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Regular research paper

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SEEDLING SURVIVAL AND DYNAMICS OF UPPER TIMBERLINE IN CENTRAL APENNINES

ABSTRACT: Despite several studies on the timberline dynamics in Europe were carried out in the last decades, very few papers refer to mountain areas where the timberline is composed of broadleaved trees, and no research was conducted on the dynamics of Apennine beech timberline in relation to seedling survival. The research aim was to analyse the beech wood timberline dynamics in the central Apennines, with reference to seedling survival. Furthermore, factors affecting seedling survival were identified. To assess the forest ecotone dynamics, vegetation layer cover, rock fragment cover and information about forest management and *krummholz* occurrence were collected in sampling plots placed over 1,600 m a.s.l., on north-facing slopes. The beech seedlings occurring in *Brachypodium genuense*-dominated stands above the timberline were counted and monitored along two growing seasons. Soil temperature, soil moisture, and photosynthetically active radiation available for seedlings (PHAR) in grasslands above timberline were measured. The research outputs indicate that timberline is not a natural boundary and that there is no evidence of its extension upwards. The greatest number of beech seedlings was recorded in late spring. The one-year mortality rate ranged from 71 to 100%. None of the seedlings still alive in the early autumn of the first year were recorded in the following spring. The competitive exclusion by *Brachypodium genuense* individuals, which limit the incident PHAR, and the low soil moisture during summer, were identi-

fied as the main factors that account for the high mortality of seedlings and affect beech regeneration above timberline. The effect of competition is probably intensified by the lack of pioneer shrubs which could otherwise serve as nurse plants for beech seedlings and protect them from browsing by wild ungulates. Thus, both the current and the past land use may be considered as driving forces in timberline dynamics.

Probably, also the trend of global warming, that in the Mediterranean and sub-Mediterranean climatic context would determine the increase of summer drought stress, could worsen the effect of competitive exclusion of beech seedlings, so that it can be hypothesized that the expansion upwards of the upper timberline in the Apennines could be totally blocked.

KEY WORDS: beech seedling, competitive exclusion, photosynthetically active radiation, soil temperature, soil moisture, timberline

1. INTRODUCTION

During the past decades abandonment of agricultural practices has led to increased forest cover, a phenomenon widely studied in European countries (e.g. Lepart and Debussche 1992, Brändli 2000, MacDonald *et al.* 2000, Mather and Fairbairn 2000, Kaligarič *et al.* 2006, Gehrig-Fasel

et al. 2007). After the World War II, the socio-economic processes that caused the abandonment of wide parts of European high hill and mountainous lands did not leave the Apennine landscape unaffected (Foglia *et al.* 2007, Geri *et al.* 2010). In fact, in the Marche Region, from 1947 to 2000 the surface area of woodlands doubled (I.P.L.A. 2001). The forest expansion took place below the timberline, mostly in mountainous rural areas, to the detriment of arable lands, grasslands and forest clearings (Picchio *et al.* 2006, Catorci *et al.* 2007a). In the central Apennines the woodland upper limit ranges from 1,600 to 1,900 m a.s.l. (Stanisci *et al.* 2000, Di Giustino *et al.* 2002, Di Pietro 2009). As described by Crawford (1989), it is often abrupt, and lacks of ecotone with shrubby communities or *krummholz* (*sensu* Holtmeier 1981).

In the Apennine ridge as well as in high-mountain areas of all continents, the upper timberline is one of the most conspicuous vegetation boundaries, affording highly interesting locations for studying how global climatic change affects the environment. According to Holtmeier (2003), the study of timberline dynamics calls for a complex approach including management history, local climate, topography, and soil features. In fact, spatial and temporal timberline structures reflect past and ongoing changes caused by many external factors (*e.g.*, macro-climate and the effects of altitude) as well as internal factors specific to the ecotone (*e.g.*, micro-climate, soil condition, succession, and competition), interacting in a complex way. Many authors have indicated that the timberline dynamics is particularly affected by grazing pressure (Hofmann 1991; Woodward 1998; Körner and Paulsen 2004, Holtmeier and Broll 2005). If not affected by orographic influences or anthropogenic disturbances, the position and dynamics of timberline depends on successful natural regeneration (Holtmeier 2009). Regeneration can be expected only if viable seeds are produced and whether seedlings survive during the first years (Rammig *et al.* 2006). The main factors and processes controlling seed-based regeneration at timberline are: competition, environmental constraints, parasitic fungi, allelopathic effects and mechanical

damage (Holtmeier 1993). Most studies of timberline dynamics refer to conifer forests (Dullinger *et al.* 2005, Caccianiga *et al.* 2008; Smith *et al.* 2009). Instead, very few articles, refer to mountain areas where the timberline is composed of broadleaved trees (Stanisci *et al.* 2000, Di Giustino *et al.* 2002, Pezzi *et al.* 2008). Most of these papers deal with floristical, structural and climatic characterization of timberlines, while no studies have been conducted on the dynamics of Apennine beech timberline in relation to seedling survival.

Because of this lack of knowledge, this study sought to analyse the beech (*Fagus sylvatica* L. subsp. *sylvatica*) wood timberline dynamics in the central Apennines, with reference to seedling survival. The specific research goals were to: i) verify whether successional processes occur above timberline, ii) assess beech seedling survival above timberline, and iii) identify the factors that affect seedling survival.

2. MATERIALS AND METHODS

2.1. Study area

The study area is a mountainous territory of the central Apennines, included in the Monti Sibillini National Park (coordinates: 43°05'–42°45'N; 13°21'–13°01'E). It is placed above 1,600 m a.s.l., and characterized by calcareous substrates, slope angles ranging from 25 to 45 degrees, and included in the Temperate Bioclimatic Region (Rivas-Martínez and Rivas-Saenz 1996–2009). The main macro-climatic features are mean annual temperature of 7–8°C, mean annual rainfall of 1,300–1,500 mm, 3–4 months with minimum temperature lower than 0°C, no summer drought stress, and a growing period of 120–150 days (Catorci *et al.* 2008a).

The woods growing at the higher altitudes are referred to the *Cardamino kitaibelii-Fagetum sylvaticae* association (Catorci *et al.* 2010) included in the *Aremonio-Fagion sylvaticae* alliance (Biondi *et al.* 2002). In the study area, as well as in the central Apennines, beech trees produce seed every year (Catorci, unpublished).

