Research paper

Growth analysis of an aged Turkey oak coppice under conversion into high forest

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ABSTRACT Most Italian research concerning the conversion of coppices analyse growth response at the stand level and adopt absolute growth as reference metric. Nonetheless, inter-individual interactions are lost when averaging tree level information at the stand level. Moreover, absolute growth ignores the initial size of individuals under comparison, the growth of large trees will thus always outperform that of small trees, and nothing can be inferred about tree-to-tree competition. We modelled the growth response after conversion thinning at the tree level using relative growth rate as a function of the initial diameter of individuals, stand density and time. Twenty years later, thinned treatments still yielded larger growth than the reference unthinned aged coppice. In the first 10-year period, the relative growth rate in all treatments decreased with increasing tree size. In the second 10-year period, the relative growth rate still decreased with increasing tree size in thinned treatments, whereas in the unthinned aged coppice, it increased with increasing tree size. The model we applied shows to what extent released individuals have grown in relation to their size and, at same time, provides information on their competitive state in relation to the overall density of stands over time.

KEYWORDS: coppice conversion, Relative Growth Rate, Turkey oak.

Introduction

The decline of coppice system

Coppicing is among the oldest forms of systematic utilization of forests carried out by human beings (Corcuera et al. 2006). However, from the second half of the 20th century, coppicing has become less important and has been abandoned in many places across Europe (Müllerová et al. 2015). Despite the ongoing shrinkage of coppice area (McGrath et al. 2015), there are still over 20 million hectares of coppice forests throughout Europe, covering over 10% of the total forest area (Unrau et al. 2018).

As a consequence of decline, very large areas of coppices (~3,200,000 ha) in Italy are approaching or beyond the formerly applied rotation age (Bertini et al. 2012). Many stands, often in marginal locations and of public ownership and/or in protected areas (i.e. Natura 2000), have been frequently left to non-intervention or converted into the high forest management system (La Marca et al. 2009, Mairota and Buckley 2018). This pattern has held not only for Italy but also for many European regions over the last 100 years (Nicolescu et al. 2017).

According to the Italian national forest inventory, the coppice area recognised as under conversion is approximately 151,000 ha (Gasparini and Tabacchi 2011), which is little more than 4% of the coppice area (3,600,000 ha). Conversions have been mainly applied to common beech (*Fagus sylvatica* L.) and Turkey oak (*Quercus cerris* L.) coppices (Amorini and Fabbio 1986).

The amount of coppice area beyond the rotation age and actually under abandonment is unknown, because these forests are still classified as "coppices" (Amorini et al. 1996) however, they supposedly constitute a significant share (Fabbio 2016). The management of these areas is one of the main problems that forestry research has to face in all Mediterranean countries (Cañellas et al. 2004).

The practice of conversion to high forest

A coppice with standards, i.e. the most frequent type in Italy (~66% of the coppice area; Gasparini and Tabacchi 2011), can be converted into high forest basically in two ways: passively by ageing (non-intervention), or actively by thinning (Nicolescu et al. 2017). The former is a long lasting process (Mairota and Buckley 2018), randomly driven by nature, with an almost unpredictable outcome, in terms of both stand structure and tree species composition. Conversely, thinning is a faster process with a fairly predictable outcome since it is driven by silvicultural choices. In Italy, a customary practice is conversion by the so-called "repeated thinnings" method, described as follows. In a coppice stand that exceeds the rotation age to some extent, standing shoots are repeatedly thinned by gradually reducing the number of shoots to one or two stems per stool until a high forest structure is achieved. Standard trees are generally removed, except for a few individuals released both for ecological and/or aesthetic reasons. Once the stand reaches its maturity (60-80 years), the high forest management system can be applied to regenerate the stand by seed. After the first intervention, 1,500 to 2,500 trees per hectare are released, and thinnings from below to mixed are repeated every 10-15 years (Amorini and Fabbio 1986). The effectiveness of the method is to adaptively shape the horizontal as well as the vertical arrangement of trees, so to resemble a high-forest structure.

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Not infrequently, however, it may happen that interventions following the first thinning are not performed, because of the unprofitability of the harvestings (La Marca et al. 2002).

Growth analysis

In Italy, a significant amount of literature concerning coppice conversion has been produced since the end of the 1950s (see supplementary material: Supp1). Some of this research has targeted the conversion of Turkey oak coppices (Supp1). A common trait of these works is that the analyses concerning growth response have been conducted at the stand level, except for a few analyses carried out at the individual level on long-term monitoring plots established since the early 1970s (Amorini and Fabbio 1986, 1989). When the tree level data are averaged at the stand level, the inter-individual interactions can not be observed. A variety of studies have stressed the importance of individual variation in competitive ability for resource acquisition with changing tree density (Evans 1972, Causton and Venus 1981, Freckleton and Watkinson 2001). Even in even-aged stands dominated by one species, the growth dynamics have different timing from the tree to the stand level (Assmann 1970). In experimental treatments that affect growth, approaching growth dynamics at the tree level would allow one to know to what extent released trees grow while accounting for individual competitiveness in resource acquisition (Oliver and Larson 1986).

Growth is a fundamental process that affects physiology, community dynamics and ecosystems (Paine et al. 2012). Consequently it has been of great concern in plant science and production biology, including forestry (Pommerening and Muszta 2016). One of the most noticeable signs of growth is the change in size over time (Vanclay 1994). Growth is a continuous process and, as such, cannot be measured in practice; growth quantification is usually obtained as the difference between measurements at two points in time (Pommerening and Muszta 2016). The simplest and most common measure of plant growth is the absolute growth rate (AGR), that is, the absolute change of a given quantity over a given time period (Rees et al. 2010). In forest studies, AGR is commonly referred to as increment and is calculated for tree diameter, basal area, height, volume or biomass (Van Laar and Akça 2007). In growth analysis, the use of AGR at tree level has been criticised because it ignores different individual sizes (Hunt 1982, Rees et al. 2010). It has indeed been observed that in many natural processes, the absolute growth of a certain quantity is proportional to the quantity itself (Blackman 1919). Even at the stand level, the AGR results are inadequate to assess the impact of density dependent competition and indicate only that the growth of large trees outperforms that of small trees at any stage of competition (Larocque and Marshall 1993, Vospernik et al. 2010).

