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Effects of climate on radial growth of Norway spruce and interactions with attacks by the bark beetle *Dendroctonus micans* (Kug., Coleoptera: Scolytidae): a dendroecological study in the French Massif Central

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Abstract

Samples of Norway spruce (*Picea abies* [L.] Karst) were dendrochronologically investigated in order to detect infestations by *Dendroctonus micans* (Kug.), the great spruce bark beetle (Col. Scolytidae), a relatively recent introduction to France. Uninfested natural forests located in the north-eastern French Alps and heavily infested plantations in the Ardèche region (Massif Central) were compared. The penetration holes bored in trunks by the bark beetle induced visible marks on wood, such as extreme ring width reductions, locally missing rings and crescent-shaped resin patches between consecutive rings that make possible a post-infestation dating.

The outbreak began in 1979, 5 years prior to first insect visual detection by foresters. In the infested forest, tree basal area growth was not as sustained as in uninfested natural stands, but showed an inflection point at an unusually young tree age (from 30 to 40 years). Ring widths showing extreme synchronous radial growth reductions were caused either by excessively cold periods (e.g. in 1948, 1980, 1984, 1992) or by summer drought (as in 1986). Most of these weak growth years were shared with uninfested sites. In healthy forests, the consequences of extremely cold years were usually recorded only in high elevation stands, especially near the timberline, whereas summer drought effects were mostly visible in low altitude forests. By contrast, both phenomena were recorded in the infested Ardèche plantation. An analysis of tree-rings and monthly climate confirmed that Norway spruce growth in Ardèche plantations was reduced by excessively low minimum temperature during most parts of the year prior to ring formation, by higher than average maximum temperature during current spring and summer, and by drought in winter, spring and summer. Thus, the regional Ardèche climate with both cold winters and dry summers (especially in July) seems to weaken spruce trees planted there. Moreover, tree sensitivity to climate was found to be greatly enhanced by insect infestation. Such interactions between climatic stress and insect outbreak led to forest dieback in a 15–20-year period, when trees were still young (less than 70 years), and without any tree recovery. Therefore, in that region spruce plantations

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31 should be replaced by non-host species of *Dendroctonus micans*, especially where soil conditions may exacerbate drought
32 effects.

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34 *Keywords:* *Dendroctonus micans*; *Picea abies*; Dendroecology; Drought; Growth; Tree-ring
35

37 1. Introduction

38 Although the vast majority of forest insects are
39 beneficial (Haack and Blyer, 1993), some particular
40 species raise problems to forest managers and can affect
41 forest sustainability (Chararas, 1979). Such insect pests
42 may lead to timber loss (Alfaro and Maclauchlan,
43 1992), forest dieback (Badot et al., 1990), changes in
44 regeneration and succession (Veblen et al., 1991) or
45 even tree mortality (Jardon et al., 1994), and hence
46 involve economic consequences (Conway et al., 1999).
47 Some insect and/or pathogens are known to cause more
48 losses than any other damaging agent, including fire
49 (Haack and Blyer, 1993). For these reasons, a detailed
50 knowledge of population dynamics of pest insects is
51 required for pest management. Unfortunately, tree
52 mortality caused by insects and/or diseases is often
53 discovered too late, after reaching a damage threshold,
54 especially for accidentally introduced exotic insect
55 species (Haack et al., 1997).

56 However, dendrochronological methods based on
57 ring-width analysis have proved their efficiency for
58 the study of insects and diseases (Brubaker, 1987;
59 Filion and Cournoyer, 1995; Weber and Schweingru-
60 ber, 1995). In particular, such techniques can date
61 outbreaks in various regions (Morin et al., 1993; Vogel
62 and Keller, 1998), estimate growth losses caused by
63 insects (Maclean, 1980; Alfaro and Maclauchlan,
64 1992), or analyse forest recovery after insect distur-
65 bance (Wickman, 1980).

66 For example, dendrochronological dating of *Abies*
67 *concolor* and *Pseudotsuga menziesii* narrow rings was
68 used to reconstruct past *Choristoneura occidentalis*
69 outbreaks (Swetnam and Lynch, 1993), as well as
70 periodic larch bud moth (*Zeiraphera diniana* Gn.)
71 defoliations of European larch (*Larix decidua*) (Pigna-
72 telli and Bleuler, 1988; Weber, 1997). *Larix laricina*
73 defoliations by the larch sawfly (*Pristiphora erichso-*
74 *nii* Htg.) were similarly dated in Quebec (Arquillière
75 et al., 1990; Filion and Cournoyer, 1995). Such insect
76 impacts on trees can be dendroecologically analysed

77 on both coniferous and deciduous trees. For instance,
78 oak (*Quercus* sp.) defoliations by cockchafers (*Melo-*
79 *lontha* sp.), winter moth (*Operophtera brumata*) or
80 leaf roller (*Tortrix viridana*) were successfully inves-
81 tigated with dendroecological tools (Varley, 1977;
82 Christensen, 1987; Vogel and Keller, 1998).

83 Furthermore, growth losses to scots pine (*Pinus*
84 *sylvestris*) caused by *Thaumtopoea pitiocampa* and
85 *Diprion Pini* (Laurent-Hervoiët, 1986) or *Bupalus*
86 *piniaria* (Straw, 1996; Armour et al., 2003; Straw et
87 al., 2001) and to *Abies balsamea* (Maclean, 1980) and
88 *Picea glauca* after *Choristoneura fumiferana* out-
89 breaks (Morin et al., 1993) have been quantified by
90 ring widths. At present, tree-ring and climate relation-
91 ships during insect outbreaks are not well understood
92 (Laurent-Hervoiët, 1986). Moreover, tree-rings
93 enable investigation of forest recovery after distur-
94 bance (Wickman, 1980; Veblen et al., 1991; Lindgren
95 and Lewis, 1997). For example, the consequences of
96 *Hemerocampa pseudotsugata* and *Choristoneura*
97 *occidentalis* defoliation on Douglas fir (*Pseudotsuga*
98 *menziesii*) (Brubaker, 1987) or on *Picea pungens*
99 (Weber and Schweingruber, 1995) were determined
100 with dendrochronological techniques.

