Dynamics and development patterns of *Pinus sylvestris* L.- *Fagus sylvatica* L. stands in Central Rhodope

MILIOS, E.

Laboratory of Silviculture, School of Forestry & Natural Environment, Aristotle University of Thessaloniki, 540 06 Thessaloniki, Greece

Abstract

The study was conducted in second growth stands in the central Rhodope mountains and (specially) in the region of Xanthi. In order to determine the dynamics and the development patterns of *Pinus sylvestris-Fagus sylvatica* stands, 39 plots were established, trees were cut, increment cores were taken, and stem analysis was conducted in 4 couples of dominant (competitive) pine and beech trees. The main results of this research indicate that a) The population structures, the regeneration and development patterns are strongly influenced by human and natural disturbances and species 'life history characteristics'. b) The difference in site quality between site types results in differences in the duration of beech invasion (under pine) and in species basal area distribution. c) In good site qualities when individual dominant beech and Scots pine (competitive) trees with a small age difference grew together, the beech trees, in some cases, have almost the same height growth as the pines and the pine trees showed a delayed (for the species) culmination in current annual volume increment which is not followed by a abrupt fall. d) The process of secondary succession is influenced by disturbances regime, environment, propagule availability and species biology.

1. Introduction

The main characteristic of the natural communities is their dynamic nature. The continuous structural and functional change in forest ecosystems is defined as forest ecosystems dynamics (Dafis 1986). In particular, according to Oliver and Larson (1996), forest stand dynamics include stand behavior during and after disturbances.

The significance of natural dynamics in ecosystems has always been accepted, but ecologists focused on successional development of equilibrium communities (Pickett and White 1985). However disturbance and ecosystem behavior after disturbances are now recognized as natural processes that lay at the core of ecosystem dynamics (Perry and Amaranthus 1997). In forest stands, disturbances result in gap creation, releasing growing space and stimulating secondary succession. Since the early days of the scientific discipline of succession many theories and models have arisen (Connell and Slatyer 1977, Osawa 1992).

In the present study, the main **objectives** are: a) to determine the origin and what age, diameter and height structures occur in *Pinus sylvestris-Fagus sylvatica* stands at the various developmental stages in the central Rhodope mountains (region of Xanthi), in good and medium site qualities, b) to reconstruct growth rates of adjacent individual dominant *P. sylvestris* and *F. sylvatica* (competitive) trees in good site qualities, c) to examine the results in relation to the ecological theories of succession, and d) to use this information to suggest silvicultural alternatives for the management of these stands.

2. Study area

The study was carried out in second growth stands in the central Rhodope mountains and specially in the region of Xanthi which lies in North-east Greece, an area close to the Bulgarian border. Our stands are located at elevations from 1230 to 1500 m. The climate is humid with harsh winters, the yearly precipitation averages 980 mm, and the mean annual temperature is 8.0 °C. Geologically, the study area belongs to Rhodope massif, and the dominant rocks are gneiss, granodiorite, rhyolite and granite (Dimadis and Zachos 1986). The forest soils are acid brown forest soils (Dystric Cambisoils).

During the last few decades of the nineteenth century and the first decades of the twentieth century, many flocks of sheep, goats and horses were grazing in the area. In fact, shepherds used to burn large areas in autumn in order to have fresh grass in summer. During these decades people fled the area many times due to war and other events. The war events between 1910-1922 in particular, led all the local people to drive their flocks away from the area. Although after the first world war, many flocks came back, the second war events were the final strike for grazing in the area. Actually today only a small number of cows browse in the area (Souliaris 1969, Koutoulas 1990).
During the 1960s the first organized cuttings took place in the area by the forest service. Before that, only shepherds and people from the nearby villages cut (illegally) trees in the area.

3. Research method

In order to study the structures of the stands, 39 representative plots of 500 m^2 were established randomly in 8 developmental stages, found in the mixed stands. These plots were established in two site types. Site type A represents the good site qualities and site type B represents the medium site qualities (Milios 2000). For every sample plot the following data were recorded: a) diameter in cm, for trees with a diameter of over 4 cm (breast height), and b) height in meters. In each plot, increment cores for all species were taken (at a height of 1.3 m) in the main diameter classes.

Sixty dominant pine and twenty dominant beech trees were cut, according to the stratified random sampling method, from all the developmental stages. The age of each tree (in the stump height) was recorded using a cross sectional disc. Stem analysis was conducted in 4 couples of dominant (competitive) pine and beech trees in a stands developmental stage of site type A. Each, couple, consists of a dominant pine and an adjacent dominant beech tree. These trees were competitors, they had almost the same height and their crowns were touching each other. They were selected according to the stratified random sampling method. From each tree, cross-sectional discs were cut and removed from a 0.3 m level, breast height 3.30 level and at a 3 meter intervals up to the bole. The last disc was collected from the 5 cm-bole diameter. These discs were taken to the Forestry laboratory in order to measure the rings' width with the ADDO instrument (Smiris 1991, 1998). In stem analysis the mathematics formulas of Regent instruments in Xlstem V1.1 were used.

Analysis of Variance was conducted, with the data of two developmental stages (one of A and one of B site type), in order to investigate: a) the main effects of species and site types and b) the interaction of the above two factors on the basal area. The experiment design was considered as a two-factor complete randomized experiment with repeated measures of one factor. The plot of 500 m^2 was considered as an experimental unit. Design = 'Site type' x 'Species' mixed factorial or split - plot design. 'Species' is a split - plot on factor 'site type'. Simple main effects Analysis was performed in order to compare basal area between the two species in each site type (Gomez and Gomez 1984, Iversen and Norpoth 1987, Brown 1990, Girden 1992, Coakes and Steed 1999). Lastly a comparison of beech basal area percentages between two developmental stages (one of A and one of B site type) was made using the Mann - Whitney test (Matis 1989, Mehta and Patel 1996, Zar 1996).

4. Results

4.1 Developmental stages

Some stands and study area characteristics as the stands structure and development patterns, the age of trees (increment cores from trees in the main diameter classes and the age of dominant trees), the area which is occupied by each of the developmental stages, their distribution in the landscape and the history of the area (social-economic conditions, population removals and land use history) gave information about the origin of the different stages and the factors which cause the stands initiating disturbances.

4.1.1. Site type A

In this site type, three developmental stages were found.

