

Tree rings show competition dynamics in abandoned *Castanea sativa* coppices after land-use changes

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Abstract

Questions: As a consequence of socio-economic changes, many *Castanea sativa* coppices have been abandoned and are now developing past their usual rotation length. Do we have to expect changes in stand structure and composition of abandoned *Castanea sativa* coppice invaded by other species? Is a tree ring-based approach adequate to early recognise changes in inter-specific competitive interaction?

Location: Lowest alpine forest belt of the southern Swiss Alps.

Methods: We selected a 60-year old abandoned *Castanea sativa* coppice stand with sporadic *Fagus sylvatica* and *Quercus cerris* mixed in. Using tree-ring based indices we analysed differences in the species-specific response to competition. Analyses were performed by comparing how subject dominant trees (10 *Castanea*, 5 *Fagus*, 5 *Quercus*) have differently faced competition from their immediate *Castanea* coppice neighbourhood, taking into account the changes over time and space.

Results: Although no species appears yet to have made a difference in the surrounding coppice mortality, there are species-specific differences in growth dominance, which indicate potential successional processes. *Castanea sativa* growth dominated in the early stages of stand development. However, after approximately 30-35 yr *Fagus sylvatica* and *Quercus cerris* became much more dominant, indicating a change in competitive potential that does not favour *Castanea sativa*.

Conclusions: Without interventions this coppice will develop into a mixed stand. A tree-ring based approach allows an early recognition of forthcoming changes in stand composition and structure and is likely to be an important tool for forest landscape management.

Keywords: Dendro-ecology; Growth; Interspecific competition; Mortality; southern Swiss Alps; Stand dynamics; Sweet chestnut.

Nomenclature: Aeschimann et al. (2004).

Abbreviations: BAI = Basal area increment; TD = Tree density.

Introduction

Human activities have a major impact on the global environment, inducing changes in global biogeochemical cycles (altering nutrient flows), land-use type and intensity, species distribution (invasions and extinction), natural disturbance regimes, and the physical environment (including climate). In a changing environment, ecosystem processes and functioning can be modified with ecological consequences that are only partially known. In forests, global changes modify, in particular, intra- and inter-specific competition processes. Such modification processes may induce changes in the composition and structure of forest ecosystems. To manage changing forests in a sustainable manner, an understanding of forest stand dynamics is needed. Studies of stand dynamics in unmanipulated forests are relatively common (e.g. Bergeron 2000; Chokkalingam & White 2000; Woods 2000; Groven et al. 2002), as are studies modelling the impact of anthropogenic disturbances on forest ecosystems (e.g. Antonić et al. 2001; Cullen et al. 2001; Ford & Brooks 2002). However, relatively few studies have analysed the development of recently abandoned forests that have been strongly impacted by human activities in the past (e.g. Amorini et al. 1996).

Dendrochronology is a tool that allows the reconstruction of stand history, disturbances and dynamics by analysing tree rings. Tree-ring analysis has been successfully used for this purpose in a variety of ecosystems (e.g. Henry & Swan 1974; Johnson & Fryer 1989; Veblen et al. 1991; Abrams et al. 1995; Rubino & McCarthy 2004; Piovesan et al. 2005). These studies are usually retrospective analyses of natural ecological successions or of stand development after disturbances. They describe past stand dynamics only after changes in stand structure and composition have already become visible. However, if disturbed forests are to be managed efficiently, an early identification of competitive changes

between species is needed. Acquiring this information is still a methodological challenge.

Competition plays a central role in mixed forest stand dynamics by reducing the growth of weaker trees and altering the number of stems. Competition is defined as an interaction between individuals, brought about by a shared recruitment for a resource in limited supply, and leading to a reduction in performance (Begon et al. 1996). Competition, however, is frequently characterized through indices based on performance variables (e.g. yield, biomass, growth rate, cover) (Weigelt & Jolliffe 2003) that are only applicable for the time period in which the data are acquired. For most forest ecosystems, trees usually are only re-measured accurately on a 5-10 year basis, so competition can typically be assessed with a frequency of once to twice per decade. Therefore, an accurate identification of a shift in competition has to be supported by repeated measurements with a finer time scale. In this regard, tree-ring based competition indices have many advantages: (1) tree-ring width can be used as a succinct indicator of the tree-growth performance; (2) tree rings have an annual resolution and (3) changes in competition processes can be readily analysed from tree-ring time series.

