1 Stand and coarse woody debris dynamics in subalpine Norway spruce forests

2 withdrawn from regular management

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12 Short title: Dynamics of overmature subalpine Norway spruce forests

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18   Abstract

19   - We studied structural characteristics, amount and quality of coarse woody debris

20   (CWD), intensity of competition and mortality in two subalpine Norway spruce stands

21   withdrawn from regular management. The stands, that we measured twice (in 1993 and

22   2005), have similar age and structure, but a different time has elapsed since the last

23   silvicultural treatments (respectively 22 and about 55 years).

24   - The main purposes were to analyze the current stage of development as compared to

25   the old-growth one and to highlight the legacies of past management.

26   - Even if relatively aged, the first plot (Valbona 1) was at the end of the pole stage.

27   CWD was low in volume and was mainly of man-made origin (stumps). A recent

28   thinning from below has reduced density-dependent competition and delayed the

29   development of old-growth characteristics. The second plot (Valbona 2a) was at the

30   beginning of the transition stage, with density-dependent and allogenic mortality both

31   active at the same time. CWD volume was higher in plot Valbona 2a than in Valbona 1,

32   but neither was comparable yet to the reference old-growth sites from Central Europe,

33   both in quantity and in quality (e.g., decay rate continuity).

34   - The effects of the past management were: (1) reducing the quality and quantity of the

35   CWD, (2) alleviating competition, (3) increasing resistance to minor disturbances and,

36   as a consequence, (4) delaying the development processes.

37   - In mature or overmature subalpine Norway spruce stands withdrawn from regular

38   management many decades are necessary to develop old-growth characteristics and a

39   longer period of time is necessary to reach a true old-growth stage.

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45   1. Introduction

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47   Since the second half of the 19th century, in most of the Italian Alps the socioeconomic

48   structure and the public attitude towards forests and forestry have dramatically changed,

49   resulting in extensive land use changes and in a noticeable reduction in human activities

50   (Motta et al., 2006). As a consequence, many forests have been withdrawn from regular

51   silvicultural management and have developed without direct human influence

52   (Vandekerkhove et al., 2009). At the same time, while the past management was

53   concentrated on extracting products from the forest, the present and the future one

54   should emphasize what is being left (Kohm and Franklin, 1997).

55   Stakeholders and foresters are increasingly aware of the unique characteristics and

56   values that overmature, late-successional and old-growth forests (sensu Oliver and

57   Larson, 1996) provide. Nevertheless, due to the past intensive management, early seral

58   stages are over-represented and late seral stages are rare or even absent (Motta, 2002).

59   Old-growth forests are later stages in forest development that are compositionally and

60   structurally distinct from earlier successional stages. The age at which stands develop

61   old-growth characteristics varies widely according to forest type, climate, site

62   conditions and disturbance regime, hence the existence of various degrees of old-growth

63   condition. In general the processes that take place in old-growth forests imply certain

64   structural characteristics with significant ecological and aesthetic values: large and old

65   trees, the abundance of dead organic material (coarse woody debris or CWD) like logs

66   and snags, and canopy gaps formed by fallen trees. Overmature or late-successional

67   forests are at a stage of stand development preceding old-growth; they encompass some

68 attributes of old-growth forests but lack other key old-growth characteristics (Foster et

69 al., 1996).

70 Due to the past human impact true old-growth stands no longer exist in the Italian Alps

71 (Motta, 2002). On the other hand, there are many stands that have been withdrawn

72 from regular management for decades. In these stands the natural processes, e.g.,

73 competition and disturbances, are superimposed on and interact with past human-

74 induced changes. Such cultural legacy has important implications for the present-day

75 structures and processes (Foster et al., 2003; Franklin et al., 2007).

76 Our specific questions were: 1) How long do old-growth characteristics take to develop

77 from over-mature subalpine Norway spruce (*Picea abies* (L.) Karst.) forests that have

78 been withdrawn from regular management respectively for 22 and 55 years? 2) Which

79 are the legacies of the past management?

80 The results will provide baseline data to support the conservation and management of

81 late successional Norway spruce subalpine forests, in order to recognize forest stands

82 that deserve protection and to devise practices that will hasten the development of late-

83 seral and old-growth characteristics, that are currently largely under-represented in the

84 whole European Alps (Marage and Lemperiere, 2005; Keeton, 2006; Bauhus et al.,

85 2009).

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88 2. Material and methods

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90 2.1. Study area

91   The study area is located in the Valbona forest reserve (lat. 46°18'N, long. 11°45'E)

92   that is part of the Paneveggio Forest at an elevation ranging from 1695 m for plot

93   Valbona 1 (VB1) to 1815 m a.s.l. for plot Valbona 2a (VB2a). The bedrock is porphyry,

94   partially covered by morainic material, and the soils are podsols and non calcareous

95   lithomorphic soils. The forest type is "Typical subalpine Norway spruce".

96   The human presence in Paneveggio started in the Mesolithic age (8000 bp) and the

97   forests of the Fiemme valley have been managed at least since the beginning of the XIII

98   century. The Forest of Paneveggio has belonged to the Austro-Hungarian Empire until

99   the end of the First World War. Since 1919, the forest has been property of the Italian

100   State and since the 1970s of the Autonomous Province of Trento. Since 1990 it has been

101   part of the "Parco Naturale Paneveggio-Pale di S. Martino". The Valbona forest reserve

102   (123 ha) was established in 1992, and contains a silvicultural reserve for experimental

103   research (43 ha) and a strict reserve (80 ha).

