Structure, dynamics and dendroecology of an old-growth *Fagus* forest in the Apennines

Piovesan, G.[1,*]; Di Filippo, A.[1]; Alessandrini, A.[1]; Biondi, F.[2] & Schirone, B.[1]

[1]*DAF, Department of Environment and Forests, University of Tuscia, Via S.C. de Lellis, I-01100 Viterbo, Italy;*
[2]*Department of Geography, University of Nevada, Reno, NV 89557-0048, USA;*
[*]*Corresponding author; Fax +39761357413; E-mail piovesan@unitus.it*

Abstract

Question: Which are the structural attributes and the history of old-growth *Fagus* forest in Mediterranean montane environments? What are the processes underlying their structural organization? Are these forests stable in time and how does spatial scale affect our assessment of stability? How do these forests compare to other temperate deciduous old-growth forests?

Location: 1600-1850 m a.s.l., *Fagus* forest near the tree line, central Apennines, Italy.

Methods: An old-growth *Fagus* forest was studied following historical, structural and dendroecological approaches. History of forest cover changes was analysed using aerial photographs taken in 1945, 1954, 1985 and 1994. The structural analysis was carried out in the primary old-growth portion of the forest using 18 circular and two rectangular plots. Dendroecological analyses were conducted on 32 dominant or co-dominant trees.

Results: These primary old-growth *Fagus* remnants consist of four patches that escaped logging after World War II. Both living and dead tree components are within the range of structural attributes recognized for old-growth in temperate biomes. Dendroecological analyses revealed the roles of disturbance, competition and climate in structuring the forest. We also identified a persistent *Fagus* community in which gap-phase regeneration has led to a mono-specific multi-aged stand at spatial scales of a few hectares, characterized by a rotated-sigmoid diameter distribution.

Conclusion: Even at the relatively small spatial scale of this study, high-elevation Apennine *Fagus* forests can maintain structural characteristics consistent with those of old-growth temperate forests. These results are important for managing old-growth forests in the Mediterranean montane biome.

Keywords: Beech; Diameter distribution; Late-successional forest; Stand structure; Temperate zone.

Nomenclature: Pignatti (1982).

Abbreviations: BAI = Basal area increment; CCTRMD = Computer controlled tree ring measuring device; CV = Coefficient of variation; CWD = Coarse wood debris; DBH = Diameter at breast height; DIB = Diameter inside bark; IGM = Istituto Geografico Militare; OG = Old-growth; PGC = Percentage growth change; PNA = Abruzzo National Park; UTM = Universal transverse Mercator.

Introduction

Understanding and maintaining old-growth forests requires a twofold approach based upon both process modelling and descriptive analysis of biophysical characteristics (Frelich & Reich 2003). The description of old-growth attributes and their spatio-temporal variations allows us to trace the processes and eventually formulate a general theory of old-growth dynamics (e.g. Coomes et al. 2003). In particular, the long-lasting debate about steady-state vs non-equilibrium forest dynamics would benefit from case studies performed in every biome under different disturbance regimes (White et al. 2000). While several studies on old-growth have been carried out in North America, poor documentation exists for Europe, especially in the Mediterranean area (Nilsson et al. 2003).

Depending on their geographic location, Mediterranean old-growth forests display different compositional characteristics with altitudinal differentiation due to the overlap of evergreen Mediterranean and deciduous temperate types (e.g. Walter 1985; Mazzoleni et al. 2004). Information on Mediterranean old-growth forest structure is scarce and the relative density of living and dead trees, in spite of their ecological importance for wildlife (Keddy & Drummond 1996; Fan et al. 2003), is practically unknown (Nilsson et al. 2003). Despite the fact that Italian landscapes have been modified for millennia, there are remote mountain areas where it is possible to find patches of old-growth forests. In the central Apennines we discovered an old-growth *Fagus* forest, which hosts some of the oldest deciduous trees in the world (Piovesan et al. 2003).

In this paper, we provide a first characterization of the structural attributes and history of this deciduous forest, as an ideal case study of an old-growth community in the Mediterranean montane environment. We addressed the following questions: What are the composition and structure of this old growth forest? What do aerial photographs tell us about the changes in the size and structure of these remnant forests? Do

monospecific *Fagus* stands develop in Mediterranean montane Europe in the absence of human disturbance? What does dendrochronology tell us about the relative effects of competition, climatic variation and disturbance on growth histories of individuals trees at different spatial and temporal scales? What is the growth increment of the old trees? Are these forests stable and how does spatial scale affect our assessment of stability? How do these forests compare to other *Fagus* forests around the world?

Material and Methods

Study area

The *Fagus* forest of Valle Cervara is located at 41°50' N, 13°44' E, in the town district of Villavallelonga, L'Aquila province, central Italy, in the northwest corner of the Abruzzo National Park (PNA; Fig. 1). The forest, located in an amphitheatre shaped valley orientates from east to west and ranges in elevation from 1200 to 1850 m a.s.l. Bedrock consists of Cretaceous limestone; soils can be referred to the brown group. Climate regime can be described as Mediterranean montane, with cold snowy winters and dry summers (Piovesan et al. 2003). However, the high elevation of our study site implies the occurrence of orographic precipitation, generating favourable conditions for the establishment of a mesic hardwood deciduous forest (*Polysticho-Fagetum*; Feoli & Lagonegro 1982).

Most of the Valle Cervara forest has been historically exploited for timber and fuel by local people. The lower part of the valley shows clear signs of exploitation, with the presence of coppice. The upper part of the valley escaped logging because of its difficult access and, probably, because of its role in maintaining a more constant source of freshwater to rural villages and, also, to increase protection from landslides and avalanches. Summer grazing in higher elevation pastures may have been for centuries the main disturbance at these sites. Thanks to its naturalistic importance, the valley is now ascribed to the integral reserve zone of PNA.

Analysis of aerial photographs

Post-war forest cover changes were studied using the Istituto Geografico Militare (IGM) aerial photographs taken in 1945, 1954, 1985 and 1994. Six structural types were recognized, based on field survey and repeated aerial photos:
1. Primary old-growth (OG) *Fagus* stand: presence of OG attributes such as all structural phases of the forest life-cycle, abundance of large trees, snags and coarse woody debris (CWD), plus absence of signs of harvest and persistence of high canopy articulation in photographic chronosequence;
2. Secondary old-growth *Fagus* stand: present day OG attributes but presence of stumps that indicated selective logging and an appreciable decrease in canopy density from the 1945 to the 1954 photo;
3. Uneven-aged *Fagus* stand: rarity of large and/or dead trees, signs of past utilization with presence of stumps;
4. Fragmented *Fagus* stand: low density stands with small patches of clearings, stunted trees;
5. Avalanche tracks: linear shape on photos, abundance of small trees, presence of maples (*Acer pseudoplatanus* and *A. platanoides*);
6. Clearings: grass dominated areas.
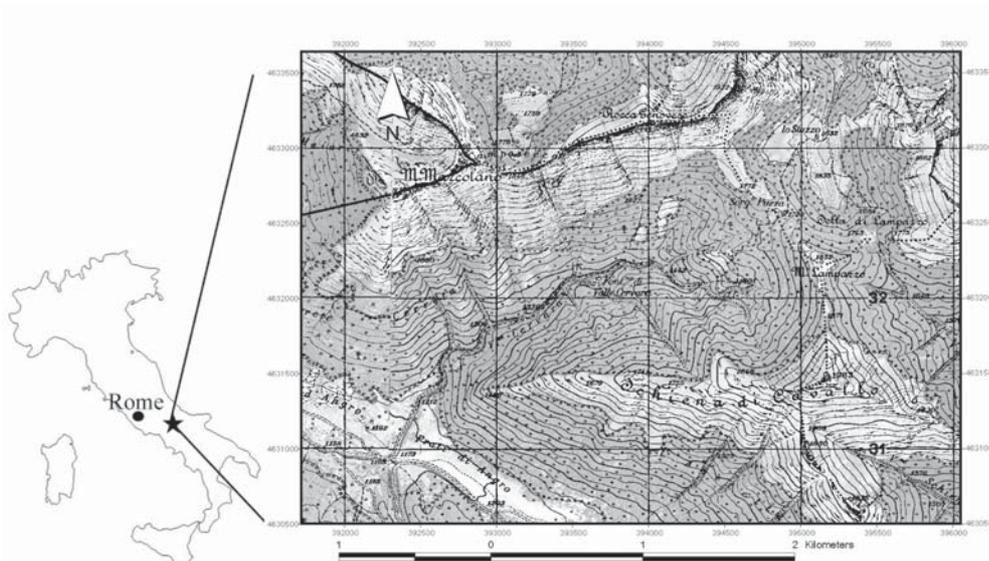
Fig. 1. Location and aerial view of Valle Cervara.

Type boundaries were identified on the aerial photographs using a stereoscope. Each photo was scanned, rectified and georeferenced in relation to the universal transverse Mercator (UTM) grid in Arcview GIS 3.1. Boundaries were checked in the field by means of a GPS receiver to calculate the relative planimetric area with regard to the 1994 aerial photos. Finally, changes in area covered by each type were computed between 1945 and 1994.

Structural analysis

Structural analysis was conducted in the primary old-growth portion of the forest (Type 1) using 18 circular plots, each with a 20 m radius. Geographic coordinates, elevation, aspect and slope were recorded at each plot. Species and DBH (1.3 m from the ground) were measured for every tree with stem ≥ 2.5 cm DBH. We also measured the heights of two to eight trees per plot representative of the different diameter classes to draw a height-DBH curve. In addition, two rectangular 1000 m^2 plots (20 m $\times$ 50 m) were established to describe the degree of vertical layering and spatial distribution of trees within the stand. Volume was calculated by the two-way volume table for *Fagus* in Italy (Castellani et al. 1984). Biomass values (Mg.ha^{-1}) were obtained by the formula for hardwood trees (Brown et al. 1997):

$$\text{Biomass} = \frac{0.5 + 25000 \times \text{DBH}^{2.5}}{\text{DBH}^{2.5} + 246872} \qquad (1)$$

Distribution and volume of dead trees were calculated for each plot. DBH and height were measured for every snag with stem ≥ 10 cm DBH and snag volume was calculated according to the formula:

$$v = g \cdot h \cdot f, \qquad (2)$$

where g = basal area, h = snag height and f = reduction factor. Compass orientation, mean diameter and length were measured for CWD with median diameter ≥ 10 cm and length ≥ 50 cm (Rubino & McCarthy 2003); CWD volume was calculated according to Huber's formula (Fridman & Walheim 2000): $v = s_{0.5} \times l$, where l = length, and $s_{0.5}$ = median sectional area. Snags and CWD were referred to one of five decay state classes (Rubino & McCarthy 2003), increasing from class I to V with decreasing integrity.