Differently, the relative growth rate (RGR), that is, the increase per unit of initial quantity in a given time period (see section Methods for details), can be advantageous compared to AGR because it accounts for growth differences that arise from different initial sizes (Wareing 1966). Accordingly, RGR was at first preferred in comparing experimental treatments that affect growth (Evans 1972, Causton and Venus 1981). Although RGR provides a common base of comparison for trees that differ in initial size, age or environmental conditions, its application in growth analysis is not common in forestry (Larocque 1998, Fabbio 1994).

Aim of the study

To improve the knowledge base on the growth response resulting after coppice conversion, this work attempts to answer the following questions: How does the release density affect the overall growth response? To what extent is growth response affected by the initial size of released individuals? How does density dependent competition affect growth over time?

The novelty of our study is that growth is analysed at the tree level and modelled in terms of relative growth rate. We report findings after twenty years of monitoring in permanent plots established in the Gargano promontory (Apulia Region) of Italy.

Materials

Study area

The experimental trials were carried out in the forest district of "Bosco di Manfredonia", in the promontory of Gargano (Apulia region). The area is located at approximately 700 m above sea level, with an average slope of 20–25% on gentle hill-slopes facing North-Northeast. The soils are mainly brown earths of organic origin. The climate is typically Mediterranean, with an average annual rainfall of 726 mm and average annual temperature of 12°C.

Woodlands are dominated by Turkey oak (*Quercus cerris* L.) with associated broadleaved tree species (*Ostrya carpinifolia* Scop., *Acer opalus* Mill., *Acer campestre* L.). The grass and shrub layers are composed of *Cyclamen neapolitanum* Aiton., *Rosa canina* L., *Prunus spinosa* L., *Crataegus oxyacantha* L., *Pteridium aquilinum* (L.) Khun., *Brachipodium pinnatum* (L.) P. Beauv., *Brachipodium sylvaticus* (Huds.) P. Beauv., *Fragaria vesca* L., and *Cornus mas* L.. The forest area may be ascribed to the phytosociological association of *Physospermum verticillata-Quercus cerris* communities (Biondi et al. 2008).

In 1996 the coppice under experimental conversion was 35 years old, which is ten years beyond rotation age. The coppice had a two-layer vertical structure: *(i)* a dominant layer composed of a few

Table 1 - Selected sample: sample size and stratification by treatment and period. In brackets the selected sample as proportion of all measured trees.

Period	Treatment			
	A	B	C	row sum
1996-2006	295 (99%)	385 (96%)	606 (55%)	1,286
2006-2016	276 (96%)	359 (98%)	448 (88%)	1,083
column sum	571	744	1,054	2,369

Table 2 - Quantile distribution of initial size (dbh) of individuals by treatment conditional to period.

Period	Treatment	q10	q20	q30	q40	q50	q60	q70	q80	q90
1996	A	9	13	14	16	17	19	20	22	26
	B	12	13	15	16	17	18	20	22	26
	C	9	11	12	13	15	16	17	19	23
2006	A	14	16	18	19	21	22	24	26	30
	B	15	17	18	19	21	22	23	26	30
	C	11	14	15	17	19	20	22	23	27

scattered Turkey oak standards (aged differently) and shoots (2-3 per stool); and *(ii)* a crowded dominated layer mainly composed of tree species other than Turkey oak, occurring as many small shoots per stool, and a few Turkey oak individuals. Further details concerning the study area can be found in Notarangelo et al. (2018).

Experimental design

The experimental design is a randomised complete block, with three theses replicated two times: 600 tree·ha⁻¹ (A), 800 tree·ha⁻¹ (B), and as control the reference density of the aged coppice (C, unthinned). The three theses were randomly assigned to six plots of 2,500 m² surrounded by a 10-m-wide buffer zone. At the onset of experimentation, all living trees with diameter at breast height (dbh) equal to or larger than 7 cm were numbered and identified by species in each plot. Full callipering was conducted in 1996 (after thinning), in 2006 and in 2016. Individual volume was assessed by a model built from sample trees felled after the experimental thinnings (La Marca et al. 2002).

Selected sample

In this study we focus on individuals selected for growth modelling (see "Grown modelling" section). A comprehensive review of data collected from repeated inventories (1996-2006-2016) can be found in Notarangelo et al. (2018).

The selected sample includes 2,369 measurements from trees found alive in the 2006 and 2016 inventories. Trees with the same dbh in the two consecutive inventories have been excluded since a null growth would be biologically inconsistent and likely due to either bark anomalies or callipering precision, based on 1 cm dbh classes. A summary of the selected sample is reported in Table 1, and, Table 2 shows the quantile distribution of individuals by initial sizes (dbh).

Methods

Experimental coppice conversion

The applied experimental conversion method forecasted a single intervention where the released individuals would have resembled an almost permanent structural and compositional arrangement. No further thinnings should have been scheduled until the regeneration cutting, or at most a preparation cut. As the number of trees before conversion was approximately 3,900 trees·ha⁻¹ (La Marca et al. 2008), the intervention would have been of heavy intensity and mainly from below since a large number of small-sized individuals would have been removed.