There is evidence that the grasslands of the study area were used for centuries as sum-

mer pasture by thousands of sheep (Anselmi 1975, Di Stefano 1988) and that in the last decades there was a strong decrease in livestock husbandry. Many mountain grasslands are abandoned since 20–25 years (Catorci *et al.* 2008b); moreover populations of wild ungulates are on the rise, particularly deer and roe deer (Vitanzi *et al.* 2010).

2.2. Experimental design

To reduce the number of environmental variables and because areas that receive less solar radiation (north-facing slopes) have a higher probability of beech forest expansion (Dittmar *et al.* 2003), only beech timberline on north-facing slopes (NW-NE) was considered. As there are evidences that altitudinal gradient affects seedling survival and forest expansion rapidity (Tasser *et al.* 2007), only slopes with altitudes ranging from 1,600 to 1,800 m a.s.l. (excluding mountain crests and troughs) were selected.

The study was carried out in three steps, as follows. In order to assess upper forest ecotone structure and dynamics, twenty-four sampling plots covering 400 m² each (40 × 10 m) laid out perpendicularly to the timberline, were selected. The a priori sites selection was based on the plant landscape geodatabase of Marches and Umbria Regions (Orsomando and Catorci 2000, Catorci *et al.* 2007b, Pesaresi *et al.* 2007). Plots were composed of four subplots (10 × 10 m), two of which placed below the timberline (in woodland: subplots 1 and 2 in Fig. 1) and two above it (in grassland: subplots 3 and 4 in Fig. 1).

To check for the presence of beech seedlings and assess their survival during the growing season, only subplots placed above the timberline (subplots no. 3), in *Brachypodium genuense* (DC.) Roem. and Schult.-dominated stands (*B. genuense* cover greater than 75%), were considered. Twelve sites were surveyed on the whole. The choice of sampling areas next to the beech forest edge was made because it is well known that the relatively heavy beech seed does not fall far from the parent tree, and that the strongest natural reforestation takes place in direct proximity to the established tree stands (Tasser *et al.* 2007).

To identify the factors that affect seedling survival above the timberline, soil tempera-

ture, soil moisture and photosynthetically active radiation (PHAR) available for seedlings were monitored in three of the twelve sites.

2.3. Data collection

In 2007, the following data were collected for each subplot of the twenty-four 400 m² plots: species cover value (%); rock fragment

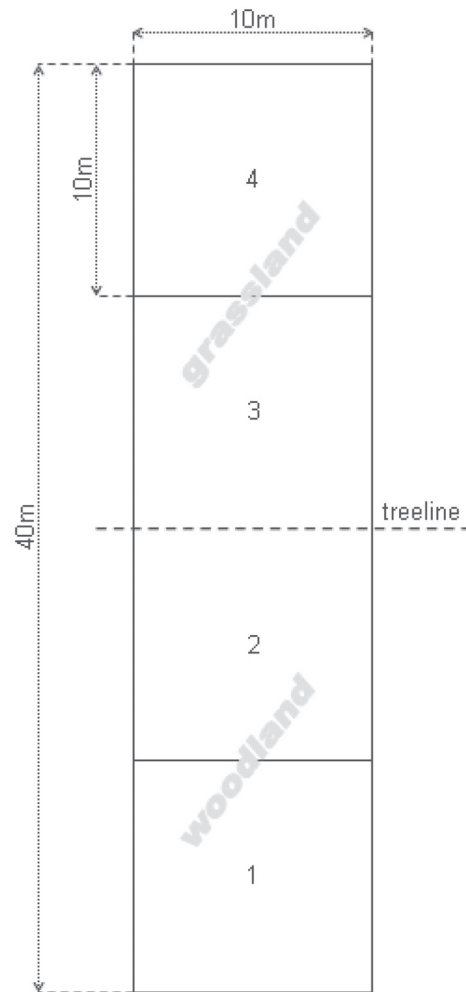


Fig. 1. Scheme of the 400 m² (40 × 10 m) sampling plot and arrangement of the four 100 m² (10 × 10 m) subplots. Subplots 1 and 2 fall in the wood below timberline; subplots 3 and 4 are placed in grasslands above timberline. In twenty-four 40 × 10 m plots information on species cover value, rock fragment cover, tree, shrub and herb layers cover (%), forest management, presence of beech *krummholz* were collected. In twelve 10 × 10 m *Brachypodium genuense*-dominated subplots (subplots no. 3) beech seedlings were counted; in three of them, soil temperature and moisture, and photosynthetically active radiation were measured.

cover (%); tree, shrub and herb layers cover (%); forest management; presence of beech *krummholz*. Information on time since last logging was drawn from forestry registers (*Corpo Forestale dello Stato* database).

In 2008, seedlings were counted in late spring (end of May), summer (early August) and early autumn (mid-September) in each of the twelve 100 m² subplots. Microsite features of surviving seedlings were noted. In 2009, these sites were examined again to count two-year-old seedlings (marked with wire flags in the previous year).

Soil temperature (°C) and moisture (%) were measured monthly from May to October 2008, at 10 cm of depth, using a digital soil temperature and moisture meter (tr-46908). PHAR ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) available for seedlings was measured at 10 cm above ground level, while the total available PHAR was measured at 50 cm above ground level (above the canopy of the herb layer). Light availability data were recorded monthly from June to September 2008 using a ceptometer (Decagon Devices, Pullman, WA, USA). In each site, data were randomly gathered between 11.00 a.m. and 2.00 p.m. on cloudless days, with twenty sampling replicates for soil temperature, thirty for soil moisture, and twenty for PHAR.

2.4. Data analysis

Average cover value and frequency of each species recorded in each 10 × 10 m subplot of the sampled twenty-four plots were calculated. Mean percent cover values of vegetation layers and rock fragments were calculated with reference to the subplots in which they occurred. Seedling mortality rates (% of dead beech seedlings at the end of the growing season compared to the number of spring seedlings) were calculated for each subplot.