Dendroecological analysis

Dendroecological studies were conducted in old-growth patches, where *Fagus* reproduces mostly by seed. In total 32 dominant or co-dominant trees were cored at breast height using an increment borer for age determination and radial growth analysis. DBH of each tree sampled was recorded.

Cores were mounted, sanded and polished; ring width was then measured to the nearest 0.01 mm using CCTRMD (Computer controlled tree ring measuring device; Aniol 1987) and the software CATRAS (Aniol 1983). Cores were aged following visual and statistical crossdating techniques (Stokes & Smiley 1996) to reveal the presence of locally absent rings. Basal area increment (BAI) curves were obtained from ring width series, and compared among trees belonging to different size classes.

Cores that reached the pith were used to analyse age-DBH relationships. Moreover, the overall trend of these tree ring series, and their initial growth rate in relation to the entire chronology were used to distinguish if trees originated in sunlight conditions or in the understorey (Frelich & Graumlich 1994; Nowacki & Abrams 1997). Trees with high initial growth rates and declining or no trend are considered to have originated in large gaps, with unobstructed access to the canopy. Trees originated in the understorey are expected to have low initial growth rates with an increasing trend afterwards. An intermediate category is made up of small gap trees, which originated in canopy openings which later closed by lateral expansion of gap bordering individuals. These small gap trees are expected to show high initial growth rates followed by a period of suppression that ends when they reach the canopy. Dates of growth release were derived from tree ring series using the criteria established by Lorimer & Frelich (1989) for the determination of major sustained and moderate temporary releases. Major and sustained release events were considered as canopy accession events: each was dated and diameter inside bark (DIB) was calculated for trees originating in the understorey or in small gaps.

Dates of moderate temporary and major sustained growth release were organized in decades to outline the canopy disturbance history. In addition, abrupt growth decreases of 25% sustained for at least 10 years in relation to the previous 10 years, were employed to point out canopy damage (Foster 1988; Orwig et al. 2001). Percentage growth change (PGC; Nowacki & Abrams 1997) was used to compare decadal growth variations in Valle Cervara with those of two other old-growth *Fagus* stands, Val Fondillo (PNA in Biondi 1993) and Mount Terminillo (Piovesan et al. unpubl.), respectively 15 km and 100 km away, with the aim of searching for common low frequency climatic signals.

Results

Forest history

Analysis of aerial photographs showed that present-day (1994) forest covers an area of ca. 300 ha. Uneven aged *Fagus* stand(Type 3), encompassing 233 ha (75% of the valley area), is the most widespread type in Valle Cervara (Figs. 2 and 3), followed by old-growth *Fagus* stand of both types (17% of the valley area; Type 1 occupies 24.2 ha, Type 2 accounts for 28.7 ha). Primary old-growth *Fagus* stand is divided into four patches: three of respectively 9, 7 and 2 ha on the northwest facing side of the valley below M. Schiena di Cavallo between 1650 and 1850 m a.s.l. and one of 6.2 ha, of slender shape or slim shape, just below the tree line. The first three patches are divided by two avalanche tracks, 5.5 and 3.3 ha, respectively (3% of total area). The secondary old-growth *Fagus* stand consists of a single stand extending for 28.7 ha on the west facing slope of M. Schiena di Cavallo. Fragmented *Fagus* stand is made of several small patches intermingled with the uneven aged stand
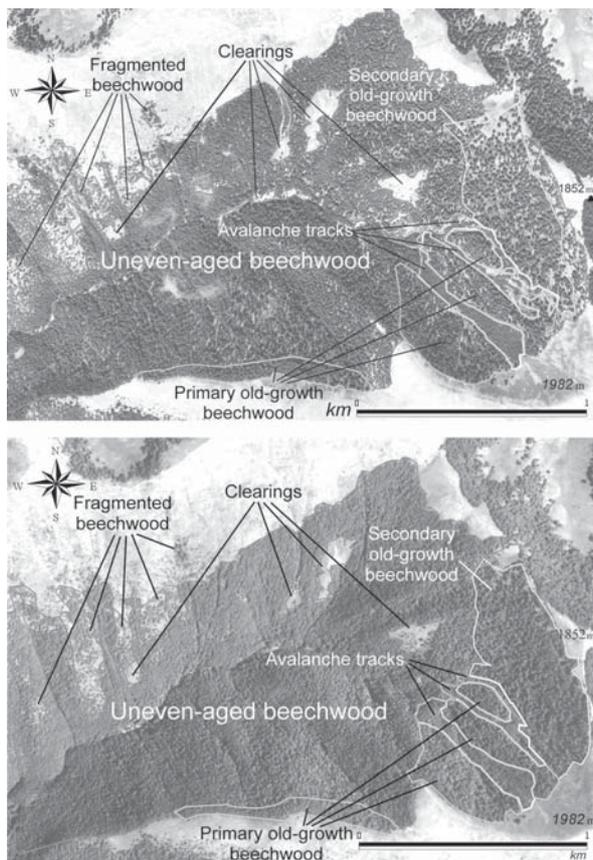
Fig. 2. Structural forest types of Valle Cervara identified on the aerial photographs taken in 1954 (above) and 1994 (below).

mainly spreading on the south facing slope of M. Marcolano and amounting to 11.4 ha. Clearings are present in the valley covering a total area of 5.7 ha (2% of total area).

Total old-growth (Type 1 plus Type 2) area remained constant (53 ha) in the aerial photo chronosequence. In 1945 it was all Type 1 old-growth but aerial photos in 1954 showed the first signs of the exploited secondary old-growth forest (Type 2; Figs. 2 and 3). Intensive logging took place in the years following World War II, and other residual old-growth forests in the Apennines and the Alps were cut during this period (Susmel 1959). The conservation of present day, primary old-growth remnants is chiefly due to the botanist Loreto Grande, who fought against the logging of this forest after the war. In the second half of the 1950s Guglielmo Giordano, a forester in charge of forest management for this area, chose to exclude these old-growth stands from logging. In the last 30 years, the conservation commitment of PNA, directed by Franco Tassi, has been the reason for protecting the Valle Cervara forest from logging.

The areas of fragmented *Fagus* stand and clearings increase between 1945 and 1954, then decrease constantly until 1994. This process suggests that even the most disturbed forest areas have been recovering from human impact. Avalanche tracks have been decreasing constantly in coverage from 15 ha in 1945 to 8.8 ha in 1994. Comparisons with 1945, 1954 and 1985 photos show that the tree line (1850 m a.s.l.) has remained relatively stable in the last 50 years (Fig. 2).

Current live tree structure

Mean density is 1590 ind.ha^{-1} for stems $\geq$ 2.5 cm, 532 ind.ha^{-1} for stems $\geq$ 7.5 cm (Table 1). The height-DBH curve can be modelled by a semi-logarithmic curve; maximum height is 29.6 m (Fig. 4A). Mean basal area is 41 m^2.ha^{-1}, ranging from 31 to 53 m^2.ha^{-1}, and has a coefficient of variation (CV) of 18%. The mean volume of living trees is 497 m^3.ha^{-1}, varying from 381 to 654 m^3.ha^{-1} with a CV of 20%. Ca. 57% of this volume belongs to trees with DBH $\geq$ 52.5 cm, 26% to trees with DBH between 32.5 and 52.4 cm and 17% to trees with DBH < 32.5 cm. Volume distribution among DBH-classes tends to be normally distributed, with modal value at 55 - 60 cm (Fig. 4B). Above-ground living woody biomass has a mean value of 328 Mg.ha^{-1}, ranging between 251 and 432 Mg.ha^{-1}.

Diameter distribution in 5-cm DBH classes can be described, after log transformation, by a fourth degree polynomial equation as described by Goff & West (1975) for old-growth forests (Fig. 5A). Interpolation with a rotated:sigmoid curve, derived by a finite mixture of two Weibull distributions (Zhang et al. 2001), also gives
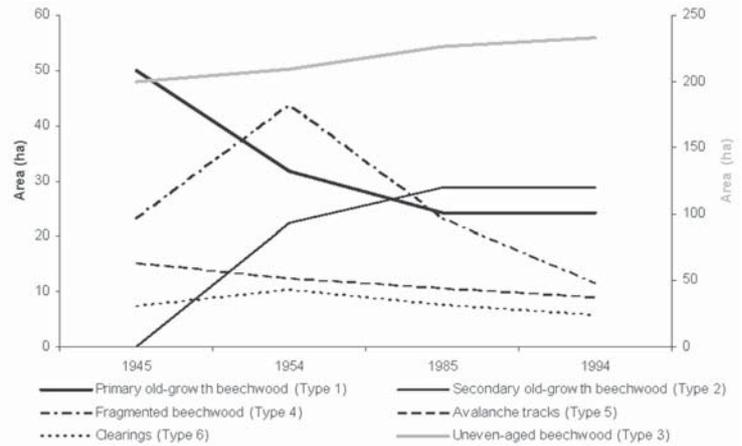
Fig. 3. Time-series changes in area occupied by the structural types. The right vertical axis shows area variation for uneven aged *Fagus* stand only.

a good fit (Fig. 5B). Transect analysis showed that stand vertical structure is complex (data not shown), being generated by a mosaic of patches belonging to different phases of stand structural development (cf. Peters 1997; Emborg et al. 2000).

Current dead tree structure

In sampled plots, snag density varies between 0 and 79 dead trees/ha (mean = 19 ± 18 snags/ha). Medium

size snags (25-40 cm DBH) represent a relatively small percentage of standing trees, but this percentage increases with snag diameter (Fig. 6B). CWD has a mean density of 40 ± 28 trunks/ha (range 0 - 95 trunks/ha). Snag volume is 24 $m^3.ha^{-1}$, concentrated in individuals with DBH ≥ 50 cm (92% of the total) (Fig. 4B). CWD volume is 41 $m^3.ha^{-1}$, more evenly distributed than snag volume. Ca. 45% of CWD is in classes with median diameter ≥ 50 cm, 51% in classes with median diameter between 30 and 50 cm and 4% in lower classes. By

Table 1. Structural variables of the 20 plots studied.