To this aim, two release densities were tested: 600 trees per hectare (treatment A) and 800 trees per hectare (treatment B). Arguments in favour of this choice are: *(i)* the incremental response of Turkey oak to thinnings of heavy intensity has been proven to be fast and evident (Amorini et al. 2006, Cañellas et al. 2004, Cutini 2006); *(ii)* the overall site conditions are good, considering the climate and soil fertility (La Marca et al. 2002); *(iii)* the planned release densities date back to the method of "balivage intensif", successfully applied by Aubert in the French oak coppices since the twenties of the former century (Hubert 1983); and *(iv)* side effects, such as resprouting, would not have been a problem since grazing is locally practiced.

To match the planned release densities, the following silvicultural criteria were applied: *(i)* removal of all stems with dbh less than 7 cm; *(ii)* release of one (sometimes two) stem of Turkey oak per stool, selected among the best shoots based on shape and vigour; *(iii)* release of a few old standards as habitat trees while removing the others; *(iv)* release of individuals of species other than Turkey oak if they were of good vigour. Each of these criteria respon-

ds to specific objectives, namely: *(i)* and *(ii)*, delay as long as possible the self-thinning phase (*sensu* Westboy 1984) while preserving released individuals in a condition of low inter-individual competitive stress; and *(iii)* and *(iv)*, improve stand structural diversity and preserve tree species richness, respectively, as premise for an overall biodiversity enhancement.

Growth measurement

We refer to growth as the increase in size of a quantity over a given period of time (Vanclay 1994). Blackman (1919), proposed a simple equation relating the production of new matter, to time, and to the initial size:

$$K_2 = K_1 \cdot e^{r \cdot \Delta t} \qquad \text{[eq. 1]}$$

where K_2 is the final size, K_1 is the initial size, r is the rate of increase, Δt is the time that has passed, and e is the exponential constant. Therefore, the final size attained depends on the initial size, the rate of increase, and the time. Solving eq.1 for the rate of increase (r) gives the relative growth rate (RGR):

$$\text{RGR} = \log_e (K_2 / K_1) / \Delta t \qquad \text{[eq. 2]}$$

RGR is defined as the rate of increase per unit of initial quantity in a unit of time (Blackman 1919, Fisher 1921, Wenk 1978, South 1991). Although eq. [1] focuses on final size, eq. [2] focuses on the amount of growth (Hoffmann and Poorter 2002). As a ratio, RGR is a measure of the efficiency of the plant's activity at producing new matter (Blackman 1919) and, at the same time, provides a common base of comparison for individuals that differ in initial sizes.

Growth modelling

To model the growth response at the tree level, the individual volume increment represents a logical and natural starting point (Assmann 1970, Wenk et al. 1990). The individual volume increment was modelled in terms of RGR and the following candidate predictors were considered: *(i)* the individual diameter (dbh), to rank trees by growth efficiency (Stoneman and Whitford 1995); *(ii)* the release densities (treatment), to assess the effect of available growing space, and *(iii)* two 10-year periods (period), to assess the effect of age-size related increase on growth decline (Coleman et al. 1994, Hoffmann and Poorter 2002, Mencuccini et al. 2005).

All candidate predictors were significantly correlated with RGR when modelled as additive terms (results not reported). Then, we increased model complexity in a stepwise fashion, including all possible combinations of interactions among those significantly correlated with RGR (results not reported). Lastly, by means of the likelihood ratio test, we compared the performance of several candidate models. The selected model, a compromise between model complexity and goodness of fit, includes three predictors and two pairwise interactions, namely:

RGR = dbh + treatment + period + dbh:treatment + dbh:period

where the colon symbol indicates a 2-way interaction term. The dbh was first log-transformed, to linearise the relationship, and was then centred to mitigate the collinearity. RGR is multiplied by 100 to ease the readability of model results.

Whenever repeated measurements are made on the same sample units, as is the case in long-term monitoring of trees in permanent plots, observations are no longer independent. Among others, mixed-effect modelling is an appropriate solution to handle data from repeated measurements (Aarts et al. 2014, Pinheiro and Bates 2000). We assigned a random intercept to individuals in order to isolate the effect of corrrelated errors.

Data management and statistical analyses were performed using "R" (R Core Team, 2019) and the "nlme" package for mixed effects modelling (Pinheiro et al. 2019).

Results

Model results

The estimates of coefficients along with associated statistics are reported in Table 3. The fixed component of the model explains more than half of the variability of the response (R^2 marginal: 57%), with an overall error of 0.8% (RMSE). The intraclass correlation coefficient (ICC) is 95.3%, and nearly all the model variance is thus due to differences in the fixed component. For details on model diagnostics, see supplementary material (Supp2).

In Table 3, the model intercept ($\beta_{w_0} = 4.5\%$) expresses the log-RGR in reference treatment A of the average tree, which has β_3 equal to 0 (dbh 17.4 cm), in the first 10-year period. The same tree in treatment B has an log-RGR equal to 3.65% ($\beta_0 - \beta_1$) and in treatment C has an log-RGR equal to 2.74% ($\beta_0 - \beta_2$). In the second 10-year period the log-RGR decreases by -1.19% (β_6) compared with the first 10-year period (Tab. 3). The log-RGR of the average tree ($\beta_3 = 0$) is equal to 3.31% ($\beta_0 + \beta_6$) in reference treatment A, 2.46% (3.65 + β_6) in treatment B and 1.55% (2.74 + β_6) in treatment C. Table 4 shows the back-transformed fitted relative growth rate for different tree size by treatment and period.

The Figure 1 depicts the interaction between the initial size of trees and treatment, and initial size of trees and period. In the first 10-year period, the RGR and initial size of trees are negatively correlated in all treatments, that is, small trees grow faster than large ones. As evidenced in Table 3, the slopes of regression lines significantly decrease from A ($\beta_3 = -4.27$) to B ($\beta_3 + 1.86 = -2.41$), and from B to C ($\beta_3 + 3.31 = -0.96$). In the second 10-year period, the sign of

the correlation between RGR and initial size of trees varies depending on treatment: it is still negative in A ($\beta_3 + \beta_7$ = -2.29) and B (-2.41 + β_7 = -0.42), whereas it becomes positive in C (-0.96 + β_7 = 1.03) such that small trees grow slower than large ones in treatment C (Tab. 3).