101 Most of the time, outbreak reconstructions are
102 easier when using comparisons with non-host tree
103 species. Eckstein et al. (1991) used non-host *Pinus*
104 *sylvestris* for the evaluation of *Betula tortuosa* defo-
105 liation impact by *Epirrita autumnata*, and Arquillière
106 et al. (1990) used non-host *Picea mariana* and *P.*
107 *glauca* for comparisons with defoliated *Larix laricina*
108 by *Pristiphora erichsonii*. However, these studies
109 suggested the use of non infested sites with the same
110 tree species as a non-host reference (Weber and
111 Schweingruber, 1995), since the climatic responses
112 of different tree species were usually different (Eck-
113 stein et al., 1991), as a result of their specific ecologi-
114 cal requirements.

115 The effectiveness of dendrochronological techni-
116 ques for investigating insect impacts on trees has
117 promoted their use as tools for the reconstruction of

118 past *Picea abies* dieback after *Dendroctonus micans*
 119 (Scolytidae) attacks in a plantation located in the
 120 Ardèche (Massif Central, France). The influence on
 121 tree-rings of some other bark borer species such as *D.*
 122 *rufipennis* has been analysed in North America
 123 (Lindgren and Lewis, 1997; Veblen et al., 1991),
 124 but to our knowledge, *D. micans* outbreaks have never
 125 been dendrochronologically investigated.

126 The Norway spruce (*Picea abies* (L.) Karst) was a
 127 common coniferous species throughout Europe and
 128 grows spontaneously in France in the Alps, the Vosges
 129 and Jura mountains. Since the beginning of the 20th
 130 century, this species has spread in many regions out-
 131 side its area of natural distribution, to form mono-
 132 specific even-aged plantations that replaced deciduous
 133 forests or covered ancient abandoned grasslands.
 134 Thus, it was introduced in the Bretagne and Pyrenées
 135 regions, and more extensively in the Massif Central
 136 (Fig. 1a) as well as in other continents (as in Quebec,
 137 for instance, Archambault et al., 1993). However,
 138 artificial even-aged monospecific spruce stands were
 139 often susceptible to insect damage when planted out-
 140 side the spruce natural distribution area. Such planta-
 141 tions were attacked by the white pine weevil *Pissodes*
 142 *strobi* in Quebec (Archambault et al., 1993), and by
 143 *Dendroctonus micans* (Kugelann) in several regions of

144 France (Lempérière, 1992, 1994; Legrand and Lévy,
 145 1995). It was especially the case in the Ardèche
 146 region, where *Picea abies* plantations cover 7154 ha
 147 (IFN, 1982) and develop there mostly on superficial
 148 volcanic soils with mor humus.

149 *Dendroctonus micans* Kug. was a widespread bark
 150 beetle species (Scolytidae) that could infest trees such
 151 as spruce or mountain pine from Asia to western
 152 Europe (Lempérière, 1992) (Fig. 1b). Adult bark
 153 beetles bore holes in tree bark to lay eggs. Three
 154 weeks later, the larva destroyed the phloem near the
 155 laying hole, during 2 or 3 years before emerging.
 156 Consequently, they reduced the sap flow in trunks
 157 (on a 1 m × 50 cm surface), that may lead to spruce
 158 mortality. This species was considered as a dangerous
 159 scolytid for spruce in France because it could infest
 160 healthy trees.

161 Among the valid 18 existing world *Dendroctonus*
 162 species (synonyms not included, Lempérière et al.,
 163 2004), *Dendroctonus micans* is the only one in France.
 164 It was first mentioned in this country in 1950 (Lem-
 165 périère, 1994), and was also recorded in England in
 166 1982 (King and Fielding, 1989). *D. micans* is an
 167 endemic scolytid in the eastern part of France, where
 168 it is found in the Cévennes, in the Savoie (Hurtières,
 169 forêt de la Table), in the Vercors and Belledonne