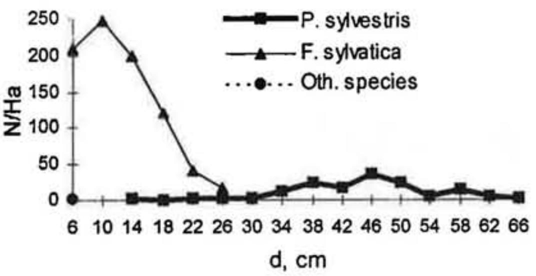
4.1.1.1. D. stage 1

In this stage 8 sample plots were established. The pine trees are 76-90 years old, except a few individuals which are younger, whereas the age of the beech trees is between 35-55 years.
This stage was initiated by stand destroying disturbances in which almost all trees were killed. The disturbances were intense and acted for a long period of time to kill even the seeds buried in the soil and extended in a relatively large area. Only a few suppressed sparsely scattered beech trees survived. At first, gaps were colonized by the 'early succession species' of *P. sylvestris*. Scots pine existed in the area as a pioneer species mainly in poor site qualities. The

'late succession species' of *F. sylvatica* appeared later, after 30-40 years (the seeds come from the suppressed survivors). The duration of beech invasion was about 20 years (in all sample plots of this stage). The few younger pines which have smaller dimensions than the others were established in gaps created later by small disturbances (windfall or the death of a few trees or cuttings).

The initiation of this stage coincides with the period of time between 1910-1922 in which the war events led all the local people to drive their flocks away from the area. This fact in relation with the large area that is covered by this stage, the age of beech and the existence of only a few beech survivors leads us to the conclusion that grazing was the agent which caused the disturbance.

The bole distribution in diameter classes is given in figure 1. Even though the beech trees are almost evenly aged, we observe a fall in diameter distribution. The pine diameter distribution shows a normal distribution with a maximum massing in the 46 diameter class. The mean stage statistics are presented in table 1.
The tree height distribution in height classes (see fig. 1) shows a two storey stand. The upper storey (26-30m) consists of pine and the lower storey consists of beech.
New seedlings of beech and fir (*Abies borisii-regis*) appear today in the growing space which is released by the death or the cutting of an overstorey or midlestorey tree.



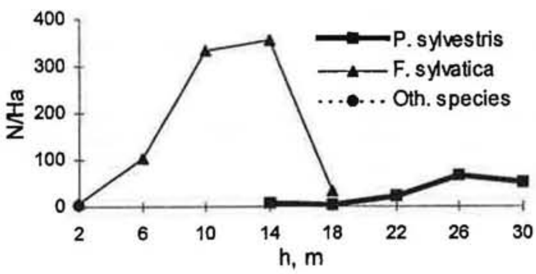


Figure 1. *Structure analysis graph of diameter and height classes of stage 1 in site type A.*

Table 1. *Mean stand statistics for stage 1 in site type A*

	Mean DBH (cm)	Mean height (m)	B. A. (m^2/ha)
P. sylvestris	44.13	25.72	24.47
F. sylvatica	11.54	11.16	10.27

4.1.1.2. D. stage 2

In this stage 7 sample plots were established. The pine trees are 76-95 years old. Beech is unevenly aged, although the older beech trees are 70-90 years old.
This stage was initiated by disturbances which destroyed all the trees. The disturbances were not so severe and did not last for a long period to destroy the forest floor and to kill the

dispersed and recently buried seeds. The disturbed area was smaller than the area in stage one.

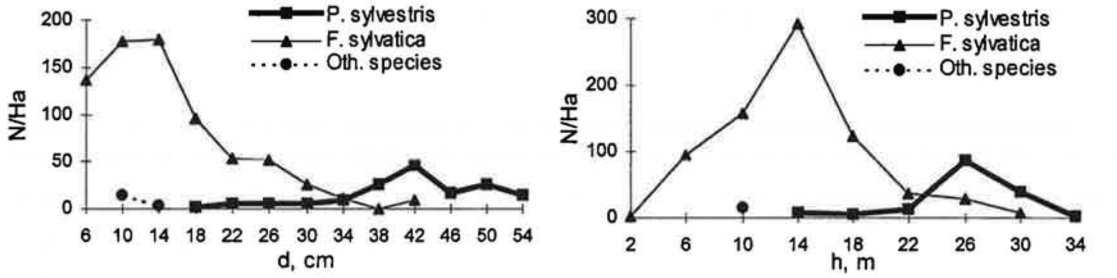


Figure 2. *Structure analysis graph of diameter and height classes of stage 2 in site type A.*

In this case the gap was invaded by a few beech trees which originated from newly dispersed and recently buried seeds but mostly by pine trees whose seeds had arrived (mainly) from distant mature trees. These few beech trees were not able to occupy all the available (for beech) growing space, so the duration of beech invasion was long.

Despite the fact that this stage was initiated in the same period with the previous one, there are many differences. The invasion pattern of beech trees in relation to the smaller from stage 1 area which is covered by these stands and their scattered distribution in the landscape, suggest that these stands originated from disturbances different from stage 1, probably illegal cuttings or windfall, or a combination of both.

Table 2. *Mean stand statistics for stage 2 in site type A*

	Mean DBH (cm)	Mean height (m)	B. A. (m^2/ha)
P. sylvestris	40.93	25.64	21.51
F. sylvatica	14.15	13.59	14.88

Figure 2 presents the bole distribution in diameter classes (see table 2 for the mean stage statistics). The beech diameter distribution is analogous to the beech trees age structure. The older trees are in the larger classes, whereas the younger trees are located in the smaller classes. The pine diameter distribution, though, shows an almost normal distribution, with a maximum massing in the 42 cm diameter class. The tree height distribution (see fig 2) shows a stand with two main storeys although there are a number of trees in all height classes. The upper storey (26-30 m) consists of some beech but mainly of pine trees while the lower storey consists of beech and few pine trees.

4.1.1.3. D. stage 3

In this stage 5 sample plots were established. The pine trees are 89-123 years old. The beech trees belong to two age groups. In the main group, trees are 85-107 years old although some trees are a few years older. In the second group, trees are 20-40 years old.

According to our data, this stage was initiated by disturbances which were not so intense and did not affect a large area. The duration of the disturbances was not long either, but they destroyed all the trees (except for some suppressed beech juveniles) in an area of 600 to 1500 m^2. The main characteristic of these gaps is that they were surrounded by groups of adult beech trees (today some of these trees are over 150 years old).