In Figure 2 the back-transformed fitted RGR curves and confidence areas for each treatment are plotted against back-transformed dbh values, separately for each period. From visual inspection, confidence intervals around the RGR of trees with dbh up to 26 cm do not overlap, and at common size, individuals in theses A and B thus have higher RGR than those of thesis C, in both periods. The same does not hold for trees with dbh above 26 cm in the right tails of the distributions (Fig. 2). The dbh range between 7 and 26 cm, encompasses from 90% (1996-2006) to 80% (2006-2016) of all individuals.

Table 3 - Estimates of coefficients and associated statistics from linear mixed model. Estimates, standard error, confidence intervals and RMSE, expressed as percentage in log-scale.

Coefficients	Estimates	Std. Error	95% Conf. Int.	t-value	p-value
β0 (Intercept)	4.50	0.06	4.37 – 4.63	70.247	<0.001
β1 B	-0.85	0.08	-1.00 – -0.69	-10.812	<0.001
β2 C	-1.76	0.07	-1.90 – -1.62	-24.432	<0.001
β3 cLog(dbh)	-4.27	0.17	-4.60 – -3.95	-25.662	<0.001
β4 cLog(dbh) : B	1.86	0.22	1.43 – 2.30	8.347	<0.001
β5 cLog(dbh) : C	3.31	0.19	2.94 – 3.68	17.556	<0.001
β6 period 2006-2016	-1.19	0.06	-1.30 – -1.08	-21.297	<0.001
β7 cLog(dbh) : period 2006-2016	1.99	0.16	1.67 – 2.30	12.268	<0.001
Observations	2,369				
ICC	0.953				
R² marginal	0.57				
RMSE	0.8				

cLog(dbh): centred logarithm of dbh; Std. Error: standad error; Conf. Int.: confidence interval; ICC: intraclass correlation coefficient; R2: coefficient of determination; RMSE: root mean square error.

Table 4 -Back-transformed fitted relative growth rate for different tree size (dbh) by period and treatment.

		Relative growth rate (%)					
		1996-2006			1996-2006		
cLog(dbh)	dbh (cm)	A	B	C	A	B	C
-0.8	8	22.1	17.5	14.2	16.7	13.2	10.8
-0.6	10	20.3	16.7	13.9	16.0	13.1	11.0
-0.4	12	18.6	15.9	13.7	15.3	13.0	11.2
-0.2	14	17.1	15.1	13.4	14.6	12.9	11.4
0*	17	15.7	14.4	13.2	13.9	12.8	11.7
0.2	21	14.4	13.7	12.9	13.3	12.7	11.9
0.4	26	13.2	13.1	12.7	12.7	12.6	12.2
0.6	32	12.1	12.5	12.4	12.1	12.5	12.4
0.8	39	11.1	11.9	12.2	11.6	12.4	12.7

* Average tree.

Figure 1 - Fitted relative growth rate at varying initial size of trees (dbh) by treatment per period. Gray shaded area represents 95% confidence intervals.
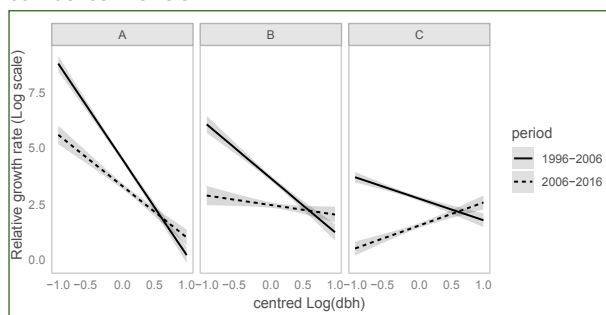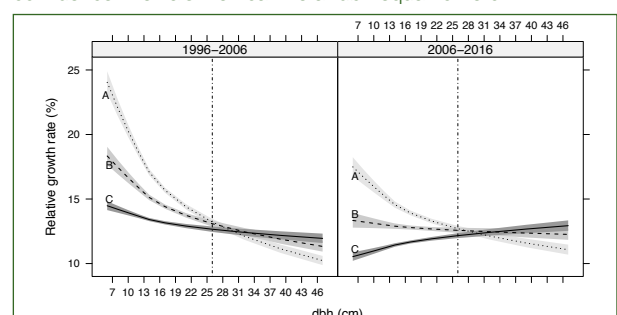

Figure 2 - Predicted relative growth rate by treatment against initial size of trees (dbh), per period. Gray shaded area represents 95% confidence intervals. Vertical line at dbh equal to 26 cm.

Discussion

At the stand level, or at least for individuals with dbh up to 26 cm, the relative growth of thinned treatments were higher than that of the coppice left to natural evolution (unthinned treatment C) for up to 20-years after the intervention. Other studies (Amorini and Fabbio 1987, Amorini et al. 2006, Corcuera et al. 2006) have reported positive effects on growth after the conversion thinning of up to 10-15 years. Moreover, the RGR of thinned treatments was negatively correlated to stand densities and decreased over time. The same relationship was found by Boncina et al. (2007) for selective thinning trials in beech (*Fagus sylvatica* L.) stands. For the cohort of individuals with dbh above 26 cm (80th-90th percentiles), which occupy the crown layer of dominant trees, light is probably not the primary limiting resource and, consequently, growth dynamics is mainly driven by environmental factors and/or site carrying capacity. Rentch et al. (2009) found that commercial thinnings in broadleaved stands of light-demanding species (*Liriodendron tulipifera* L.), from light to heavy intensity, did not affect the crown class transition rates of dominant trees.

