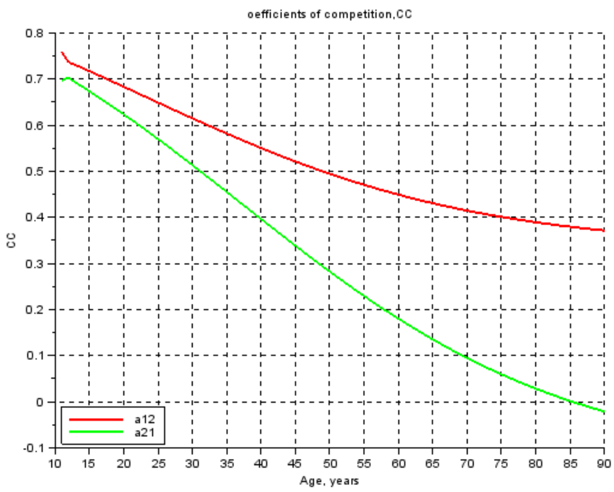

Figure 39.A. SEMS with Fsy+Psy, initially with 2000 trees of Fsy, and 8000 trees of Pab. Both mutualism, and asymmetric competition occur

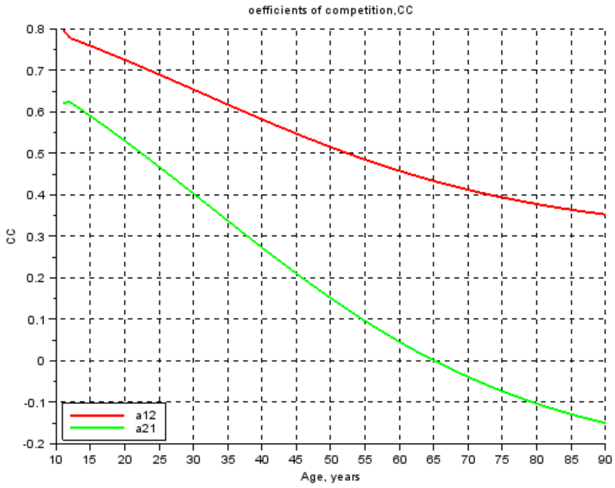

Figure 39.B. SEMS with Fsy+Psy, initially with 5000 trees of Fsy, and 5000 trees of Pab. Both mutualism, and asymmetric competition occur

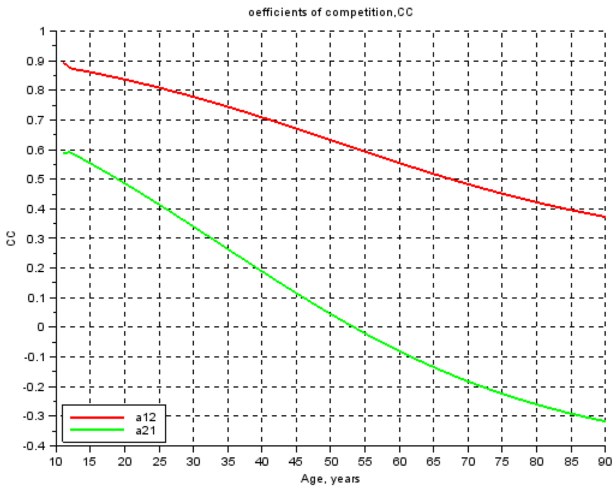

Figure 39.C. SEMS with Fsy+Psy, initially with 8000 trees of Fsy, and 2000 trees of Pab. Both mutualism, and asymmetric competition occur

The SEMS with *Pinus nigra*, and *Pinus sylvestris*

In figure 40, for the SEMS with Pni+Pab, I display the graphic with rmr, and the rgrt. At about age 45 a shift of dominance occurs.

In figure 41, I present the graphics of the emergence of OY, at age 90 years. The close bionomic strategy of the species, and the occurrence of a shift of dominance make the emergence of underyielding residual.

In figure 42, I display the graphics with the coefficients of competition. As both species are not strong K strategists, and a shift of dominance occurs, both mutualism, and asymmetric competition emerge only when the initial proportion of trees of Pni are 80%.