There was an almost parallel invasion of beech and pine trees. In many cases, the pine trees preceeded the beech trees for 5-15 years. The area was refilled a) by pine individuals growing from propagules which arrived (mainly) from distant seed trees, b) by beech individuals which originated from recently buried seeds, or from seeds of surrounding adults, and c) by growth of surviving beech juveniles. The pine and beech trees occupied all available growing space. The new beech trees (the younger age group) were established in the last 30-35 years in the growing space that was created by the cuttings.

The stands of this stage are sparsely scattered in the area. The difference between this stage and stage 2 invasion pattern of beech and the consequent different development pattern of these stands is the result of the different size of the gaps which were created by the same, as we assume, disturbances (illegal cuttings or windfall, or a combination of both) that were not so severe as in the case of the stage 2, and acted in a smaller area.

Today, the overstorey consists of pine and mainly beech trees. Beech dominates in the midlestorey and understorey. In this case the beech trees show different patterns in diameter distribution and age structure. As we mentioned earlier, age structure has a discontinuous pattern.

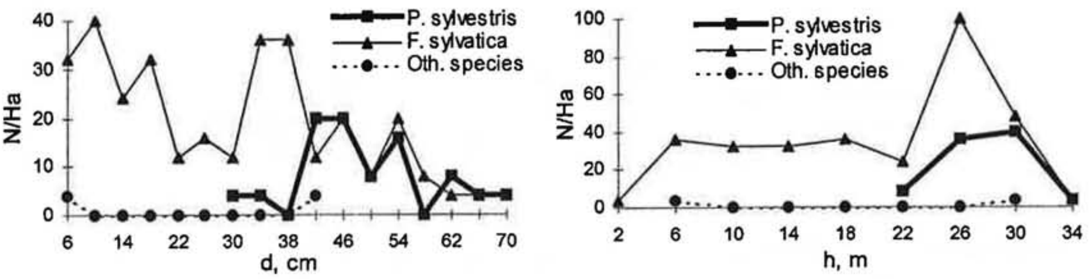


Figure 3. *Structure analysis graph of diameter and height classes of stage 3 in site type A.*

Table 3. *Mean stand statistics for stage 3 in site type A*

	Mean DBH (cm)	Mean height (m)	B. A. (m^2/ha)
P. sylvestris	48.64	27.75	17.00
F. sylvatica	28.08	19.80	26.38

The continuous pattern of diameter distribution (see fig. 3) was affected by growth differences among trees in each age group (see table 3 for the mean stage statistics). The pine diameter distribution shows an almost normal distribution. The tree height distribution shows a one storey stand (26-30 m) which consists of both pine but mainly of beech trees. New seedlings of beech and fir (*Abies borisii-regis*) appear today in the growing space which is released by the death or the cutting of an overstorey tree. A few pine seedlings have also been established in large openings.

4.1.2. Site type B

In this site type, three main developmental stages and two substages were found. These two substages followed almost analogous development patterns with two of the main stages. The difference is that they were initiated several decades later by the same kind of disturbances.

4.1.2.1. D. stage 1

In this stage 4 sample plots were established. The pine trees are 105-125 years old, except a few individuals which are younger. The age of the beech trees is between 45-75 years.
This stage was initiated by disturbances which had the same characteristics as in stage 1 of A site type. In this case, the duration of beech invasion was about thirty years (in all sample plots of this stage). The few younger pines which have smaller dimensions than the others were established in gaps created later by small disturbances (windfall or death of a few trees or cuttings).
The mean stage statistics are presented in table 4 and the bole distribution in diameter classes is given in figure 4. In beech, we observe a exponential distribution, but the pine has an almost bell shaped distribution. The tree height distribution (see fig. 4) shows a two storey stand. The upper storey (22-26 m) consists of pines and the lower storey of beech.

