Stand and coarse woody debris dynamics in subalpine Norway spruce forests withdrawn from regular management

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Short title: Dynamics of overmature subalpine Norway spruce forests

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Abstract

- We studied structural characteristics, amount and quality of coarse woody debris (CWD), intensity of competition and mortality in two subalpine Norway spruce stands withdrawn from regular management. The stands, that we measured twice (in 1993 and 2005), have similar age and structure, but a different time has elapsed since the last silvicultural treatments (respectively 22 and about 55 years).

- The main purposes were to analyze the current stage of development as compared to the old-growth one and to highlight the legacies of past management.

- Even if relatively aged, the first plot (Valbona 1) was at the end of the pole stage. CWD was low in volume and was mainly of man-made origin (stumps). A recent thinning from below has reduced density-dependent competition and delayed the development of old-growth characteristics. The second plot (Valbona 2a) was at the beginning of the transition stage, with density-dependent and allogenic mortality both active at the same time. CWD volume was higher in plot Valbona 2a than in Valbona 1, but neither was comparable yet to the reference old-growth sites from Central Europe, both in quantity and in quality (e.g., decay rate continuity).

- The effects of the past management were: (1) reducing the quality and quantity of the CWD, (2) alleviating competition, (3) increasing resistance to minor disturbances and, as a consequence, (4) delaying the development processes.

- In mature or overmature subalpine Norway spruce stands withdrawn from regular management many decades are necessary to develop old-growth characteristics and a longer period of time is necessary to reach a true old-growth stage.

Keywords: competition, coarse woody debris (CWD), stand density index (SDI), age structure, old-growth.

1. Introduction

Since the second half of the 19th century, in most of the Italian Alps the socioeconomic structure and the public attitude towards forests and forestry have dramatically changed, resulting in extensive land use changes and in a noticeable reduction in human activities (Motta et al., 2006). As a consequence, many forests have been withdrawn from regular silvicultural management and have developed without direct human influence (Vandekerkhove et al., 2009). At the same time, while the past management was concentrated on extracting products from the forest, the present and the future one should emphasize what is being left (Kohm and Franklin, 1997).

Stakeholders and foresters are increasingly aware of the unique characteristics and values that overmature, late-successional and old-growth forests (sensu Oliver and Larson, 1996) provide. Nevertheless, due to the past intensive management, early seral stages are over-represented and late seral stages are rare or even absent (Motta, 2002).

Old-growth forests are later stages in forest development that are compositionally and structurally distinct from earlier successional stages. The age at which stands develop old-growth characteristics varies widely according to forest type, climate, site conditions and disturbance regime, hence the existence of various degrees of old-growth condition. In general the processes that take place in old-growth forests imply certain structural characteristics with significant ecological and aesthetic values: large and old trees, the abundance of dead organic material (coarse woody debris or CWD) like logs and snags, and canopy gaps formed by fallen trees. Overmature or late-successional forests are at a stage of stand development preceding old-growth; they encompass some attributes of old-growth forests but lack other key old-growth characteristics (Foster et al., 1996).

Due to the past human impact true old-growth stands no longer exist in the Italian Alps (Motta, 2002). On the other hand, there are many stands that have been withdrawn from regular management for decades. In these stands the natural processes, e.g., competition and disturbances, are superimposed on and interact with past human-induced changes. Such cultural legacy has important implications for the present-day structures and processes (Foster et al., 2003; Franklin et al., 2007).

Our specific questions were: 1) How long do old-growth characteristics take to develop from over-mature subalpine Norway spruce (*Picea abies* (L.) Karst.) forests that have been withdrawn from regular management respectively for 22 and 55 years? 2) Which are the legacies of the past management?

The results will provide baseline data to support the conservation and management of late successional Norway spruce subalpine forests, in order to recognize forest stands that deserve protection and to devise practices that will hasten the development of late-seral and old-growth characteristics, that are currently largely under-represented in the whole European Alps (Marage and Lemperiere, 2005; Keeton, 2006; Bauhus et al., 2009).

2. Material and methods

2.1. Study area

The study area is located in the Valbona forest reserve (lat. 46°18'N, long. 11°45'E) that is part of the Paneveggio Forest at an elevation ranging from 1695 m for plot Valbona 1 (VB1) to 1815 m a.s.l. for plot Valbona 2a (VB2a). The bedrock is porphyry, partially covered by morainic material, and the soils are podsols and non calcareous lithomorphic soils. The forest type is "Typical subalpine Norway spruce".

The human presence in Paneveggio started in the Mesolithic age (8000 bp) and the forests of the Fiemme valley have been managed at least since the beginning of the XIII century. The Forest of Paneveggio has belonged to the Austro-Hungarian Empire until the end of the First World War. Since 1919, the forest has been property of the Italian State and since the 1970s of the Autonomous Province of Trento. Since 1990 it has been part of the "Parco Naturale Paneveggio-Pale di S. Martino". The Valbona forest reserve (123 ha) was established in 1992, and contains a silvicultural reserve for experimental research (43 ha) and a strict reserve (80 ha).

Most of the reserve is characterized by monolayered Norway spruce stands. In the most mature part of the reserve we selected two study areas according to a chronosequence in the human abandonment process, ranging from the recent end of the silvicultural treatments up to a few decades of abandonment. The disturbance history and, particularly, the cessation of silvicultural treatments was estimated in 22 years for plot VB1 and about 55 years for plot VB2a using release from suppression in cross-dated cores and validated using Management plans (Motta et al., 1999).

2.2. Stand structure

The size of the two permanent plots is, respectively, 10267 (VB1) and 14046 m^2 (VB2a). The two plots were established and mapped in 1993 (Motta et al., 1999). In the initial inventory we recorded species, tree topographic coordinates and diameter at breast height (dbh) for all living trees ≥ 7.5 cm in dbh. Total height, height to the lowest live branch in two opposite directions and crown projections on the ground in four directions were also measured. One core was extracted at 50 cm height from all living trees in 1995. In the lab, following optimization of surface resolution, radial increments to the nearest 0.01 mm were measured and cross-dated against available and updated site chronologies (Motta et al., 2002).