Plot	N5[*1]	N10[*1]	G5[*2]	G10[*2]	Volume				Biomass	Dead volume					
					Total	5-30[*3]	35-50[*3]	>50[*3]	Total	Total	Snags	CWD	10-30[*3] snag/CWD	35-50[*3] snag/CWD	> 50[*3] snag/CWD
	n.ha^{-1}	nha^{-1}	m²ha^{-1}	m²ha^{-1}	m³ha^{-1}	m³ha^{-1}	m³ha^{-1}	m³ha^{-1}	Mg.ha^{-1}	m³ha^{-1}	m³ha^{-1}	m³ha^{-1}	m³ha^{-1}	m³ha^{-1}	m³ha^{-1}
1	272	185	34	34	434	9	182	243	290	93	67	26	0/0.9	7.5/25.2	59.2/0
2	2731	977	48	45	529	191	122	217	345	68	15	53	0/0	0/9.5	15.3/43.4
3	302	169	33	33	425	8	146	272	283	201	58	143	0/0	1.4/112.2	56.6/31.3
4	1073	183	31	29	392	23	162	206	257	92	34	58	0/0.5	0/5.1	33.9/52.7
5	1740	369	40	37	489	44	103	342	324	0	0	0	0/0	0/0	0/0
6	343	299	47	47	597	41	281	275	399	0	0	0	0/0	0/0	0/0
7	314	224	45	45	573	8	278	287	383	93	43	50	0/2.0	4.5/25.0	38.3/23.2
8	3857	1268	38	33	400	140	17	243	253	31	0	31	0.2/9.4	0/7.1	0/14.4
9	2811	471	33	29	393	66	121	206	251	104	10	94	0/4.8	0/23.6	10.2/65.5
10	1191	206	32	30	398	29	235	134	259	38	5	33	0/0	0/32.9	5.5/0
11	1719	367	51	49	654	40	152	462	432	56	14	42	0/2.8	0/3.7	14.5/35.0
12	1257	1239	53	53	586	360	161	64	394	15	10	4	10.3/4.4	0/0	0/0
13	1388	1228	41	41	381	353	28	0	253	2	0	1	0.5/1.2	0/0	0/0
14	1291	313	48	46	597	49	158	390	396	106	9	97	0/5.7	0/46.6	8.9/44.9
15	3016	543	44	39	539	65	57	417	350	122	55	67	0/0	0/22.6	55.5/44.5
16	2435	672	33	29	389	63	9	317	251	57	11	46	0/0	0/46.4	10.6/0
17	1244	245	48	46	625	50	13	561	418	34	0	34	0/0	0/16.3	0/17.2
18	1629	946	37	29	400	111	31	260	273	26	17	9	0/4.3	0/4.9	17.1/0
19	-	429	-	39	506	15	137	349	337	70	57	13	0/0	0/12.8	56.8/0
20	-	298	-	48	624	6	156	462	416	86	65	21	0/0	15.2/20.8	49.4/0
Mean	1590	532	41	39	497	84	127	285	328	65	24	41	0.6/1.8	1.4/20.7	21.1/18.6
SD	1031	384	7	8	97	105	83	136	66	50	24	37	2.3/2.6	3.8/25.9	22.7/22.1
CV	65	72	18	20	20	125	65	48	20	77	104	91	383/144	271/80	105/119

[*1] N5 = number of stems with DBH > 2.5 cm.ha^{-1}; N10 = number of stems with DBH > 7.5 cm.ha^{-1};
[*2] G5 = Basal area per ha of all stems with DBH > 2.5 cm; G10 = Basal area per ha of all stems with DBH > 7.5 cm.ha^{-1};
[*3] Total values are divided into three DBH classes.
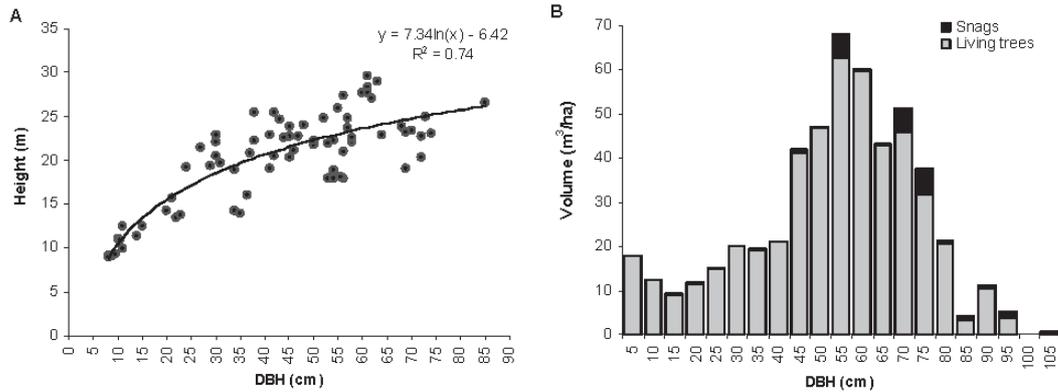
Fig. 4. A. Height-DBH relationship. **B.** Living (grey) and snag (black) volume distribution among DBH classes.
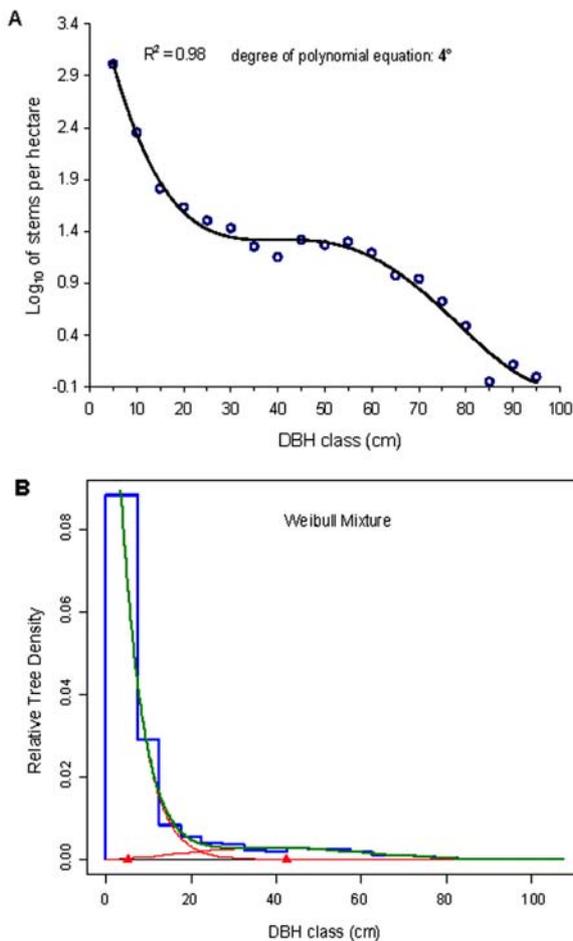
Fig. 5. A. Density by DBH class interpolated with a 4th degree polynomial equation. **B.** Diameter distribution modelled using a finite mixture of two Weibull distributions.

combining the data for snags and CWD we found that the mean volume of dead woody material ≥ 10 cm was 65 $m^3.ha^{-1}$, ranging between 0 and 201 $m^3.ha^{-1}$ with a CV of 77%. CWD contributes 64% of this volume, snags 36%. The sum of live and dead trees volume is ca. 562 $m^3.ha^{-1}$, with 88% in live individuals and 12% in dead ones. Most CWD volume can be referred to 2nd (32%) and 3rd (43%) decay classes. Ca. 90% of snag volume is in the first three decay classes, only 10% in the last two. CWD orientation is greater in N, NE and NW directions (52%) than S and SW (32%).