104   Most of the reserve is characterized by monolayered Norway spruce stands. In the most

105   mature part of the reserve we selected two study areas according to a chronosequence in

106   the human abandonment process, ranging from the recent end of the silvicultural

107   treatments up to a few decades of abandonment. The disturbance history and,

108   particularly, the cessation of silvicultural treatments was estimated in 22 years for plot

109   VB1 and about 55 years for plot VB2a using release from suppression in cross-dated

110   cores and validated using Management plans (Motta et al., 1999).

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112   2.2. Stand structure

113   The size of the two permanent plots is, respectively, 10267 (VB1) and 14046 m^2

114   (VB2a). The two plots were established and mapped in 1993 (Motta et al., 1999). In the

115   initial inventory we recorded species, tree topographic coordinates and diameter at

116   breast height (dbh) for all living trees ≥ 7.5 cm in dbh. Total height, height to the lowest

117   live branch in two opposite directions and crown projections on the ground in four

118   directions were also measured. One core was extracted at 50 cm height from all living

119   trees in 1995. In the lab, following optimization of surface resolution, radial increments

120   to the nearest 0.01 mm were measured and cross-dated against available and updated

121   site chronologies (Motta et al., 2002).

122   The inventory was repeated in 2005 and tree lists were updated with ingrowth; dbh,

123   heights and crown projections were re-measured and ingrowth cores were collected and

124   cross-dated. Volume for living trees was calculated according to local yield tables. We

125   tested a) the normality of size distributions in the two plots by the Shapiro-Wilk test; b)

126   the statistical differences in paired data (size distribution in two different inventories

127   and trees/CWD size distribution in the same plot) by a Wilcoxon non-parametric test

128   and c) the statistical differences in independent samples (size distribution in two

129   different plots) by a Kolmogorov-Smirnov non-parametric test. Statistical analyses were

130   performed using PAST 1.90 (Hammer et al., 2001).

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132   2.3. CWD (Coarse woody debris)

133   We grouped CWD into snags (standing dead trees, dbh ≥ 7.5 cm and height ≥ 1.3 m),

134   downed logs (fallen stems or branches ≥ 7.5 cm diameter and length ≥ 1 m) and stumps

135   (short, vertical remains from cutting or windthrow, top diameter ≥ 7.5 cm and height $<$

136   1.30 m). A stump was classified as man-made if the exposed surface was straight,

137   indicating felling by saw. The separation of snags from logs was established at a 45°

138   angle. Volumes for non-broken snags were calculated according to methods described

139   in Motta, Berretti et al. (2006). The decay stage (Tab. 1) was classified according to a

140   four-class system (Sollins, 1982). We extracted, prepared and cross-dated one core

141   from snags and logs in decay classes 1 and 2.

142

143   2.4. Competition and mortality

144   We assessed crowding in plot VB1 and plot VB2a by means of Reineke's (1933) Stand

145   Density Index (SDI), using the summation method proposed by Shaw (2000). Relative

146   density, i.e., the percent ratio between observed stand density and its theoretical

147   maximum, describes the intensity of competition acting in the stand, and can be linked

148   to specific stand developmental stages (Smith and Long, 2001). The maximum SDI for

149   Norway spruce in the Paneveggio-Pale di San Martino Natural Park was calculated as

150   1380 from a dataset of 291 sample plots already available (Castagneri et al., 2008). We

151   computed percent relative density in the two permanent plots for both inventory years as

152   the ratio between observed and maximum SDI. We also computed mortality rates on an

153   annual basis.

154   We determined the year of death of log and snags (decay classes 1 and 2) by cross-

155   dating and rounded to the nearest decade. Logs and snags mortality causes were

156   classified as follows:

157   -allogenic: logs from windthrow (uprooted or snapped trees with marked fracture and

158   splintering);

159   -autogenic and unknown: logs from snags (trees that died standing and after some time

160   fell on the ground) and snags with no evidence of primary mortality agents (Dobbertin,

161   2005).

162   Mortality induced by competition or other unknown were partitioned in two classes: i)

163   trees showing a growth decline before death, or suppressed trees characterized by very

164   narrow rings during all their life and ii) trees without evident signs of growth decline

165   before death (Bigler and Bugmann, 2003)

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167   3. Results

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169   3.1. Stand structure

170   Tree density was respectively 466 (Plot VB1) and 513 (Plot VB2a) trees ha^{-1} (Tab. 2).

171   Standing volume was respectively 841.4 and 914.5 m^3 ha^{-1}. In 2005 the tree size

172   distributions were unimodal (Castagneri et al., 2008) but didn't have a normal

173   distribution (Shapiro-Wilk test). Density slightly decreased in both plots the between

174   the two measurements (-1.7% in Plot VB1 and -12.1% in Plot VB2a), high and

175   medium-low diameter classes experienced increased and reduced frequencies

176   respectively. The size distribution has not changed across time in both plots (P>0.05).

177   Size distribution differences between the two plots were not significant in year 2005

178   (P>0.05).

179   We were able to determine the age at a height of 50 cm of 94.9% of the individuals.

180   Stem and root rot was the main obstacle to age determination. The age structure (Fig. 1)

181   pinpointed the time of establishment of the current stands: about 200 years before

182   present in plot VB1 and about 220 years in plot VB2a. The establishment period after

183   the disturbance lasted approximately one century in both plots. There were some very

184   old individuals in both plots, the oldest ones being 279 and 447 years old in plot VB1

185   and VB2a respectively.