The inventory was repeated in 2005 and tree lists were updated with ingrowth; dbh, heights and crown projections were re-measured and ingrowth cores were collected and cross-dated. Volume for living trees was calculated according to local yield tables. We tested a) the normality of size distributions in the two plots by the Shapiro-Wilk test; b) the statistical differences in paired data (size distribution in two different inventories and trees/CWD size distribution in the same plot) by a Wilcoxon non-parametric test and c) the statistical differences in independent samples (size distribution in two different plots) by a Kolmogorov-Smirnov non-parametric test. Statistical analyses were performed using PAST 1.90 (Hammer et al., 2001).

2.3. CWD (Coarse woody debris)

We grouped CWD into snags (standing dead trees, dbh ≥ 7.5 cm and height ≥ 1.3 m), downed logs (fallen stems or branches ≥ 7.5 cm diameter and length ≥ 1 m) and stumps (short, vertical remains from cutting or windthrow, top diameter ≥ 7.5 cm and height < 1.30 m). A stump was classified as man-made if the exposed surface was straight, indicating felling by saw. The separation of snags from logs was established at a 45° angle. Volumes for non-broken snags were calculated according to methods described in Motta, Berretti et al. (2006). The decay stage (Tab. 1) was classified according to a four-class system (Sollins, 1982). We extracted, prepared and cross-dated one core from snags and logs in decay classes 1 and 2.

2.4. Competition and mortality

We assessed crowding in plot VB1 and plot VB2a by means of Reineke's (1933) Stand Density Index (SDI), using the summation method proposed by Shaw (2000). Relative density, i.e., the percent ratio between observed stand density and its theoretical maximum, describes the intensity of competition acting in the stand, and can be linked to specific stand developmental stages (Smith and Long, 2001). The maximum SDI for Norway spruce in the Paneveggio-Pale di San Martino Natural Park was calculated as 1380 from a dataset of 291 sample plots already available (Castagneri et al., 2008). We computed percent relative density in the two permanent plots for both inventory years as the ratio between observed and maximum SDI. We also computed mortality rates on an annual basis.

We determined the year of death of log and snags (decay classes 1 and 2) by cross-dating and rounded to the nearest decade. Logs and snags mortality causes were classified as follows:

-allogenic: logs from windthrow (uprooted or snapped trees with marked fracture and splintering);

-autogenic and unknown: logs from snags (trees that died standing and after some time fell on the ground) and snags with no evidence of primary mortality agents (Dobbertin, 2005).

Mortality induced by competition or other unknown were partitioned in two classes: i) trees showing a growth decline before death, or suppressed trees characterized by very narrow rings during all their life and ii) trees without evident signs of growth decline before death (Bigler and Bugmann, 2003)

3. Results

3.1. Stand structure

Tree density was respectively 466 (Plot VB1) and 513 (Plot VB2a) trees ha^{-1} (Tab. 2). Standing volume was respectively 841.4 and 914.5 m^{3} ha^{-1}. In 2005 the tree size distributions were unimodal (Castagneri et al., 2008) but didn't have a normal distribution (Shapiro-Wilk test). Density slightly decreased in both plots the between the two measurements (-1.7% in Plot VB1 and -12.1% in Plot VB2a), high and medium-low diameter classes experienced increased and reduced frequencies respectively. The size distribution has not changed across time in both plots ($P>0.05$). Size distribution differences between the two plots were not significant in year 2005 ($P>0.05$).

We were able to determine the age at a height of 50 cm of 94.9% of the individuals. Stem and root rot was the main obstacle to age determination. The age structure (Fig. 1) pinpointed the time of establishment of the current stands: about 200 years before present in plot VB1 and about 220 years in plot VB2a. The establishment period after the disturbance lasted approximately one century in both plots. There were some very old individuals in both plots, the oldest ones being 279 and 447 years old in plot VB1 and VB2a respectively.

3.2. CWD profile

The total volume of CWD was 27.6 m^3 ha^{-1} in plot VB1 and 79.6 m^3 ha^{-1} in plot VB2a (Tab. 3). Stumps (exclusively of man-made origin in plot VB1 and almost exclusively so in plot VB2a) had an irregular diameter distribution, ranging from 15 to 70 cm in plot VB1 and from 10 to 100 cm in plot VB2a, with a modal value of 40 cm in both plots (Fig. 2). Snags had reverse J-shaped distribution in plot VB2a, while they were scarce in plot VB1. Logs showed a unimodal distribution in both plots with a modal value of 15 cm in plot VB1 and 20 cm in plot VB2a. Size distribution of snags, logs and stumps were significantly different from that of live trees in both plots ($p<0.05$) taking into account that CWD size were measured in part of the trunk different form the dbh and the original trunk can produce more than one log resulting in a potential overestimation of this CWD type. CWD volume amounted to 3.3% of living tree volume in plot VB1 and 8.7% in plot VB2a (Tab. 2). The volume of stumps was relevant in plot VB1, where they represented 64.5% of the total CWD volume, but scarce in plot VB2a (7.7%). On the other hand, the volume of snags was relevant in plot VB2a, where they accounted for more than 67% of the CWD total volume. The logs represented 15.9% and 25.0% of the total CWD volume respectively in plot VB1 and VB2a. We assume that logs were over-represented in plot VB1, due to the presence of many short logs from a 1993 thinning.

Regarding decay class, we detected opposite trends between stumps, on one side, and snags and logs on the other (Tab. 4). Most of the stumps in both plots were in classes 3 and 4, i.e., the most decayed ones (84.0% in plot VB1 and 97.2% in plot VB2a). On the other hand, 100.0% of the snags in plot VB1 and 97.2% in plot VB2a were in the lower decay classes (1 and 2). There was a higher incidence of snags in class 1 in plot VB2a

(88.4%) than in plot VB1 (60.9%). If compared to snags, logs generally showed a more advanced decay status: class 2 was the most represented one in both plots (71.0% and 52.6% of total logs respectively).