Castanea sativa has been intensively cultivated for centuries as a monoculture (coppices and orchards), even far outside its natural range (Pitte 1986; Bernetti 1987), e.g. in many regions of the southern Alps. These strongly human-impacted forest ecosystems are still important landscape components in the mountainous regions around the European Mediterranean basin and in the southern Alps, covering more than 2.2 million ha (Conedera et al. 2004). Since the early 1950s, however, a progressive decline in the rural economy and the onset of *Cryphonectria parasitica* (Murrill) Barr., a pathogen responsible for bark canker, has caused a decreasing interest in the cultivation of *Castanea sativa* (Pitte 1986). This has led to the abrupt reduction of cultural practices in both coppices and orchards. Short rotation coppices (< 20 year), which for millennia had been regularly and intensively managed, were abruptly abandoned during the 1950s. These coppices are thus developing past their usual rotation length and without any further human intervention. In some cases the absence of management is also associated with a slow invasion of other species (Amorini et al. 1997; Conedera et al. 2001). Analyses of stand development and of competition processes between *Castanea sativa* and other species are crucial for understanding current and future forest succession processes and for anticipating landscape development within the extended chestnut belt of the southern Alps.

In this study, we use tree rings as indicators of the competitive strength of different tree species growing in the same abandoned *Castanea sativa* coppices. The

study aims to reconstruct past changes in competition among trees in order to anticipate expected changes in stand structure and composition in a disturbed forest. We studied a 60 year old abandoned *Castanea sativa* coppice stand in the southern Alps, and competition processes with *Fagus sylvatica* and *Quercus cerris*. The response to neighbouring coppice competition of dominant *Castanea sativa* plants was compared to that of *Fagus sylvatica* and *Quercus cerris* to determine which species will win or lose. Comparisons are allowed since all subject trees are embedded in a homogeneous structured *Castanea sativa* coppice with comparable competitive power. The variation in time and space of species-specific responses to surrounding coppice competition was investigated and compared. As indicators of competition performance, we considered the simple ratio of radial-growth performance between subject trees and their coppice competitors as well as the intensity of neighbourhood mortality.

Material and Methods

Study site

The study site is located in the lowest alpine forest belt of the southern Swiss Alps (45°59'00" N, 8°51'50" E). These forests belong to the non-native chestnut forest belt, and are naturally dominated by various broad-leaved species. The study area is located at an elevation ranging from 600 to 660 m a.s.l. and the slope (ca. 10%) has a southwest exposure. The soil type is a typical cryptopodzol rich in humus (Blaser et al. 1997) and the vegetation is between a *Cruciatum glabrae-Quercetum castanosum* (Gianoni et al. 1988) and an *Ilici-Fagetum typicum* (Carraro et al. 1999). The site is well-supplied with water and nutrients. The meteorological station at Lugano, eight km from the site, recorded for the period 1901-2002 an average annual precipitation of 1678 mm, with a maximum in summer and a minimum in winter, and a mean annual temperature of 11.8 °C (MeteoSwiss, Locarno-Monti, Switzerland). The forest is a *Castanea sativa* coppice with sporadic single *Fagus sylvatica* and *Quercus cerris* trees. The coppice forest structure is homogeneous with regard to stump and shoot density, as well as the distribution of stem diameter and tree height. The forest canopy is composed of a single layer, regeneration is rare and consists mainly of *Fagus sylvatica*. At this site, the last coppicing occurred between 1946 and 1952.

Plot selection and study material

Nine *Castanea sativa*, five *Fagus sylvatica* and five *Quercus cerris* dominant stems were selected as subject trees for studying competition dynamics. These trees were almost exclusively surrounded by *Castanea sativa* coppice stumps. With the exception of two *Fagus sylvatica* trees established ca. 10 yr prior to the last coppicing (1946-1954), all subject trees were established in the same period and are comparable in tree height and stem diameter. Due to the high density of trees the zone of influence of subject trees is not expected to exceed 10 m. Therefore, circular study plots 10 m in radius were established and centred on the selected dominant trees. All plots were located in the same forest with a maximum distance between plots of 500 m.

During 2003 all stems (each coppice shoot was considered as a single stem) in the plots, both living and dead, with a diameter at 1.3 m above ground greater than 4 cm were identified, labelled and mapped. Fallen dead trees were also recorded but only if the corresponding stump could be identified. All living trees were cored, whereas dead trees were cut and cross sections collected. Cores and discs were collected at 1 m above ground level and perpendicular to the slope direction.