186

187   3.2. CWD profile

188   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

189   (Tab. 3). Stumps (exclusively of man-made origin in plot VB1 and almost exclusively

190   so in plot VB2a) had an irregular diameter distribution, ranging from 15 to 70 cm in

191   plot VB1 and from 10 to 100 cm in plot VB2a, with a modal value of 40 cm in both

192   plots (Fig. 2). Snags had reverse J-shaped distribution in plot VB2a, while they were

193   scarce in plot VB1. Logs showed a unimodal distribution in both plots with a modal

194   value of 15 cm in plot VB1 and 20 cm in plot VB2a. Size distribution of snags, logs and

195   stumps were significantly different from that of live trees in both plots (p<0.05) taking

196   into account that CWD size were measured in part of the trunk different form the dbh

197   and the original trunk can produce more than one log resulting in a potential

198   overestimation of this CWD type. CWD volume amounted to 3.3% of living tree

199   volume in plot VB1 and 8.7% in plot VB2a (Tab. 2). The volume of stumps was

200   relevant in plot VB1, where they represented 64.5% of the total CWD volume, but

201   scarce in plot VB2a (7.7%). On the other hand, the volume of snags was relevant in plot

202   VB2a, where they accounted for more than 67% of the CWD total volume. The logs

203   represented 15.9% and 25.0% of the total CWD volume respectively in plot VB1 and

204   VB2a. We assume that logs were over-represented in plot VB1, due to the presence of

205   many short logs from a 1993 thinning.

206   Regarding decay class, we detected opposite trends between stumps, on one side, and

207   snags and logs on the other (Tab. 4). Most of the stumps in both plots were in classes 3

208   and 4, i.e., the most decayed ones (84.0% in plot VB1 and 97.2% in plot VB2a). On the

209   other hand, 100.0% of the snags in plot VB1 and 97.2% in plot VB2a were in the lower

210   decay classes (1 and 2). There was a higher incidence of snags in class 1 in plot VB2a

211   (88.4%) than in plot VB1 (60.9%). If compared to snags, logs generally showed a more

212   advanced decay status: class 2 was the most represented one in both plots (71.0% and

213   52.6% of total logs respectively).

214

215   3.3. Competition and mortality

216   SDI (2005) was 1051 in plot VB1 and 1114 in plot VB2a. The log-slope of the self-

217   thinning trajectory for the study period (1993-2005) was -4.802 in plot VB1, and -1.139

218   in plot VB2a (Fig. 3). In the last decade relative density increased in plot VB1 from

219   67.7 to 76.1% and in plot VB2a from 76.7 to 80.8% (Tab. 1).

220   Mortality rate was 0.21% year^{-1} in plot VB1 and 1.01% year^{-1} in plot VB2a. In plot

221   VB1 living biomass increased with very limited mortality, while plot VB2a suffered

222   mortality that was mainly concentrated on the smaller and intermediate diameter classes

223   (Fig.4a).

224   We analyzed mortality dynamics in plot VB2a only, because sample size in plot VB1

225   was insufficient. In plot VB2a the date of death was successfully determined for 70% of

226   the tree samples (n = 179). The earliest identified year of death belonged to the 1920

227   decade, while more than 55% of the tree death was observed in the decades 1970 and

228   1980 (Fig.5).

229   The causes of death were mainly autogenic or unknown (81%). Allogenic mortality was

230   exclusively concentrated in the last decade (2000) and was due to wind or to wind-snow

231   (snapped or uprooted trees); we didn't find any biotic primary mortality agents (e.g.

232   insects and pathogens). The autogenic-unknown mortality involved trees with a dbh

233   ranging from 10 to 55 cm, but was mainly concentrated in smaller diameters. Allogenic

234   mortality had a higher incidence in dbh classes 30-60 cm (Fig. 4b).

235 Most of the trees (54.8%) defined as competition-induced or unknown mortality died

236 after a perceptible decline or chronic slow growth observed in the tree-ring series

237 (Bigler and Bugmann, 2003). Nevertheless, other trees died while growing at the

238 normal rate with no indication of impeding mortality in the tree-ring patterns.

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241 4. Discussion

242

243 The two permanent plots showed some common characteristics: both established (about

244 200 years ago plot VB1 and 220 years plot VB2a) after a shelterwood felling and were

245 respectively managed until 1983 (plot VB1) and about 1950 (plot VB2a) (Motta et al.,

246 1999). Both were monolayered and were overstocked if compared with central

247 European Norway spruce old-growth forests (Fig. 3; Tab. 5).

248 A first difference between the two plots was the CWD profile (Stokland, 2001;

249 Woodall and Nagel, 2006). Plot VB1 was poor in CWD, there were stumps in all decay

250 classes (even if only 16.1% in the classes 1-2) and there were no snags and logs in

251 classes 3-4. Plot VB2a was richer in CWD, the stumps showed a high decay rate (there

252 were no stumps in the decay class 1 and very few in class 2), there were logs in all

253 decay classes (52.6% in class 2) and so were snags, even if more than 88% in class 1.

254 Even if Norway spruce is considered very susceptible to windthrow because of its

255 shallow root system, uprooted trees were absent in plot VB1 and rare in plot VB2a.