3.3. Competition and mortality

SDI (2005) was 1051 in plot VB1 and 1114 in plot VB2a. The log-slope of the self-thinning trajectory for the study period (1993-2005) was -4.802 in plot VB1, and -1.139 in plot VB2a (Fig. 3). In the last decade relative density increased in plot VB1 from 67.7 to 76.1% and in plot VB2a from 76.7 to 80.8% (Tab. 1).

Mortality rate was 0.21% year^{-1} in plot VB1 and 1.01% year^{-1} in plot VB2a. In plot VB1 living biomass increased with very limited mortality, while plot VB2a suffered mortality that was mainly concentrated on the smaller and intermediate diameter classes (Fig.4a).

We analyzed mortality dynamics in plot VB2a only, because sample size in plot VB1 was insufficient. In plot VB2a the date of death was successfully determined for 70% of the tree samples (n = 179). The earliest identified year of death belonged to the 1920 decade, while more than 55% of the tree death was observed in the decades 1970 and 1980 (Fig.5).

The causes of death were mainly autogenic or unknown (81%). Allogenic mortality was exclusively concentrated in the last decade (2000) and was due to wind or to wind-snow (snapped or uprooted trees); we didn't find any biotic primary mortality agents (e.g. insects and pathogens). The autogenic-unknown mortality involved trees with a dbh ranging from 10 to 55 cm, but was mainly concentrated in smaller diameters. Allogenic mortality had a higher incidence in dbh classes 30-60 cm (Fig. 4b).

Most of the trees (54.8%) defined as competition-induced or unknown mortality died after a perceptible decline or chronic slow growth observed in the tree-ring series (Bigler and Bugmann, 2003). Nevertheless, other trees died while growing at the normal rate with no indication of impeding mortality in the tree-ring patterns.

4. Discussion

The two permanent plots showed some common characteristics: both established (about 200 years ago plot VB1 and 220 years plot VB2a) after a shelterwood felling and were respectively managed until 1983 (plot VB1) and about 1950 (plot VB2a) (Motta et al., 1999). Both were monolayered and were overstocked if compared with central European Norway spruce old-growth forests (Fig. 3; Tab. 5).

A first difference between the two plots was the CWD profile (Stokland, 2001; Woodall and Nagel, 2006). Plot VB1 was poor in CWD, there were stumps in all decay classes (even if only 16.1% in the classes 1-2) and there were no snags and logs in classes 3-4. Plot VB2a was richer in CWD, the stumps showed a high decay rate (there were no stumps in the decay class 1 and very few in class 2), there were logs in all decay classes (52.6% in class 2) and so were snags, even if more than 88% in class 1. Even if Norway spruce is considered very susceptible to windthrow because of its shallow root system, uprooted trees were absent in plot VB1 and rare in plot VB2a. Until the last decade mortality was confined to the suppressed trees and dead trees only reached the ground (logs) after a first stage as a snag. This explains why there are only a few logs in the first decay class (Motta et al., 2006). The rate of CWD accumulation was slow (the total amount is 27.6 and 79.6 m^3 ha^{-1} after about 22 and 55 years from the cessation of silvicultural interventions) as compared, for example, to that observed in mixed mountain forests (Motta et al., 2008).

Another difference was represented by the intensity of competition (Castagneri et al., 2010) and, consequently, the mortality rate. At the beginning of the study period, relative density in both plots was already above the 60% threshold (Tab. 1; Fig. 3), which represents complete resource exploitation and marks the onset of the self-thinning process (Drew and Flewelling, 1979). The size-density trajectory (Fig. 3) for the last decade in plot VB1 showed a period of increase in mean tree size without density-related mortality (annual mortality rate = 0.21%) as a consequence of the last thinning. Plot VB2a showed an increase in mean tree size and reduction in density (annual mortality rate = 1.01%) but, in the same time, due to the size increment, reached the 80% of maximum SDI, meaning that the biological carrying capacity of the site was nearly totally exploited (Long and Shaw, 2005). In plot VB2a competition for resources was extreme and has been high for an extended period. In this plot the date of tree death showed that the autogenic-unknown mortality reached the maximum in the decades 1970 and 1980 (Fig. 5), and subsequently declined (1990 and, even more, 2000). In the last decade overall mortality was higher than in the previous decade because of the onset of allogenic mortality, that has involved dominant and co-dominant trees (Fig. 4b). We found some discrepancies for autogenic-unknown mortality: a few trees according to crown assessment, were alive in 1993 and dead in 2005 but their last cross-dated tree-ring was formed before 1993. Autogenic-unknown mortality dates should be to be taken with caution, because the formation of tree rings may stop for years or even for decades prior to mortality (Cherubini et al., 2002).

Both plots have developed very few old-growth characteristics: even if the average size of the trees is higher if compared with the old-growth ones (Fig. 3), this is the result of a different size distribution. The studied plots have an "unimodal" distribution while a true old-growth is expected to have a "negative exponential" distribution. As a consequence the average size value is high, if compared with a true old-growth, but both stands lack or have very few very large trees that are one of the characteristics of an old-growth. The same is for the CWD: large piece of CWD are mainly stumps (Fig. 2) and the quantity and the quality (stage of decay) of the CWD is not comparable with the old-growth (Tab. 4). According to the structure, CWD profile, competition intensity and mortality rate, plot VB1 was classified as being at the end of the stem exclusion stage, while plot VB2a was assigned to a initial transition stage between stem exclusion and understory re-initiation (Oliver and Larson, 1996). In the next decades, VB1 will probably follow the same dynamics recently observed in VB2a (increment of competition and autogenic mortality), while plot VB2a will continue the structural re-organisation that is leading it from a monolayered to a multilayered structure. During such transition, allogenic disturbances will increase their importance, and the decrement of tree density will lead to QMD/density relationships more and more close to those observed for subalpine Norway spruce in a true old-growth stage (Tab. 5). This process results in a progressive accumulation of gaps as the stand gets older, so that the stand development trajectory drops below the maximum density line resulting in a SDI decline (Smith and Long, 2001). The decrement of the intensity of the competition is due to the fact that the death of old and large trees may exceed the capability of lateral growth of surviving crowns and ingrowth in overmature stands (Zeide, 1995). There are also other ecophysiological explanations for the age-related decline of radial growth

(Binkley et al., 2002).