Growth history and dendroecology

Mean diameter increment in dominant and co-dominant trees is 2.03 ± 0.71 mm.a^{-1}, ranging from 0.75 to 3.81 mm.a^{-1}. Annual basal area increment (BAI) from 1700 to 2001 ranges from 0 (locally absent rings) to 88.54 $cm^2.a^{-1}$. In the 1997-2001 interval, there is no relationship between diameter increment and DBH (Fig. 7A). Older trees have a tendency to produce smaller ring widths ($n = 19$, $r = -0.40$, $p < 0.1$). However, old trees retain a remarkable vegetative vigour in spite of age (e.g. age > 400 a, $n = 5$, mean DIB increment 1997-2001 = 1.53 ± 0.51mm.a^{-1}). BAI is linked to present day DBH: there is a tendency for higher growth rates to be expressed in larger trees (Fig. 7B). The last five years BAI varies between 9 and 37 $cm^2.a^{-1}$. BAI is clearly superior in trees with DBH ≥ 70 cm (Fig. 7C). The difference was increasing from 1740 to ca. 1950; since then, the difference between the two size classes has lessened, and both appear to be exhibiting decreased BAI with the larger class beginning to decrease around 1960, and the smaller one decreasing in the last 20 years. Volume increment is directly correlated with DBH ($r = 0.52$, $p < 0.01$). Using Schneider's formula (Hellrigl 1986), it was estimated that dominant trees (DBH ≥ 55 cm, 57% of total volume) contribute to
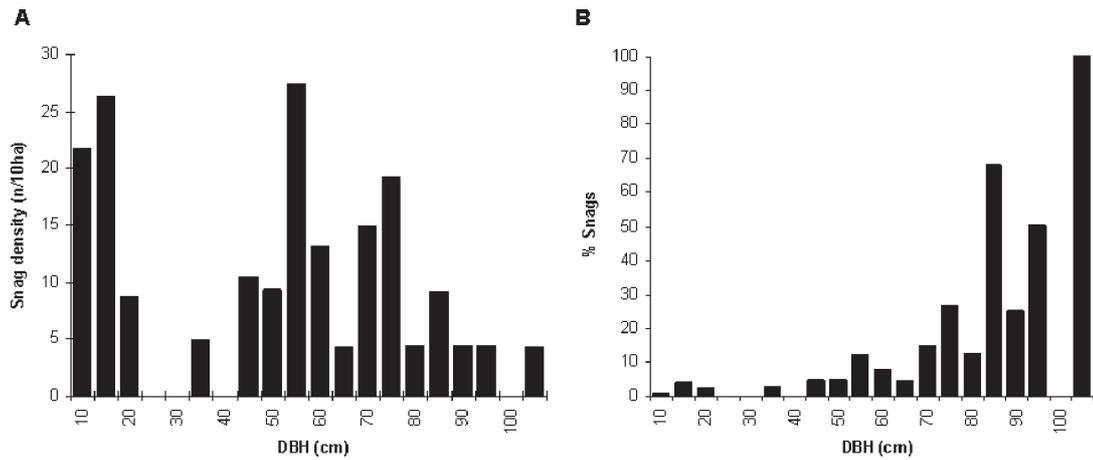
Fig. 6. A. Density of snags. **B.** Percentage of snags to standing trees by DBH class.
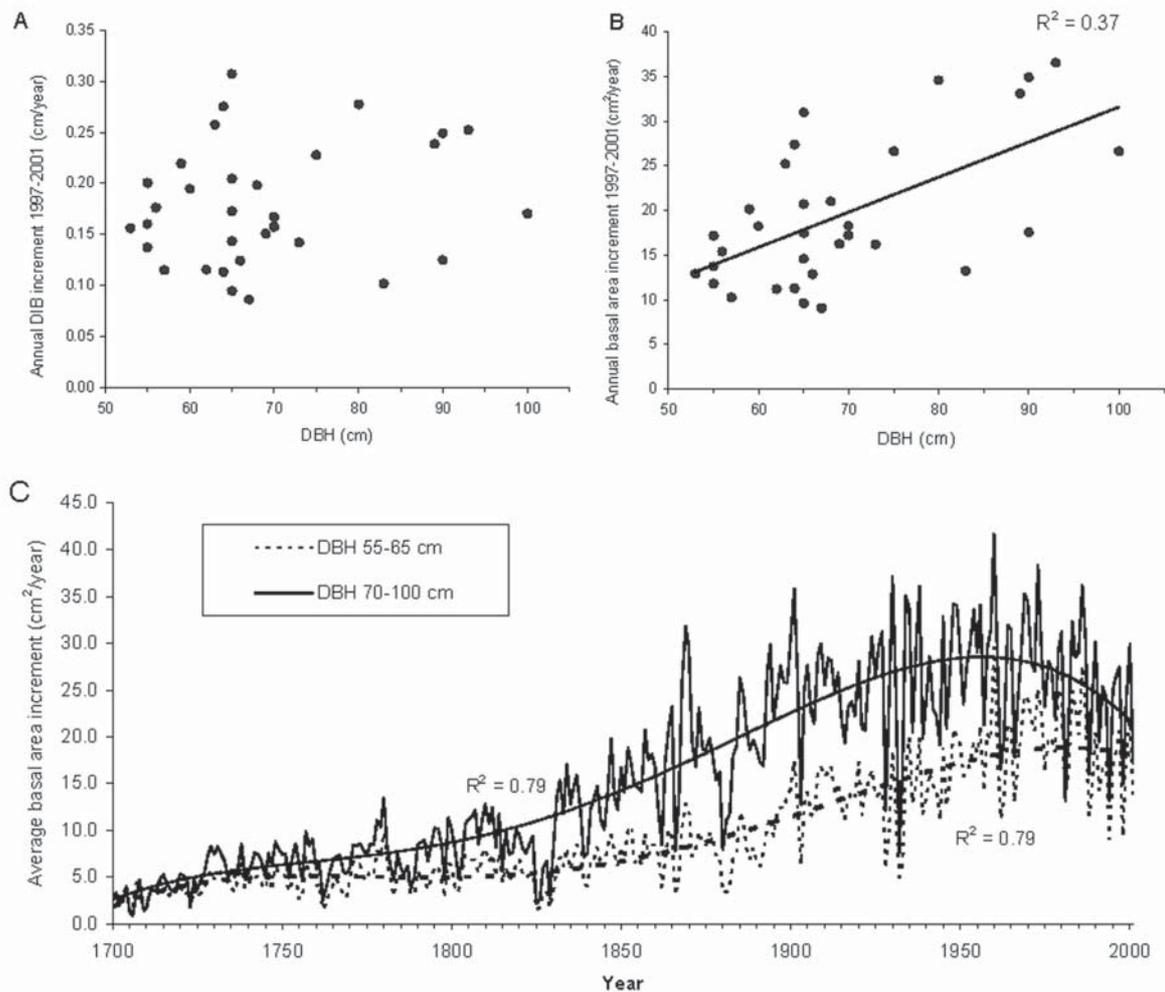
Fig. 7. A. Relationship between diameter increment and DBH. **B.** Relationship between BAI and DBH ($p < 0.01$). **C.** Mean BAI over time for trees with present day DBH comprised between 55 - 65 cm and between 70 - 100 cm.

annual biomass production with 1.79 m^3.ha^{-1}.a^{-1}.

In total, 19 cores (59% of the total) reached the pith and were used for age analysis. Age at breast height varies between 131 and 501 a, with a mean age of 314 ± 105 a (Fig. 8A), 42% of all trees are between 250 and 300 years old. No significant relationship was found between age and present day DBH of dominant trees. This is due to the different growth history of trees (Fig. 8B). Ca. 47% of pith-cored trees originated in small gaps, 37% in the understorey and the remaining 16% in large gaps. However, some individuals had intermediate characteristics, most likely due to the continuum of light levels that lies between gap and non-gap definitions (Lieberman et al. 1989). Canopy accession from understorey was attained with a mean DIB of 5 cm (range: 1-11 cm). Mean understorey residence time was 70 a and ranged from 15 to 165 a. Before canopy accession, mean annual radial growth was 0.41 mm.a^{-1} and ranged between 0.28 and 0.57 mm.a^{-1}. As reported in previous works (Bernabei & Piovesan 1997; Rozas 2001), 0.5 mm.a^{-1} could be considered a boundary value to distinguish radial growth rate between suppressed and gap exploiting *Fagus* trees. For small gap trees the first major sustained release occurs later, at a mean age of 96 a and up to a maximum of 257 a. They tend to have larger DIB (mean = 13 cm, range = 2-31 cm) and greater mean annual radial growth (0.64 mm.a^{-1}, range: 0.47 - 0.91 mm.a^{-1}) at canopy accession.

Sampled trees experienced 0 to 3 major sustained releases: these events were detected even in old trees, up to a maximum age of 358 a. Ca. 31% of cored trees ($n = 10$) showed more than one major sustained release. Gradual release was noticed in four trees and dated according to Lorimer & Frelich (1989) methods. Considering the period 1700-1990, when sample depth is higher, periods of widespread growth release occurred in the 1720s, 1770s, 1830s and 1880s - 1890s (Fig. 9A). Major sustained releases, which best identify stable canopy accessions, occurred more frequently in 1700s -1710s, 1830s and 1880s-1890s. Moderate releases seem to have a 40-50 year periodicity. In several decades, 50% or more of sampled trees experienced growth reductions (1780s, 1870s, 1910s and 1980s). A significant inverse relationship exists between percentage of trees showing growth decrease and moderate release ($r = -0.75$, $p < 0.001$). The same variables are directly correlated at lag two ($r = 0.39$, $p < 0.05$), suggesting that tree growth increases two decades after an appreciable growth decrease, possibly in response to weakened competition mediated by dieback of surrounding trees.

The reported events coincide with peaks in PGC observed at another PNA site (Val Fondillo) and at M. Terminillo (Fig. 9B). PGC analysis showed good synchronization in the occurrence of growth releases and suppressions ($r = 0.59$ with PNA, $r = 0.70$ at M. Terminillo, considering the common period 1700-1978), pointing to the effect of climatic factors in determining forest dynamics. Valle Cervara PGC agrees more with M. Terminillo than with PNA; although further away, the former presents ecological conditions more similar to those of the study site. In central Italy, high elevation Apennine *Fagus* forests appear, therefore, to be characterized by a common climatic signal at all frequencies (for the high frequency see Piovesan et al. 2003).

Discussion

Forest history

The four primary old-growth *Fagus* forest remnants of Valle Cervara have maintained an area of ca. 25 ha. We identified a persistent *Fagus* community in which gap-phase regeneration has led to a monospecific fine-grained structure (multi-aged stand) that is large enough to be representative of a steady-state forest (Shugart 1984). Korpel (1982) and Koop (1989) found that areas of 25 - 40 ha were required to continuously represent the shifting mosaic steady-state in *Fagus* dominated forests. In another European *Fagus* forest with disturbance dynamics similar to those at Valle Cervara, Emborg et al. (2000) found that an area of 10.7 ha can satisfy the quasi-equilibrium landscape criteria (Busing & White 1993) of a 'steady-state' forest. Our results confirm that even small patches can be in dynamic stability (White et al. 2000).

In spite of its position at the upper forest border, the *Fagus* forest of Valle Cervara has shown great recovery capability since logging in the 1950s. Large gaps and clearings have often been closed by growth of remaining trees and abundant establishment of new individuals. The exclusion of human activities in the valley since the 1960s has allowed secondary old-growth patches to join the primary ones, and the lower woods to regrow and form a forested buffer zone. With a total present day area of 50 ha, the old-growth stand meets the minimum area required in conservation biology for maintaining the long-term viability of gene pool in late-successional mesic tree species (Bücking 2003; Mosseler et al. 2003). It thus represents a relatively small area of the *Fagus* forest that needs to be protected for its uniqueness.