Trends of soil temperature, soil moisture, and PHAR% (ratio of the PHAR measured at 10 cm above ground level to the incident PHAR, above the canopy of the herbaceous layer) were presented in graphs. Normality distribution and variance homogeneity of environmental data series were assessed using Kolmogorov-Smirnov test and Levene test, respectively. Because data did not meet assumptions for parametric tests, Friedman non-parametric test was used to detect statistically significant differences ($P < 0.05$) in environmental parameters between consecutive months along the growing season. After rejection of null hypothesis of Friedman test, in order to understand which months are significantly different from each other in terms of soil temperature, soil moisture, and PHAR%,

Table 1. Mean rock fragment cover and mean cover percent values of vegetation layers (\pm standard deviation), calculated on the subplots in which they occurred. Percentages of occurrence are also reported. Subplots falling in the wood below timberline (1–2) and in grassland above timberline (3–4) are reported. Timberline lies between subplots 2 and 3.

Sub-plot	Rock fragment		High forest	<i>Krummholz</i>	Tree layer		Shrub layer				Herb layer			
	Occurrence (%)	Cover (%)			Occurrence (%)	Cover (%)	Low shrub (height <2.5 m)	Tall shrub (height 2.5–5.0 m)	Total	Occurrence (%)	Cover (%)			
1	92	16 \pm 13.8	92	8	100	92 \pm 8.5	83	9 \pm 5.5	67	7 \pm 5.9	92	11 \pm 8.0	100	10 \pm 4.0
2	25	14 \pm 12.0	83	17	100	88 \pm 14.5	83	8 \pm 5.6	42	11 \pm 9.3	92	12 \pm 10.0	100	18 \pm 9.0
3	75	19 \pm 18.3	–	8	8	2 \pm 1.8	33	5 \pm 4.7	8	2 \pm 1.8	42	8 \pm 7.8	100	82 \pm 14.8
4	67	23 \pm 18.6	–	0	0	0	33	1 \pm 0.3	0	0	33	1 \pm 0.3	100	87 \pm 14.5

non-parametric Wilcoxon matched-pairs tests were performed. A Bonferroni adjustment for multiple comparisons of Wilcoxon test results was used to avoid Type I error.

Statistical elaborations were run using SPSS software, version 8.0 (SPSS Inc. 1997).

3. RESULTS

The average cover values and frequencies of the species recorded in the twenty-four plots were reported in the Appendix. Very few young, mostly shrubby, beech individuals were recorded in about 12% of subplots above the timberline, covering 11–20% of their surface (on average less than 1% per subplot). Low shrubs were observed in 33% of subplots and tall shrubs in 4% of them, covering 1–20% and about 10% of their surface, respectively (on average 1% and less than 0.5% per subplot).

The analysed beech woods are managed as high forest (88% of forest subplots) and have not been cut down for at least fifty years. Mature beech even-aged individuals cover 100% of the forest subplots surface; thus, the potential seed trees grow near and along the forest edge. *Krummholz* were found in the remaining 12% of subplots, most of which are located near rock walls and have a higher percentage of rock fragment cover (20–65% of the subplot surface). Grasslands were ob-

served in all subplots above timberline; they are mostly characterized by *Brachypodium genuense* (recorded in all the subplots, with an average coverage of about 50% of their surface). Table 1 shows the cover and occurrence percentages of rock fragment, tree, shrub and herb layers, and the occurrence percentages of high forest beech woods and *krummholz*.

The greatest number of seedlings in *Brachypodium genuense*-dominated stands was observed in late spring, at the end of May. In 50% of subplots, less than 10 seedlings (0.10 individuals m⁻²) were recorded, while the other subplots had numbers of seedlings ranging from 12 to 80 (0.12 to 0.80 individuals m⁻²) (Table 2). Mortality rate of seedlings during the growing season ranged from 71 to 100%. In the second year, none of the 51 seedlings still alive in the early autumn (61% of which growing near or in the shadow of rocks, 30% in grass turf gaps, and 9% under the canopy of *Brachypodium genuense*) of the first year were recorded.

Regarding trends of the environmental features of the *Brachypodium genuense*-dominated stands, soil temperature peaked in July (around 13–15°C), when soil moisture had its minimum values (around 2–3%) (Fig. 2). The highest values of available PHAR% (Fig. 3) were recorded in June (82%) and the lowest in July (11%). Statistically significant differences ($P < 0.05$) were recorded for soil tem-

Table 2. Number of *Fagus sylvatica* seedlings per square metre in the twelve *Brachypodium genuense*-dominated subplots, and their respective one-year mortality rates in 2008.

No.	Seedlings m ⁻²			One-year mortality rate (%)
	Late spring	Summer	Early autumn	
1	0.80	0.50	0.23	71
2	0.08	0.05	0.01	88
3	0.04	0.02	0.01	75
4	0.65	0.35	0.18	72
5	0.14	0.03	0.01	93
6	0.06	0.03	0.00	100
7	0.12	0.08	0.03	75
8	0.00	0.00	0.00	–
9	0.01	0.01	0.00	100
10	0.01	0.01	0.00	100
11	0.21	0.08	0.04	81
12	0.42	0.21	0.00	100