In any case, the time requested to develop a multilayered structure is still long. Besides the further creation of new gaps, that cannot be accurately foretold, the establishment and growth of new cohorts will be postponed by many decades for the following reasons:

1) seed production is irregular, with adequate quantity and quality for seedling establishment only after a mast year, that occurs every 8-10 years on average (Mencuccini et al., 1995);

2) seedling establishment requires a favorable seedbed. Different types of microsites, e.g., CWD, mounds, and uprooting pits, are vital for regeneration establishment and early growth (Motta et al., 2006). However, microsite diversity and CWD quantity and quality are greatly reduced in managed stands. Besides, the process of wood decay in subalpine Norway spruce forests is very slow (Storaunet and Rolstad, 2002; Holeksa et al., 2008), so that it will take many more decades to develop a decay rate continuity favorable to seedling establishment and comparable to those of true old-growth forests;

3) early regeneration growth is slow. Norway spruce in Paneveggio requires an average of 18 years to reach 50 cm height and more than 40 years to reach 130 cm height (Piussi, 1976; Motta et al., 2002).

The legacies of past management are dense stands with higher resistance to small scale allogenic disturbances, low mortality rate, limited CWD accumulation and unfavorable conditions for natural regeneration establishment. Other potential legacies, such as old logging damages that could have enhanced the spread of decay fungi (Vasiliauskas, 2001) and monolayered structure that could be more vulnerable to wind disturbances (Zeng et al. 2010), at the present have no evident consequences in the two studied plots.

As a consequence we expect that these previously managed stands will reach more advanced stages of development far later than natural stands.

In previously managed, subalpine Norway spruce forests of the Alps, structure, CWD profile, competition and mortality were useful parameters to delineate the present development stage, as compared to the old-growth one. Further studies documenting natural disturbance regimes and associated stand structures and dynamics of late successional stages are much needed to refine silvicultural systems meant to develop and maintain old-growth characteristics (Long, 2009). For this reason, it is crucial to develop a network of forest reserves in previously managed forests that have been withdrawn from regular management, in order for natural processes to be allowed to take place and to provide a reference for ordinary managed forests (Motta, 2002; Brang, 2005; Bauhus et al., 2009).

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Captions

Tab. 1. Decay class system for coarse woody debris elements.

Tab. 2. Stand characteristics (1993 and 2005)

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* data from stumps not available (snags and stumps are presented together).

	Snag	Log	Stump
1	Complete or partial bark, most of the branches intact, hard wood	Bark intact, small branches present, shape round, wood texture intact, log elevated on support point or slightly sagging	Bark intact, texture intact, original surface cut and original color
2	Partial/almost absent bark, no twigs, hard wood	Trace of bark, no twigs, shape round, wood hard, texture in large pieces, log sagging near the ground	Bark almost intact, texture partly soft (in the outermost part), original surface cut and original color,
3	No bark, no twigs, wood hard to soft (soft sapwood < 70%)	No bark, no twigs, shape round to oval, wood hard to soft, texture with blocky pieces, all of log on the ground	Trace of bark, texture in large pieces, surface cut original but decay spread in most of the stump , color becoming brown
4	No bark, no twigs, wood hard to soft (soft sapwood > 70%)	No bark, no twigs, oval shape, soft and powdery wood structure, log completely sagging on the ground	Bark absent, texture soft and powdery, surface cut almost absent ad color brown

Tab. 1. Decay class system for coarse woody debris elements

Plot	Living trees N ha^{-1}	Volume living trees (m^3 ha^{-1})	Basal area (m^2 ha^{-1})	Mean diameter (cm)	Mean height (m)	SDI	Relative density %
Plot VB1 (1993)	474	725.7	54.8	38.4	29.7	935	67.7
Plot VB1 (2005)	466	841.4	63.3	41.6	30.8	1051	76.2
Plot VB2a (1993)	584	829.6	63.2	37.1	28.0	1058	76.7
Plot VB2a (2005)	513	914.5	69.2	41.5	29.6	1114	80.8

Tab. 2. Stand characteristics (1993 and 2005)

Plot	Snags (m^3 ha^{-1})	Logs (m^3 ha^{-1})	Stumps (m^3 ha^{-1})	Total CWD (m^3 ha^{-1})	CWD/living %
1	5.4	4.4	17.8	27.6	3.3
2	53.6	19.9	6.1	79.6	8.7

Tab.3. Volume of snags, logs and stumps in the two plots.

	Plot 1			Plot 2		
Decay stage	snags	logs	stumps	snags	logs	stumps
1	60.9	29.0	0.4	88.4	31.8	0.0
2	39.1	71.0	15.7	8.7	52.6	2.8
3	0.0	0.0	18.7	1.4	13.3	29.9
4	0.0	0.0	65.3	1.4	2.4	67.3