Worldwide, *Fagus* usually grows in forests with other species, and is often of secondary importance (Peters 1997). Patches of mono-dominant *Fagus* forest have been reported in the range of *Fagus moesiaca* and

F. orientalis in Asia (Zohary 1973) and *F. grandifolia* in North America (Russell 1953), but are considered rare. In contrast, in montane areas of Europe *Fagus* commonly occurs in single species stands (Ellenberg 1988). In Italy this is observed in most *Fagus* forests, including those at the southern limit of the species range, in Aspromonte and on Mount Etna. The monospecificity of European *Fagus* forests appears to be the combined result of Quaternary climatic change (Adams & Woodward 1989) and the inability of other tree species to coexist with the long-lived shade tolerant *Fagus* along edaphic and climatic gradients (Keddy & MacLellan 1990). *Taxus baccata* (yew) and *Abies alba* (silver fir), the other two late successional species of this region, are probably outside their ecological niche because of continentality and thick snow cover due to high altitude. The frost resistant *Acer pseudoplatanus* (sycamore maple) is limited to a successional role after the formation of large canopy gaps (Remmert 1990). The presence of *Acer* does not lead to a stable mixed coenosis, since it persists for just one or few generations during the forest life cycle until *Fagus* again becomes dominant. Life strategy of *Acer* is based on occupying the most difficult sites (e.g. ravines), where it can escape *Fagus* competitive exclusion (e.g. light competition), disseminate and eventually colonize new sites (Schirone et al. in press). The Valle Cervara old-growth forest, considering the long time it
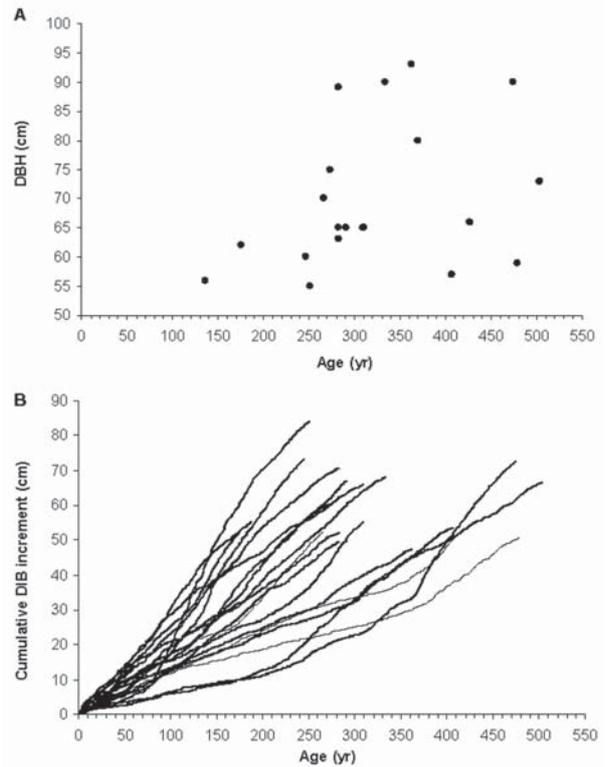
Fig. 8. A. Diameter vs age at breast height for trees with cores reaching the pith (*n* = 19). **B.** Cumulative DBI increment for the same trees shown in **A**.
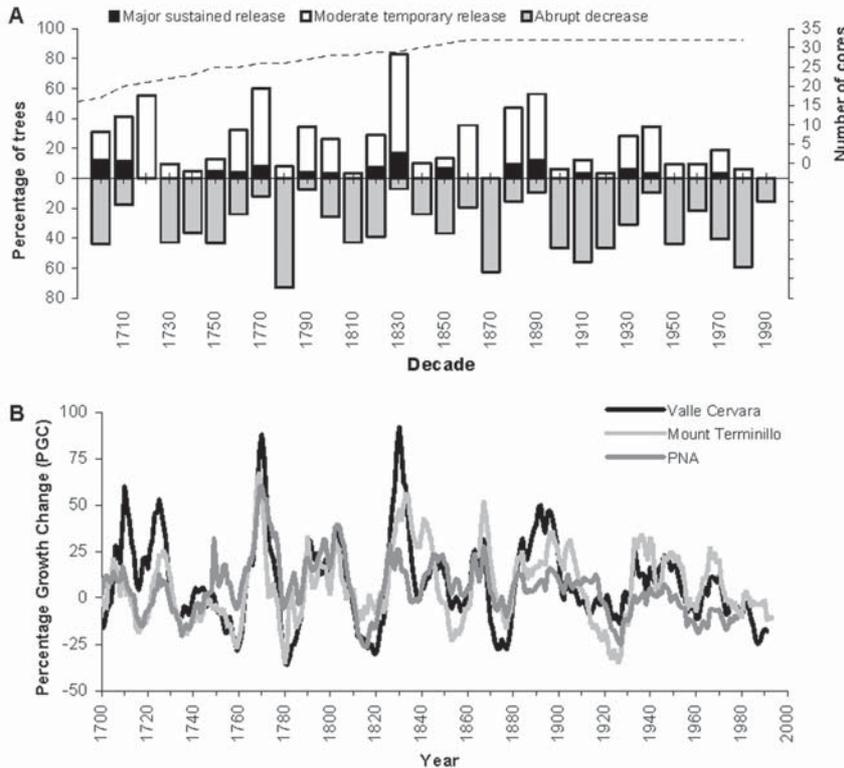
Fig. 9. A. Decadal distribution of major sustained releases, moderate temporary releases and abrupt decreases as percentage of trees cored. Dashed line represents the number of cores in each decade (left axis). **B.** Mean PGC of Valle Cervara (*n* = 32), Mount Terminillo (*n* = 35) and PNA (*n* = 22).

has had to develop its structure as well as the sporadic human disturbance, can testify that Apennine high altitude (1600-1900 m a.s.l.) pure *Fagus* forests are the result of environmental selection, such as *Nothofagus* forests at the timberline in the southern hemisphere (Cuevas 2002). This is the first study to show that Mediterranean montane *Fagus* forests can be mono-specific in the absence of human disturbance.

Living tree structure

Maximum diameter and height reached in Valle Cervara old-growth forest are within the range reported for mesic broad-leaved forests, where canopy height is 25-45 m and maximum DBH is 100 cm (Peterken 1996; Greenberg et al. 1997). Considering that this stand is at the altitudinal limit for the species, the size of the largest trees is quite remarkable.

The number of stems, basal area, volume and bio-mass per ha are comparable with those in other old-growth hardwood deciduous forests (Table 2). How-ever, basal area, volume and biomass are better descriptors for between stand comparison, for they are less affected than number of stems by size thresholds (Peterken 1996; Nilsson et al. 2003). In Valle Cervara basal area has a mean value of 41 m^2.ha^{-1}, which is within the control/normal category (>29 m^2.ha^{-1}) pro-posed by Keddy & Drummond (1996) for old-growth mesic hardwood deciduous forests. Greenberg et al. (1997) report a mean of 38 ± 11 (range 26-68) m^2.ha^{-1} and Nilsson et al. (2003) list a range of 34-40 m^2.ha^{-1}. With regard to volume, some authors have reported higher values, especially for mixed *Fagus* stands (cf. Korpel in Table 2). A *Fagus* dominated old-growth forest in Denmark was reported having 700 m^3.ha^{-1} (Emborg et al. 2000). However, above-ground bio-mass agrees with published estimates for hardwood old-growth forests (Table 2; Brown et al. 1997). These results are also interesting for carbon cycle modelling. Carbon stored in live above-ground biomass at Valle Cervara (ca. 164 t-C.ha^{-1}, if carbon is estimated as 50% of dry matter) confirms the high carbon storage capacity of natural forest vegetation (Adams & Piovesan 2002).

Another important old-growth feature is represented by the density of large trees, which account for a large portion of total volume (Brown et al. 1997; Greenberg et al. 1997; Nilsson et al. 2003). Valle Cervara values (Table 1) are within the standards formulated in the previously cited literature. Schütz (in Sagheb-Talebi & Schütz 2002) found, in a Swiss Jura *Fagus* stand, that trees with DBH > 50 cm contributed 51% of the total biomass, trees in intermediate size classes accounted for 34% and trees with < 30 cm DBH were responsible for

the remaining 15%. Density of trees ≥ 75 cm DBH ranged from 8.5 to 44.3 stems/ha and had a mean of 27.8 ± 12 stems/ha in Greenberg et al. (1997). Valle Cervara (11.7 stems/ha) is within this range. Nilsson et al. (2003) report that density of living trees with DBH > 70 cm in *Fagus* dominated forests of central Europe is ca. 30 stems/ha. Valle Cervara is characterized by a lower density of such trees, i.e. 20 stems/ha, but has 24% of the total biomass in trees with DBH ≥ 70 cm, which is included in the range of variation established by Brown et al. (1997) for old-growth forests (20-30% in trees > 70 cm DBH). In that study, as in ours, biomass has a normal distribution centred on the 60-cm DBH class (see Fig. 3 in Brown et al. 1997).

Decaying wood: snags and CWD

As a consequence of no logging activities, one of the most tangible features of old-growth forests is decaying wood (dead biomass; e.g. Butler et al. 2002). Snag and CWD densities in our study area are within the range reported in review studies (e.g. Runkle 2000). Greenberg et al. (1997) calculated a mean of 31 ± 19 (range 10-70) standing dead trees per ha. Nilsson et al. (2003), taking into consideration stands in North America and Europe, reported a wider range (29-187) and, based on the litera-ture, proposed a 'standard' range of 20-80 snags/ha. Valle Cervara, with 19 snags/ha, is very close to the lower end of that range. Percentage of dead trees per DBH class is not constant, and the observed snag distri-bution suggests a U-shaped mortality curve (Runkle 2000; Lorimer et al. 2001). In accordance with Coomes et al. (2003), we argue that the smallest individuals die from asymmetric competition (self-thinning), which is less severe for medium size individuals (Wolf et al. 2004). Intermediate size trees, thanks to their better position in the stand, undergo lower mortality rates (Goff & West 1975), as can be seen in the snag distribu-tion at our study area (Fig. 6B). Increasing snag density with larger DBH implies greater mortality (Runkle 2000; Miura et al. 2001), even if mortality has not necessarily a constant rate. Individuals in larger DBH classes have bigger crowns and are probably more exposed to exog-enous climatic disturbances (e.g. wind, summer drought) (Fig. 6B; Batista et al. 1998; Ida 2000; Runkle 2000; Lorimer et al. 2001). At the same time, older trees may become more vulnerable to natural disturbance (Goff & West 1975; Lorimer et al. 2001). Another explanation for our results is that larger diameter snags persist longer in the field than small ones and are, therefore, more likely to be measured (e.g. Cline et al. 1980).

CWD density is within the range of temperate old-growth forests, especially when considering mixed *Fagus* forests (range of 33-110 stems/ha according to Nilsson

Table 2. Comparison of structural variables for *Fagus* stands in different countries; symbols are the same used in Table 1.