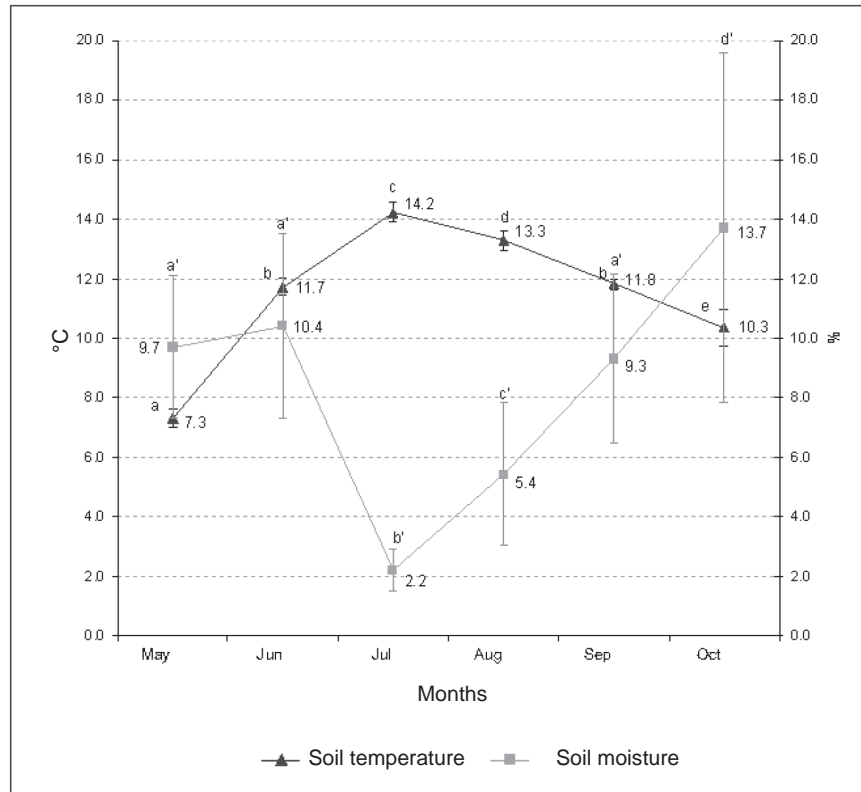


Fig. 2. Trends in soil temperature and moisture in the grassland during the growing season. Vertical bars indicate standard deviation. Different letters above bars indicate statistical difference ($P < 0.003$).

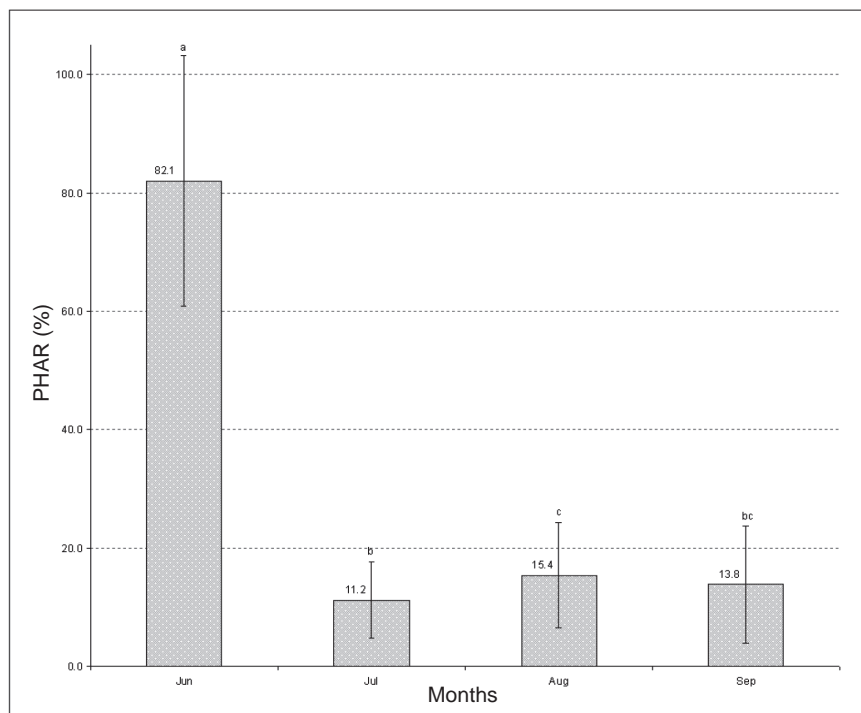


Fig. 3. Photosynthetically active radiation (PHAR in %) available for beech seedlings (ratio of the PHAR measured below the vegetation at 10 cm above ground to the total incident PHAR). Error bars indicate standard deviation. Different letters above bars indicate statistical difference ($P < 0.008$).

perature ($X^2(5) = 284.829$, $P = 0.000$), soil moisture ($X^2(5) = 319.434$, $P = 0.000$), and PHAR ($X^2(3) = 126.000$, $P = 0.000$). Significant variations ($P < 0.003$) in soil temperature and moisture were observed from May to October, except between May and June with regard to soil moisture ($Z = -1.690$, $P = 0.091$). About PHAR, statistically significant variations ($P < 0.008$) were recorded from June to July ($Z = -6.737$, $P = 0.000$), and from July to August ($Z = -6.739$, $P = 0.000$).

4. DISCUSSION

The research outputs indicate that there is no evidence of timberline extension upwards. Indeed, the forest edge was characterized by old high trees able to produce seeds and the border between forest and grassland is mostly abrupt, namely without a gradient of tree age and size. Also the absence or very low frequency and cover value of young beech or shrub individuals above the beech forest edge indicate the absence of successional processes, except for very few areas where the presence of young beech individuals was detected. These findings are in accordance with Pezzi *et al.* (2007), who observed limited and extremely localized upwards extension of the beech wood upper limit in the northern Apennines.

The presence in the study area of mature and high trees at timberline and the absence of *krummholz* (recorded only in harsh environmental conditions due to high outcropping rock cover) lead us to consider the current upper limit of the woods as unnatural. In fact, natural tree lines usually show a transition between forest and herbaceous vegetation, in which the growth of individuals is usually very stunted, with the uppermost ones forming low, densely matted bushes (Holtmeier 2009). Moreover, Tasser *et al.* (2007) argued that in central Apennines the potential climatic tree line lies approximately at 2,000 m a.s.l. Hence, timberline naturalness cannot be considered the reason for general timberline stability in the study area.

In addition, grazing is not a constraint for the upwards expansion of woods: the grasslands above timberline here are mainly *Brachypodium genuense*-dominated stands, and it is well known that they develop due to

abandonment of grazing (Wilson *et al.* 1995, Buckland *et al.* 2001, Catorci *et al.* 2011a).

Rammig *et al.* (2006) argued that seed availability, seedling survival and the presence of advance regeneration are key processes for successful reforestation. Seasonal monitoring of beech seedlings highlighted that most of them die before the growing season ends. Surviving ones were found in shelter niches near rocks or in *Brachypodium genuense* canopy openings. This is consistent with Vanderberghe *et al.* (2006), who demonstrated that gaps in grass turf have a positive influence on the early stages of tree development. Moreover, it is known that the eco-physiological characteristics of *Fagus sylvatica* make the survival of isolated young individuals difficult (Crawford 1989, Pezzi *et al.* 2008). Indeed, the survival rate of seedlings within shrub communities is higher than that of appearing in pure grass communities (Hiroki and Matsubara 1995). Hence, the very low cover of pioneer shrubs recorded in this study, inside the subplots placed above the timberline, might negatively affect the extension upwards of the beech woods upper limit.