Tab.4. CWD type and decay stage (%) in the two plot

	Volume	Basal Area	Density	Mean dbh	Volume Snags	Volume Logs	Volume Stumps	Total CWD volume	CWD/live trees	Total volume Living tree + CWD	Reference
	(m^3 ha^{-1})	(m^2 ha^{-1})	(N ha^{-1})	(cm)	(m^3 ha^{-1})	(m^3 ha^{-1})	(m^3 ha^{-1})	(m^3 ha^{-1})	%	(m^3 ha^{-1})	
Babia Gora 1	407.0	36.4	258	42.4	58.5	72.6	*	131.1	32.2	538,1	(Holeksa, 2001)
Babia Gora 2	387.2	35.3	255	42.0	54.4	76.0	6.0	136.4	35.2	523.6	(Zielonka, 2006)
Babia Gora 3	412.1	32.7	258	40.2	71.0	73.4	8.2	152.6	37.0	564.7	(Zielonka, 2006)
Babia Gora 4	511.2	37.4	230	45.5	73.8	110.1	9.2	193.1	37.8	704.3	(Zielonka, 2006)
Babia Gora 5	465.9	36.0	288	39.9	106.1	145.5	9.7	261.3	56.1	727.2	(Zielonka, 2006)
Babia Gora 6	540.3	38.7	378	36.1	58.3	78.8	4.5	141.6	26.2	681.8	(Zielonka, 2006)
Tatra Mountains 1	351.5	27.3	414	29.0	119.4	82.1	5.1	206.6	58.8	558.1	(Zielonka, 2006)
Tatra Mountains 2	306.9	23.4	327	30.2	185.3	88.2	8.9	292.4	95.5	599.3	(Zielonka, 2006)
Tatra Mountains 3	486.4	42.1	290	43.0	72.2	60.4	4.0	136.6	28.0	623.1	(Zielonka, 2006)
Tatra Mountains 4	622.3	44.6	383	38.5	90.7	104.5	8.1	203.3	32.3	825.6	(Zielonka, 2006)
Tatra Mountains 6	453.8	36.1	314	38.3	92.4	92.1	7.1	191.5	42.2	645.3	(Zielonka, 2006)
Polana	500.0	41.0	290	37.3	48.6	94.9	*	143.5	28.7	643,5	(Holeksa et al., 2007)
Sumava NP 1	351.0	32.0	131	53.0	196.0	115.0	*	311.0	88.6	662.0	(Svoboda and Pouska, 2008)
Sumava NP 2	447.0	45.0	310	43.0	96.0	60.0	*	156.0	34.9	603.0	(Svoboda and Pouska, 2008)
Valbona 1	841.4	63.2	463	41.6	5.4	4.4	17.8	27.6	3.3	868,9	This study
Valbona 2a	945.3	71.2	489	42.9	53.6	19.9	6.1	79.6	8.4	1025.0	This study

Tab.5. Stand characteristics for some subalpine Norway spruce old-growth forest from the Carpathians, the Tatra mountains and from the Valbona forest Reserve in Paneveggio. In all the stands the lowest measured dbh was 10 cm (density and mean dbh data from Valbona Reserve were harmonized according to this threshold). Data from Babia Gora 1, Polana and Sumava NP are means from a network of sampling plots. The other data are from individual permanent plots.

* data from stumps not available (snags and stumps are presented together).

Fig.1. Age structure in the two plots

Fig. 2. Size class distribution for the three CWD types (snags, logs and stumps) in the two plots.

Fig. 3. Size (QMD: quadratic mean diameter)-density relationships for the studied plots (1993 and 2005) and for some subalpine, old-growth Norway spruce forest in central Europe.

Solid dots represent the Valbona plots respectively in 1993 and in 2005. VB2a is currently above 80% of the SDI that represents the biological carrying capacity of the site. VB1 is very close to this threshold. Empty dots represents size-density pairs for central European old-growth stands (see Tab. 5). The relative density in old-growth stands ranges between 35 and 60% (OGZ: old-growth zone) suggesting that old-growth stage processes occur after a reduction of competition intensity due to both autogenic and allogenic disturbances

Fig. 4. Diameter distribution (a) and incidence of mortality (both snags and logs) in the different size classes (b) in plot VB2a

Fig. 5. Decade and cause of death for cross-dated snags and logs in decay classes 1 and 2 in plot VB2a