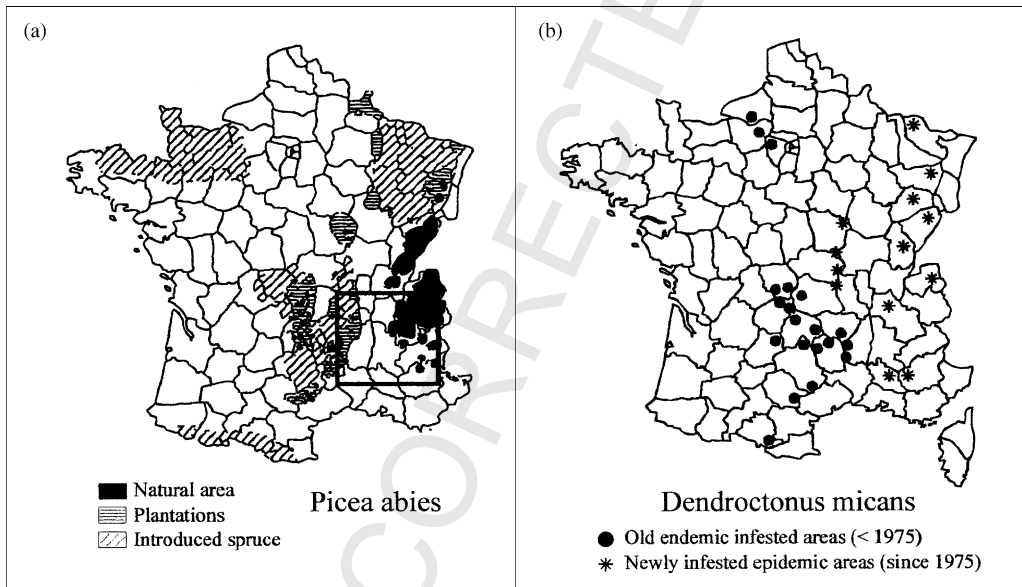


Fig. 1. (a) Map of natural distribution area and recent plantations of spruce (*Picea abies*) in France with locations of sampled sites. (b) Natural distribution area of *Dendroctonus micans* (Coleopter: Scolytidae) covering Asia and Europe.

170 massifs (Prémol, Luitel), in the Jura, Marne, Meurthe
171 et Moselle, Bourgogne (Saint Prix) and Aube (Schve-
172 ster, 1985; Lempérière, 1992; Legrand and Lévy,
173 1995). The infested area has recently expanded to
174 the Pyrénées in the south and to Normandy–Brittany in
175 north-western France. For this reason, better knowl-
176 edge is required about the impact of *D. micans* on
177 spruce.

178 As this pest completes most of its life cycle under
179 bark, it is difficult to detect in the early stages of
180 infestation. Small holes in bark and resin lumps melted
181 with sawdust glued on stems are the only visible
182 symptoms on trees (Lempérière, 1996), since healthy
183 spruce trees react to bark beetle attacks by resin
184 exudation. *Dendroctonus micans* was observed for
185 the first time in the Ardèche region in 1984, where
186 it caused extensive tree mortality (Lempérière, 1996).
187 Cold winters and dry summers in the Ardèche were
188 responsible for a long *D. micans* life cycle, during
189 which it remained 3 years under bark (Lempérière,
190 1992). It was hypothesised that such harsh climatic
191 conditions may also be unfavourable for spruce and
192 hence they favoured *Dendroctonus* attacks.

193 *Dendroctonus* species were able to colonize
194 healthy trees and even to kill them (e.g. see Logan
195 et al. (1998), Wilson et al. (1998) for *D. ponderosa*,
196 Lempérière (1992, 1994) for *D. micans*, and Veblen et
197 al. (1991) for *D. rufipennis*).

198 Prior to this study there has been little known about
199 the consequences of *D. micans* infestation for *Picea*
200 *abies* radial growth and its ability to survive. Since there
201 was a lack of forest archive sources, only a posteriori
202 studies were feasible. Therefore the main purposes of
203 this paper were to use dendrochronology to date the first
204 bark beetle attacks in a heavily infested site located in
205 the Ardèche, where *D. micans* was accidentally intro-
206 duced—to compare radial tree growth in infested and
207 uninfested sites—to determine to what extent spruce
208 trees could recover from an outbreak, and to analyse the
209 interactions between climatic events, tree growth and
210 *Dendroctonus micans* attack.

211 2. Materials and methods

212 2.1. Sampling sites

213 Three sites were assessed:

- The first forest was a Norway spruce monoculture, 214
that was planted with *Picea abies* (L.) Karst on an 215
ancient abandoned grassland. The oldest spruce 216
were 74 years in 1997 (planted in 1924). This forest 217
was called “Forêt de la Clède” (in the Domaniel 218
Forest of Bonnefoi). It was located at 1600 m on a 219
western slope in the Ardèche region (Fig. 1) near 220
Les Estables and Mont-Mézenc (Massif Central, 221
France). This plantation was heavily infested by 222
Dendroctonus micans (Kug.) (Coleoptera, Scolyti- 223
dae) and is hereafter called “INF” (infested) (Fig. 224
2). All trees were felled (in 1997) because of a 225
strong *Dendroctonus* infestation that severely 226
affected more than 50% of the trees. Samples were 227
taken at stem base with a chain saw on 62 trunk 228
sections randomly chosen within a 1 ha area of the 229
stand. According to a survey made in 1996, more 230
than 50% of the Norway spruces were obviously 231
infested (with about 10% of dead trees), before the 232
site was clear felled in 1998. Ring-widths were 233
measured on two opposite radii per tree (126 indi- 234
vidual series, 6705 ring widths, chronology from 235
1923 to 1997). 236
- A second plantation with a very low infestation 237
level (but unfortunately with younger trees) was 238
chosen close to the previous one (hereafter coded 239
NonInf: non-infested). Twenty-six trees were cored 240
with one core per tree in four different locations 241
with a Pressler borer at tree base. Ring-widths (716) 242
were measured, providing a master chronology 243
from 1966 to 1998 (latitude 44°53'40"N, longitude 244
4°08'02"E, altitude 1375 m). On both sites, soils 245
were brown acid soils on granite, andosols on 246
volcanic substrates. 247
- A third non-infested natural population (NAT) with 248
older trees was also sampled in the Belledonne 249
mountain (Taillefer, Isère), located in the spruce 250
natural distribution area (Petitcolas, 1993). Thirty- 251
six cores were sampled there, with 5219 ring- 252
widths, from 1801 to 1993. 253