256 Until the last decade mortality was confined to the suppressed trees and dead trees only

257 reached the ground (logs) after a first stage as a snag. This explains why there are only a

258 few logs in the first decay class (Motta et al., 2006). The rate of CWD accumulation

259 was slow (the total amount is 27.6 and 79.6 m^3 ha^{-1} after about 22 and 55 years from the

260 cessation of silvicultural interventions) as compared, for example, to that observed in

261 mixed mountain forests (Motta et al., 2008).

262 Another difference was represented by the intensity of competition (Castagneri et al.,

263 2010) and, consequently, the mortality rate. At the beginning of the study period,

264 relative density in both plots was already above the 60% threshold (Tab. 1; Fig. 3),

265 which represents complete resource exploitation and marks the onset of the self-

266 thinning process (Drew and Flewelling, 1979). The size-density trajectory (Fig. 3) for

267 the last decade in plot VB1 showed a period of increase in mean tree size without

268 density-related mortality (annual mortality rate = 0.21%) as a consequence of the last

269 thinning. Plot VB2a showed an increase in mean tree size and reduction in density

270 (annual mortality rate = 1.01%) but, in the same time, due to the size increment, reached

271 the 80% of maximum SDI, meaning that the biological carrying capacity of the site was

272 nearly totally exploited (Long and Shaw, 2005). In plot VB2a competition for resources

273 was extreme and has been high for an extended period. In this plot the date of tree death

274 showed that the autogenic-unknown mortality reached the maximum in the decades

275 1970 and 1980 (Fig. 5), and subsequently declined (1990 and, even more, 2000). In the

276 last decade overall mortality was higher than in the previous decade because of the

277 onset of allogenic mortality, that has involved dominant and co-dominant trees (Fig.

278 4b). We found some discrepancies for autogenic-unknown mortality: a few trees

279 according to crown assessment, were alive in 1993 and dead in 2005 but their last cross-

280 dated tree-ring was formed before 1993. Autogenic-unknown mortality dates should be

281 to be taken with caution, because the formation of tree rings may stop for years or even

282 for decades prior to mortality (Cherubini et al., 2002).

283   Both plots have developed very few old-growth characteristics: even if the average size

284   of the trees is higher if compared with the old-growth ones (Fig. 3), this is the result of a

285   different size distribution. The studied plots have an "unimodal" distribution while a

286   true old-growth is expected to have a "negative exponential" distribution. As a

287   consequence the average size value is high, if compared with a true old-growth, but

288   both stands lack or have very few very large trees that are one of the characteristics of

289   an old-growth. The same is for the CWD: large piece of CWD are mainly stumps (Fig.

290   2) and the quantity and the quality (stage of decay) of the CWD is not comparable with

291   the old-growth (Tab. 4). According to the structure, CWD profile, competition intensity

292   and mortality rate, plot VB1 was classified as being at the end of the stem exclusion

293   stage, while plot VB2a was assigned to a initial transition stage between stem exclusion

294   and understory re-initiation (Oliver and Larson, 1996). In the next decades, VB1 will

295   probably follow the same dynamics recently observed in VB2a (increment of

296   competition and autogenic mortality), while plot VB2a will continue the structural re-

297   organisation that is leading it from a monolayered to a multilayered structure. During

298   such transition, allogenic disturbances will increase their importance, and the decrement

299   of tree density will lead to QMD/density relationships more and more close to those

300   observed for subalpine Norway spruce in a true old-growth stage (Tab. 5). This process

301   results in a progressive accumulation of gaps as the stand gets older, so that the stand

302   development trajectory drops below the maximum density line resulting in a SDI

303   decline (Smith and Long, 2001). The decrement of the intensity of the competition is

304   due to the fact that the death of old and large trees may exceed the capability of lateral

305   growth of surviving crowns and ingrowth in overmature stands (Zeide, 1995). There

306   are also other ecophysiological explanations for the age-related decline of radial growth

307   (Binkley et al., 2002).

308   In any case, the time requested to develop a multilayered structure is still long. Besides

309   the further creation of new gaps, that cannot be accurately foretold, the establishment

310   and growth of new cohorts will be postponed by many decades for the following

311   reasons:

312   1) seed production is irregular, with adequate quantity and quality for seedling

313   establishment only after a mast year, that occurs every 8-10 years on average

314   (Mencuccini et al., 1995);

315   2) seedling establishment requires a favorable seedbed. Different types of microsites,

316   e.g., CWD, mounds, and uprooting pits, are vital for regeneration establishment and

317   early growth (Motta et al., 2006). However, microsite diversity and CWD quantity and

318   quality are greatly reduced in managed stands. Besides, the process of wood decay in

319   subalpine Norway spruce forests is very slow (Storaunet and Rolstad, 2002; Holeksa et

320   al., 2008), so that it will take many more decades to develop a decay rate continuity

321   favorable to seedling establishment and comparable to those of true old-growth forests;

322   3) early regeneration growth is slow. Norway spruce in Paneveggio requires an average

323   of 18 years to reach 50 cm height and more than 40 years to reach 130 cm height

324   (Piussi, 1976; Motta et al., 2002).

325   The legacies of past management are dense stands with higher resistance to small scale

326   allogenic disturbances, low mortality rate, limited CWD accumulation and unfavorable

327   conditions for natural regeneration establishment. Other potential legacies, such as old

328   logging damages that could have enhanced the spread of decay fungi (Vasiliauskas,

329   2001) and monolayered structure that could be more vulnerable to wind disturbances

330   (Zeng et al. 2010), at the present have no evident consequences in the two studied plots.