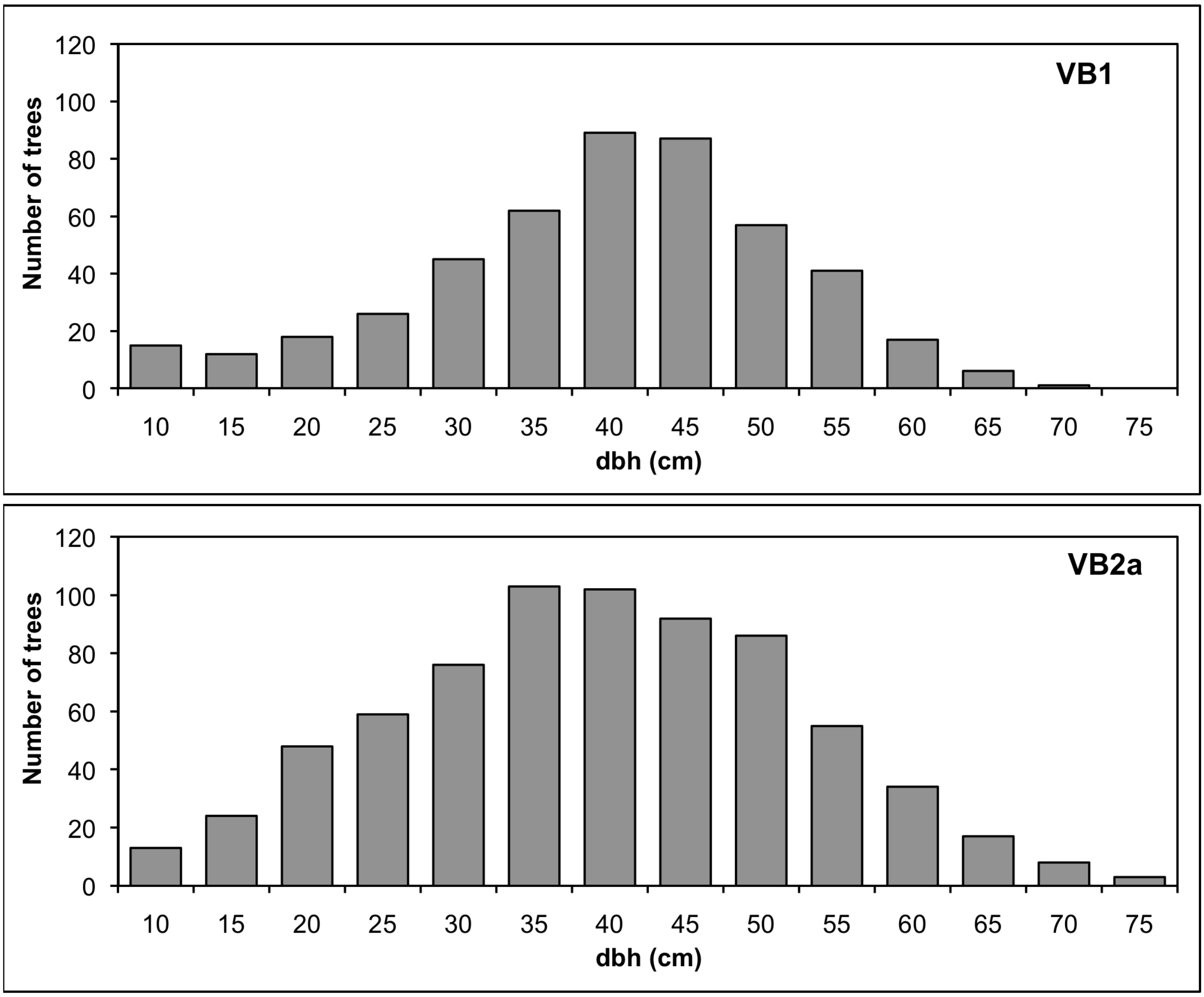

VB1
Number of trees
0
20
40
60
80
100
120
10
15
20
25
30
35
40
45
50
55
60
65
70
75
dbh (cm)
VB2a
Number of trees
0
20