Dendrochronological analyses

Cross sections and cores were sanded and tree-ring widths measured to the nearest 0.01 mm with a standard tree-ring measuring device (Measuring table Dendrotab Walesch, Effretikon, Switzerland). Raw ring-width data were visually crossdated with the Time Series Analysis Program TSAPWIN v0.53 (Frank Rinn, Heidelberg, Germany) and subsequently checked with the COFECHA v6.06p computer program (Holmes 1983; Grissino-Mayer 2001). Cross-dating of short time series (< 10 year) was simplified because all trees belonging to the same circular plot were coppiced in the same year. To determine the age and growth of trees when increment cores failed to reach the pith, we calculated the number of rings missing to reach the coppicing date and we estimated their ring widths using the average ring-width value of the same year on the cross sections belonging to the same plot. The year of death of the dead trees was determined by identifying the calendar year of the last ring formed by cross-dating the ring-width series. Possible bias due to missing rings as a result of wood decay should be limited to a maximum of only a few years because *Castanea sativa* heartwood is very resistant to decay and the sapwood is very thin (Bosshard 1984; Leibundgut 1984).

Since the current basal area increment (BAI) is less biased by stem geometry and therefore less dependent on tree age (West 1980), our ring-width series used for

competition analyses were converted into BAIs, assuming a circular outline of stem cross sections (Visser 1995). A species effect on growth has been tested for each calendar year t through one-way ANOVA.

Competition analyses

Differences in competition strength among species was analysed by comparing how *Castanea sativa*, *Fagus sylvatica* and *Quercus cerris* subject trees have differently faced the competition of surrounding coppice. Recall that the plots were chosen so that the subject trees were surrounded by a comparable and homogeneous pure *Castanea sativa* coppice. Thus the only real difference in growth performance and mortality between plots is due to the presence of the subject trees of various species. We posit that if there are differences between the plots it is due primarily to the competitive ability of the subject tree species. The analyses took into account the changes through time and space by using a tree-ring based competition index.

The annual growth rate was used to compare growth performance of a subject tree with the growth performance of adjacent trees. The average basal area increment ratio (BAI-ratio) of subject tree j to all competitor trees i in calendar year t is defined as:

$$BAI - ratio_t = \frac{1}{n} \sum_{i \neq j} \frac{BAI_{j,t}}{BAI_{i,t}} \quad (1)$$

where n is the number of competitors. A value of 1 implies that on average the subject tree j has no competitive growth advantage, whereas values greater than 1 indicate that the subject tree j has, on average, a competitive growth advantage over its competitors. The larger the BAI-ratio, the larger the competitive growth advantage of the subject tree at a given time.

The reduction in the density of living neighbouring trees through time (number of trees/unit area) was considered as an indicator of the mortality induced by the subject tree. The tree density around subject trees (TD) was used as an indicator of the neighbourhood mortality and calculated as follows:

$$TD_t = \frac{n}{A} \quad (2)$$

where n is the number of living competitors that in calendar year t were growing in the surrounding area A .

For the spatial analysis the plot area around the subject tree (A) was split into four concentric circles with radii of 2.5, 5.0, 7.5 and 10 m (an example is given in Fig. 1). The analyses were conducted on a 2.5 m circle ($C_{2.5}$) and three annuli (i.e. the region lying between two concentric circles) with a depth of 2.5 m each up to the maximum radius of 10 m ($A_{2.5-5.0}$, $A_{5.0-7.5}$, $A_{7.5-10}$) around

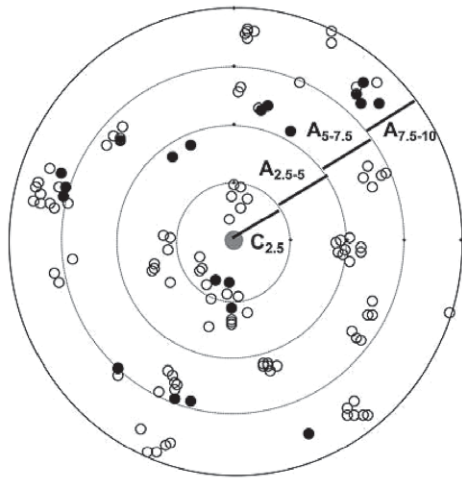


Fig. 1. Map of the 10-m radius circular study plot F4. The large grey point in the centre represents the *Fagus sylvatica* subject tree. Dots are the neighbouring competitors (filled circles for the living stems and empty circles for dead stems: status 2002). Circles delimit the four subplots considered for the analysis.

the subject tree. The two indices were then calculated using the competitors within a specific annulus only. Differences in competition strength among species were finally analysed by comparing species-specific differences in both indices over time and zones. For summary purposes the indices were analysed as a time series and were averaged by species and location within the plot. The analysis by zone (annulus) allowed us to examine the rate of decrease in competitive effects with increasing distance from the plot centre and also to examine the relative differences in these relationships for the three species considered in this study.