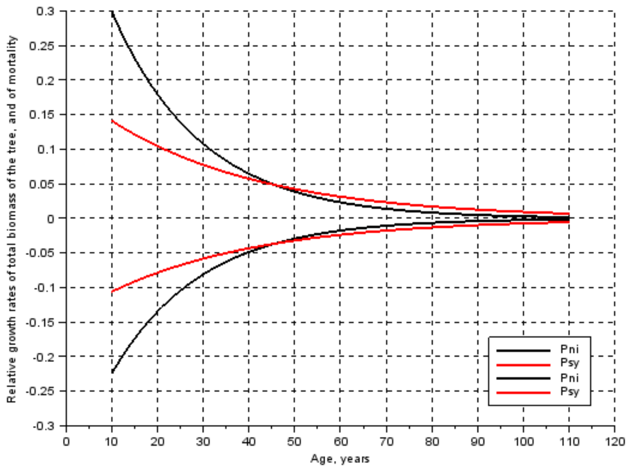

Figure 40. The dynamics of the rmr, and rgrt of Pni, and Psy. At about age 45 a shift of dominance occurs

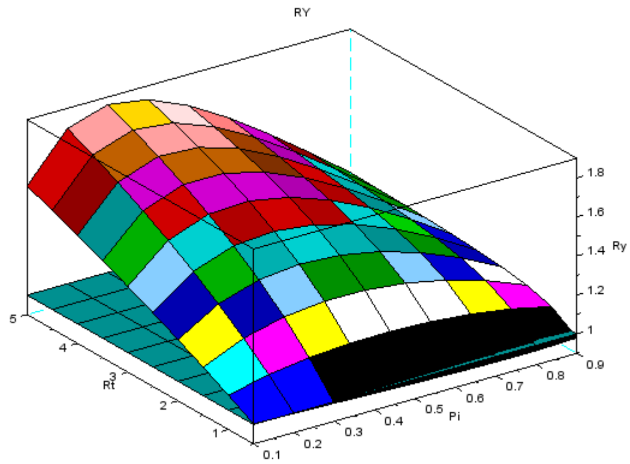

Figure 41. Simulated representation of the emergence of overyielding (RY>1) in mixed stands with Pni, and Psy, at age 90 years

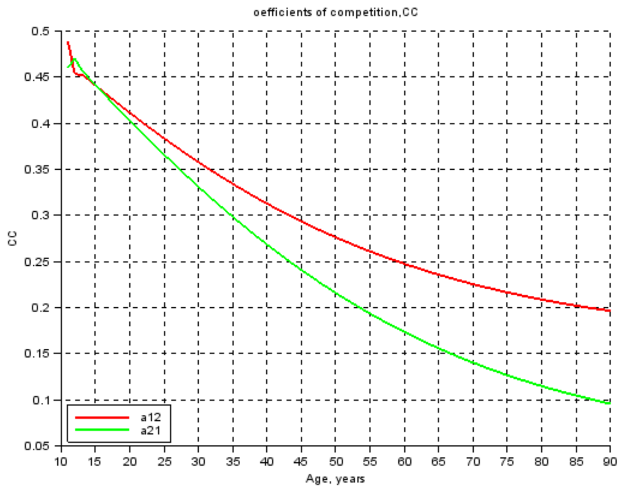

Figure 42.A. SEMS with Pni+Psy, initially with 2000 trees of Pni, and 8000 trees of Psy. Only mutualism occurs

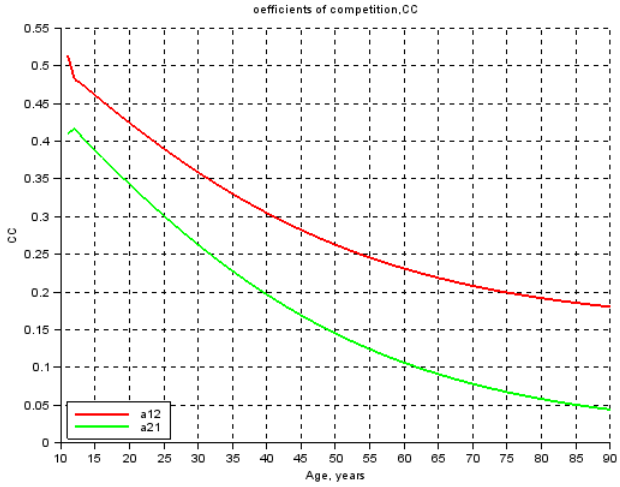

Figure 42.B. SEMS with Pni+Psy, initially with 5000 trees of Pni, and 5000 trees of Psy. Only mutualism occurs