40
60
80
100
120
10
15
20
25
30
35
40
45
50
55
60
65
70
75
dbh (cm)

Fig.1

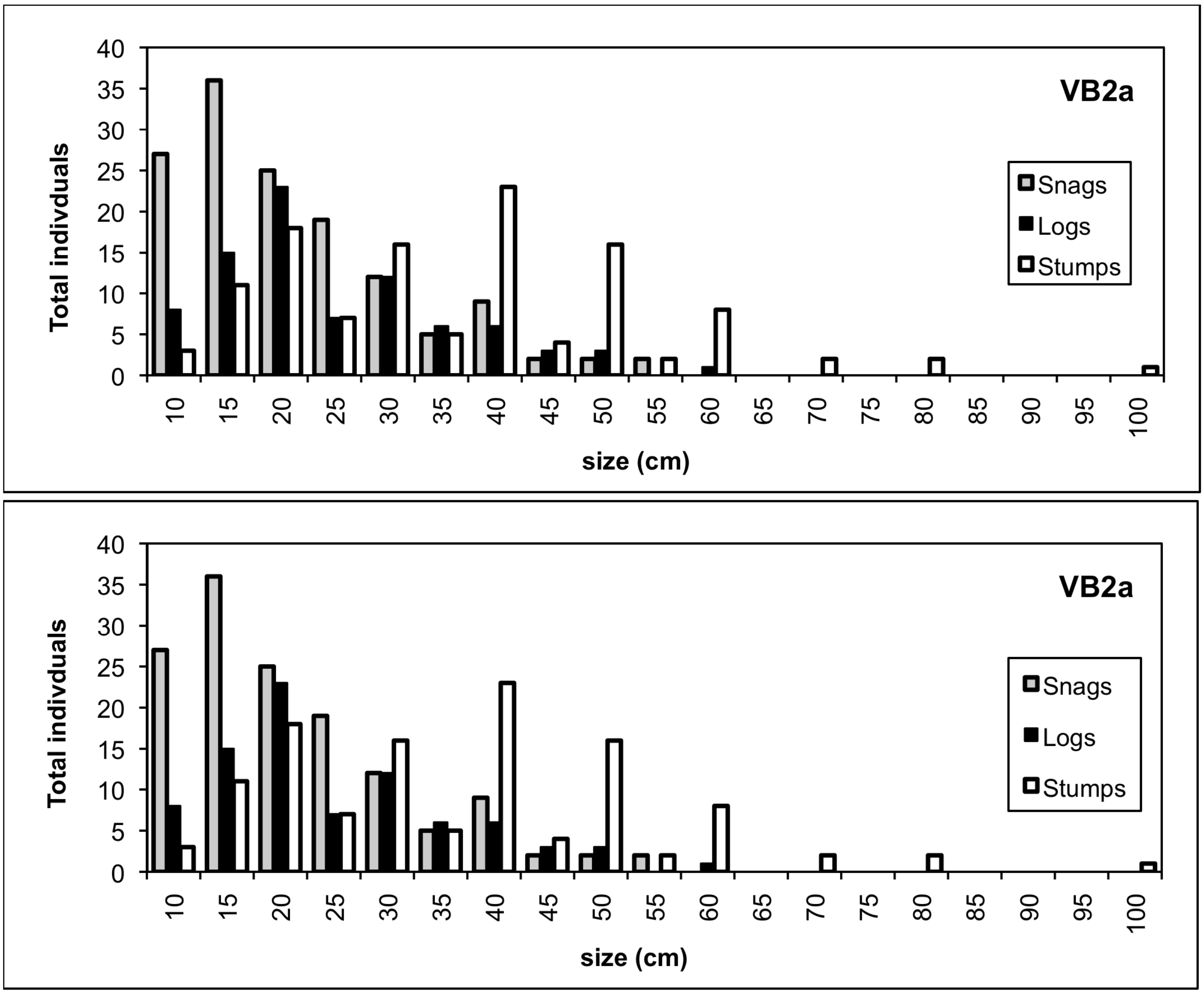
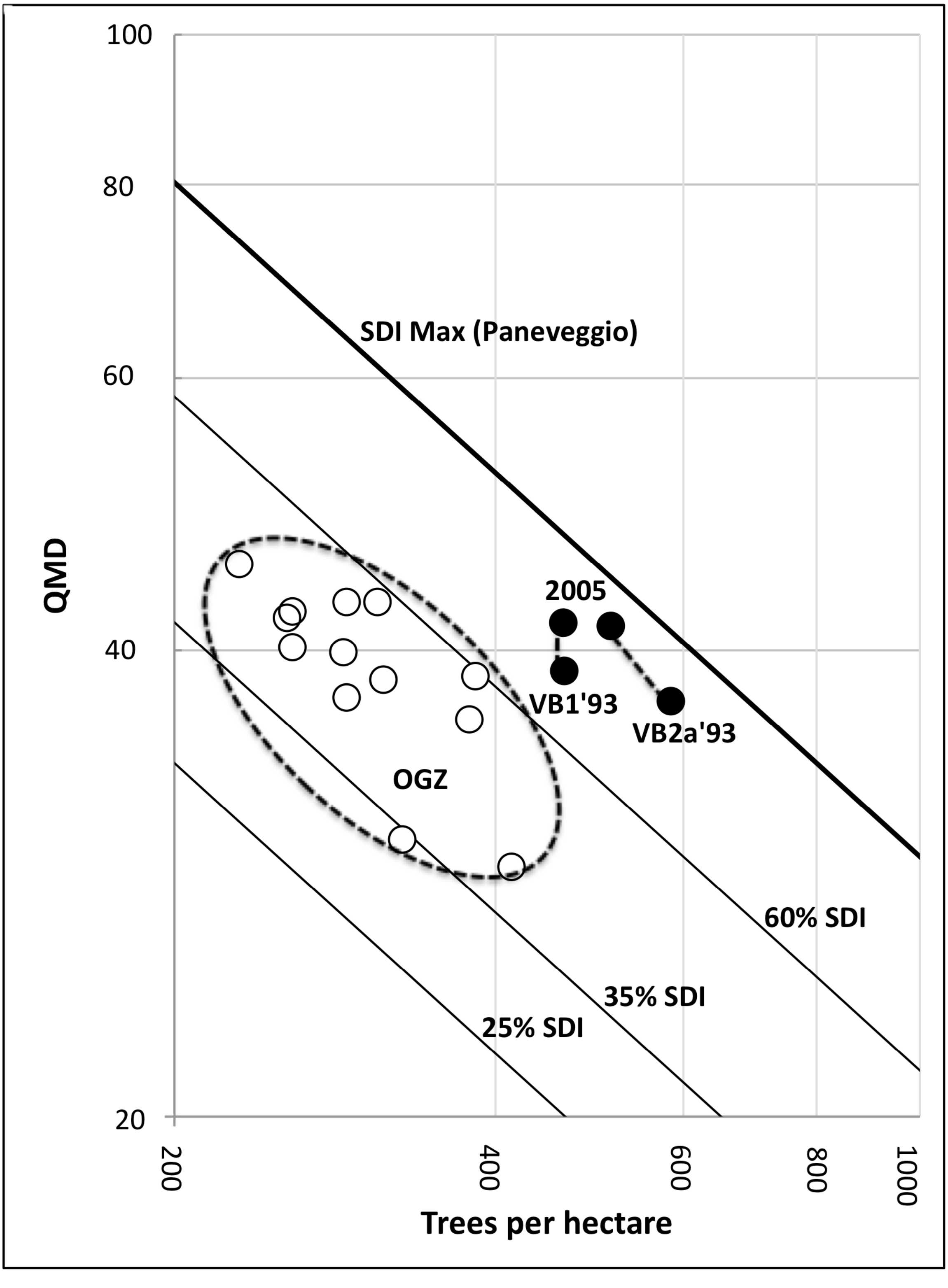