254 Several other natural spruce forests were also den- 255
droecologically investigated around our study area by 256
different authors (Petitcolas, 1993; Bocquet, 1994; 257
Rolland and Schueller, 1995; Petitcolas et al., 1997; 258
Rolland et al., 1998, 2000; Desplanque et al., 1998, 259
1999). Their results were used in order to compare 260
radial tree growth in the Ardèche region with those in 261
262
263
264

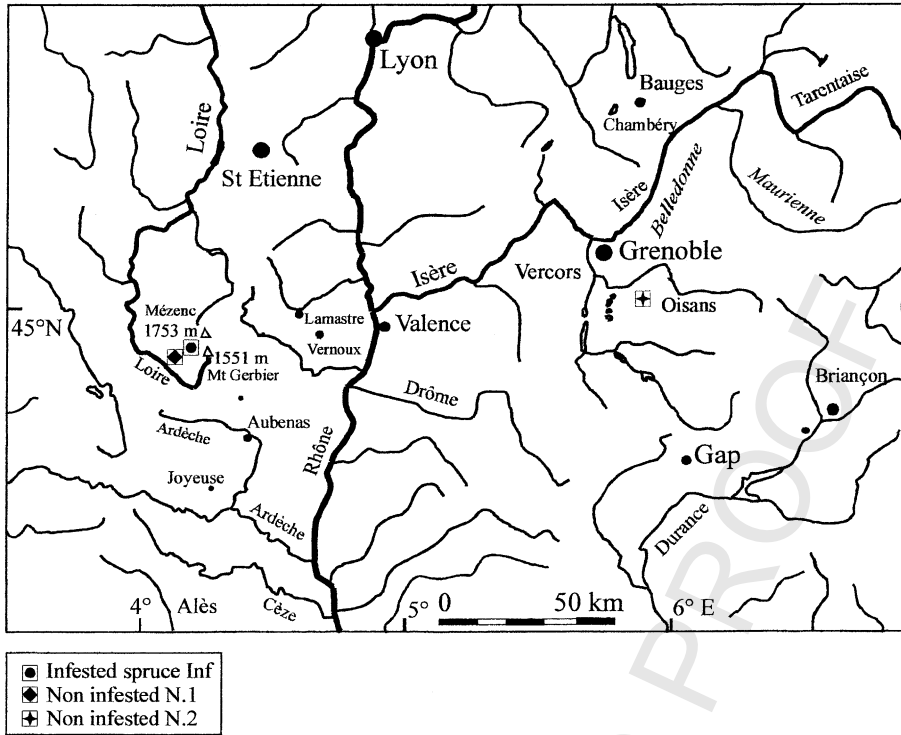


Fig. 2. Map of sampling sites in France.

265 surrounding sites. These sites were located both in
 266 Italy (two stands, with 47 cores near Cesana-Torinese,
 267 and two other sites, with 41 cores near Susa), and in
 268 the French Alps, with 5 stands in the Maurienne valley
 269 (124 cores), two stands in the Briançonnais region (47
 270 cores, near Névache), and 6 stands in the Tarentaise
 271 valley (145 cores) (in Desplanque et al., 1998, 1999);
 272 15 other spruce trees in the Vercors mountains (Roll-
 273 and and Schueller, 1995), and 106 *Picea abies* in the
 274 Bauges mountains (Boquet, 1994) were also used for
 275 comparisons. Data from several subalpine spruce
 276 stands were also available near the timberline in the
 277 Belledonne mountains (2 forests, 72 cores), in the
 278 Maurienne (3 forests, 108 cores), and in the Tarentaise
 279 regions (3 stands, 108 cores) (Petitcolas et al., 1997;
 280 Rolland et al., 1998).

281 2.2. Regional climate

282 The nearest weather station to our sampling sites in
 283 the Ardèche was located at “Les Estables” (altitude
 284 1486 m, 3 km distance). The regional climate was

285 characterized by low winter temperatures (-7°C at
 286 Les Etables). On average (1961–1990), 164 frost days/
 287 year were recorded at “Cros de Géorand” (located at
 288 1000 m above sea level, 13.5 km from the infested
 289 sampling site), and 152 frost days at Issanlas (at
 290 1252 m, 21 km) (Fig. 3). Mean yearly temperature
 291 was cold (6.35°C at Cros de Géorand, and average
 292 January minimum temperature was only -5.4°C).

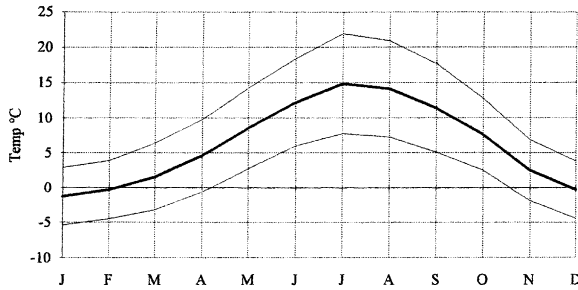
293 Snowfall was usually high, from 3 to 3.5 m per year
 294 on the Ardèche plateau, during a period of up to 60
 295 days. Drought months (with a precipitation amount in
 296 mm two times lower than the temperature in $^{\circ}\text{C}$) were
 297 observed in 1966, 1970, 1976, 1985, 1989–1990 and
 298 summers were often dry (called “Cévenol summer”).
 299 Thus, cold and snowy winters followed by dry sum-
 300 mers were the main characteristics of the regional
 301 climate.