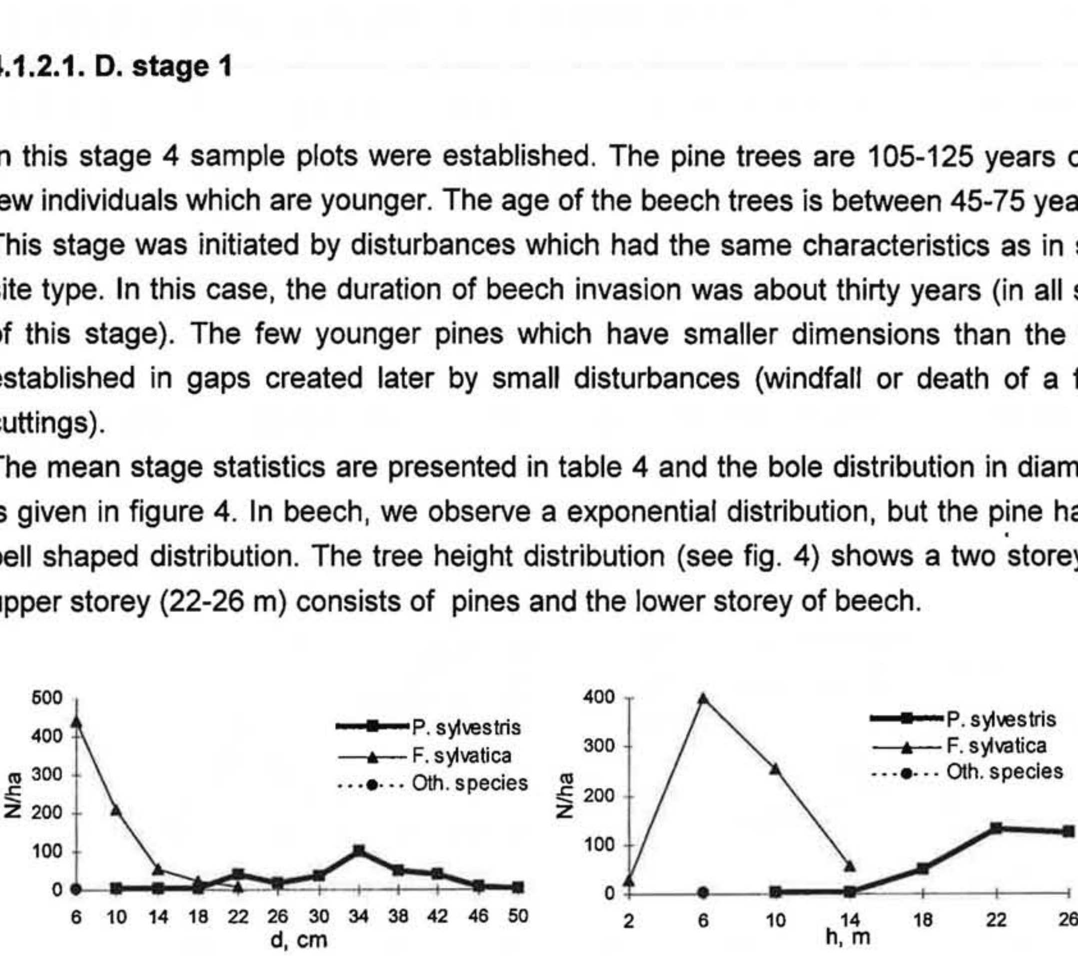


Figure 4. *Structure analysis graph of diameter and height classes of stage 1 in site type B.*

Table 4. *Mean stand statistics for stage 1 in site type B*

	Mean DBH (cm)	Mean height (m)	B. A. (m^2/ha)
P. sylvestris	32.30	22.28	27.34
F. sylvatica	7.77	7.62	4.25

4.1.2.2. D. stage 1a

In this stage 2 sample plots were established. The pine trees are 49-63 years old, except for some individuals which are younger. The age of the beech trees (with a diameter of over 4 cm) is between 25-33 years.

This stage was initiated by the same kind of disturbances as in stage 1 which acted some decades later. Its main characteristic is that even today beech continues to invade under pine canopy in order to occupy all the available growing space.

The initiation of this stage coincides with the second war events that led all the remaining local people to drive their flocks away from the area. The total disturbed (by grazing) area was smaller than in the previous cases due to the fact that the flocks were fewer than in the past.

The bole distribution in diameter classes is given in figure 1. The beech trees appear only in the 6 cm diameter class. The pine diameter distribution has a maximum massing in the 26 cm diameter class, the younger pines, that were established in the gaps created later by small disturbances (windfall or the death of a few trees or cuttings), appear in the small diameter classes. The mean stage statistics are presented in table 5.

The tree height distribution in height classes (see fig. 1) shows a two storey stand. The upper storey (18-22m) consists of pine and the lower storey consists mainly of beech and partly of younger or damaged, by various agents (wind, cuttings), pines.

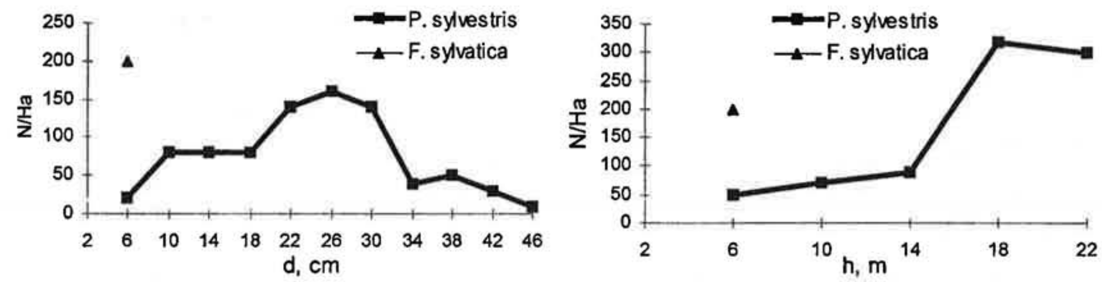


Figure 5. *Structure analysis graph of diameter and height classes of stage 1a in site type B.*

Table 5. *Mean stand statistics for stage 1a in site type B*

	Mean DBH (cm)	Mean height (m)	B. A. (m^2/ha)
P. sylvestris	23.46	17.54	41.15
F. sylvatica	4.90	4.95	0.39

Even thought these stands originated from disturbances which had the same characteristics as in stage 1 of the same site type, there is a differentiation in the development process, in the last 30-35 years, as a result of the cuttings that took place when the age of the stands was much smaller than in stage 1.

4.1.2.3. D. stage 2

In this stage 6 sample plots were established. The pine trees are 100-120 years old, except for a few individuals which are younger. Beech is unevenly aged. The older beech trees are 85-110 years old although several trees are a few years older.

This stage was initiated by disturbances which had almost the same characteristics as in stage 2 of site type A. The main difference is that in this case, some suppressed beech juveniles survived the disturbances.

In the beech trees diameter distribution (see fig. 6), we observe an exponential distribution which is analogous to the trees age structure. The older trees are in the larger diameter classes, and the younger trees are located in the smaller classes. Pine has an almost bell shaped distribution, in the small diameter classes appear the few younger individuals which were established in gaps created later by small disturbances. The diameter differences between the trees in the other diameter classes are the result of growth differences among trees in the same age group. Although there are a number of trees in all height classes the tree height distribution (see fig. 6) shows a stand with two main storeys. The upper storey (22-26 m) consists of beech and mainly of pine trees and the lower storey consists mainly of beech trees and partly of a few (younger than the others) pine trees. The mean stage statistics are presented in table 6.

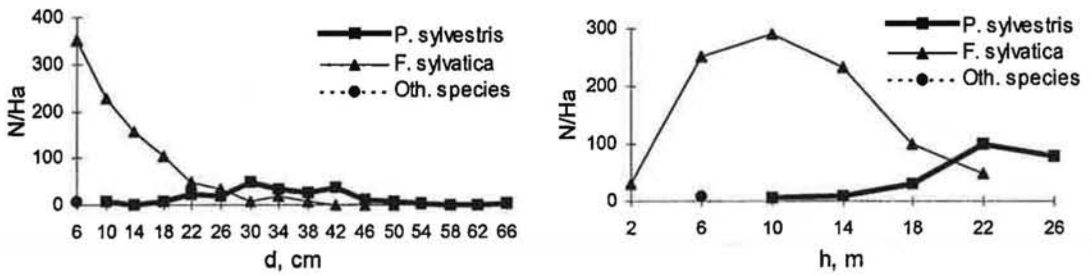


Figure 6. *Structure analysis graph of diameter and height classes of stage 2 in site type B.*

Table 6. *Mean stand statistics for stage 2 in site type B*

	Mean DBH (cm)	Mean height (m)	B. A. (m^2/ha)
P. sylvestris	33.29	21.94	21.51
F. sylvatica	11.42	10.81	13.72

4.1.2.4. D. stage 3

In this stage 5 sample plots were established. The pine trees are about 120 years old, except for a few individuals which are younger. The beech trees belong to two age groups. In the main group, the trees are 83-112 years old, but some trees are a few years older. In the second group, the trees are 25-40 years old.