Some authors (Ford 1982, Cannel et al. 1984, Perry 1985) have suggested the use of the relationship between RGR and tree size as a measure for inter-individual competitive stress. Larocque and Marshall (1993) found that RGR decreased with increasing tree size before the onset of inter-individual competition. This is because until available resources, especially light for Turkey oak, feed the demand of individuals, trees with medium-sized crowns are more efficient than trees with large crowns at producing new biomass (Assmann 1970, Oliver and Larson 1986), although larger trees have higher absolute growth.

At the tree level, in the first 10-year period and in all treatments, the RGR decreases with increasing tree size so that the small trees grow faster than the large ones, although at different magnitudes depending on treatment. The same relationship is reported by Mayor and Rodà (1993) for holm oak (*Quercus ilex* L.), by Cañellas et al. (2004) for *Quercus pyrenaica* L., and by Cannell et al. (1984) for *Pinus contorta* Douglas ex Loudon and *Picea sitchensis* (Bougard) Carrière.

The modelled slopes for the first 10-year period provide a measure of how the inter-individual competition is lowered in thinned treatments, depending on individual size: the steeper the slope, the higher the gap in RGR between smaller and larger trees in favour of the former. In the first 10-year period, RGR decreases with increasing tree size even for the unthinned coppice (treatment C), although at minimum magnitude. For the same period, a decrease of density by more than 42% was recorded in treatment C (Notarangelo et al. 2018), which means that a self-

thinning phase was already ongoing at the trial onset. Additionally, within 40 and 50 years, the coppices of light-demanding oaks left to natural evolution, experience a heavy competition and a suppression phase (Amorini et al. 1996, Cañellas et al. 2004, Amorini et al. 2006). The suppressed trees were mostly small-sized so that little growing space was made available and, thus, the slope in the modelling results were lower than for the thinned treatments.

In the second 10-year period, RGR still decreases with increasing tree size in the density release of 600 trees·ha^{-1}, even though at lower magnitude compared with the first 10-year period. This means that, notwithstanding an increased inter-individual competition, after twenty years the level of competitive stress is not yet so heavy and small trees still outperform large trees in terms of RGR. The same cannot be said for the density release of 800 trees·ha^{-1}, even though the sign of the model slope is negative, since the regression line exhibits a nearly flat trend with increasing tree size. According to Larocque and Marshall (1993), an almost constant RGR with increasing size should indicate the onset of significant inter-individual competitive stress (i.e. the phase of crown interlock). Indeed, less growing space is available at a density release of 800 trees·ha^{-1} compared with a density release of 600 trees·ha^{-1}, and the threshold for the onset of significant inter-individual competitive stress will thus be reached more quickly, other parameters being equal. Conversely, the unthinned coppice (treatment C) has increasing RGR with increasing size, in the second 10-year period. According to Larocque and Marshall (1993) this means that inter-individual competition is so severe that the size hierarchy favors the larger trees. Asymmetric competition occurs where light, which is an asymmetric resource, is the primary limiting factor (Ford and Diggle 1981, Weiner 1990). The slope sign in the regression model provides evidence of asymmetric competition, and the slope magnitude provides a measure of the strength of inter-individual competitive stress. It is likely that a new self-thinning phase is ongoing that will end up suppressing the smaller individuals.

The modelled relationship of RGR with tree size, seems to support the hypothesis of Larocque and Marshall (1993) even for aged Turkey oak coppice under conversion into high forest.

Competition influences both the growth of individuals and how this growth is allocated (Perry 1985). When the resource availability (e.g. light, water, nutrients) drops below the combined demands of individuals, competition ensures that the resources are shared unequally between individuals in relation to their size (DeMalach et al. 2016, Soares et al. 2016). However, determining when inter-individual competition begins to negatively affect stand growth is difficult since many factors would need to be weighted.

Tree size is recognized as one of the most important predictors of growth (Zhang et al. 2017), and tree growth is the basic unit to model the liberating effect of (self-) thinning on released individuals (Franklin at al. 2009). Our modelling approach showed to what extent released individuals grew in relation to size hierarchy and, at same time, provided information concerning their competitive status conditional to overall stand density, over time.

Conclusions

Despite the large countrywide production of literature concerning coppice conversions, a lack of knowledge about optimal age, intensity, type, and timing of interventions still exists (Amorini and Fabbio 1987, Mariotti et al. 2017). The proposed modelling approach could be effectively applied either in coppices to be converted or to be left to natural evolution, the growth dynamics of which are still partly unknown (Fabbio 2016). For coppices to be converted, it could be applied to disclose the variability of individual growth responses at varying density releases and types of thinnings. In addition, the pattern of RGR as a function of tree size can be used to detect the optimal timing for further interventions.

For abandoned coppices, it could be helpful to increase knowledge (Amorini and Fabbio 1987, 1991, Amorini et al. 1996, 2006, 2010, Fabbio and Amorini 2006) of the growth hypotheses for coppice stands beyond the customary rotation ages (Bernetti 1981, Clauser 1981).

Growth dynamics of forests have usually been analysed in terms of absolute growth (increment per unit of time); nonetheless, RGR should be also considered for at least three reasons: *(i)* the absolute growth depends on initial sizes of individuals under comparison (Rees et al. 2010); *(ii)* large trees will always outperform small trees in absolute growth (Vospernik et al. 2010); and *(iii)* absolute growth only indicates that the growth of large trees is higher at any stage of competition and its relationship with tree size thus cannot be used to draw inferences regarding the effect of tree-to-tree competition (Larocque and Marshall 1993, Mayor and Rodà 1993, Cañellas et al. 2004).

Finally, the proposed experimental method of conversion represents a sound option for aged coppices of light-demanding species (e.g. oaks) under the uncertainty of repeated thinnings feasibility. It must be considered that conversion to high forest with customary protocols (e.g. repeated thinnings) requires rather intensive management, and single interventions may not always be economically sustainable for the owner (Motta et al. 2015). Moreover, we would also emphasize that the release densities we applied are quite unusual, both in the provisions of local laws (Apulia Region 2010) and in the scientific literature (La Marca et al. 2002).