302 2.3. Measurements and calculations

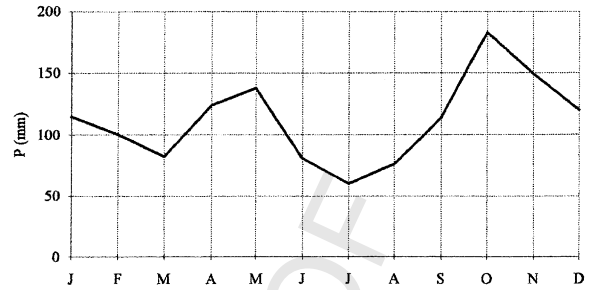
303 Cross sections or cores were machine sanded in the
 304 laboratory, before measuring all ring-widths along two

Climat in "Cros de Géorand" (1000 m.) 1961-1990

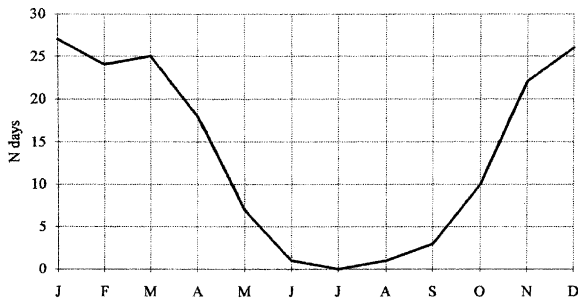
Air monthly temperature



Mean monthly precipitation



Frost days per month



Precipitation min, Q1, Q4, max

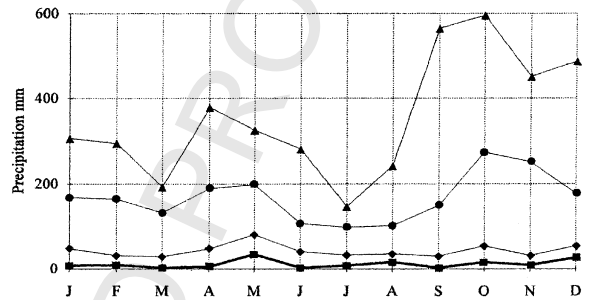


Fig. 3. Monthly climate in "Cros de Géorand" (altitude 1000 m, at 13.5 km from the studied forest) calculated during the period 1961–1990: (a) mean, maximum and minimum monthly air temperature in °C; (b) mean monthly precipitation (mm); (c) number of frost days per month; (d) minimum, maximum and Q₁, Q₄ precipitation quartiles.

305 radii in opposite directions under a binocular micro-
 306 scope, to the nearest 0.01 mm. Individual tree-ring
 307 chronologies were visually cross-dated, and dating
 308 was controlled with the Holmes (1983) computer
 309 method.

310 Extreme tree-ring widths with more than—40%
 311 growth reduction compared to the average width of
 312 the four previous rings are called "event years"
 313 (Schweingruber et al., 1990). Event years that syn-
 314 chronously occurred on many trees were called
 315 "pointer years" (PY) (Schweingruber et al., 1990,
 316 1991). Such pointer year chronologies were calcu-
 317 lated for each population to detect important radial
 318 growth disturbances. For each tree, ring-widths were
 319 transformed into growth indices in order to remove
 320 the age trend (i.e. the ring-width decrease with tree
 321 age), using autoregressive modelling (Rolland et al.,
 322 1998). Three master chronologies were obtained, one

for each tree population, by averaging all growth
 indices of the same year (Rolland and Schueller,
 1995).

Tree responses to climate were analysed using
 "correlation functions". They were based on linear
 correlation coefficients between master chronologies
 of ring-width indices and climatic data. Precipitation
 amount and maximum/minimum temperature series
 were used, with monthly data. Twenty-one months
 were used, comprising the complete year prior to
 ring formation (12 months, hereafter coded "n - 1"
 year) and the first 9 months of the current radial
 growth period (coded "n" year) from January to
 September.

Monthly precipitation data extended from 1880 to
 1990 (in the Ardèche) and monthly minimum and
 maximum temperature series extended from 1907 to
 1993 (in the Isère).

341 Spruce radial growth was reconstructed using all
 342 individual ring-width measurements, in order to cal-
 343 culate mean basal area growth curves as a function of
 344 cambial age (Petitcolas et al., 1997). A mean growth
 345 curve was computed for each tree population, by
 346 combining data from all trees (Rolland and Schueller,
 347 1995).

348 **3. Results**

349 *3.1. Infested tree ages and radial growth*

350 In the infested stand (INF), the oldest tree was only
 351 74 years, that is far less than spruce trees growing in
 352 natural forests such as in the Vercors (255 years)
 353 (Rolland and Schueller, 1995), in the Bauges (251
 354 years) (Bocquet, 1994) or in the Belledonne moun-
 355 tains (NI₂ site, 193 years) (Petitcolas, 1993). Near
 356 timberline, spruce forests were often more than 300
 357 years (Petitcolas et al., 1997). Obviously, infested
 358 trees did not reach their maximum potential age,
 359 because they were all declining. In the same region,
 360 uninfested trees could be found, but with very low
 361 ages (NonInf site, 34 years), and such stands were
 362 expected to decline during the subsequent decades
 363 since *Dendroctonus micans* attack usually occurred
 364 there after spruce reached 40–50 years.

365 *3.2. Radial growth*

366 The basal area growth curves as a function of tree
 367 age showed a slower growth rate for infested trees in
 368 the Ardèche (Inf), compared to uninfested ones (Non-
 369 Inf) after 15 years (Fig. 4). However, the most striking
 370 observation was the difference between growth pat-
 371 terns in the Ardèche plantations (both Inf and NonInf)
 372 compared with those in natural spruce stands (Bauges,
 373 Susa, Maurienne, Tarentaise, Italy, Belledonne, and
 374 Névache). Despite high growth rates in the Ardèche,
 375 higher than in many natural forests, the basal area
 376 growth curves showed inflexions at early tree ages of
 377 about 35 years. Such inflexions were usually observed
 378 after trees reached 140 or 160 years in healthy natural
 379 forests (Roland and Schueller, 1995; Petitcolas et al.,
 380 1997). Therefore it might be interpreted as accelerated
 381 tree senescence. Such a result was supported by
 382 Schvester (1985), who suggested that important *Den-*
 383 *droctonus micans* attacks occurring in the Haute-Loire
 384 and the Lozère areas (France) might be linked to
 385 spruce over-maturity.