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

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

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463   Captions

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

466   Tab. 2. Stand characteristics (1993 and 2005)

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

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

469   Tab.5. Stand characteristics for some subalpine Norway spruce old-growth forest from

470   the Carpathians, the Tatra mountains and from the Valbona forest Reserve in

471   Paneveggio. In all the stands the lowest measured dbh was 10 cm (density and mean

472   dbh data from Valbona Reserve were harmonized according to this threshold). Data

473   from Babia Gora 1, Polana and Sumava NP are means from a network of sampling

474   plots. The other data are from individual permanent plots.

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

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	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

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

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491   Tab. 2. Stand characteristics (1993 and 2005)
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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

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

	Volume (m³ ha⁻¹)	Basal Area (m² ha⁻¹)	Density (N ha⁻¹)	Mean dbh (cm)	Volume Snags (m³ ha⁻¹)	Volume Logs (m³ ha⁻¹)	Volume Stumps (m³ ha⁻¹)	Total CWD volume (m³ ha⁻¹)	CWD/live trees %	Total volume Living tree + CWD (m³ ha⁻¹)	Reference
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

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528 Tab.5. Stand characteristics for some subalpine Norway spruce old-growth forest from the

529 Carpathians, the Tatra mountains and from the Valbona forest Reserve in Paneveggio. In all the

530 stands the lowest measured dbh was 10 cm (density and mean dbh data from Valbona Reserve were

531 harmonized according to this threshold). Data from Babia Gora 1, Polana and Sumava NP are

532 means from a network of sampling plots. The other data are from individual permanent plots.

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

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536   Fig.1. Age structure in the two plots

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

538   Fig. 3. Size (QMD: quadratic mean diameter)-density relationships for the studied plots (1993 and

539   2005) and for some subalpine, old-growth Norway spruce forest in central Europe.

540   Solid dots represent the Valbona plots respectively in 1993 and in 2005. VB2a is currently above

541   80% of the SDI that represents the biological carrying capacity of the site. VB1 is very close to this

542   threshold. Empty dots represents size-density pairs for central European old-growth stands (see

543   Tab. 5). The relative density in old-growth stands ranges between 35 and 60% (OGZ: old-growth

544   zone) suggesting that old-growth stage processes occur after a reduction of competition intensity

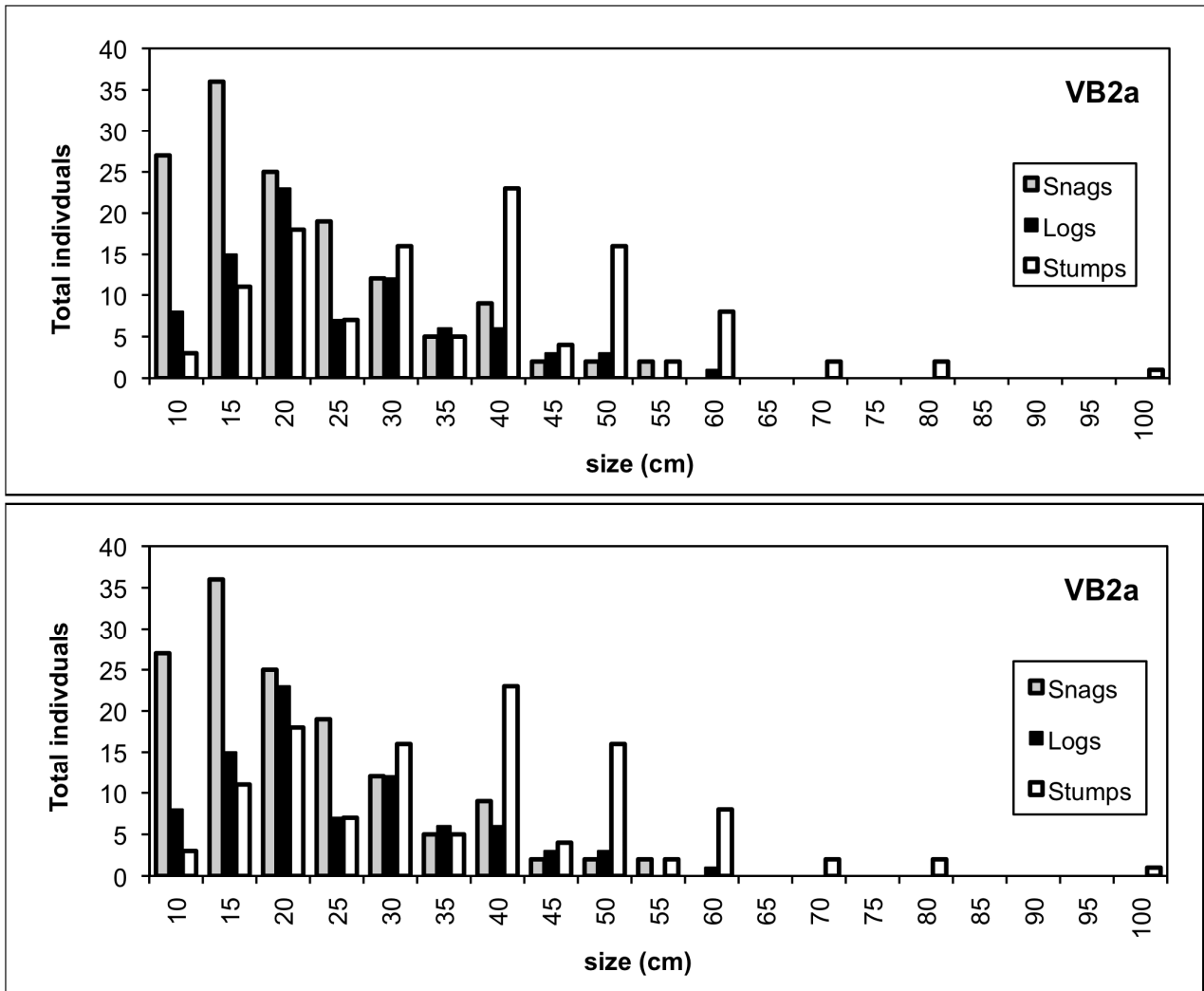545   due to both autogenic and allogenic disturbances