References

Aarts E., Verhage M., Veenvliet J.V., Dolan C.V., van der Sluis S. 2014 – *A solution to dependency: using multi-level analysis to accommodate nested data.* Nature Neuroscience Nature Research 17: 491–496. doi.org/10.1038/nn.3648

Amorini E., Bruschini S., Cutini A., Di Lorenzo M.G., Fabbio G. 1996 – *Treatment of Turkey oak (*Quercus cerris *L.) coppices. Structure, biomass and silvicultural options.* Annali Istituto Sperimentale per la Selvicoltura 27: 121-129.

Amorini E., Fabbio G. 1986 - *L'avviamento all' altofusto nei cedui a prevalenza di cerro. Risultati di una prova sperimentale a 15 anni dalla sua impostazione. Primo contributo.* Annali Istituto Sperimentale per la Selvicoltura XVII: 7-101.

Amorini E., Fabbio G. 1987 - *Studio auxometrico in un ceduo invecchiato e in una fustaia da polloni di faggio, sull'Appennino toscano: Primo contributo.* Annali Istituto Sperimentale per la Selvicoltura XIV: 283-328.

Amorini E., Fabbio G. 1989 – *L'avviamento all'altofusto nei cedui a prevalenza di cerro. Risultati di una prova sperimentale a 15 anni dalla sua impostazione. Studio auxometrico. Secondo contributo.* Annali Istituto Sperimentale per la Selvicoltura XVIII: 19-70.

Amorini E., Fabbio G. 1991- *Ricerche sull'invecchiamento dei cedui: riflessi sul trattamento di conversione.* L'Italia Forestale e Montana XLV (3): 193-204.

Amorini E., Fabbio G. 1992 - *The coppice area in Italy. General aspects, cultivation trends and state of knowledge.* In: Proceeding of workshop 'Improvement of coppice forests in the Mediterranean region'. Arezzo, 1992. Annali Istituto Sperimentale per la Selvicoltura XXIII: 292-298.

Amorini E., Fabbio G., Cantiani P. 2006 – *Avviamento ad altofusto e dinamica naturale nei cedui a prevalenza di cerro. Risultati di una prova sperimentale a 35 anni dalla sua impostazione. Il protocollo di Valsavignone (Arezzo).* Annali Istituto Sperimentale per la Selvicoltura 33: 115-132. ISSN 0390-0010.

Amorini E., Fabbio G., Frattegiani M., Manetti M.C. 1988 - *L'affrancamento radicale dei polloni. Studio sugli apparati radicali in un soprassuolo avviato ad altofusto di faggio.* Annali Istituto Sperimentale per la Selvicoltura XIX: 201-261.

Amorini E., Fabbio G., Bertini G. 2010 – *Dinamica del ceduo oltre turno e avviamento ad alto fusto dei cedui di faggio. Risultati del protocollo "Germano Gambi" sull'Alpe di Catenaia (Arezzo).* Annali del Centro di Ricerca per la Selvicoltura 36: 151–172.

Apulia Region 2010 – *Regional Council Resolution n. 2250 (26/10/2010) – Interventi forestali e selvicolturali nelle aree protette: indicazioni tecniche.* Bollettino Ufficiale della Regione Puglia n. 166.

Assmann E. 1970 – *The principles of Forest Yield Study.* Pergamon Press Ltd.

Bernetti G. 1981 – *Ipotesi sullo sviluppo dei boschi cedui e relative considerazioni selvicolturali e assestamentali*. Monti e Boschi (5): 61-66.

Bertini G., Fabbio G., Piovosi M., Calderisi M. 2012 – *Densità di biomassa e necromassa legnosa in cedui invecchiati di leccio in Sardegna e di faggio in Toscana. [Tree biomass and deadwood density into aged holm oak (Sardinia) and beech coppices (Tuscany)]*. Forest@ 9: 108-129. doi.org/10.3832/efor0690009

Biondi E., Casavecchia S., Biscotti N. 2008 – *Forest biodiversity of the Gargano Peninsula and a critical revision of the syntaxonomy of the mesophilous woods of southern Italy*. Fitosociologia 45 (2): 93–127.

Blackman V.H. 1919 – *The compound interest law and plant growth*. Annals of Botany 33 (3): 353–360. doi.org/10.1093/oxfordjournals.aob.a089727

Boncina A., Kadunc A., Robic D. 2007 - *Effects of selective thinning on growth and development of beech (*Fagus sylvatica *L.) forest stands in south-eastern Slovenia*. Annals of Forest Science 64: 47–57. doi.org/10.1051/forest:2006087

Cañellas I., Del Río M., Roig S., Montero G. 2004 – *Growth response to thinning in Quercus pyrenaica coppice stands in Spanish central mountain*. Annals of Forest Science 61: 243–250. doi.org/10.1051/forest:2004017

Cannel M.G.R., Rothery P., Ford E.D. 1984 – *Competition within stands of* Picea sitchensis *and* Pinus contorta. Annals of Botany 53: 349-362.

Causton D.R., Venus J.C. 1981 – *The Biometry of Plant Growth*. Edward Arnold, London. 307 p.

Clauser F. 1981 – *Un'ipotesi auxonomica da verificare*. Monti e Boschi XXXII (2-3): 98-98.

Coleman J.S., McConnaughay K.D.M., Ackerly D.D. 1994 – *Interpreting phenotypic variation in plants*. Tree 9 (5).

Corcuera L., Camarero J.J., Sisó S., Gil-Pelegrin E. 2006 – *Radial-growth and wood-anatomical changes in overaged* Quercus pyrenaica *coppice stands: functional responses in a new Mediterranean landscape*. Trees 20: 91–98. doi.org/10.1007/s00468-005-0016-4

Cutini A. 2006 – *Taglio di avviamento, ceduazione e matricinatura: effetti sulle caratteristiche della copertura forestale in cedui a prevalenza di cerro*. Annali Istituto Sperimentale per la Selvicoltura 33: 21-30.