386 *3.3. Response to climate*

387 Monthly precipitation and both maximum and
 388 minimum monthly temperature values were used to
 389 calculate spruce response to climate.
 390

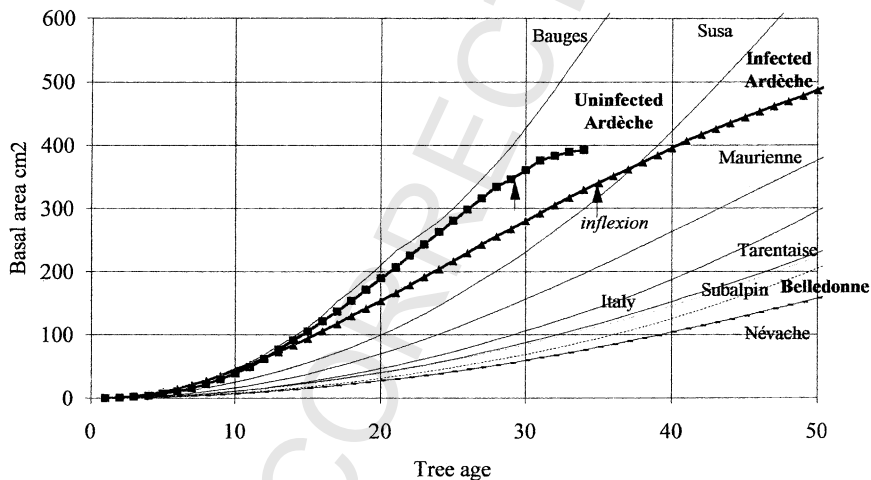


Fig. 4. Basal area (in cm²) growth curves as a function of cambial age for the spruce stand infested by *Dendroctonus micans* (INF), compared with the non infested stand (NonInf), both located in the Ardèche. Other results for natural uninfested spruce forests located in Bauges, Maurienne, Belledonne, Névache, Susa and Italy were calculated using data from Boquet (1994), Desplanque et al. (1998), Petitcolas et al. (1997).

Precipitation data were recorded in the Ardèche, whereas temperature series were from the Isère where longer time series were available. The same climatic data set was used for all the forests permitting easier comparisons. Linear correlation coefficients R were transformed into Student's t -values.

In all stands, spruce trees reacted to both precipitation and temperature (Fig. 5), as already observed by Desplanque et al. (1998) in the Tarentaise and Maurienne mountains.

For the natural spruce forest (located within the *Picea abies* distribution area), radial growth was found to be positively correlated with higher than average rainfall during a long period, from May ($n - 1$) to November ($n - 1$) in the year prior to ring formation (n) (Fig. 5a). Conversely, unfavourable effect of warm air temperature from May ($n - 1$) to September ($n - 1$) were recorded at the same time. Both of these features might be interpreted as an influence of favourable water balance. Climate during the current year of ring formation was also involved, since high temperature in May (n) followed by abundant rainfall in July (n) appeared to be beneficial, probably for cambial initiation and water supply during cambial cell division and expansion.

The non-infested plantation in the Ardèche followed the same general pattern, with unfavourable consequences of warmth in the previous July ($n - 1$), and enhanced tree growth associated with high precipitation from August ($n - 1$) to November ($n - 1$) (Fig. 5b). Current June and July (n) precipitations were similarly found beneficial for tree growth, whereas April ($n - 1$) snowfall had a negative influence and was specific to the Ardèche region. Therefore, the main difference between the natural forest and the spruce plantation was the shorter period of climate influence observed in the Ardèche during the previous year.

In the infested stand, the response to climate appeared to be sharply modified compared to healthy sites (Fig. 5c). In such a situation, the respective responses to minimum and maximum temperature were quite different to those previously observed. The response pattern to minimum temperature was roughly comparable to that found in healthy stands, but reinforced, whereas the response to maximum temperature revealed specific features. Thus, infested spruce required higher than average maximum tem-

perature in March ($n - 1$) and June ($n - 1$) for their growth, and during the whole current summer. Hence, they seemed to suffer more from insufficient spring and summer warmth. Moreover, the positive response to precipitation was found to be stronger in August ($n - 1$) and March (n) compared to that of healthy trees, demonstrating a stronger drought susceptibility.

3.4. Years with extreme growth reductions

Ring-widths with growth increase (more than +30%) were as numerous in both the infested plantation and uninfested natural forest (Fig. 6). However, the percentage of ring-widths with sharp growth reductions (compared with the mean of four previous rings) was higher in the infested site, especially for severe growth reductions (−50% and less).

Since 1920, infested spruces recorded several important growth reduction events in their rings, such as those in 1948, 1963, 1968, 1975, 1980, 1984, 1986, 1992 and 1997. The most striking feature was a gradual increase during recent times in the percentage of trees that showed growth reductions at a given year, compared to healthy forests (Fig. 7). In this way, the infested forest demonstrated a gradual dieback of the entire stand. Most of these pointer years were linked with extreme climatic events, and were also found by several other authors in *Picea abies* dendroecological studies.