VB2a
Total indivduals
size (cm)
Snags
Logs
Stumps
0
5
10
15
20
25
30
35
40
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100

Fig. 2

Fig. 3


100
80
60
40
20
QMD
SDI Max (Paneveggio)
2005
VB1'93
VB2a'93
OGZ
60% SDI
35% SDI
25% SDI
200
400
600
800
1000
Trees per hectare

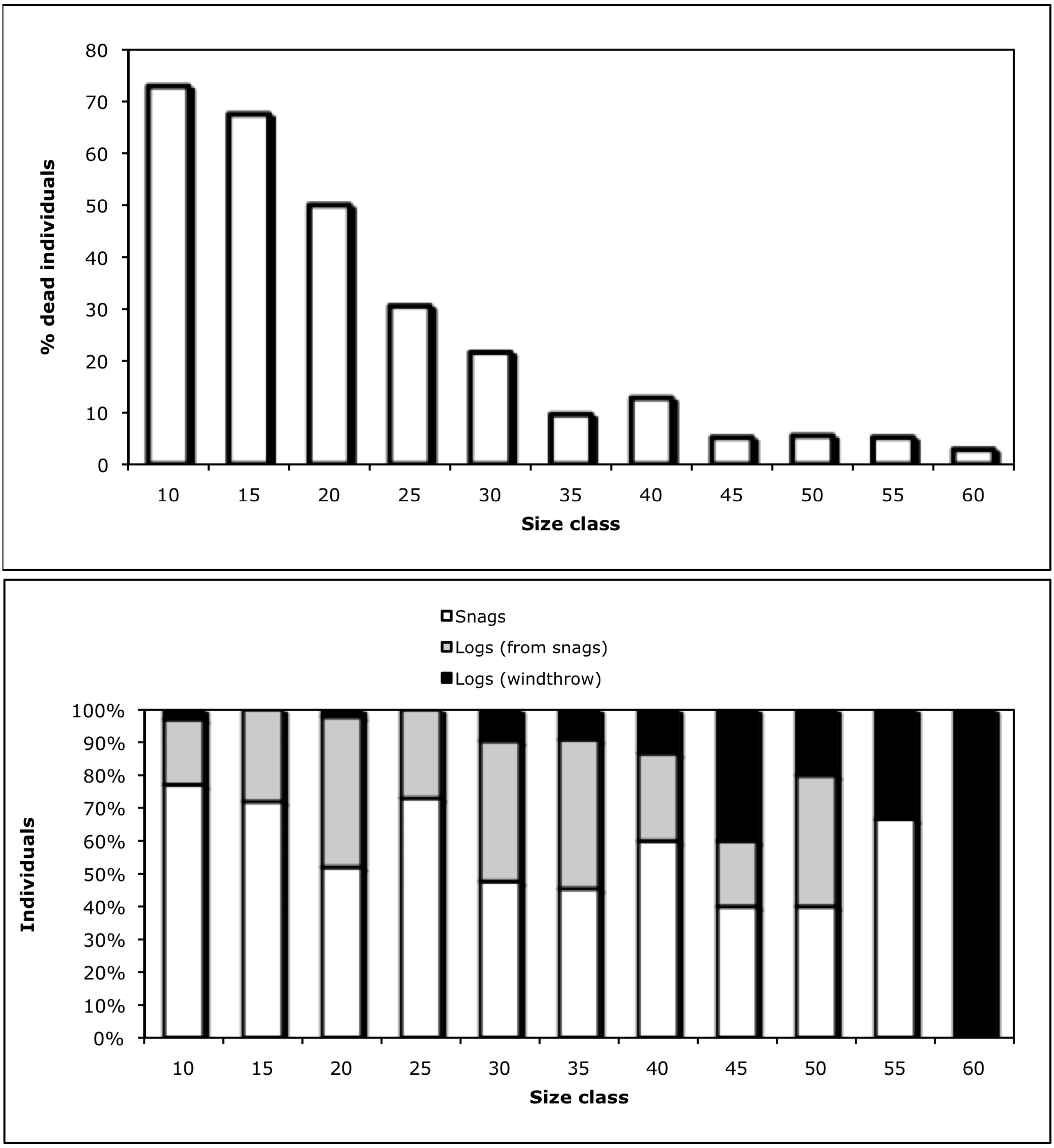
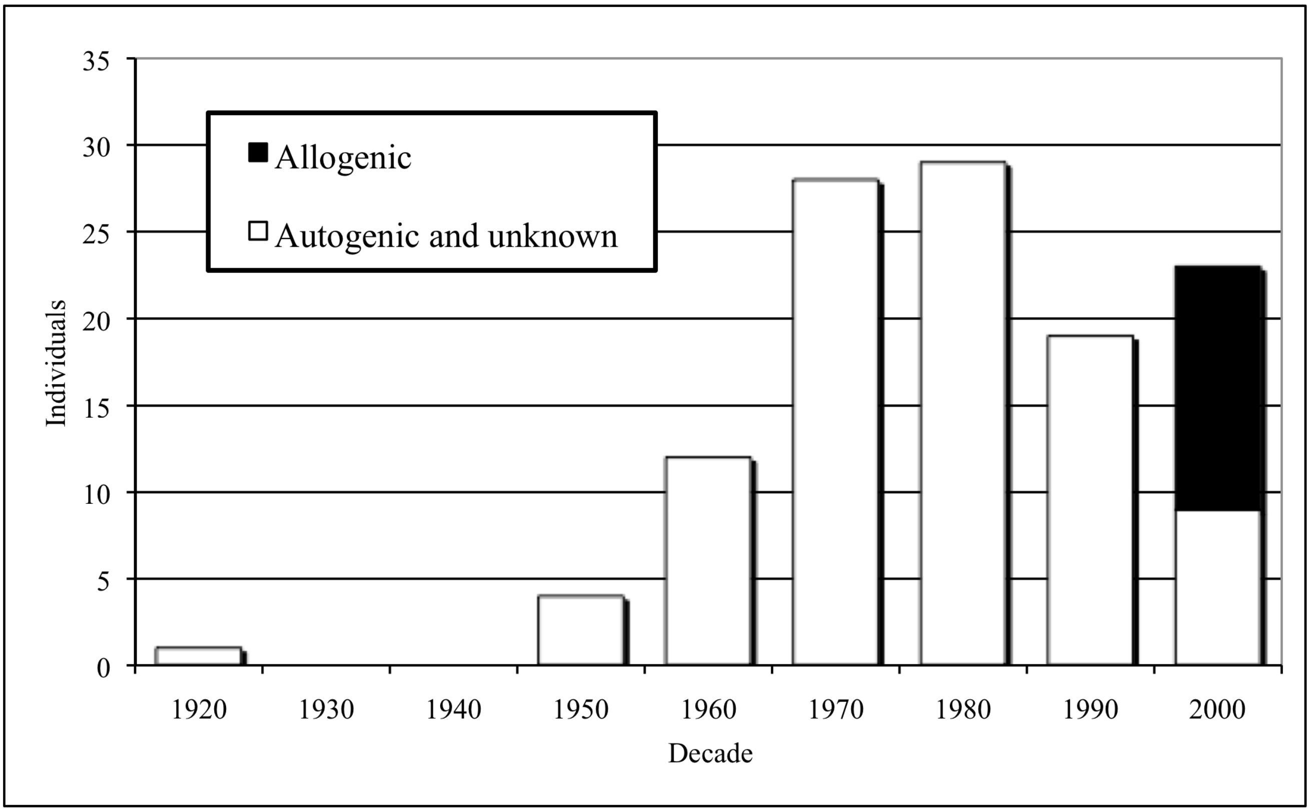

% dead individuals
80
70
60
50
40
30
20
10
0
10
15
20
25
30
35
40
45
50
55
60
Size class
□ Snags
▨ Logs (from snags)
■ Logs (windthrow)
Individuals
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
10
15
20
25
30
35
40
45
50
55
60
Size class

Fig. 4

Fig. 5


■ Allogenic
□ Autogenic and unknown
Individuals
35
30
25
20
15
10
5
0
1920
1930
1940
1950
1960
1970
1980
1990
2000
Decade