DeMalach N., Zaady E., Weiner J., Kadmon R. 2016 – *Size asymmetry of resource competition and the structure of plant communities*. Journal of Ecology 4: 899–910. doi.org/10.1111/1365-2745.12557

Evans G.C. 1972 – *The Quantitative Analysis of Plant Growth*. University of California Press.

Fabbio G. 1994 - *Dinamica della popolazione arborea in un ceduo di cerro in invecchiamento*. Annali Istituto Sperimentale per la Selvicoltura XXIII: 41-72.

Fabbio G. 2016 – *Coppice forests, or the changeable aspect of things, a review*. Annals of Silvicultural Research 40 (2): 108-132.

Fabbio G., Amorini E. 2006 – *Avviamento ad altofusto e dinamica naturale nei cedui a prevalenza di cerro. Risultati di una prova sperimentale a 35 anni dalla sua impostazione. Il protocollo di Caselli (Pisa)*. Annali Istituto Sperimentale di Selvicoltura Arezzo 33: 79–104.

Fisher R.A. 1921 – *Some remarks on the methods formulated in a recent article on 'The quantitative analysis of plant growth'*. Annals of Applied Biology 7: 367-372.

Ford E.D., Diggle P.J. 1981 – *Competition for light in a plant monoculture modelled as a spatial stochastic process*. Annals of Botany 48: 481-500.

Ford E.D. 1982 – *High Productivity in a Polestage Sitka Spruce Stand and its Relation to Canopy Structure*. Forestry 55(1). doi.org/10.1093/forestry/55.1.1

Franklin O., Aoki K., Seidl R. 2009 – *A generic model of thinning and stand density effects on forest growth, mortality and net increment*. Annals of Forest Science 66: 815. doi.org/10.1051/forest/2009073

Freckleton R.P., Watkinson A.R. 2001 – *Asymmetric competition between plant species*. Functional Ecology 15: 615 – 623.

Gasparini P., Tabacchi G. (a cura di) 2011 – *L'Inventario Nazionale delle Foreste e dei serbatoi forestali di Carbonio INFC 2005. Secondo inventario forestale nazionale italiano. Metodi e risultati*. Edagricole-Il Sole 24 ore, Bologna. 653 p. ISBN 978-88-506-5394-2.

Hoffmann W.A., Poorter H. 2002 – *Avoiding Bias in Calculations of Relative Growth Rate*. Annals of Botany 90 (1): 37–42. doi.org/10.1093/aob/mcf140

Hubert M. 1983 – *L'amélioration des taillis par balivage intensif*. Institut pour le Development Forestier, Paris.117 p.

Hunt R. 1982 - *Plant Growth Curves. The Functional Approach to Plant Growth Analysis*. Edward Arnold (Publishers) Limited.

La Marca O., Avolio S., Tomaiuolo M. 2008 – *Prove di avviamento ad altofusto in un ceduo di cerro (*Quercus cerris *L.) del Gargano: primi risultati*. Annali del Centro di Ricerca per la Selvicoltura 35: 25–33.

La Marca O., Marziliano P.A., Moretti N., Perna A., Santoro A. 2002 – *Prove di conversione in un ceduo di cerro (*Quercus cerris*) del Gargano*. L'Italia Forestale e Montana 6: 533–552.

La Marca O., Scopigno D., Tomaiuolo M. 2009 – *Primi risultati in prove di avviamento in un ceduo misto del Gargano*. Forest@ 6: 120–128.

Larocque G.R. 1998 – *Functional growth analysis of red pine trees under variable intensities of competition*. The Forestry Chronicle 74 (5).

Larocque G.R., Marshall P.R. 1993 – *Evaluating the impact of competition using relative growth rate in red pine (*Pinus resinosa *Ait.) stands*. Forest Ecology and Management 58 (1–2): 65-83. doi.org/10.1016/0378-1127(93)90132-7

Mairota P., Buckley P. 2018 – *The Status of Coppice Management within Forested Natura 2000 Sites*. In: "Coppice Forests in Europe". A. Unrau, G. Becker, R. Spinelli, D. Lazdina, N. Magagnotti, V.N. Nicolescu, P. Buckley, D. Bartlett, P.D. Kofman (Eds.). Freiburg i. Br., Germany: Albert Ludwig University of Freiburg: 135-138.

Mariotti B., Alberti G., Maltoni A., Tani A., Piussi P. 2017 – *Beech coppice conversion to high forest: results from a 31-year experiment in Eastern Pre-Alps*. Annals of Forest Science 74: 44. DOI: doi.org/10.1007/s13595-0170642-1

Mayor X., Rodà F. 1993 – *Growth response of holm oak (*Quercus ilex *L.) to commercial thinning in the Mont-*

seny mountains (NE Spain). Annales des sciences forestières, INRA/EDP Sciences 50 (3): 247-256. https://hal.archives-ouvertes.fr/hal-00882844

McGrath M.J., Luyssaert S., Meyfroidt P., Kaplan J.O., Bürgi M., Chen Y., Erb K., Gimmi U., McInerney D., Naudts K., Otto J., Pasztor F., Ryder J., Schelhaas M.J., Valade A. 2015 – *Reconstructing European forest management from 1600 to 2010.* Biogeosciences 12: 4291-4316. doi.org/10.5194/bg-12-4291-2015

Mencuccini M., Martínez Vilalta J., Vanderklein D., Hamid H.A., Korakaki E., Lee S., Michiels B. 2005 – *Size mediated ageing reduces vigour in trees.* Ecology Letters 8 (11): 1183-1190. doi.org/10.1111/j.1461-0248.2005.00819.x

Motta R., Berretti R., Dotta A., Motta Fre V., Terzuolo P.G. 2015 – *Il governo misto [Mixed management].* Sherwood - Foreste e alberi oggi 211: 5-9.