546   Fig. 4. Diameter distribution (a) and incidence of mortality (both snags and logs) in the different

547   size classes (b) in plot VB2a

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

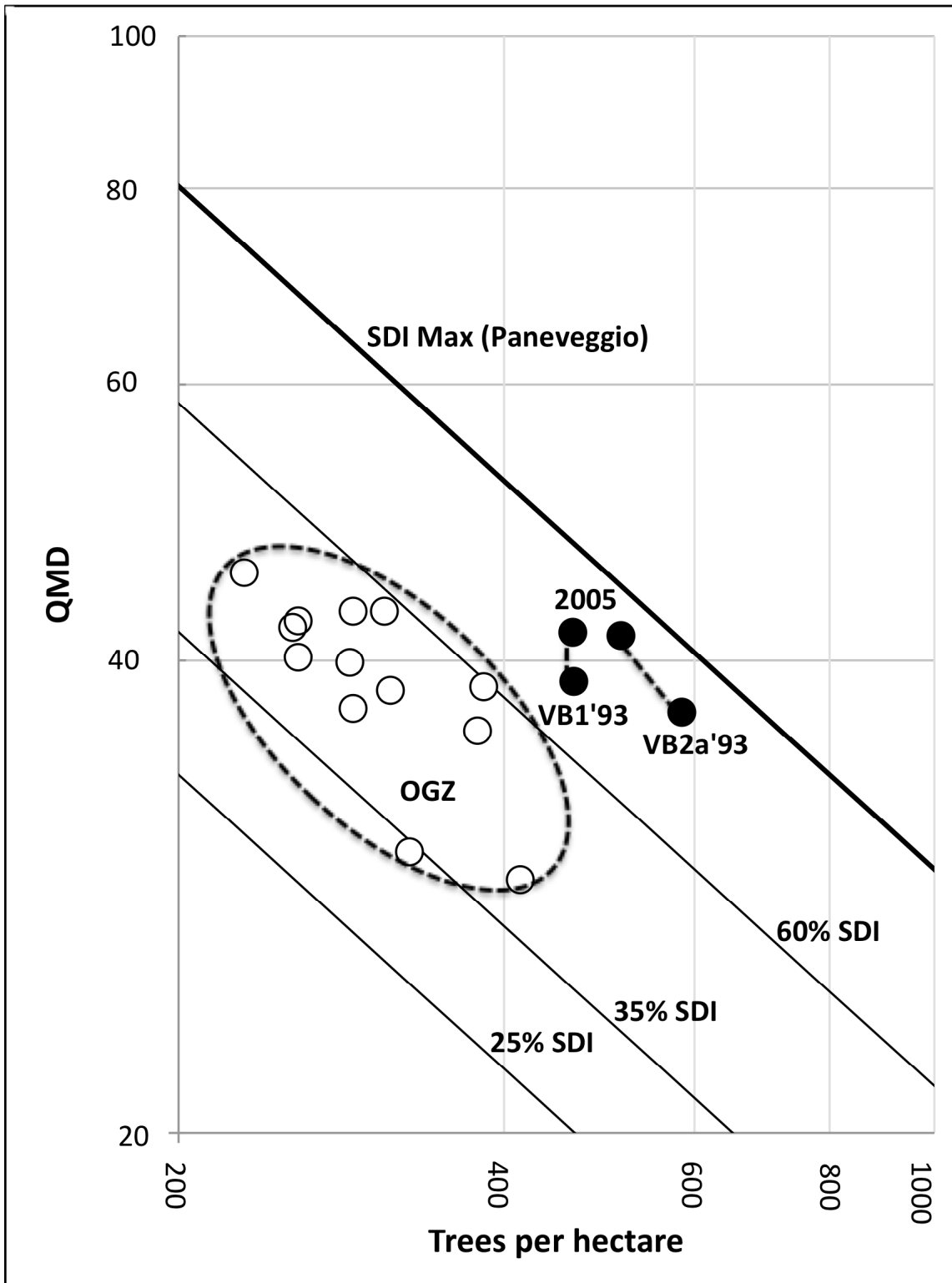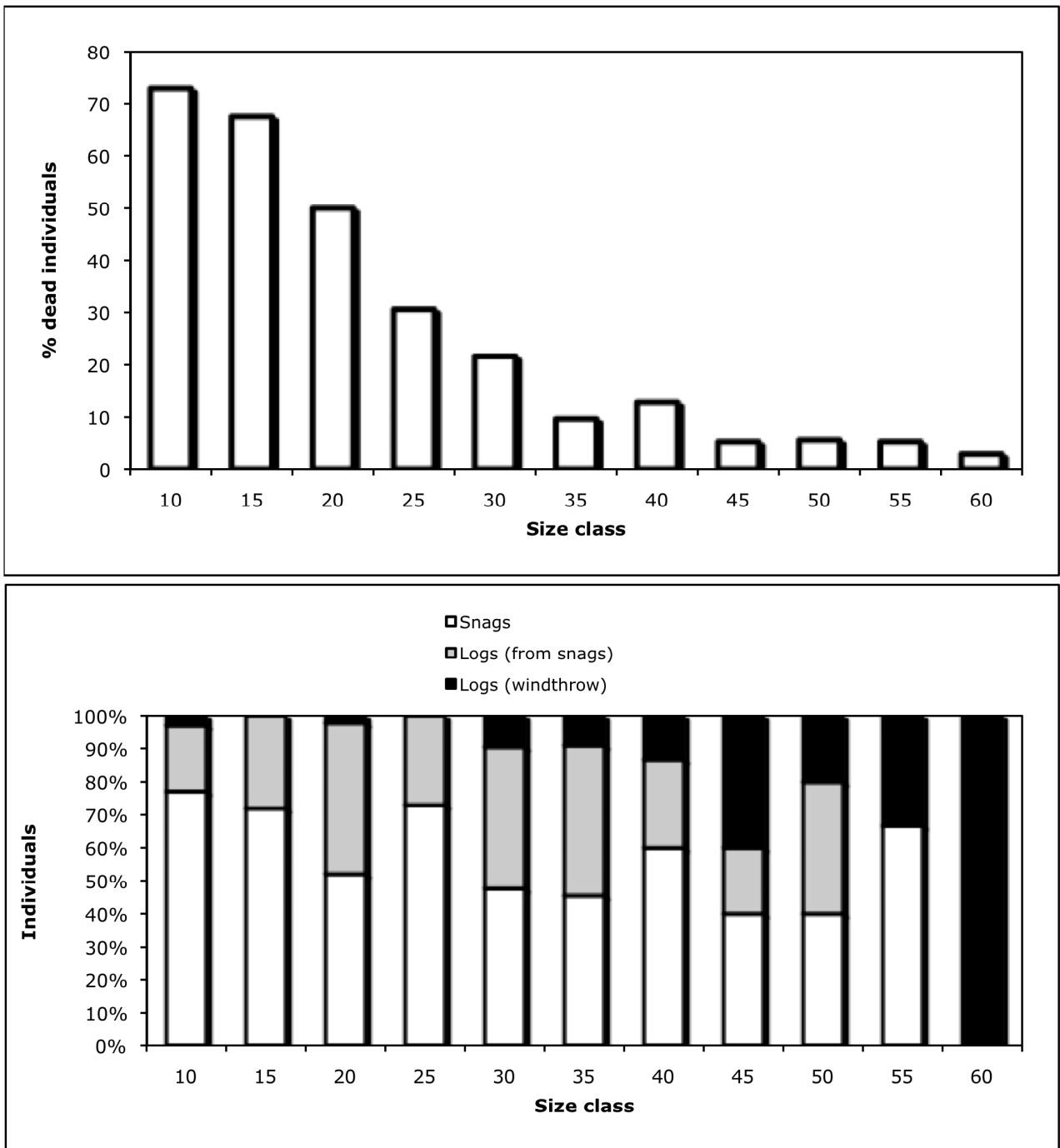549   VB2a