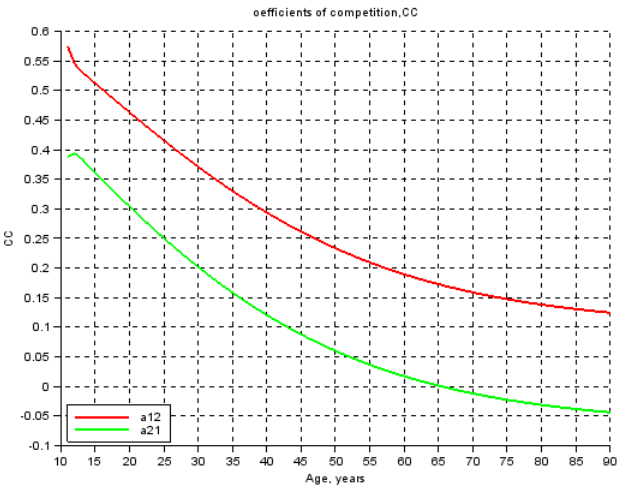

Figure 42.C. SEMS with Pni+Psy, initially with 8000 trees of Pni, and 2000 trees of Psy. Both mutualism, and asymmetric competition occur

The SEMS with *Picea abies*, and *Larix decidua*

In figure 43, for the SEMS with Pab+Lde, I display the graphic with rmr, and the rgrt.

In figure 44, I present the graphics of the emergence of OY, at age 90 years.

In figure 45, I display the graphics with the coefficients of competition. Pab is a K-2 strategist, and Lde is a K-1 strategist. This hierarchy in competitive ability causes the occurrence in all three graphics of both mutualism, and asymmetric competition occur. The greater is the initial proportion of Pab, the shorter is th phase of mutualism, as expected.

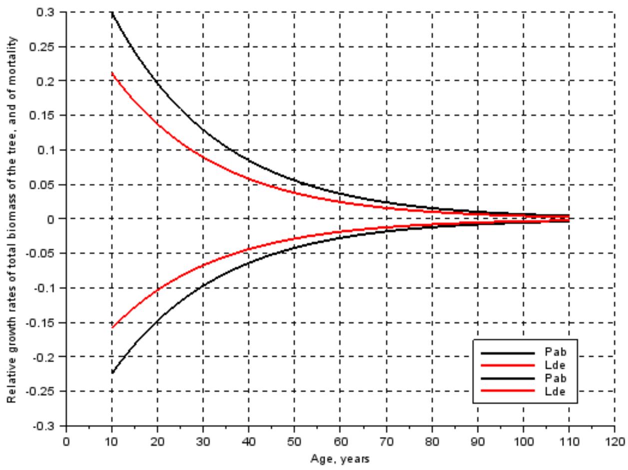

Figure 43. The dynamics of the rmr, and rgrt of Pab, and Lde

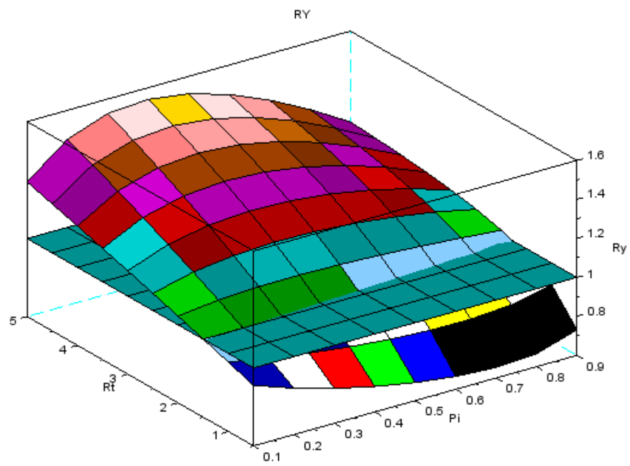

Figure 44. Simulated representation of the emergence of overyielding (RY>1) in mixed stands with Pab, and Lde, at age 90 years