Müllerová J., Hédl R., Szabó P. 2015 – *Coppice abandonment and its implications for species diversity in forest vegetation.* Forest Ecolology and Management 343: 88-100. doi.org/10.1016/j.foreco.2015.02.003

Nicolescu V.N., Carvalho J., Hochbichler E., Bruckman V., Piqué-Nicolau M., Hernea C., Viana H., Štochlová P., Ertekin M., Tijardovic M., Dubravac T., Vandekerkhove K., Kofman P.D., Rossney D., Unrau A. 2017 – *Silvicultural guidelines for European coppice forests.* COST Action FP1301 Reports. Freiburg, Germany: Albert Ludwig University of Freiburg.

Notarangelo M., La Marca O., Moretti N. 2018 – *Long-term effects of experimental cutting to convert an abandoned oak coppice into transitional high forest in a protected area of the Italian Mediterranean region.* Forest Ecology and Management 430: 241-249. doi.org/10.1016/j.foreco.2018.08.012

Oliver C.D., Larson B.C. 1986 – *Forest Stand Dynamics, Update Edition.* Yale School of Forestry & Environmental Studies Other Publications.

Paine C.E.T., Marthews T.R, Vogt D.R., Purves D., Rees M., Hector A., Turnbull L.A. 2012 – *How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists.* Methods in Ecology and Evolution 3: 245–256. doi.org/10.1111/j.2041-210X.2011.00155.x

Perry D.A. 1985 – *The competition process in forest stands.* In: "Attributes of Trees as Crop Plant ". M.G.R. Cannell and J.E. Jackson, eds. Institute of Terrestrial Ecology, Abbots Ripton, Hunts: 481-506.

Pinheiro J., Bates D., DebRoy S., Sarkar D., R Core Team 2019 – *nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1.* https://CRAN.Rproject.org/package=nlme

Pinheiro J., Bates D. 2000 – *Mixed-Effects Models in S and S-PLUS.* SpringerVerlag New York.

Pommerening A., Muszta A. 2016 – *Relative plant growth revisited: Towards a mathematical standardisation of separate approaches.* Ecological Modelling 320: 383–392. dx.doi.org/10.1016/j.ecolmodel.2015.10.015

R Core Team 2019 – *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

Rees M., Osborne C.P., Woodward I., Hulme S.P., Turnbull L.A., Taylor S.H. 2010 – *Partitioning the Components of Relative Growth Rate: How Important Is Plant Size Variation?* The American Naturalist 176 (6). doi.org/10.1086/657037

Rentch J.S., Miller G.W., Gottschalk K.W. 2009 – *Crown Class Dynamics of Oaks, Yellow-Poplar, and Red Maple after Commercial Thinning in Appalachian Hardwoods: 20-Year Results.* Northern Journal of Applied Forestry 26(4).

Soares A.A.V., Leite H.G., Souza A.L., Silva S.R., Lourenço H.M., Forrester D.I. 2016 – *Increasing stand structural heterogeneity reduces productivity in Brazilian Eucalyptus monoclonal stands.* Forest Ecology and Management 373: 26-32. doi.org/10.1016/j.foreco.2016.04.035

South D.B. 1991 – *Testing the hypothesis that mean relative growth rates eliminate size-related growth differences in tree seedlings.* New Zealand Journal of Forestry Science 21(2/3): 144-164.

Stoneman G.L., Whitford K. 1995 – *Analysis of the concept of growth efficiency in Eucalyptus marginata (jarrah) in relation to thinning, fertilising and tree characteristics.* Forest Ecology and Management 76: 47-53.

Unrau A., Becker G., Spinelli R., Lazdina D., Magagnotti N., Nicolescu V.N., Buckley P., Bartlett D., Kofman P.D. 2018 – *Coppice Forests in Europe.* Freiburg i. Br., Germany: Albert Ludwig University of Freiburg. ISBN 978-39817340-2-7.

Van Laar A., Akça A. 2007 – *Forest Mensuration.* Springer, P.O. Box 17, 3300 AA Dordrecht, The Netherlands. ISBN-13 978-1-4020-5991-9.

Vanclay J.K. 1994 – *Modelling forest growth and yield : applications to mixed tropical forests.* CAB International, Wallingford, UK.

Vospernik S., Monserud R.A., Sterba H. 2010 – *Do individual-tree growth models correctly represent height: diameter ratios of Norway spruce and Scots pine?* Forest Ecology and Management 260: 1735–1753. dx.doi.org/10.1016/j.foreco.2010.07.055

Wareing P.F. 1966 - *The physiologist's approach to tree growth.* In: Physiology in Forestry (R.W.V. Palmer Ed.), Supplement to Forestry, Oxford University press, London: 7–18.

Weiner J. 1990 - *Asymmetric competition in plant populations.* Trends in Ecology and Evolution 5 (11): 360-364. doi.org/10.1016/0169-5347(90)90095-U

Wenk G., Antanaitis V., Smelko S. 1990 – *Waldertragslehre. [Forest growth and yield science].* Deutscher Landwirtschaftsverlag, Berlin.

Wenk G. 1978 – *Mathematische Formulierung von Wachstumsprozessen in der Forstwirtschaft. [Mathematical formulation of growth processes in forestry].* Beiträge für die forstwirtschaft 1: 25–30.

Westboy M. 1984 – *The self-thinning rule.* Advances in Ecological Research 14: 167–225.Zhang Z., Papaik M.J., Wang X., Hao Z., Ye J., Lin F., Yuan Z. 2017 – *The effect of tree size, neighborhood competition and environment on tree growth in an old-growth temperate forest.* Journal of Plant Ecology 10 (6): 970–980. doi.org/10.1093/jpe/rtw126