The high mortality of seedlings during the first year is probably due to local environmental constraints. It is well known that soil temperature, water availability, and light intensity are limiting factors for beech seedling establishment and growth (Larcher 1980, Stephenson 1990, Minotta and Pinzauti 1996, Scarascia-Mugnozza 1999, Coll *et al.* 2003). In the study area, assessment of light availability for seedlings inside the *Brachypodium genuense*-dominated stands indicated a strong decrease at ground level in July and August (11–15% of incident radiation), when *Brachypodium genuense* individuals reach their maximum height and cover value (Catorci *et al.* 2011b). Since about 40% of incident radiation at ground level is optimal for beech seedling growth (Oswald 1981), it is possible to state that during July and August, the solar incident radiation is insufficient for beech seedling survival. Beech seedlings only have optimal light conditions in June, and this could explain why they start to die after this period.

Furthermore, in July and August the soil moisture value is very low (ranging from 2 to 6%). This may be due to the summer decrease

in rainfall and increase in temperature, and to the strong water demand of growing individuals of *Brachypodium genuense*, because of their increasing photosynthetic activity and evapotranspiration rate. Seedlings are prone to water deficit because they have not yet developed a root system capable of replacing water loss through transpiration (Baeza *et al.* 1991, Espelta *et al.* 2003), subsequently low moisture availability limits seedlings survival (Rey Benayas *et al.* 2005). All these findings are in accordance with those of Frochot *et al.* (1986), Davies (1987) and Davies *et al.* (1999), who demonstrated that tall grasses are the most harmful for young tree growth through competition for water or nutrients. Furthermore, Husheer *et al.* (2006) demonstrated that turf removal increased beech seedling growth and survival, indicating that competition with grasses has a direct effect on beech regeneration.

Seedling that survived the first growing season were not found in the second year of data collection, probably because of browsing pressure from wild ungulates, which is known to be a key factor in failure of broad-leaf seedling establishment (Kuiters *et al.* 1996, Husheer *et al.* 2006).

5. CONCLUSIONS

The findings of the present research indicate that in the study area, forest expansion upwards is blocked by the combination of different environmental constraints, and that the decrease in livestock grazing does not facilitate the upwards expansion of beech woods. However, multi-year environmental data collection could be useful for assessing the effects of inter-annual climatic variability on beech seed production and seedling viability.

The most important driving force for timberline stability turns out to be the competitive exclusion of beech seedlings due to the dominance of *Brachypodium genuense* in abandoned stands, given the low value of summer soil moisture and light intensity at ground level. The effect of competition is probably intensified by the lack of pioneer shrubs, which could otherwise serve as nurse plants (*sensu* Padilla and Pugnaire 2006) for beech seedlings and protect them from

browsing by wild ungulates, as demonstrated by Rousset and Lepart (1999) and Smit *et al.* (2006). Their absence is due to the destruction of the natural subalpine shrub communities by farmers in the past century (Marchesoni 1957). Thus, it is possible to state that, in the study area, also the past land use may be considered as driving force in timberline dynamics. Humans not only lowered the upper timberline, but also considerably changed the floristic composition of the timberline ecotone, and this change seems to interfere with the current timberline extension upwards.

Finally, the trend of global warming, which in temperate mountains seems to favour the expansion upwards of forest upper limit (Caccianiga *et al.* 2008, Smith *et al.* 2009), probably will have the opposite effects in the mediterranean and sub-mediterranean climatic context, because it would increase summer drought stress, which in turn could worsen the effect of competitive exclusion of beech seedlings.

Furthermore, our findings indicated that in Mediterranean mountain the beech seedling survival is very hard even in the north-facing slopes, so that one can hypothesize that beech expansion could be impossible in south-facing slopes, where high radiation dramatically reduces the soil water content (Joffre and Rambal 1993). So that it is possible to state that nowadays the expansion upwards of the upper timberline in the Apennines could be totally blocked. More studies are needed to clarify this issue and to assess its implications from the ecosystem management viewpoint.

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APPENDIX. Mean cover and occurrence percent values of species in each subplot of the sampled twenty-four plots. Values lower than 0.5 are indicated with "r".

Species	Subplot no.							
	1		2		3		4	
	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)
Tree layer								
<i>Fagus sylvatica</i> L. subsp. <i>sylvatica</i>	100	91	100	88	8	r	0	0
<i>Sorbus aria</i> (L.) Crantz subsp. <i>aria</i>	25	1	17	1	8	r	0	0
<i>Sorbus aucuparia</i> L. subsp. <i>aucuparia</i>	25	1	33	2	0	0	0	0
<i>Laburnum anagyroides</i> Medik. subsp. <i>anagyroides</i>	25	1	8	r	0	0	0	0
Shrub layer								
<i>Fagus sylvatica</i> L. subsp. <i>sylvatica</i>	67	8	75	9	17	3	0	0
<i>Rubus idaeus</i> L.	50	1	25	1	0	0	0	0
<i>Rosa pendulina</i> L.	17	r	17	1	0	0	0	0
<i>Juniperus communis</i> L. var. <i>saxatilis</i> Pall.	0	0	0	0	25	1	25	r
<i>Rosa arvensis</i> Huds.	0	0	17	1	0	0	0	0
<i>Rosa canina</i> L.	0	0	0	0	0	0	8	r
Herb layer								
<i>Achillea millefolium</i> L.	0	0	0	0	17	1	25	1
<i>Achillea tenorii</i> Grande	0	0	8	0	25	1	25	1
<i>Acinos alpinus</i> (L.) Moench	0	0	0	0	25	1	25	1
<i>Adenostyles australis</i> (Ten.) Nyman	83	1	58	1	0	0	0	0
<i>Aethionema saxatile</i> (L.) R. Br.	0	0	0	0	17	1	17	1
<i>Agrostis capillaris</i> L.	0	0	0	0	25	1	50	3
<i>Ajuga reptans</i> L.	0	0	43	1	8	r	0	0
<i>Alchemilla nitida</i> Buser	0	0	0	0	50	2	67	5
<i>Allium sphaerocephalon</i> L.	0	0	0	0	25	1	17	1
<i>Anthemis cretica</i> L. subsp. <i>columnae</i> (Ten.) Franzén	0	0	8	0	8	r	17	1
<i>Anthoxanthum odoratum</i> L. subsp. <i>odoratum</i>	0	0	0	0	0	0	17	1
<i>Anthyllis vulneraria</i> L. subsp. <i>rubriflora</i> (DC.) Arcang.	0	0	0	0	33	2	33	2
<i>Arabis collina</i> Ten.	0	0	0	0	8	r	17	1
<i>Arabis hirsuta</i> (L.) Scop.	0	0	25	r	58	3	50	2
<i>Arenaria serpyllifolia</i> L.	0	0	8	0	17	1	25	1
<i>Armeria canescens</i> (Host) Boiss.	0	0	0	0	50	2	83	3
<i>Asperula cynanchica</i> L.	0	0	8	r	75	3	83	7
<i>Asplenium trichomanes</i> L. subsp. <i>quadrivalens</i> D.E. Mey.	0	0	8	r	0	0	0	0
<i>Astragalus sempervirens</i> Lam.	0	0	8	0	17	1	8	r
<i>Avenula praetutiana</i> (Parl.) Pignatti	0	0	0	0	42	2	58	4
<i>Biscutella laevigata</i> L. subsp. <i>laevigata</i>	0	0	8	r	25	1	42	2
<i>Bellardiochloa variegata</i> (Lam.) Kerguélen	0	0	0	0	0	0	8	r
<i>Bellis perennis</i> L.	0	0	0	0	8	r	0	0
<i>Brachypodium genuense</i> (DC.) Roem. & Schult.	0	0	75	2	100	49	100	48
<i>Briza media</i> L.	0	0	0	0	0	0	17	1
<i>Bromus erectus</i> Huds. subsp. <i>erectus</i>	0	0	0	0	0	0	17	2
<i>Bunium bulbocastanum</i> L.	0	0	25	r	58	2	58	2