Country	Survey year	Min DBH cm	N	G m².ha⁻¹	Living trees volume m³.ha⁻¹¹	Bio-mass Mg.ha⁻¹	Dead trees volume m³.ha⁻¹	Snags Volume m³.ha⁻¹	Snags Density n.ha⁻¹	CWD Volume m³.ha⁻¹	Reference
PURE *FAGUS* FORESTS											
Europe											
		2.5	1590	41	497	328	65	24	19	41	This study
			(272-3857)	(31-53)	(381-654)	(251-432)	(0-201)	(0-67)	(0-79)	(0-143)	This study
UK, lower Wye valley		5					47-129	3-42		15-113	Green & Peterken 1997
Poland, *Fagus-Abies*	1988	8	160-288	33-32	611-632		74-102	17-47	14-36	57-55	Jaworski et al. 2002
	1998	8	158-288	33-35	600-610		142-118	12-29	14-28	130-89	Jaworski et al. 2002
Slovakia, Stužica	1971	7			549-709						Saniga & Schütz 2002
	2001	7			481-677		60-200				Saniga & Schütz 2002
Slovakia		16	112-272		490-778		65-201			159	Korpel 1989
Asia											
Iran, *Fagus orientalis*		7.5		32	484						Sagheb-Talebi & Schütz 2002
MIXED *FAGUS* FORESTS											
Europe											
Slovenia, *Fagus-Abies*		10	265		799		138				Boncina 2000
France, *Fagus-Quercus*		5								142-256	Mountford 2002
Poland, *Fagus-Abies-Picea*	1988	8	183	32	547		306	101	81	205	Jaworski et al. 2002
	1998	8	189	33	578		289	63	48	226	Jaworski et al. 2002
Poland, *Fagus-Abies-Picea*	1986	8	145-324	34-44	442-691						Jaworski & Paluch 2002
	1996	8	140-346	35-44	464-693						Jaworski & Paluch 2002
Spain, *Fagus-Quercus*		2	1081-1169	32							Rozas 2003
Slovakia, Sitno, hardwood-conifers	1977	7			530-661						Saniga & Schütz 2002
	1998	7			346-617		50-250				Saniga & Schütz 2002
Slovakia, Hrončokovský grúň, hardwood-conifers	1972	7			839-1102						Saniga & Schütz 2002
	1992	7			702-1115		50-250				Saniga & Schütz 2002
Slovakia, Badín, *Fagus-Abies*	1970	7			648-968						Saniga & Schütz 2002
	1997	7			502-736		200-450				Saniga & Schütz 2002
Slovakia, Dobroč, *Fagus-Abies-Picea*	1968	7			565-1075						Saniga & Schütz 2002
	1998	7			600-853		150-440				Saniga & Schütz 2002
Sweden		10	402-445	37-40					31-39		Nilsson et al. 2003
Slovakia. *Abies-Fagus, Acer, Picea*		10	173	37				53	34		Nilsson et al. 2003
Slovakia. *Fagus-Abies*		16	179-594	37-56	251-1046						Korpel 1989
Asia											
Iran		7.5		41	603						Sagheb-Talebi & Schütz 2002
North America											
USA		2	877	52		440					Busing & White 1993
USA		9.5	475-649	26-34			29-64				Chokkalingam & White 2000
USA	1974	1		27-30							Martin & Bailey 1999
	1994	1	5047-5072	30-35		185-225					Martin & Bailey 1999
USA	1979	5	576	33							Olano & Palmer 2003
	1994	5	574	34							Olano & Palmer 2003
USA		8	470-590	27-34			20-34		85-115		Orwig et al. 2001
USA	1976	25	171-279	37-77							Runkle 2000
	1990	25	159-271	36-74					15-18		Runkle 2000

et al. 2003). Dead material (snags plus CWD) in Valle Cervara has a mean of 65 m³.ha⁻¹, equivalent to 12% of the total volume. Considering that mean volume of dead material estimated for Italian stands (mainly logged forests) by the National Forest Inventory is 4% of live biomass (Wolynski 2001), this represents another distinctive characteristic of our study area. Estimated carbon content in dead material is 18-20 t-C.ha⁻¹, which demonstrates its importance for storing carbon (Adams & Piovesan 2002). The range for European *Fagus* forests is 50-200 m³.ha⁻¹ (Table 2); similar values can be found in Nilsson et al. (2003). Rauh & Schmitt (1991) found 105 m³.ha⁻¹ in Bavaria. Koop &

Hilgen (1987) reported a range of 92-145 m³.ha⁻¹ for the natural reserve of Fontainebleau, France. CWD often contributes more than snags to dead biomass volume (snags account for 36% in our stand, 20-40% in Nilsson et al. 2003; Table 2; see also Stewart et al. 2003). Another important old-growth feature is the amount of large diameter dead material (e.g. Keddy & Drummond 1996). In Valle Cervara, 92% of snag volume comes from stems with DBH ≥ 50 cm, whereas CWD volume is equally divided between intermediate and large individuals. Spetich et al. (1999) reached similar conclusions for old-growth forests of central-western USA.

Generally, production of dead material is expected

to be greater on more productive sites, and maximum tree height at Valle Cervara qualifies for medium-low productivity classes. Low values of dead wood volume found at Valle Cervara can be related to high altitude ecology and site productivity. However, it should be considered that our stand lacks widespread diseases (e.g. *Fagus* bark disease) and dieback phenomena, which cause high mortality in forests (Innes 1992). This study confirms that primary old-growth forests with a fine-grained mosaic also show remarkable resilience to wind disturbance, even to ice storms (Hooper et al. 2001), while in secondary old-growth forests severe wind-storms can cause high levels of dead material (e.g. Mountford 2002). Furthermore, abundant dead material of large dimension was observed in avalanche tracks suggesting translocation of CWD by gravity or by down-ward snow movement from the upper primary old-growth (Rubino & McCarthy 2003).

The degree of wood decay is another important characteristic of old-growth stands. CWD in Valle Cervara is mostly (58%) in the last three decay classes, i.e. more advanced decomposition, while more than 50% of snag volume is in the first two classes. Stewart et al. (2003) reported similar patterns, which can be related to the fact that CWD is more exposed to soil humidity and saproxylic organisms, so that wood decay is faster, while progressive degradation in snags leads to struc-tural instability and transition to CWD, thereby prevent-ing snags from being listed in the more advanced decay classes. CWD orientation follows down slope direction, as slope at the study area reaches 70%, and is mostly N – NW. Therefore, gravity is the major driver; wind direction is usually responsible for CWD orientation in flat-land forests (Mason 2002; Wolf et al. 2004).

Recruitment, growth and disturbance history

High altitude *Fagus* forests in the Apennines yield multi century old trees (Biondi 1993). Some individuals in Valle Cervara exceed 500 a in age, and are the oldest known broad-leaved trees in the northern hemisphere (Piovesan et al. 2003). The short vegetative period near the tree line (Peters 1997), combined with Mediterra-nean summer drought, produce small annual growth increments (Piovesan et al. 2003). The oldest trees are usually found on extreme sites (Schulman 1954). *Fagus* trees with similar age have been recently discovered in the Pyrenees (Bourquin-Mignot & Girardclos 2001). North American *Fagus* (*Fagus grandifolia*) can live more than four centuries (412 a in Greenberg et al. 1997; Tubbs & Houston 1990). The age of large trees is an important attribute of an old-growth forest: maximum age is always superior to that of secondary woods. Age of several trees could not be measured because of heart rot or hollow stems. This is a common feature of domi-nant trees in old-growth forests, where more than 50% of trees with DBH > 50 cm, either live or dead, have holes that are crucial for wildlife preservation (Fan et al. 2003).

In spite of their old age, large trees maintain high growth rates, as was also found in other *Fagus* old-growth forests (Jaworski & Paluch 2002). Growth rate increase after selective logging has demonstrated the importance of competition as a main limiting factor in these stands (Latham & Tappeiner 2002; Bebber et al. 2004). BAI curves in old-growth forests can peak at great age because of strong competition before stable canopy recruitment. The descending growth trend of BAI at Valle Cervara in recent decades may also be related to climatic changes (e.g. Piovesan & Schirone 2000). Other studies have demonstrated how much cli-mate influences growth of dominant *Fagus* trees (e.g. Biondi 1993; Batista et al. 1998).

Sampled dominant and co-dominant trees have an age range of more than 350 a (Fig. 8A). Such multi-aged structure is typical of the last phase of stand develop-ment (Frelich 2002). Release and decrease events are present in almost all decades during 1700-1990: this underlines the importance of gap dynamics and ex-cludes the possibility of stand-replacing disturbance, which would synchronize recruitment and canopy ac-cession. However, peaks in release frequency during the 1720s, 1770s and 1830s allows us to hypothesize about exogenous events of major severity shaping these ecosystems. PGC analysis confirmed that climate is important in controlling *Fagus* growth through sum-mer drought (Piovesan et al. 2003), but wind storms, ice storms and avalanches may have generated the lower frequency patterns mentioned above.

Canopy processes are very complex, being linked to high variability in competition and gap characteristics. Runkle (1990) reports for mesic hardwood forests of eastern North America a mean gap area of 200 m^2, but gaps can be formed by a fallen branch as well as by several trees falling at once. So, individuals can be affected by disturbances of different intensity at diverse places and times: this generates a myriad of different life histories among trees of the same stand, leading to complexity in age and diameter structure (Fig. 8B). Gap-phase dynamics at Valle Cervara are evident in radial growth patterns: large gaps are scarce, gradual release occurs in some individuals and, in addition, some trees experienced multiple gap episodes: this is a common feature of temperate forests (Runkle 1985). The occurrence of several periods of suppression and release during canopy recruitment has previously been observed in *Fagus sylvatica* (Peters 1997; Di Filippo et al. 2004). This phenomenon has also been reported for

F. grandifolia in North America (Canham 1988, 1990) and *F. crenata* in Japan (Cao & Ohkubo 1999). Individuals that remain in the understorey or in small gaps undergo severe competition from dominant trees, grow slowly and reach the canopy at a later age and with a small diameter (lower curves in Fig. 8B). These become the oldest trees in the stand. Individuals that originated in large gaps show the fastest growth rates because of low competition from above, reach the canopy at a younger age and with a large diameter (upper curves in Fig. 8B).

Fagus is well adapted to a frequent, small-gap disturbance regime, thanks to its physiological and morphological plasticity (Canham 1988; Poulson & Platt 1996; Peters 1997; Batista et al. 1998); this would explain its dominance and the exclusion of other species from these ecosystems (Poulson & Platt 1989). We found that *Fagus sylvatica* can survive in the understorey up to 165 a, maintaining a mean radial growth rate of 0.28 mm.a^{-1}. At the time of release from suppression, growth increases as large as 501 PGC have been observed at the study area.