Results

Subject trees and plot characteristics

Subject trees are very similar in ring width and BAI pattern and no clear differences were found between species by visual inspection. Statistical differences in ring width among species (ANOVA, $p < 0.01$) occur in only a few specific years (Fig. 2). These minor differences however are not continuous enough to identify stable, significant differences in the tree-specific competitive power.

Plots were also tested for equality of neighbouring tree density over time. In case of significant differences (ANOVA, $p < 0.01$) in density among species, the relationship held over the entire time span (1955-2002) (Fig. 3). The density of stems observed within the 10-m

radius circular plot at the time of survey is summarized in Table 1.

The relationships of the BAI-ratio to tree density on each 10 m circular plot for three selected years (1965, 1985 and 2002) are shown in Fig. 4. Species differences in BAI-ratio, which were not evident in 1965 (ANOVA, $p = 0.37$) and 1985 ($p = 0.10$), became more evident over time and were significantly different in the year 2002 ($p = 0.006$). To test the influence of the factors species and year on the BAI-ratio we performed an analysis of covariance with density as a covariate. While the species and year factors were individually significant ($p < 0.001$), the interaction of these two factors on the BAI-ratio was not significant ($p = 0.142$). Thus, when accounting for density as a covariate it was not possible to find a consistent influence of time and species on the BAI-ratio. In this study, it is reasonable to assume that the BAI-ratio is a stable enough variable to judge the species-specific response to competition.

Effect on neighbourhood mortality

The development of tree densities surrounding the selected dominant subject trees was used to estimate the intensity of mortality of neighbouring trees. The development over time and space of tree density per subject species is shown in Fig. 3. For each subplot and species, the pattern of reduction in tree density follows a negative power function with the exception of the early years after coppicing, i.e. prior to 1962. In the last 40 years (from 1962 to 2002), the living tree density within a 10-m radius was reduced on average from 3846 to 1113 trees/ha for *Castanea sativa*, 3298 to 847 for *Fagus sylvatica* and 3124 to 999 for *Quercus cerris*. The yearly mortality rate over the 40-year period ranged from a maximum of 68 trees/ha for *Castanea* to a minimum of 53 trees/ha for *Quercus*.

Effect on growth performance

The current BAI was used to estimate differences in the growth performance between the subject tree and its competitors. Fig. 5 shows how the BAI-ratio has developed over time and space. There are clear differences over time between the pattern of development of *Castanea*, *Fagus* and *Quercus*. On average, in the early stages individual *Castanea* subject trees, in comparison with the neighbouring trees, had higher relative growth rates than *Fagus* and *Quercus*. In 1965, for example, the subject *Castanea* in the $A_{5-7.5}$ annulus grew 4.29 times faster than its neighbours, whereas in comparison subject *Fagus* and *Quercus* grew on average only 3.09 and 2.77 times faster on average. However, after about 28 year (in 1993) a shift in competition potential occurred:

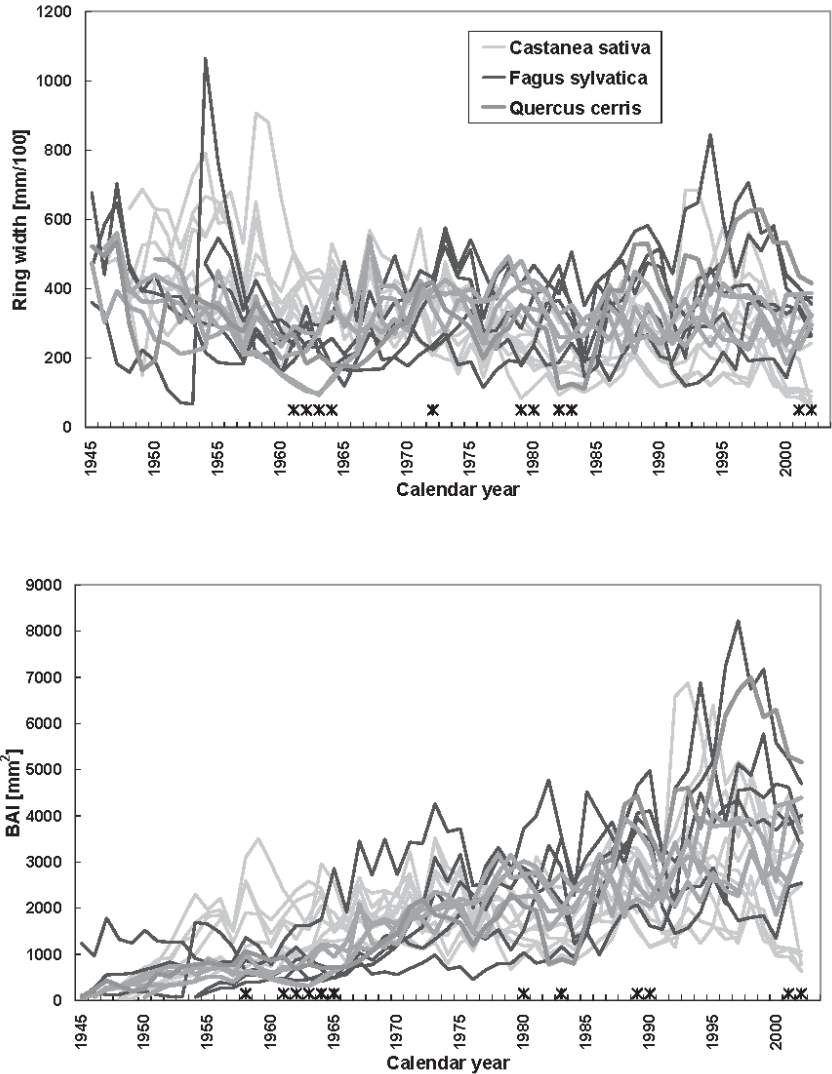


Fig. 2. Ring widths (above) and basal area increment (below) of the selected dominant subject trees from 1945 to 2002. Light grey lines = *Castanea sativa*; black lines = *Fagus sylvatica*; dark grey lines = *Quercus cerris*. Asterisks indicate significant statistical differences in ring width among species (one-way ANOVA between species, $p < 0.01$).

the average BAI-ratio of subject *Castanea* trees remained constant, whereas the average BAI-ratio of *Quercus* and *Fagus* subject trees strongly increased. In 2002 the average BAI-ratios for the $A_{5-7.5}$ annulus increased up to 6.41 for *Castanea*, 14.73 for *Fagus* and 15.62 for *Quercus*.

The change in BAI-ratios occurred in later years with increasing distance from the subject tree, in 1977 for $C_{2.5}$, 1985 for $A_{2.5-5.0}$, in 1993 for $A_{5.0-7.5}$ and in 1999 for $A_{7.5-10}$. This means there is a time lag of about seven years per 2.5 m of increasing distance from the plot centre (see arrows in Fig. 5). The differences in the average growth ratio between species are maximally expressed in the $A_{2.5-5.0}$ annulus.

Discussion

Validation of past competition reconstruction

Considering all plots together, in 2002 only 51 (26%) of the 195 trees recorded as living in 1962 were still alive. High mortality rates are common in *Castanea sativa* coppices, where the high density of shoots resprouting from the stumps after coppicing is rapidly reduced in the first decade after coppicing (Pagès & Cabanettes 1993). Before 1962 (Fig. 3) the decreasing pattern, however, did not correspond to the negative power function that at least theoretically should exist in even-aged (coppice) forest stands (Cappelli 1991). This means that the dendrochronologically based reconstruction of the past stand population and derived competition can only be applied for the last 40 years,

Table 1. Stem density observed within the 10-m radius circular plots at the time of survey in 2002. Tree density values between species are not statistically different (one-way ANOVA, $p > 0.05$).

Plot	Density [stems/ha]		
	Total	Alive	Dead (%)
<i>Castanea sativa</i>			
C1	5032	1274	3758 (75%)
C2	4548	1204	3344 (74%)
C3	4080	933	3147 (77%)
C4	4354	1272	3082 (71%)
C5	7427	1612	5815 (78%)
C6	5090	1307	3783 (74%)
C7	3503	629	2874 (82%)
C8	4223	920	3303 (78%)
C9	4461	872	3589 (80%)
Mean	4746	1113	3633 (77%)
SD	1114	297	874
<i>Fagus sylvatica</i>			
F1	7707	1009	6698 (87%)
F2	2951	1215	1736 (59%)
F3	3256	729	2517 (77%)
F4	2747	530	2217 (81%)
F5	3962	752	3210 (81%)
Mean	4123	847	3276 (79%)
SD	2056	267	1986
<i>Quercus cerris</i>			
Q1	5359	1580	3779 (71%)
Q2	4137	839	3298 (80%)
Q3	3209	706	2503 (78%)
Q4	4731	1010	3721 (79%)
Q5	5417	861	4556 (84%)
Mean	4571	999	3572 (78%)
SD	923	342	751

back to 1962. Despite the high decay-resistance of *Castanea* wood (Bossard 1984), it is likely that some trees that died prior to this date were not recorded in 2003. Furthermore, we observed that the outermost rings of some dead trees were partly decayed, and therefore an error in the estimate of the year of tree death would be possible. Fortunately, *Castanea* usually has only a few sapwood rings (< 5 years) (Bossard 1984) and therefore the error is limited to a few years at most.