This stage was initiated by disturbances which had the same characteristics as in stage 3 of site type A.

The beech trees, as in stage 3 of site type A, show different patterns in diameter distribution and age structure. In this stage there is a significant larger number of young trees, with small dimensions (diameter and height), than in stage 3 of site type A (see fig. 3, 7). The pine diameter distribution shows an almost normal distribution (see fig. 7), in the small diameter classes appear the few younger individuals which were established in gaps created later by small disturbances. The diameter differences between the trees in the other diameter classes are the result of growth differences among trees in the same age group. The tree height distribution shows a multistorey stand. The upper storeys consist of pine and beech trees and the lower storeys are dominated by beech, there are also few (younger than the others) pine trees. The mean stage statistics are presented in table 7.

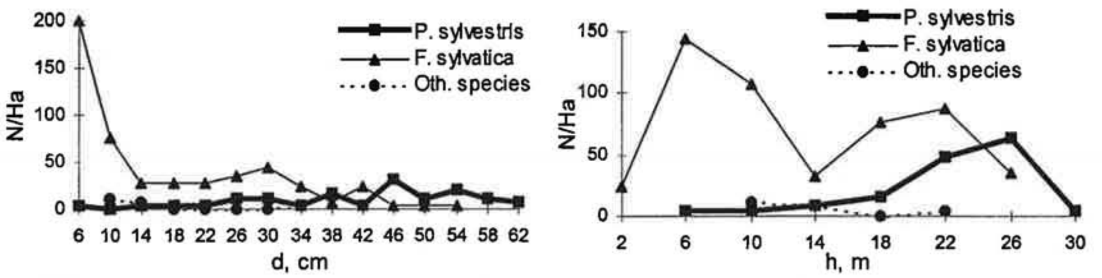


Figure 7. *Structure analysis graph of diameter and height classes of stage 3 in site type B.*

Table 7. *Mean stand statistics for stage 3 in site type B*

	Mean DBH (cm)	Mean height (m)	B. A. (m^2/ha)
P. sylvestris	41.43	22.38	22.15
F. sylvatica	15.84	12.90	16.09

4.1.2.5. D. stage 3a

In this stage 2 sample plots were established. The pine trees are 59-76 years old. The age of the beech trees is between 40-73 years, though there are some aged trees (a few years older). This stage was initiated by the same kind of disturbances as in stage 3 which acted some decades later. The difference in this case is that the trees in the stands of this stage were significantly younger than the trees in stage 1 when the cuttings began. As a result there is one age group of beech trees with a diameter of over 4 cm.

The mean stage statistics are presented in table 8 and the bole distribution in diameter classes is given in figure 8. The beech diameter distribution has a maximum massing in the 14 cm diameter class. The diameter differences are the result of growth differences and the small age difference among trees. The pine trees, also, show a considerable diameter differentiation due to growth differences among trees. The tree height distribution (see fig. 8) shows an almost multistorey stand. The upper storeys consist of pine and a few beech trees and the lower storeys are dominated by beech.

Table 8. *Mean stand statistics for stage 3a in site type B*

	Mean DBH (cm)	Mean height (m)	B. A. (m^2/ha)
P. sylvestris	27.16	18.95	20.18
F. sylvatica	12.47	10.62	10.49

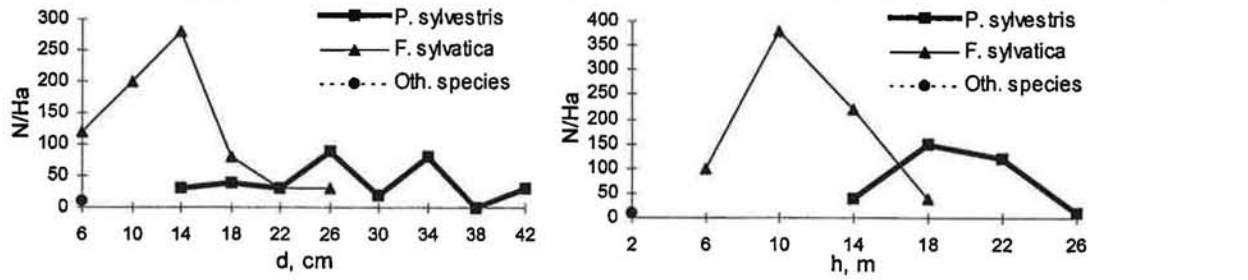


Figure 8. *Structure analysis graph of diameter and height classes of stage 3a in site type B.*

4.2. Basal area distribution

In mixed stands, the basal area of the different species is one of the stand features which shows the dominant degree of each species. Basal area is affected by several factors such as species ecology, ecology of the other constituent species, site type etc. In this study, with the basal area data of the developmental stages 3 in the two site types, we try to investigate a) the main effects of species and site types and b) the interaction of the above two factors on the basal area using the 'Site type' x 'Species' mixed factorial or split - plot design. 'Species' is a split - plot on factor 'site type'. We use these two stages due to the fact that we measured the same number of sample plots in each stage, the ages of the two species are about the same and the influence of the other factors (size and shape of the initial gaps, vicinity of seed trees, survivors from the disturbance trees etc.) which affect the basal area distribution was considered the same

Even though there were many similarities in the initiation and development processes between the developmental stages 1 in the two site types we compare only the beech basal area percentages between them because of the different number of sample plots which were established and the age differences between species in the two stages. Lastly we did not investigate any basal area differences between the developmental stages 2 in the two site types due to the different number of sample plots that was measured, the age differences between species in the two stages and mainly because of the slight differentiation's in the stages initiation process, which are substantial for the species basal area distribution (e.g. in stage 2 of site type B there were some suppressed beech juveniles which had survived the disturbance).
The Analysis of Variance, using the basal area data (see table 9) of the developmental stages 3 in the two site types (see table 10a, 10b), showed that a) the factor 'site type' does not affect basal area ($F=1.159$, $p=0.313$) b) the factor 'species' does not affect basal area ($F=0.645$, $p=0.445$) and c) there is a statistically significant interaction between the factors 'site type' and 'species' ($F=14.716$, $p=0.005$, eta squared=0.648, Observed Power=0.917).
As for the comparisons between the means of basal area of beech and pine (see table 9, 10c, 10d), the analysis shows that a) for site type A, there is a statistically significant difference between beech and pine mean basal area, beech has a larger mean basal area than pine ($F=10.760$, $p=0.011$, eta squared=0.574, Observed Power=0.819) and b) there is no statistically significant difference between beech and pine basal area for site type B ($F=4.600$, $p=0.064$). Although no statistically significant difference was detected at $a=0.05$ (the difference is significant at $a=0.10$), from a practical point of view the difference is considered substantial.