Diameter distribution

Diameter distribution in Valle Cervara can be modelled by a rotated-sigmoid curve (Goff & West 1975; Zhang et al. 2001). This distribution is typical of old-growth forests, especially those of limited area (Goodburn & Lorimer 1999; De Long & Kessler 2000). The genesis of a rotated-sigmoid shape is complex because it is affected by multiple processes, such as stem recruitment, growth and mortality (Leak 2002; Coomes et al. 2003).

Climate driven disturbance can spatially synchronize cohort growth and thus partially explain the rotated-sigmoid distribution. Mortality can vary according to social position and, consequently, diameter (Zhang et al. 2001; Wolf et al. 2004). Simulation of forest structural dynamics based on a U-shaped mortality-size relationship has generated a rotated-sigmoid diameter distribution (Lorimer & Frelich 1984; Coomes et al. 2003); this is probably the case at Valle Cervara as well.

Conclusion

In this study an Apennine high altitude old-growth *Fagus* forest is described for the first time. The attributes of such stands are within the ranges reported in the literature for deciduous hardwood old-growth forests. The monospecific dominance of *Fagus* is probably due to its shade tolerance and ability to regenerate under a conspecific canopy. Moreover, these *Fagus* forests are less species-rich than those reported elsewhere, most likely because of the high altitude environment and the extinction of potential competitors during the Quaternary glaciations. Dendroecological analysis indicates that *Fagus* forests in this study do not undergo stand-replacing disturbance events. The disturbance regime in these forests is characterized by small to intermediate gap-phase processes that favour *Fagus* regeneration and exclude competitors. Our results suggest that even at the relatively small spatial scale of this study, high altitude Apennine *Fagus* forests can maintain structural characteristics consistent with those of old-growth forests. Therefore, on the basis of reported evidence, and in analogy with other biomes, high altitude Apennine landscapes have the potential for restoration to old-growth status.

References

Adams, J.M. & Piovesan, G. 2002. Uncertainties in the role of land vegetation in the carbon cycle. *Chemosphere* 49: 805-819.

Adams, J.M. & Woodward, F.I. 1989. Patterns in tree species richness as a test of the glacial extinction hypothesis. *Nature* 339: 699-701.

Aniol, R.W. 1983. Tree-Ring Analysis using Catras. *Dendrochronologia* 1: 45-53.

Aniol, R.W. 1987. A new device for computer assisted measurement of tree-ring widths. *Dendrochronologia* 5: 135-141.

Batista, W.B., Platt, W.J. & Macchiavelli R.E. 1998. Demography of a shade-tolerant tree (*Fagus grandifolia*) in a hurricane-disturbed forest. *Ecology* 79: 38-53.

Bebber, D.P., Thomas, S.C., Cole, W.G. & Balsillie, D. 2004. Diameter increment in mature eastern white pine *Pinus strobus* L. following partial harvest of old-growth stands in Ontario, Canada. *Trees Struct. Funct.* 18: 29-34.

Bernabei, M. & Piovesan, G. 1997. Alcune osservazioni sugli accrescimenti anulari del faggio del Lazio settentrionale. *Monti e Boschi* 5: 52-56. (In Italian.)

Biondi, F. 1993. Climatic signals in tree-rings of *Fagus sylvatica* L. from the central Apennines, Italy. *Acta Oecol.* 14: 57-71.

Boncina, A. 2000. Comparison of structure and biodiversity in the Rajhenav virgin forest remnant and managed forest in the Dinaric region of Slovenia. *Global Ecol. Biogeogr.* 9: 201-211.

Bourquin-Mignot, C. & Girardclos, O. 2001. Construction

d'une longue chronologie de hêtres au Pays Basque. La forêt d'Iraty et le Petit Age Glaciaire. Sud-Ouest Européen. *Rev. Géogr. Pyrénées Sud-Ouest* 11: 59-71.

Brown, S.L., Schroeder, P. & Birdsey, R. 1997. Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. *For. Ecol. Manage.* 96: 37-47.

Bücking, W. 2003. Are there threshold numbers for protected forests? *J. Environ. Manage.* 67: 37-45.

Busing, R.T. & White, P.S. 1993. Effects of area on old-growth forest attributes: implication for the equilibrium landscape concept. *Landscape Ecol.* 8: 119-126.

Butler, J., Alexander, K. & Green, T. 2002. *Decaying wood: an overview of its status and ecology in the United Kingdom and Continental Europe.* In: Laudenslayer, W.F.jr., Shea, P.J., Valentine, B.E., Weatherspoon, C.P. & Lisle, T.E. (tech. coord.) Proceedings of the Symposium on the ecology and management of dead wood in Western forests, pp. 11-19. USDA For. Serv. Res. Pap., PSW-GTR-181. Albany, CA, US.

Canham, C.D. 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69: 786-795.

Canham, C.D. 1990. Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bull. Torrey Bot. Club* 117: 1-7.

Cao, K.-F. & Ohkubo T. 1999. Suppression and release during canopy recruitment in *Fagus crenata* and *Acer mono* in two old-growth beech forests in Japan. *Plant Sci.* 145: 281-290.

Castellani, C., Scrinzi, G., Tabacchi, G. & Tosi, V. 1984. *Inventario forestale nazionale italiano (I.F.N.I.), Tavole di cubatura a doppia entrata,* pp. 71-75. Istituto Sperimentale per l'Assestamento Forestale e per l'Alpicoltura. Trento, IT. (In Italian.)

Chokkalingam, U. & White, A. 2000. Structure and spatial patterns of trees in old-growth northern hardwood and mixed forests of northern Maine. *Plant Ecol.* 156: 139-160.

Cline, S.P., Berg, A.B. & Wright, H.M. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *J. Wildl. Manage.* 44: 773-786.

Coomes, D.A., Duncan, R.P., Allen, R.B. & Truscott, J. 2003. Disturbances prevent stem size-density distributions in natural forests from following scaling relationships. *Ecol. Lett.* 6: 980-989.

Cuevas, J.C. 2002. Episodic regeneration at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego, Chile. *J. Ecol.* 90: 52-60.

De Long, S.C. & Kessler, W.B. 2000. Ecological characteristics of mature forest remnants left by wildfire. *For. Ecol. Manage.* 131: 93-106.

Di Filippo, A., Piovesan, G. & Schirone, B. 2004. La dendroecologia applicata alle foreste vetuste: il caso delle faggete italiane. In: Casagrandi, R. & Melià, P. (eds.) *Atti del XIII Congresso Nazionale della Società Italiana di Ecologia*, pp. 49-54. Aracne, Roma, IT. (In Italian.)

Di Filippo, A., Piovesan, G. & Schirone, B. 2004. *La dendroecologia applicata alle foreste vetuste: il caso delle faggete italiane.* Proceedings of the XIII National Congress of the Italian Society of Ecology (S.It.E.), 8-10 September 2003, pp. 49-54. Como, Roma, IT. (In Italian.)

Ellenberg, H. 1988. *Vegetation ecology of Central Europe.* Cambridge University Press, Cambridge, UK.

Emborg, J., Christensen, M. & Heilmann-Clausen, J. 2000. The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. *For. Ecol. Manage.* 126: 173-189.

Fan, Z., Shifley, S.R., Spetich, M.A., Thompson F.R. III & Larsen, D.R. 2003. Distribution of cavity trees in Midwestern old-growth and second-growth forests. *Can. J. For. Res.* 33: 1481-1494.

Feoli, E. & Lagonegro, M. 1982. Syntaxonomy of beech-woods of Apennines based on IAHOPA. *Vegetatio* 50: 129-173.

Foster, D.R. 1988. Disturbance history, community organization and vegetation dynamics of old-growth Pisgah Forest, South-Western New Hampshire, USA. *J. Ecol.* 76: 105-134.

Frelich, L.E. 2002. *Forest dynamics and disturbance regimes, studies from temperate evergreen-deciduous forests.* Cambridge University Press, Cambridge, UK.

Frelich, L.E. & Graumlich, L.J. 1994. Age-class distribution and spatial patterns in an old-growth hemlock-hardwood forest. *Can. J. For. Res.* 24: 1939-1947.

Frelich, L.E. & Reich, P.B. 2003. Perspectives on development of definitions and values related to old-growth forests. *Environ. Rev.* 11: 9-22.

Fridman, J. & Walheim, M. 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *For. Ecol. Manage.* 31: 23-26.

Goff, F.G. & West, D. 1975. Canopy-understory interaction effects on forest population structure. *For. Sci.* 21: 98-108.

Goodburn, J.M. & Lorimer, C.G. 1999. Population structure in old-growth and managed northern hardwoods: an examination of the balanced diameter distribution concept. *For. Ecol. Manage.* 118: 11-29.

Green, P. & Peterken, G.F. 1997. Variation in the amount of dead wood in the woodlands of the Lower Wye Valley, UK in relation to the intensity of management. *For. Ecol. Manage.* 98: 229-238.

Greenberg, C.H., McLeod, D.E. & Loftis, D.L. 1997. *An old-growth definition for western and mixed mesophytic forests.* USDA For. Serv. Tec. Rep. GTR-SRS-16. Asheville, NC, US.

Hellrigl, B. 1986. Il rilevameto dendro-crono-auxometrico. In: Hellrigl, B., Bernetti, G., Bagnaresi, U. & Cantiani, M. (eds.) *Nuove metodologie nella elaborazione dei piani di assestamento dei boschi*, pp. 399-704. I.S.E.A., Litografia Lorenzini, Bologna, IT. (In Italian.)

Hooper, M.C., Arii, K. & Lechowicz, M.J. 2001. Impact of a major ice storm on an old-growth hardwood forest. *Can. J. Bot.* 79: 70-75

Ida, H. 2000. Treefall gap disturbance by a catastrophic typhoon in southwestern Japan. *J. Veg. Sci.* 11: 825-832.

Innes, J.L. 1992. Forest decline. *Prog. Phys. Geogr.* 16: 1-64.

Jaworski, A. & Paluch, J. 2002. Factors Affecting the Basal

Area Increment of the primeval forests in the Babia Góra National Park, southern Poland. *Forstwiss. Centralbl.* 121: 97-108.