Plot comparability

In this study we tested for competition effects within 10-m radius plots. We wanted to measure the ability of subject trees to suppress their surrounding neighbours. This design implicitly assumes that plot conditions are comparable. Total tree densities (live and dead) observed in the plot do not statistically differentiate between species (Table 1). So, due to the homogeneous and hierarchical structure of the surrounding coppices,

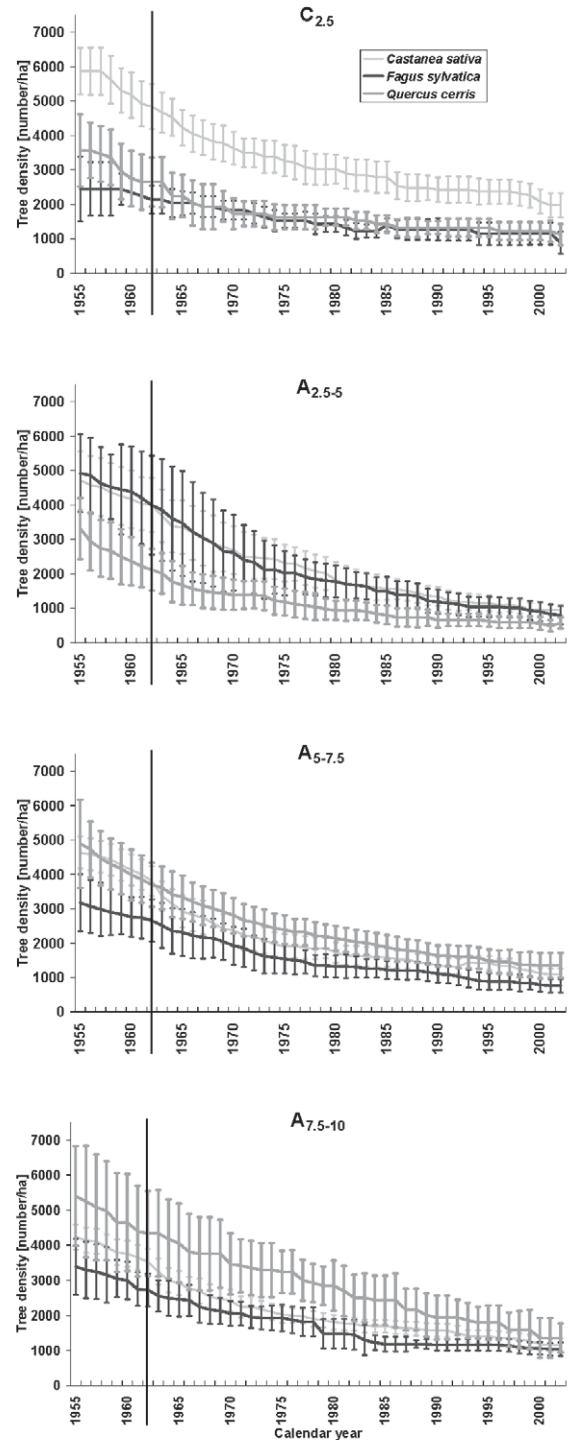


Fig. 3. Development of the density of living stems in all 19 study locations considered from 1955 to 2002. Lines refer to mean values and bars to standard error. Light grey line = *Castanea sativa*; black line = *Fagus sylvatica*; dark grey line = *Quercus cerris*. The vertical line delimits the validity in the reconstruction of past stand populations. C_{2.5}, A_{2.5-5.0}, A_{5.0-7.5}, A_{7.5-10} refer to the four subplots.