Species	Subplot no.							
	1		2		3		4	
	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)
<i>Bupleurum falcatum</i> L. subsp. <i>cernuum</i> (Ten.) Arcang.	0	0	8	r	17	1	17	1
<i>Cachrys ferulacea</i> (L.) Calestani	0	0	8	0	8	r	8	r
<i>Campanula glomerata</i> L.	0	0	42	1	58	3	42	2
<i>Campanula micrantha</i> Bertol.	25	r	42	r	58	2	67	3
<i>Cardamine bulbifera</i> (L.) Crantz	50	1	42	r	8	r	0	0
<i>Cardamine enneaphyllos</i> (L.) Crantz	33	r	33	r	8	r	0	0
<i>Carduus carlinaefolius</i> Lam.	0	0	0	0	0	0	17	1
<i>Carduus nutans</i> L.	0	0	8	r	75	3	83	3
<i>Carex caryophyllea</i> La Tourr.	0	0	0	0	8	r	25	1
<i>Carex macrolepis</i> DC.	0	0	0	0	58	3	58	7
<i>Carlina acaulis</i> L. subsp. <i>caulescens</i> (Lam.) Schubl. & G. Martens	0	0	0	0	8	r	25	1
<i>Carum flexuosum</i> (Ten.) Nyman	0	0	8	r	8	r	17	1
<i>Cerastium arvense</i> L. subsp. <i>suffruticosum</i> (L.) Ces.	25	r	17	r	100	4	100	7
<i>Cerastium tomentosum</i> L.	0	0	0	0	8	r	8	r
<i>Chaerophyllum aureum</i> L.	0	0	8	r	0	0	0	0
<i>Cirsium morisianum</i> Rchb.	0	0	0	0	8	r	8	r
<i>Coeloglossum viride</i> (L.) Hartm.	0	0	0	0	0	0	8	r
<i>Coronilla minima</i> L.	0	0	0	0	8	r	0	0
<i>Corydalis cava</i> (L.) Schweigg. & Koerte subsp. <i>cava</i>	0	0	8	r	0	0	0	0
<i>Cruciata glabra</i> (L.) Ehrend. subsp. <i>glabra</i>	0	0	8	r	8	r	8	r
<i>Cruciata laevipes</i> Opiz	0	0	0	0	8	r	0	0
<i>Cyanus triumfetti</i> (All.) Dostál ex Á. & D. Löve	0	0	0	0	8	r	8	r
<i>Cynoglossum magellense</i> Ten.	0	0	8	r	25	r	50	2
<i>Cynosurus cristatus</i> L.	0	0	0	0	0	0	8	r
<i>Cynosurus echinatus</i> L.	0	0	0	0	8	r	0	0
<i>Cystopteris montana</i> (Lam.) Desv.	25	r	0	0	8	r	8	r
<i>Dactylis glomerata</i> L. subsp. <i>glomerata</i>	0	0	17	r	25	1	0	0
<i>Delphinium fissum</i> Waldst. & Kit.	0	0	8	r	8	r	8	r
<i>Dianthus carthusianorum</i> L. subsp. <i>carthusianorum</i>	0	0	0	0	8	r	8	r
<i>Dianthus monspessulanus</i> L.	0	0	17	r	58	2	67	2
<i>Dianthus sylvestris</i> Wulfen subsp. <i>longicaulis</i> (Ten.) Greuter & Burdet	0	0	8	r	25	1	33	2
<i>Digitalis lutea</i> L. subsp. <i>australis</i> (Ten.) Arcang.	0	0	8	r	0	0	0	0
<i>Doronicum columnae</i> Ten.	50	1	67	1	58	2	75	4
<i>Edraianthus graminifolius</i> (L.) DC.	0	0	0	0	17	1	8	r
<i>Erysimum pseudorhaeticum</i> Polatschek	0	0	0	0	8	r	8	r
<i>Euphorbia cyparissias</i> L.	0	0	0	0	42	1	42	1
<i>Festuca dimorpha</i> Guss.	25	r	25	r	42	4	42	5
<i>Festuca heterophylla</i> Lam.	0	0	33	r	33	2	42	3
<i>Festuca laevigata</i> Gaudin subsp. <i>laevigata</i>	0	0	33	1	75	8	83	21
<i>Fragaria vesca</i> L. subsp. <i>vesca</i>	0	0	17	r	0	0	8	r
<i>Galium anisophyllum</i> Vill.	25	r	17	r	42	2	67	3