Jaworski, A., Kolodziej, Z.B. & Porada, K. 2002. Structure and dynamics of stands of primeval character in selected areas of the Bieszczady National Park. *J. For. Sci.* 48: 185-201.

Keddy, P.A. & Drummond, C.G. 1996. Ecological properties for the evaluation, management, and restoration of temperate deciduous forest ecosystems. *Ecol. Appl.* 6: 748-762.

Keddy, P.A. & MacLellan, P. 1990. Centrifugal organization in forests. *Oikos* 59: 75-84.

Koop, H. 1989. *Forest Dynamics. SILVI-STAR: A comprehensive monitoring system.* Springer, Berlin, DE.

Koop, H. & Hilgen, P. 1987. Forest dynamics and regeneration mosaic shifts in unexploited beech (*Fagus sylvatica*) stands at Fontainebleau (France). *For. Ecol. Manage.* 20: 135-150.

Korpel, S. 1982. Degree of equilibrium and dynamical changes of the forest on example of natural forests of Slowakia. *Acta Fac. For. Zvolen* 24: 9-30.

Korpel, S. 1989. *Pralesy Slavenska.* Academia Bratislava, SL.

Latham, P. & Tappeiner, J. 2002. Response of old-growth conifers to reduction in stand density in western Oregon forests. *Tree Physiol.* 22: 137-146.

Leak, W.B. 2002. *Origin of sigmoid diameter distributions.* USDA For. Serv. Res. Pap. NE-718. Newton Square, PA, US.

Lieberman, M., Lieberman, D. & Peralta, R. 1989. Forests are not like Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology* 70: 550-552.

Lorimer, C.G. & Frelich, L.E. 1984. A simulation of equilibrium diameter distributions of sugar maple (*Acer saccharum*). *Bull. Torrey Bot. Club* 111: 193-199.

Lorimer, C.G. & Frelich, L.E. 1989. A methodology for estimating canopy disturbance frequency in dense temperate forests. *Can J. For. Res.* 19: 651-663.

Lorimer, C.G., Dahir, S.E. & Nordheim, E.V. 2001. Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. *J. Ecol.* 89: 960-971.

Martin, C.W. & Bailey, A.S. 1999. Twenty years of change in a northern hardwood forest. *For. Ecol. Manage.* 123: 253-260.

Mason, F., 2002. *Dinamica di una foresta della Pianura Padana. Bosco della Fontana. Primo contributo, monitoraggio 1995. Rapporti scientifici 1. Centro Nazionale Biodiversità Forestale Verona, Bosco della Fontana.* Arcari Editore, Mantova, IT. (In Italian.)

Mazzoleni, S., Di Pasquale, G., Mulligan, M., Di Martino, P. & Rego, F. 2004. *Recent dynamics of Mediterranean vegetation and landscape.* Wiley, New York, NY, US.

Miura, M., Manabe, T., Nishimura, N. & Yamamoto, S. 2001. Forest canopy and community dynamics in temperate oldgrowth evergreen broad-leaved forest, south-western Japan: a 7-year study of a 4-ha plot. *J. Ecol.* 89: 841-849.

Mosseler, A., Lynds, J.A. & Major, J.E. 2003. Old-growth forests of the Acadian Forest Region. *Environ. Rev.* 11: 47-77.

Mountford, E.P. 2002. Fallen dead wood levels in the nearnatural beech forest at la Tillaie reserve, Fontainebleau, France. *Forestry* 75: 203-208.

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusínski, G. & Ranius, T. 2003. Densities of large and dead trees in old-growth temperate and boreal forests. *For. Ecol. Manage.* 161: 189-204.

Nowacki, G.J. & Abrams, M.D. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecol. Monogr.* 67: 225-249.

Olano, J.M. & Palmer, M.W. 2003. Stand dynamics of an Appalachian old-growth forest during a severe drought episode. *For. Ecol. Manage.* 174: 139-148.

Orwig, D.A., Cogbill, C.V., Foster, D.R. & O'Keefe, J.F 2001. Variations in old-growth structure and definitions: forest dynamics on Wachusett Mountain, Massachusetts. *Ecol. Appl.* 11: 437-452.

Peterken, G.F. 1996. *Natural woodland. Ecology and conservation in northern temperate regions.* Cambridge University Press, Cambridge, UK.

Peters, R. 1997. *Beech Forests.* Geobotany 24. Kluwer, Dordrecht, NL.

Pignatti, S. 1982. *Flora d'Italia.* Edagricole, Bologna, IT.

Piovesan, G. & Schirone, B. 2000. North Atlantic Oscillation effects on Italian beech (*Fagus sylvatica* L.). *Int. J. BioMeteorol.* 44: 121-127.

Piovesan, G., Bernabei, M., Di Filippo, A., Romagnoli, M. & Schirone, B. 2003. A long-term tree ring beech chronology from a high-elevation old-growth forest of central Italy. *Dendrochronologia* 21: 1-10.

Poulson, T.L. & Platt, W.J. 1989. Gap light regimes influence canopy tree diversity. *Ecology* 70: 553-555.

Poulson, T.L. & Platt, W.J. 1996. Replacement patterns of beech and sugar maple in Warren Woods, Michigan. *Ecology* 77: 1234-1253.

Rauh, J. & Schmitt, M. 1991. Methodik und Ergebnisse der Totholzforschung in Naturwaldreservaten. *Forstwiss. Centralbl.* 110: 114-127.

Remmert, H. 1990. *The mosaic-cycle concept of ecosystem.* Ecological Studies 85. Springer Verlag, Berlin, DE.

Rozas, V. 2001. Detecting the impact of climate and disturbances on tree-rings of *Fagus sylvatica* L. and *Quercus robur* L. in a lowland forest in Cantabria, Northern Spain. *Ann. For. Sci.* 58: 237-251.

Rozas, V. 2003. Regeneration patterns, dendroecology, and forest-use history in an old-growth beech-oak lowland forest in Northern Spain. *For. Ecol. Manage.* 182: 175-194.

Rubino, D.L. & McCarthy, B.C. 2003. Evaluation of coarse woody debris and forest vegetation across topographic gradients in a southern Ohio forest. *For. Ecol. Manage.* 183: 221-238.

Runkle, J.R. 1985. Disturbance regimes in temperate forests. In: Pickett S.T.A. & White P.S. (eds.) *The ecology of natural disturbance and patch dynamics*, pp. 17-33. Academic Press, San Diego, CA, US.

Runkle, J.R. 1990. Gap dynamics in an Ohio *Acer-Fagus* forest and speculations on the geography of disturbance.

Can. J. For. Res. 20: 632-641.

Runkle, J.R. 2000. Canopy tree turnover in old-growth mesic forests of Eastern North America. *Ecology* 81: 554-567.

Russell, N.H. 1953. The beech gaps of the Great Smoky Mountains. *Ecology* 34: 366-374.

Sagheb-Talebi, K. & Schütz, J.P. 2002. The structure of natural oriental beech (*Fagus orientalis*) forests in the Caspian region of Iran and potential for the application of the group selection system. *Forestry* 75: 465-472.

Saniga, M. & Schütz, J.P. 2002. Relation of dead wood course within the development cycle of selected virgin forests in Slovakia. *J. For. Sci.* 48: 513-528.

Schirone, B., Pedrotti, F., Spada, F., Bernabei, M., Di Filippo, A. & Piovesan, G. In press. L'hêtraie de plusieurs siècles de la Vallée Cervara (Parc National des Abruzzes, Italie). Colloque International de Phytosociologie et Dynamique des Végétations de Montagne 6-13 juillet 2002. Peiresc, France. *Acta Bot. Gall*.

Shugart, H.H. 1984. *A theory of forest dynamics*. Springer-Verlag, New York, NY, US.

Schulman, E. 1954. Longevity under adversity in conifers. *Science* 119: 396-399.

Spetich M.A., Shifley S.R. & Parker, G.R. 1999. Regional distribution and dynamics of coarse woody debris in midwestern old-growth forests. *For. Sci.* 45: 302-312.

Stewart, B.J., Neily, P.D., Quigley, E.J., Duke, A.P. & Benjamin, L.K. 2003. Selected Nova Scotia old-growth forests: Age, ecology, structure, scoring. *For. Chron.* 79: 632-644.

Stokes, M.A. & Smiley, T.L. 1996. *An Introduction to Tree-Ring Dating.* Reprint of 1968. U. of Chicago Press ed.

University of Arizona Press, Tucson, AZ, US.

Susmel, L. 1959. Riordino su basi bioecologiche delle faggete di Corleto Monforte (Salerno). Pubbl. n. 12 della Stazione Sperimentale per la Selvicoltura, Firenze, IT. (In Italian.)

Tubbs, C.H. & Houston, D.R. 1990. *Fagus grandifolia* Ehrh. American beech. In: Burns, R.M. & Honkala, B.H. (techn. coord.) *Silvics of North America. Vol. 2. Hardwoods,* pp 325-332. Agric. Handb. 654. USDA For. Serv., Washington, DC, US.

Walter, H. 1985. *Vegetation of the earth and ecological systems of the Geo-biosphere.* Springer-Verlag, Berlin, DE.

White, P.S., Harrod, J., Walker, J.L. & Jentsch, A. 2000. Disturbance, scale, and boundary in wilderness management. In: McCool, S.F., Cole, D.N., Borrie, W.T. & O'Loughlin, J. (eds.) *Wilderness science in a time of change conference - Volume 2: Wilderness within the context of larger systems*, pp. 27-42. USDA Forest Service Proceedings RMRS-P-15-VOL-2. Ogden, UT, US.

Wolf, A., Møller, P.F., Bradshaw, R.H.W. & Bigler, J. 2004. Storm damage and long-term mortality in a semi-natural, temperate deciduous forest. *For. Ecol. Manage*. 188: 197-210.

Wolynski, A. 2001. Significato della necromassa legnosa in bosco in un'ottica di gestione forestale sostenibile. *Sherwood* 67: 5-12. (In Italian.)

Zhang, L., Gove, J.H., Liu, C. & Leak, W.B. 2001. A finite mixture of two Weibull distributions for modelling the diameter distributions of rotated-sigmoid, uneven-aged stands. *Can. J. For. Res.* 31: 1654-1659.

Zohary, M. 1973. *Geobotanical foundations of the Middle East.* Fischer Verlag, Stuttgart, DE.