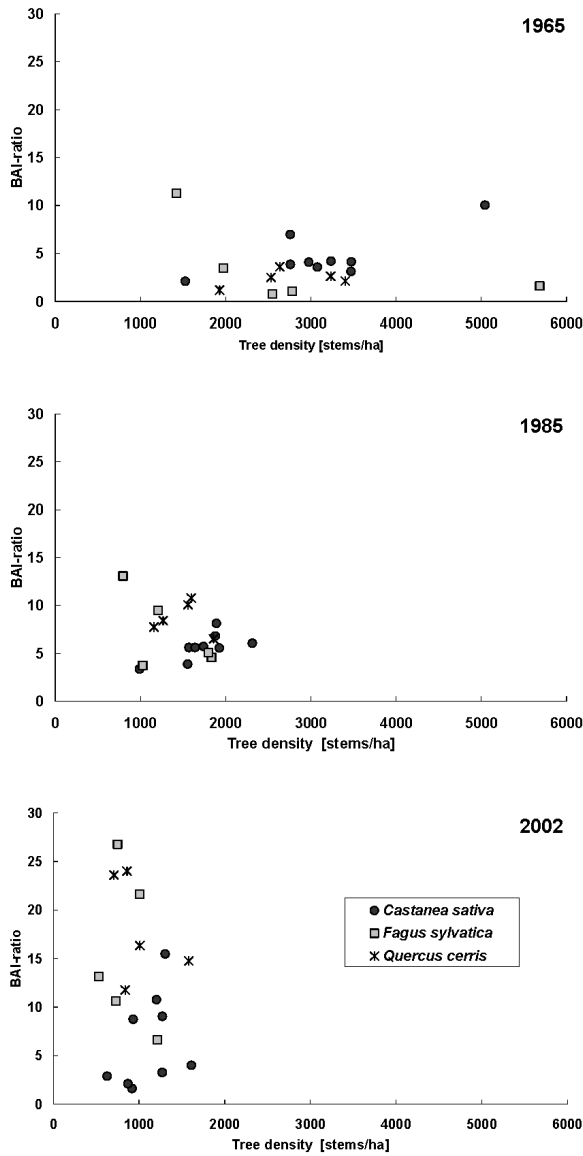


Fig. 4. Relationships between BAI-ratios and stem densities in the whole 10-m circular plots for three selected years: 1965, 1985 and 2002.

we can reasonably assume that each subject tree faces approximately the same level of competition from its neighbouring trees. We assume that coppice-coppice competition processes among neighbouring trees inside and outside the 10 m circular plot are not appreciably affecting our results since they are equal in the whole stand.

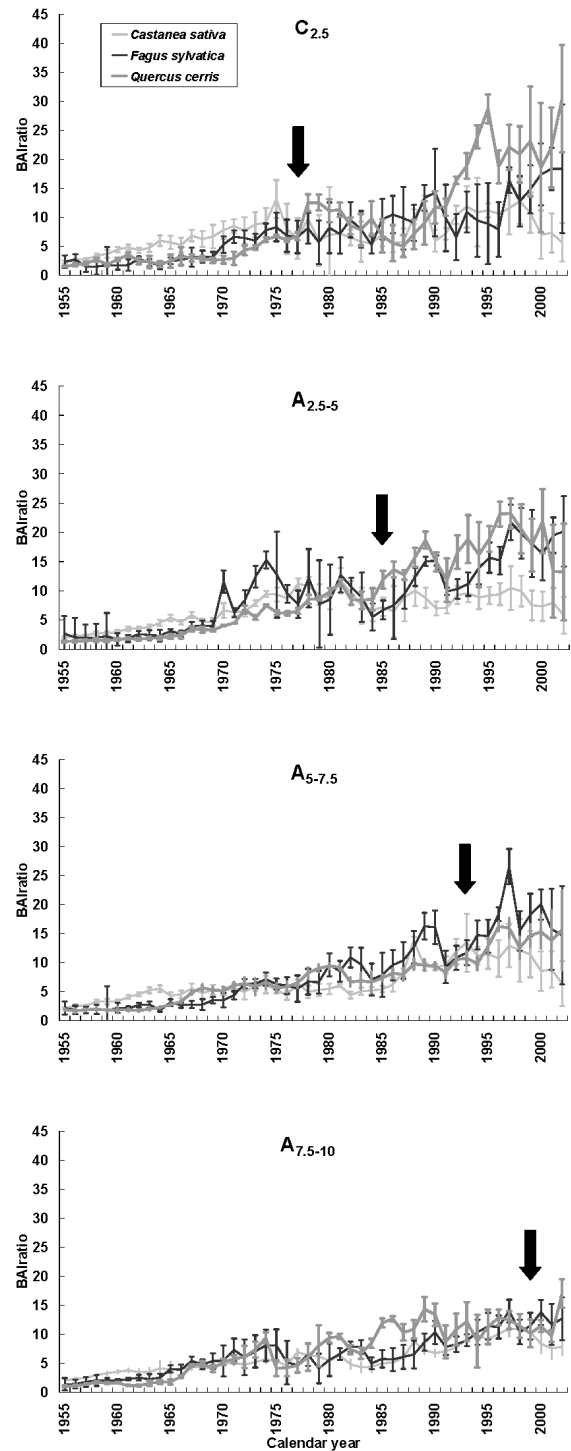


Fig. 5. Development of the average BAI-ratios for all 19 study locations considered from 1955 to 2002. Lines refer to mean values and bars to SE. Light grey line = *Castanea sativa*; black line = *Fagus sylvatica*; dark grey line = *Quercus cerris*. Arrows and dark lines mark the time the BAI-ratio of *Castanea sativa* is surpassed by those of *Fagus sylvatica* and *Quercus cerris*. C_{2.5}, A_{2.5-5.0}, A_{5.0-7.5}, A_{7.5-10} refer to the four subplots.