Species	Subplot no.							
	1		2		3		4	
	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)
<i>Galium corrudifolium</i> Vill.	25	r	17	r	42	2	42	2
<i>Galium odoratum</i> (L.) Scop.	50	1	42	1	25	1	8	r
<i>Galium verum</i> L.	0	0	8	0	33	3	17	2
<i>Gentiana lutea</i> L.	0	0	0	0	50	2	50	2
<i>Gentiana verna</i> L.	0	0	0	0	8	r	17	1
<i>Geum urbanum</i> L.	0	0	8	0	8	r	17	1
<i>Globularia meridionalis</i> (Podp.) O. Schwarz	0	0	0	0	17	r	17	1
<i>Grafia golaka</i> (Hacq.) Rchb.	0	0	8	0	17	r	17	r
<i>Helianthemum nummularium</i> (L.) Miller subsp. <i>grandiflorum</i> (Scop.) Sch. & Th.	0	0	0	0	58	2	42	2
<i>Helianthemum nummularium</i> (L.) Miller subsp. <i>obscurum</i> (Celak.) Holub	0	0	0	0	8	r	0	0
<i>Helianthemum oelandicum</i> (L.) DC. subsp. <i>alpestre</i> (Jacq.) Breistr.	0	0	0	0	8	r	8	1
<i>Helleborus bocconeii</i> Ten. subsp. <i>bocconeii</i>	0	0	8	0	17	1	17	1
<i>Hepatica nobilis</i> Schreb.	25	r	17	r	8	0	8	r
<i>Hieracium cymosum</i> L.	0	0	0	0	33	1	50	2
<i>Hieracium glaucinum</i> Jordan	0	0	8	r	0	0	0	0
<i>Hieracium murorum</i> L. (group)	0	0	0	0	17	1	8	r
<i>Hieracium pilosella</i> L.	0	0	0	0	0	0	25	1
<i>Hieracium piloselloides</i> Vill.	0	0	0	0	33	1	25	1
<i>Hieracium pilosum</i> Schleich. ex Froel.	25	r	8	r	8	r	25	1
<i>Hieracium sabaudum</i> L.	0	0	0	0	8	r	17	1
<i>Hippocrepis comosa</i> L.	0	0	0	0	25	1	8	r
<i>Hypericum montanum</i> L.	0	0	0	0	8	r	8	r
<i>Knautia purpurea</i> (Vill.) Borbas	0	0	0	0	8	r	17	1
<i>Koeleria lobata</i> (M. Bieb.) Roem. & Schult.	0	0	0	0	8	r	25	2
<i>Lactuca muralis</i> (L.) Gaertn.	83	2	67	1	17	1	8	r
<i>Lamium bifidum</i> Cirillo	0	0	17	r	0	0	0	0
<i>Lamium maculatum</i> L.	0	0	8	r	0	0	0	0
<i>Laserpitium latifolium</i> L.	0	0	17	r	0	0	8	r
<i>Laserpitium siler</i> L. subsp. <i>siculum</i> (Spreng.) Santangelo, F. Conti & Gubellini	0	0	0	0	17	1	17	1
<i>Lathyrus venetus</i> (Mill.) Wohlf.	0	0	8	r	0	0	0	0
<i>Leontodon cichoraceus</i> (Ten.) Sanguin.	0	0	0	0	0	0	17	1
<i>Leontodon hispidus</i> L.	0	0	8	r	25	1	25	1
<i>Leontodon montanus</i> Lam.	0	0	8	r	8	r	0	0
<i>Leucanthemum adustum</i> (Koch) Gremler	0	0	0	0	58	2	83	4
<i>Lilium bulbiferum</i> L. subsp. <i>croceum</i> (Chaix) Jan	0	0	8	r	17	1	17	1
<i>Lilium martagon</i> L.	0	0	17	r	8	r	8	r
<i>Linaria purpurea</i> (L.) Mill.	0	0	8	r	8	r	8	r
<i>Linum alpinum</i> Jacq.	0	0	0	0	25	1	17	1
<i>Linum catharticum</i> L. subsp. <i>catharticum</i>	0	0	0	0	8	r	25	1
<i>Lotus corniculatus</i> L. subsp. <i>corniculatus</i>	0	0	8	r	83	4	100	6
<i>Luzula sylvatica</i> (Huds.) Gaudin subsp. <i>sieberi</i> (Tausch) K. Richt.	0	0	17	r	50	2	58	1