Table 9. *The basal area data of the developmental stages 3 in the two site types*

	Basal area m^2							
	plot	1	2	3	4	5	mean	S. D.
S. type A	Beech	1.04	1.49	1.45	1.60	1	1.32	0.28
	Pine	0.85	1.1	0.9	0.52	0.88	0.85	0.21
S. type B	Beech	0.65	0.98	1.01	0.78	0.59	0.80	0.19
	Pine	1.3	1.3	1.37	0.81	0.76	1.11	0.3

Using the Mann-Whitney test, the comparison of beech basal area percentages between stage 1 of site type A and stage 1 of site type B (see table 11, 12) shows that there is a statistically significant difference between the distribution of basal area in the two types ($Z=-2.386$, $p=0.013$). This p-value is computed with the Monte Carlo simulation method and is based on 10,000 random samples. The percentage of beech basal area of the total stands basal area in site type A is greater than in site B.

Table 10. *Analysis of basal area data with regards to the developmental stages 3 in the two site types*

a) *Pooled Analysis of Variance for Two-Factor Experiment with Repeated Measures of One Factor Design = Site Type x (Species) Mixed Factorial or Split-Plot Design*

Source of Variation	df	Sum of Squares	Mean quare	F	Sig
Site Type	1	0.0416	0.0416	1.159	0.313
Error a	8	0.287	0.0359		
Species	1	0.033	0.033	0.645	0.445
Site Type × Species	1	0.75	0.75	14.716	0.005*
Error b	8	0.407	0.051		

b) *Statistical Power and Effect Size of Hypothesis Testing*

Source of Variation	Partial Effect Size Eta Squared	Observed Power[c]
Site Type	0.127	0.158
Error a		
Species	0.075	0.110
Site Type × Species	0.648	0.917
Error b		

c Computed using alpha = 0.05

c) *Simple Main Effects Analysis*

Site Type		Value	F	df	Error df	Sig.
A	Pillai's trace	0.574	10.760	1	8	0.011
	Wilks' lambda	0.426	10.760	1	8	0.011
B	Pillai's trace	0.365	4.600	1	8	0.064
	Wilks' lambda	0.635	4.600	1	8	0.064
	Wilks' lambda	0.635	4.600	1	8	0.064

d) Statistical Power and Effect Size of Hypothesis Testing

Site Type		Eta Squared	Observed Power[d]
A	Pillai's trace	0.574	0.819
	Wilks' lambda	0.574	0.819
B	Pillai's trace	0.365	0.471
	Wilks' lambda	0.365	0.471

d Computed using alpha = 0.05

Table 11. *The percentages of beech basal area of the developmental stages 1 in the two site types*

		Basal area percentage %								
	plot	1	2	3	4	5	6	7	8	mean %
Site type A	Beech	36	36	26 .	34	1 3	38	28	34	30.63
Site type B	Beech	12	21	20	4	-	-	-	-	14.25

Table 12. *Mann-Whitney Test for comparing the distributions of percentages of beech basal area of the developmental stages 1 in the two site types*

a) Ranks

SITE	N	Mean Rank	Sum of Ranks
A	8	8.25	66.00
B	4	3.00	12.00
Total	12		

a) Test Statistics

Mann-Whitney U				2.000
Wilcoxon W				12.000
Z				-2.386
Monte Carlo Sig. (2-tailed)	Sig.			0.013
	99% interval	Confidence	Lower Bound	0.010
			Upper Bound	0.016

4.3. Stem analysis

Today the beech and pine trees in the four competing couples (from stage 3 in site type A) have almost similar heights (see fig. 9). The pine trees are taller than the beech trees except in couple 1. In this case, the two trees are older than the trees of the other couples (see table 13). We observe that the beech trees in all the couples have a higher periodic annual height increment than the pines in the last (at least) 15 years, due to their younger, in most cases, age and to their growth ecology (see fig. 9). Pine is a pioneer species which has an early culmination in height increment. On the contrary, beech is a shade tolerant species that shows a more sustained height increment. After some decades, the beech trees in almost all the couples will be taller than the pines.

Table 13. *The ages, heights and volumes of trees in the four competing couples*

	Pine				Beech			
	Age (years)	Height (m)	Volume (m^3)	(dm^3)	Age (years)	Height (m)	Volume (m^3)	(dm^3)
Couple 1	122	28.26	2.00	1999	106	29.35	1.38	1379
Couple 2	114	31.50	2.21	2210	100	29.96	2.59	2591
Couple 3	87	31.89	1.46	1457	101	27.63	1.42	1422
Couple 4	88	30.62	2.54	2536	84	28.03	1.55	1548

In the third couple, the beech tree is older than the pine, probably because it was a suppressed survivor from the disturbance. As we observe, after the gap creation, when the pine tree was established, the beech tree showed high periodic annual height increment due to released growing space.
As far as the volume is concerned, today, in two couples the beech trees has a similar or greater volume than the pine trees (see table 13, fig. 10). In the other two couples the pine trees has a significantly higher volume than the beech trees. However in all couples, the beech trees show a more delayed culmination in current annual volume increment than the pine trees (see fig. 10) due to their species' growth ecology.

The pine trees in some cases showed a delayed (for the species) culmination in current annual volume increment which is not followed by a abrupt fall. On the contrary afterwards they have a more or less sustained current annual volume increment.