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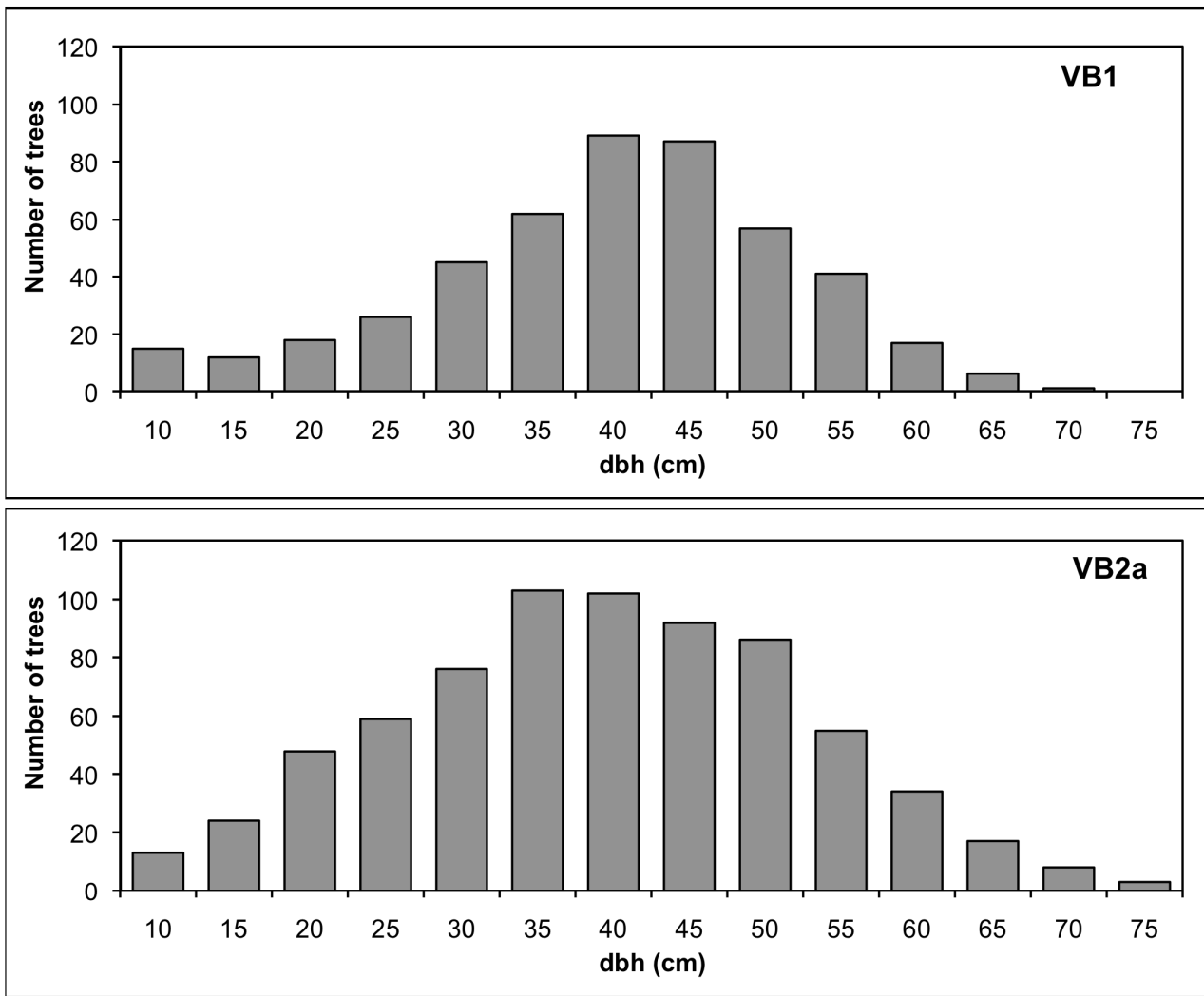
551   Fig.1