Year 1948 was also described as a negative pointer year in France by Petitcolas (1998) in subalpine stands (especially in the Belledonne massif), by Desplanque et al. (1999) on north facing slopes and high elevation spruce forests, and by Brugnoli and Gandolfo (1991) in Italy (Trentino region). It was probably caused by frost during the vegetative period (Desplanque et al., 1999). Many other authors observed this narrow ring (Lingg, 1986 in Switzerland; Becker et al., 1990 in France, Germany and Switzerland; Kontic et al., 1990; Schweingruber et al., 1990, 1991; Picard, 1995). The previous dry year might also have been involved (Schweingruber et al., 1991).

Year 1963 narrow ring followed the 1962 extreme dry year (Desplanque et al., 1999), and was also recorded by *Picea abies* in other forests (Desplanque et al., 1999), as well as by *Fagus sylvatica* (Becker et al., 1990).

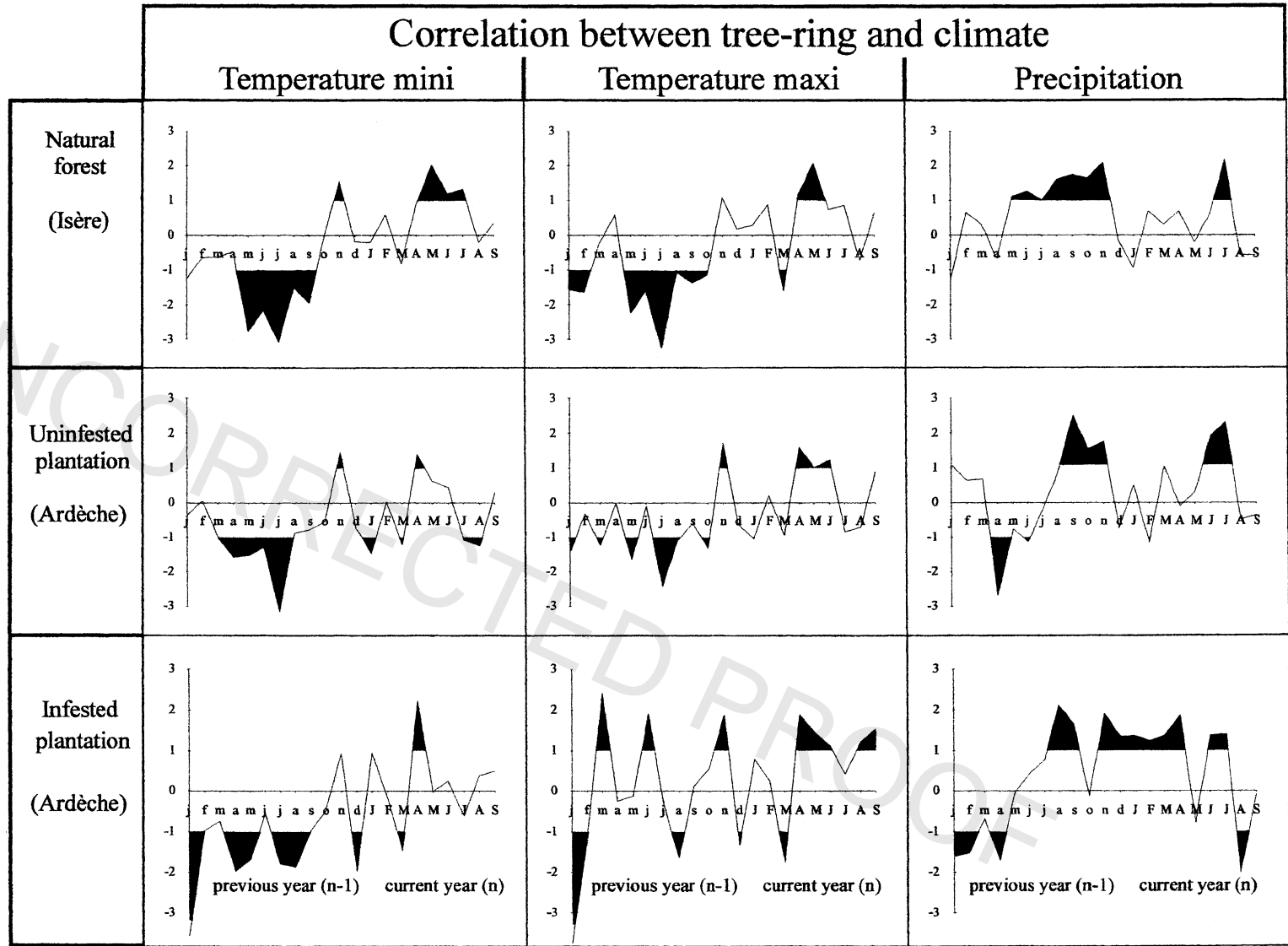


Fig. 5. Tree-ring and climate relationships in a natural healthy spruce forest (in Belledonne, Isère), in an uninfested plantation and in a heavily infested plantation, both in the Ardèche. Linear correlation coefficients (transformed into Student's *t*-values) between master chronologies of indices and monthly climatic data were calculated for each month of the year prior to ring formation ($n - 1$), and with current year data from January to September (n). Positive values stand for positive correlations.