Species	Subplot no.							
	1		2		3		4	
	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)
<i>Luzula sylvatica</i> (Huds.) Gaudin subsp. <i>sylvatica</i>	0	0	0	0	8	r	8	r
<i>Medicago lupulina</i> L.	0	0	0	0	25	1	17	1
<i>Melica uniflora</i> Retz.	0	0	17	r	0	0	0	0
<i>Melittis melissophyllum</i> L. subsp. <i>melissophyllum</i>	25	r	17	r	8	r	0	0
<i>Minuartia verna</i> (L.) Hiern subsp. <i>collina</i> (Neilr.) Halliday	0	0	0	0	17	1	50	2
<i>Muscari neglectum</i> Guss.	0	0	1	0	1	17	0	17
<i>Myosotis alpestris</i> F. W. Schmidt	0	0	0	0	1	8	0	17
<i>Orchis mascula</i> L.	0	0	0	0	0	0	0	8
<i>Pedicularis comosa</i> L.	0	0	1	0	1	25	0	17
<i>Pedicularis elegans</i> Ten.	0	0	1	0	1	17	0	25
<i>Phleum rhaeticum</i> (Humphries) Rauschert	0	0	1	0	1	17	0	17
<i>Phyteuma orbiculare</i> L.	0	0	1	33	2	33	0	50
<i>Plantago media</i> L.	0	0	8	r	8	r	8	r
<i>Poa alpina</i> L.	25	r	33	r	83	3	67	5
<i>Poa nemoralis</i> L.	50	r	33	r	8	r	0	0
<i>Polygala vulgaris</i> L.	0	0	0	0	0	0	8	r
<i>Polystichum lonchitis</i> (L.) Roth	33	1	33	r	8	r	8	r
<i>Potentilla rigoana</i> Th. Wolf	0	0	0	0	50	2	67	3
<i>Prenanthes purpurea</i> L.	50	1	8	r	0	0	8	r
<i>Primula veris</i> L. subsp. <i>columnae</i> (Ten.) Lüdi	0	0	8	r	17	1	17	1
<i>Pulsatilla alpina</i> (L.) Delarbre subsp. <i>millefoliata</i> (Bertol.) D.M. Moser	0	0	0	0	33	1	25	1
<i>Ranunculus apenninus</i> (Chiov.) Pignatti	0	0	0	0	0	0	8	r
<i>Ranunculus lanuginosus</i> L.	50	1	33	r	17	1	8	r
<i>Ranunculus millefoliatus</i> Vahl	0	0	0	0	8	r	17	1
<i>Ranunculus oreophilus</i> Bieb.	0	0	8	r	25	1	33	1
<i>Rhinanthus wettsteinii</i> (Sterneck) Soó	0	0	0	0	17	1	42	2
<i>Robertia taraxacoides</i> (Loisel.) DC.	0	0	0	0	0	0	8	r
<i>Rumex alpestris</i> Jacq.	0	0	8	r	0	0	0	0
<i>Rumex nebroides</i> Campd.	0	0	50	1	92	3	83	4
<i>Rumex scutatus</i> L.	0	0	0	0	0	0	17	1
<i>Saxifraga bulbifera</i> L.	0	0	0	0	25	1	42	2
<i>Saxifraga paniculata</i> Miller subsp. <i>paniculata</i>	0	0	8	r	17	1	0	0
<i>Saxifraga rotundifolia</i> L. subsp. <i>rotundifolia</i>	25	r	17	r	8	r	8	1
<i>Saxifraga tridactylites</i> L.	0	0	0	0	8	r	0	0
<i>Scilla bifolia</i> L.	0	0	8	r	0	0	0	0
<i>Sedum acre</i> L.	0	0	0	0	25	1	17	1
<i>Sedum dasyphyllum</i> L.	0	0	0	0	8	r	0	0
<i>Sedum hispanicum</i> L.	0	0	17	r	8	r	8	r
<i>Sedum rupestre</i> L. subsp. <i>rupestre</i>	0	0	17	r	58	3	58	2
<i>Sedum sexangulare</i> L.	0	0	0	0	0	0	17	1
<i>Sempervivum arachnoideum</i> L.	0	0	0	0	0	0	8	r

Species	Subplot no.							
	1		2		3		4	
	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)	occurrence (%)	mean cover (%)
<i>Senecio doronicum</i> L.	25	1	17	r	83	4	75	3
<i>Seseli libanotis</i> (L.) Koch	0	0	17	r	8	r	8	r
<i>Sesleria juncifolia</i> Suffren subsp. <i>juncifolia</i>	0	0	8	r	17	1	17	2
<i>Sesleria nitida</i> Ten.	0	0	25	r	17	1	17	3
<i>Silene ciliata</i> Pourr. subsp. <i>graefferi</i> (Guss.) Nyman	0	0	0	0	50	2	50	2
<i>Silene dioica</i> (L.) Clairv.	25	r	8	r	0	0	0	0
<i>Silene italica</i> (L.) Pers. subsp. <i>italica</i>	0	0	17	r	17	1	17	1
<i>Silene italica</i> (L.) Pers. subsp. <i>nemoralis</i> (W.aldst. & Kit.) Nyman	0	0	17	r	0	0	0	0
<i>Silene multicaulis</i> Guss.	0	0	0	0	17	1	25	1
<i>Silene otites</i> (L.) Wibel subsp. <i>otites</i>	0	0	8	r	8	r	25	1
<i>Silene vulgaris</i> (Moench) Garcke subsp. <i>vulgaris</i>	0	0	0	0	8	r	8	r
<i>Solidago virgaurea</i> L. subsp. <i>virgaurea</i>	0	0	17	1	0	0	0	0
<i>Stachys alopecuroides</i> (L.) Bentham subsp. <i>divulsa</i> (Ten.) Pignatti	0	0	8	r	25	1	17	1
<i>Stellaria holostea</i> L.	0	0	8	r	8	r	0	0
<i>Stellaria media</i> (L.) Vill. subsp. <i>media</i>	33	r	25	r	0	0	0	0
<i>Stellaria nemorum</i> L. subsp. <i>nemorum</i>	25	r	8	r	8	r	0	0
<i>Thymus longicaulis</i> C. Presl	0	0	0	0	0	0	8	r
<i>Thymus praecox</i> Opiz subsp. <i>polytrichus</i> (Borbás) Jalas	0	0	0	0	33	1	58	2
<i>Trifolium alpestre</i> L.	0	0	0	0	17	1	25	1
<i>Trifolium montanum</i> L. subsp. <i>rupestre</i> (Ten.) Pign.	0	0	8	r	92	3	100	6
<i>Trifolium ochroleucum</i> Huds.	0	0	0	0	8	r	17	1
<i>Trifolium pratense</i> L. subsp. <i>semipurpureum</i> (Strobl) Pignatti	0	0	33	r	75	3	67	3
<i>Trifolium repens</i> L. subsp. <i>prostratum</i> (Biasoletto) Nyman	0	0	0	0	0	0	25	1
<i>Trinia dalechampii</i> (Ten.) Janchen	0	0	0	0	17	1	17	1
<i>Trinia glauca</i> (L.) Dumort.	0	0	0	0	8	r	25	1
<i>Valeriana tuberosa</i> L.	0	0	0	0	17	1	17	r
<i>Veratrum nigrum</i> L.	0	0	17	r	17	1	25	1
<i>Verbascum densiflorum</i> Bertol.	0	0	17	r	25	1	8	r
<i>Veronica arvensis</i> L.	0	0	0	0	8	r	8	r
<i>Veronica orsiniana</i> Ten.	0	0	8	r	33	1	42	2
<i>Vicia tenuifolia</i> Roth	0	0	8	r	8	r	0	0
<i>Viola alba</i> Besser subsp. <i>dehnhardtii</i> (Ten.) W. Becker	33	r	8	r	0	0	0	0
<i>Viola reichenbachiana</i> Jord. ex Boreau	0	0	8	r	0	0	0	0