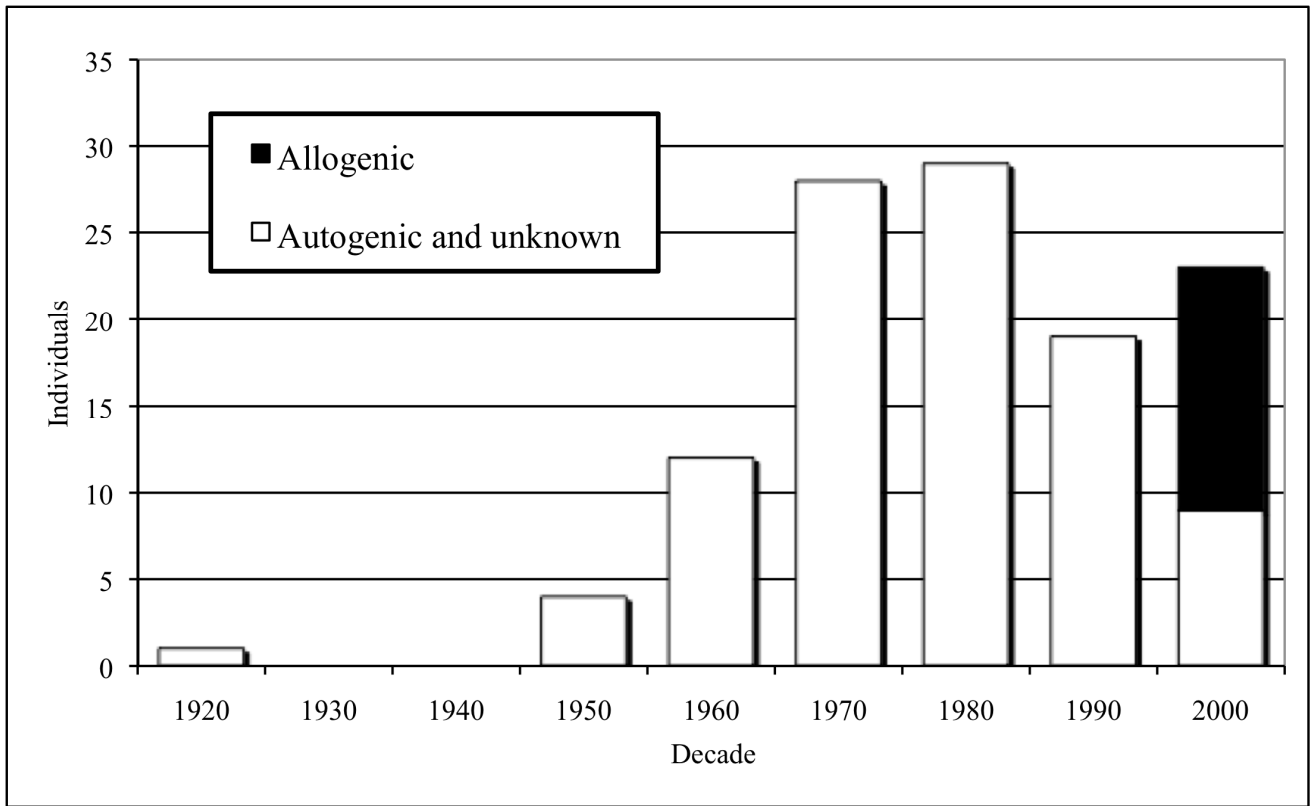552 Fig. 2
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