5. Discussion

The different developmental stages of *P. sylvestris-F. sylvatica* stands originated from different kind of disturbances. The population structures, the regeneration and development patterns are strongly influenced by human and natural disturbances and species 'life history characteristics'. Similar processes have been mentioned elsewhere. Stewart (1986) describes how disturbance features and species' life history characteristics affect population structures and regeneration patterns in a montane conifer forest, and Smiris (1995) mentions that *Quercus sp.-Pinus nigra* mixed stands in Olympus undergo disturbances by heavy grazing which favour the invasion of P. nigra. According to Fajvan and Seymour (1993), in *Picea ruben-Tsuga canadensis-Pinus strobus* mixed stands, spatial and temporal variability in disturbances result in a complex stand development pattern.
Furthermore differences in the sizes of gaps result in differences in species composition (Connell and Slatyer 1977, Whitemore 1989), stands structure and development patterns. Large gaps were colonized by pines whereas beech trees appeared later (stage 1 site type A, stages 1, 1a site type B). When the size of gaps was smaller, we had an almost parallel invasion of pine and a few beech trees. However, the duration of beech invasion was long (stage 2 site type A, stage 2 site type B). In small gaps, all the growing space was occupied by beech and pine trees (stage 3 site type A, stages 3, 3a site type B) which later had almost the same growth rates. Today, most developmental stages of the stands have irregular shelterwood structure.

The difference in site quality between site types resulted in differences in the duration of beech invasion in stage 1 of the two site types. In addition in all stages of site type B, there is a significant larger number of young trees, with small dimensions, than in stages of site type A. The worse site quality than site type A, did not enable beech seedlings and samplings to rapidly occupy the available growing space and excluded the establishment of many individuals for a long period of time, see also Oliver and Larson (1996). In stage 3, of site type A, beech has a larger basal area than pine, also the percentage of beech basal area of the total stands basal area in stage 1 of site type A seems to be greater than in stage 1 of site type B due to the fact that in type A the site conditions favour the demanding shade tolerant species of beech. Development patterns and other stands characteristics as basal area were strongly influenced by other factors such as the spatial distribution of seed resources (after the gaps creation) and the timing of cuttings as well as their intensity.

In many cases, both pioneer and non-pioneer species grow in gaps (Poulson and Platt 1989, Spies and Franklin 1989, Veblen 1989, Whitmore 1989). In stage 3 of site type A, beech and pine trees grow together competing with each other. In fact the beech trees in some cases have almost the same height growth rates as the pines which usually have higher growth rates than beech. This happens because the beech trees were dominant from the beginning, they had to compete only with shade intolerant trees such as pines. In addition the pine trees probably showed slower than usual growth rates because, in many cases, for a long period of their life they were shaded by mature beech trees which were at the edges of the gaps.

The pine trees in some cases showed a delayed (for the species) culmination in current annual volume increment which is not followed by an abrupt fall. On the contrary, afterwards, they have a more or less sustained current annual volume increment.
Many reasons may be responsible for that fact, a) the pines grow in mixed (with beech trees of similar age) stands b) in these stands the cuttings started, in the last 30-35 years, giving more growing space to dominant pines, and c) the pines are in the southern limit of their species expansion.

Connell and Slatyer (1977) mention that in small gaps, which were created by extreme disturbances, 'early succession species' may not grow as quickly as usual, since resources are reduced by the neighboring adults. According to Assman (1970), in *Pinus sylvestris-Fagus sylvatica* mixed stands the beech understorey probably reduces the increment of Scots pine.
In this study, the plant succession phenomenon has elements from all the ecological theories (models) of succession. The conclusion is the same as Pickett et al. (1997). Site-specific predictions about vegetation dynamics require a complex scientific framework as well as information and knowledge about disturbance, environment, propagule availability and species biology. If stands remain undisturbed for many decades, pine will be replaced by the more shade tolerant species of beech and fir (Milios 2000). The forest practice must favour pine in the forest edges and in small areas in medium and poor site qualities in order: a) to exist as a pioneer species (well distributed in the area) after a possible disturbance (Smiris 1999, Milios 2000) and b) to maintain species diversity.