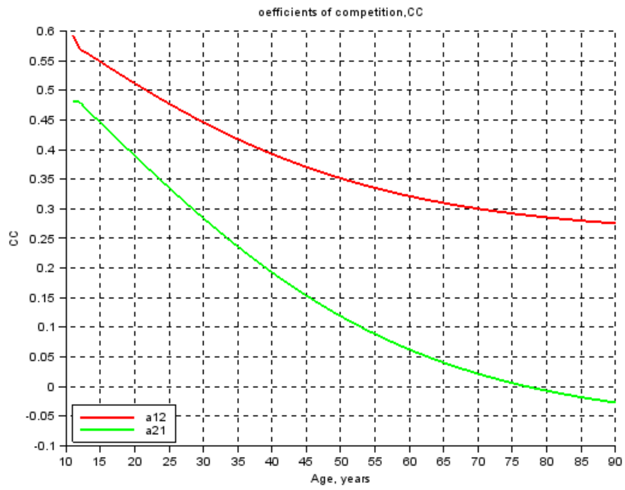

Figure 45.A. SEMS with Pab+Lde, initially with 2000 trees of Pab, and 8000 trees of Lde. Both mutualism, and asymmetric competition occur

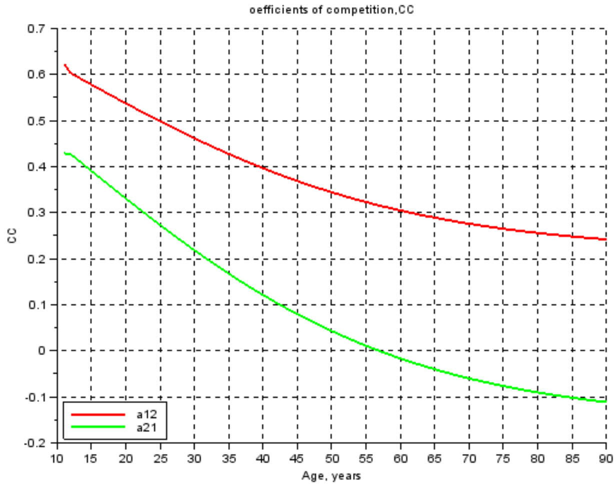

Figure 45.B. SEMS with Pab+Lde, initially with 5000 trees of Pab, and 5000 trees of Lde. Both mutualism, and asymmetric competition occur

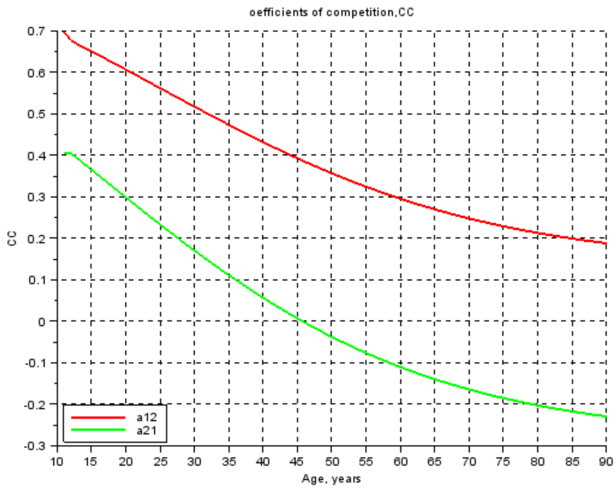

Figure 45.C. SEMS with Pab+Lde, initially with 8000 trees of Pab, and 2000 trees of Lde. Both mutualism, and asymmetric competition occur

Conclusive Remarks

The comparisons of the simulations of the emergence of OY, underpinned by my theory, and connected models, agree with the empirical results I used as paradigms. The only discrepancy occurred is related to the precocity of the emergence of OY, in stands of Fsy+Pme.

This achievement reinforces the truthfulness of my theory for the structure, and dynamics of forests.

I can understand how niche separation can contribute to the coexistence of species but I am not capable to conceive how niche separation can cause OY.

The harmonization of the shade tolerance of the species and their varying competitive dominances can occur in nature, as I showed in Barreto (2011: subsection 15.2.2).

The explanation for OY is rooted in the simultaneous occurrence of competitive dominance and greatest rgrt. This is a consequence of physical constraints on the relations between the physical space, and the forest variables. For more detail see figure 1.1, and related text in Barreto (2017).

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