Successional trends in abandoned Castanea coppices

Suppression and death is a natural result of stand development. In mixed stands mortality depends on the species-specific competition potential. As tree crowns expand and dominant trees encroach on the growing space of suppressed trees, the number of trees decreases (Oliver & Larson 1996).

Although there were differences in BAI-ratio patterns between different species (Fig. 5), the mortality around the different subject tree species did not substantially differ in the various annuli (Fig. 3), except for $C_{2.5}$. The observed mortality is a function of the regular inter-tree competition which is accentuated in *Castanea* coppices due to the high stem density and good site fertility. For our data, it appears that 60 years since the last coppicing is too short a period to detect differences in species-induced mortality. The stand-dynamic patterns observed in this study are largely the result of the growth responses to interactions between different species.

Castanea sativa is a fast growing and shade intolerant species, especially when managed as a coppice (Bernetti 1995), whereas *Quercus cerris* and especially *Fagus sylvatica* have slower growth rates and are less light demanding (Bernetti 1995).

Our results (Fig. 5) show that individual *Castanea* trees dominate their neighbours during the early stages of stand development, beginning immediately after the coppicing. However, after ca. 30-35 year (1980-1985) the pattern begins to change with increased BAI-ratio values for individual *Fagus* and *Quercus* trees, but constant BAI-ratio values for *Castanea* trees. *Fagus* and *Quercus* slowly occupy the growing space as it is freed. Once they become dominant they reach average BAI-ratio values higher than 15 within a few years. Thus, the neighbouring *Castanea* are progressively suppressed.

The change in the BAI-ratio between the species occurs with a delay depending on the distance from the subject tree: an increase in distance of 2.5 m corresponds to a delay of about 7 years (Fig. 5) in our data. Hence on a 10-m radius circle (314 m²) around the subject tree, *Fagus* and *Quercus* need ca. 55 year to establish their growth dominance over all the *Castanea* coppice trees. It is sufficient to have a density of 32 subject trees/ha regularly distributed on the surface to guarantee a stand-wide successional change within this period.

Abandoned *Castanea sativa* coppices with a similar mix of sporadic *Fagus sylvatica* and *Quercus cerris* are frequent on mesic soils in many regions in the southern Alps. Without silvicultural interventions these coppices will probably develop within a few decades into mixed stands of *Fagus sylvatica* and *Quercus cerris*, which would fundamentally change the characteristics of these landscapes.

Evaluation of the methods used

Competition indices are widely used in interpreting and summarizing plant competition (Weigelt & Jolliffe 2003). The use of dynamic competition indices which include time as part of the calculations is, however, new. Combinations of spatial and dendrochronological data have been used in several other studies for reconstructing past forest dynamics (e.g. Lorimer 1984; Cherubini et al. 1996; Harrod et al. 1999; Parish et al. 1999; Dobbertin et al. 2001; Anton & Parish 2002; Motta et al. 2002).

In this study, we used tree rings for the first time as retrospective dynamic indicators of the competitive strength of different tree species growing in abandoned *Castanea* coppices. Tree rings enable us to reconstruct the annual past growth and mortality of the trees in the stand, focusing on the interactions between a subject tree and its close neighbours. Our innovative approach of selecting subject trees from trees embedded in the same homogeneous coppice forest has allowed an unbiased analysis of the species-specific competitive power. It was thus possible to clearly identify which species has relative growth advantages over neighbouring *Castanea* coppice competition and under what conditions and time that takes place. In particular, it was possible to quantify the timing and rate of competition processes, which allowed us to predict how the stand composition and structure are likely to change without management intervention. Abandoned coppice stands are very suitable for such studies because the abandonment occurred homogeneously within the stand, competition processes were from the beginning extremely pronounced, and dead suppressed trees are still found.

We combined dendrochronological and competition analysis method in an ideal case. We believe that, according to our results, the method has a more general potential for the early detection of stand altering processes in mixed stands caused by competition shifts following (1) different types of disturbances such as fire, insects or drought, and (2) changing environmental conditions such as changes in climate and land use. The method should prove useful in landscape management to predict future development of forest ecosystems.

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