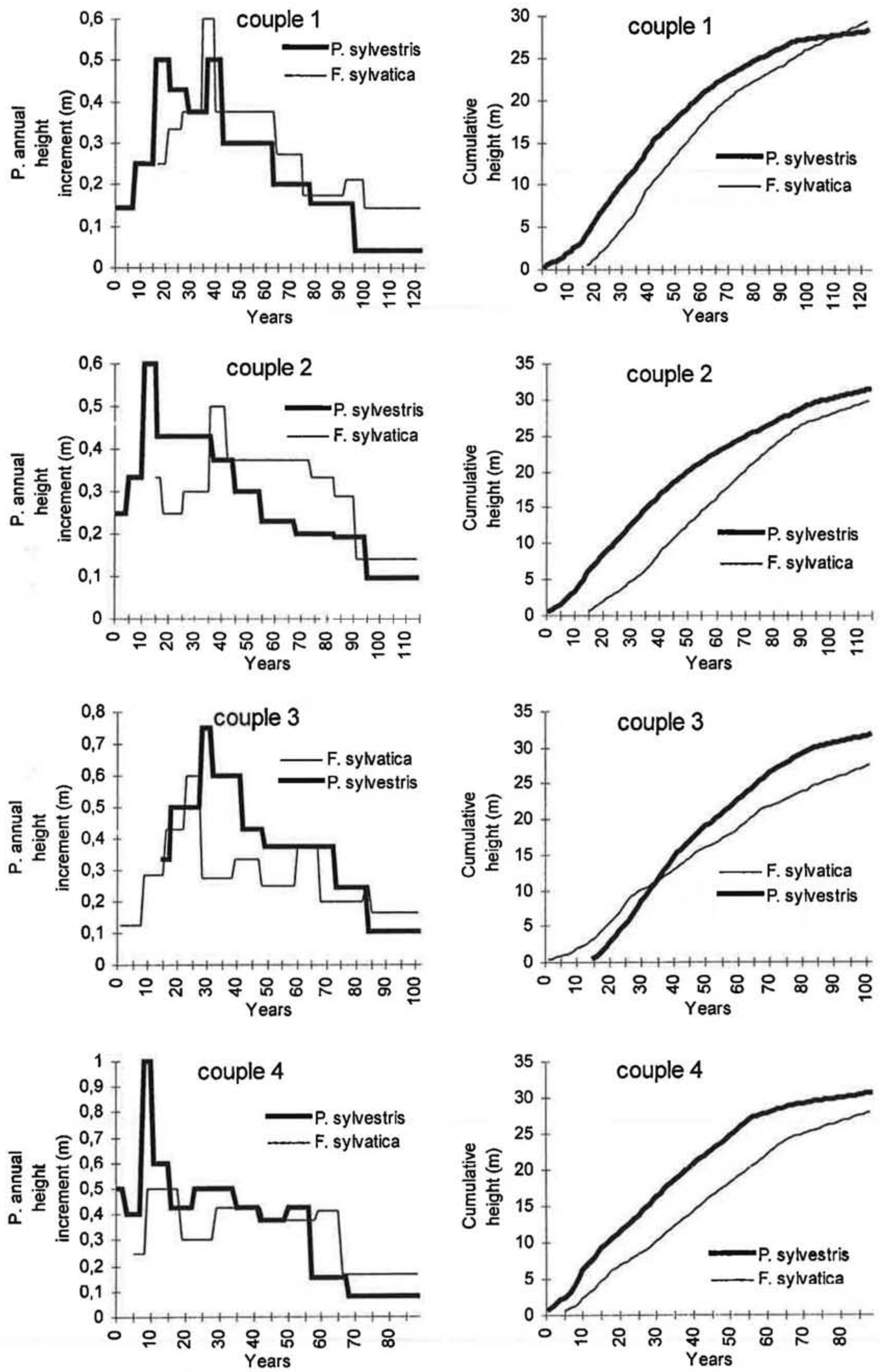


Figure 9. *Periodic annual height increment and cumulative curves in the four competing pine-beech couples.*

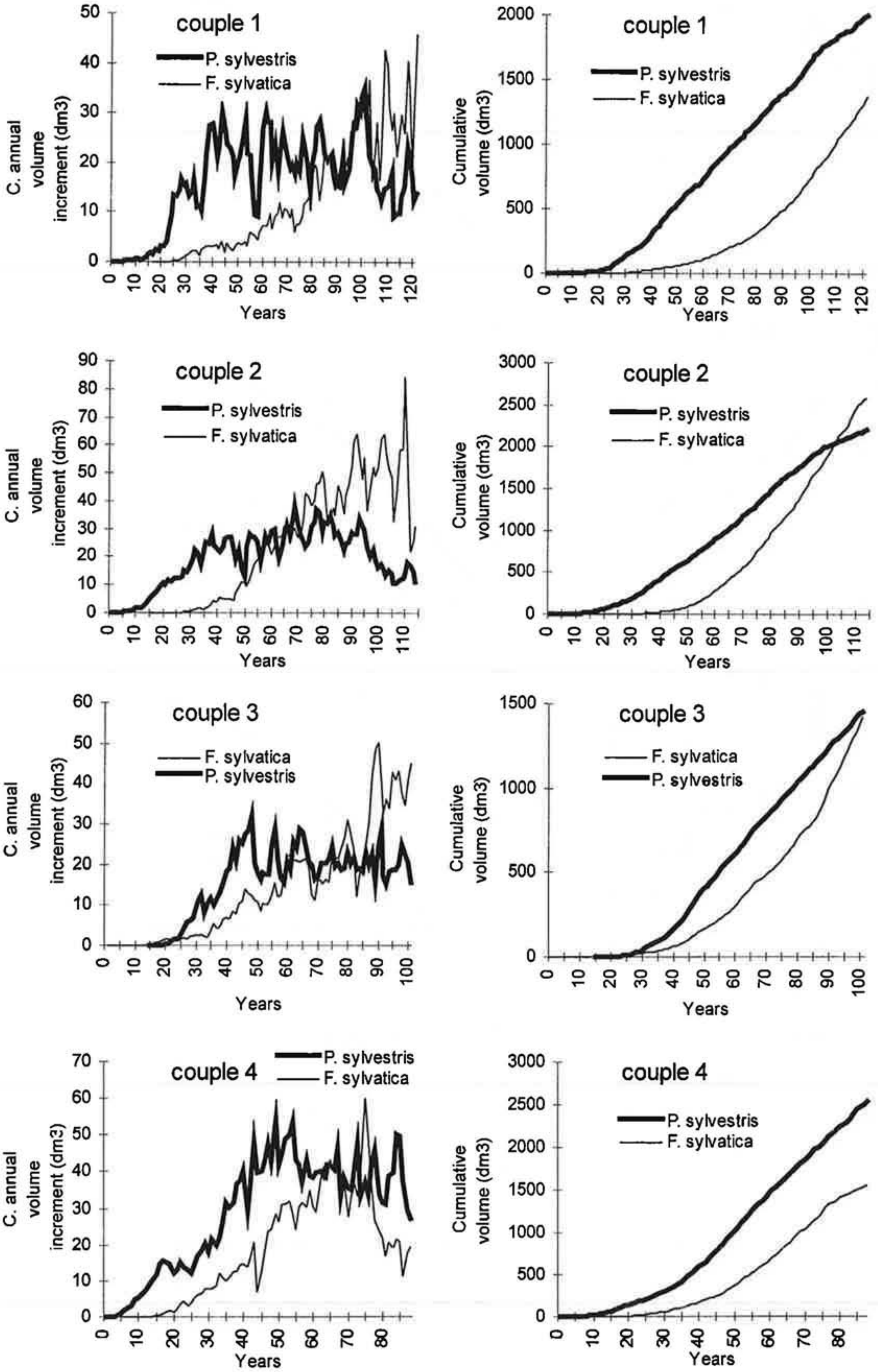


Figure 10. *Current annual volume increment and cumulative curves in the four competing pine-beech couples.*

6. Conclusions

a) The population structures, the regeneration and development patterns of *Pinus sylvestris-Fagus sylvatica* stands are strongly influenced by human and natural disturbances and species 'life history characteristics'.

b) The difference in site quality between site types results in differences in the duration of beech invasion (under pine) and in species basal area distribution.

c) In good site qualities when individual dominant beech and Scots pine (competitive) trees with a small age difference grew together, the beech trees, in some cases, have almost the same height growth as the pines and the pine trees showed a delayed (for the species) culmination in current annual volume increment which is not followed by an abrupt fall.

d) The process of secondary succession is influenced by disturbances regime, environment, propagule availability and species biology.

e) The forest practice must favour pine at the edges of the forest and in small areas in medium and poor site qualities.

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