Percentage of ring-widths with growth changes

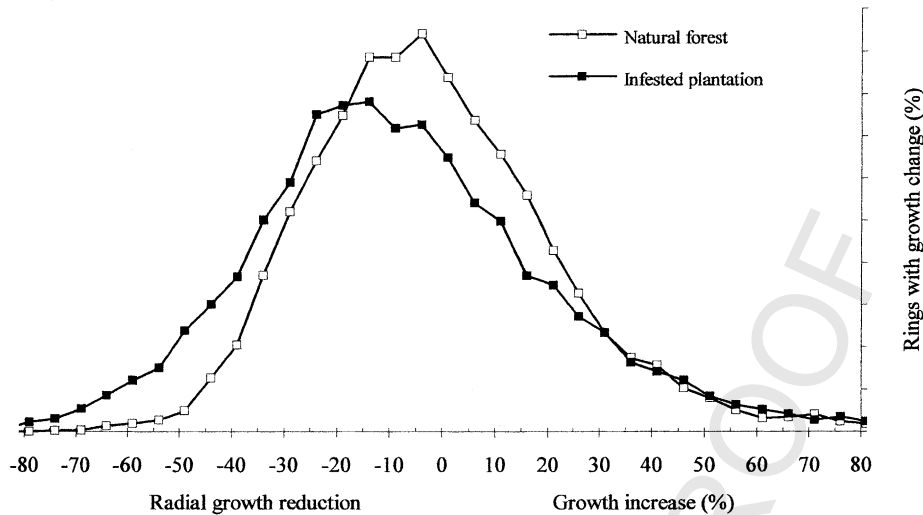


Fig. 6. Percentages of individual ring-widths with growth changes (compared with the mean of four previous widths), in the Ardèche plantation infested by *Dendroctonus micans*, and in healthy forest in Isère.

484 Year 1968 was also a slight pointer year in the
485 Maurienne spruce stands (Desplanque et al., 1999).

486 Year 1975 was described by Petitcolas (1998) as the
487 most important negative pointer year observed for
488 subalpine spruce in the French Alps during the last
489 200 years. It followed a very snowy 1974 winter and
490 extremely cold October ($n - 1$). This pointer year was
491 also described in the Maurienne, but only for high
492 elevation spruce stands (Desplanque et al., 1999).

493 Year 1980 was a cold year (Petitcolas, 1998) in
494 French Alps from March to August (n). This negative
495 pointer year was also found by Sander et al. (1995) for
496 spruce in Giant-Mountains in Czechoslovakia, and
497 was attributed to a cold summer.

498 Year 1984 was similarly observed in the Tarentaise
499 (Desplanque et al., 1999) at low elevations, as
500 observed in Switzerland by both Kontic et al.
501 (1990) near Zürich, and by Becker et al. (1990). It
502 was a cold year (Petitcolas, 1998), with exceptional
503 snowfall in June at 800–1000 m above sea level, and
504 also with a dry July (n). *Pinus cembra* and *Pinus*
505 *uncinata* growth were also reduced (Petitcolas, 1998).

506 Year 1986 was a drought year in June and July, with
507 a cold February (Desplanque et al., 1999). Low elevation
508 spruce stands were also affected both in the
509 Tarentaise and the Maurienne massifs (Desplanque

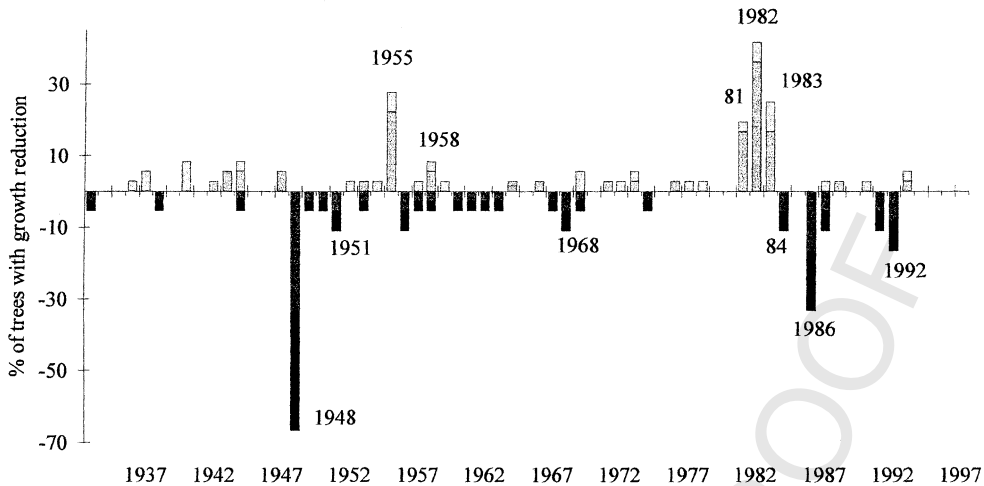
et al., 1999), as in east and southern France (Lebour- 510
geois, 1997). 511

512 Year 1992 was characterized by two different limit-
513 ing factors at the same time, with both a drought in
514 August ($n - 1$) unfavourable for hot and dry spruce
515 stands (in Upper Maurienne) and a cold June (n)
516 unfavourable for north facing and moist sites (in
517 Belledonne) according to Petitcolas (1998). Desplan-
518 que et al. (1999) also reported narrow spruce ring
519 widths during this year.

4. Discussion 520

521 Our results underline the importance of a favour-
522 able water balance for spruce growth (high precipita-
523 tion associated with cool temperature and low
524 evapotranspiration), especially during the year prior
525 to ring formation. They could be compared with those
526 of Feliksik (1993), who studied spruce growth in the
527 Bukowiek Forest (Beskid Mountains, Poland). Tree
528 growth there was negatively correlated with high
529 temperature during the previous summer (from June
530 to September [$n - 1$]), as we observed. However,
531 current year temperature also affected the trees in
532 Poland (from June to September [n]), contrary to

Uninfested natural spruce forest



Infested spruce plantation

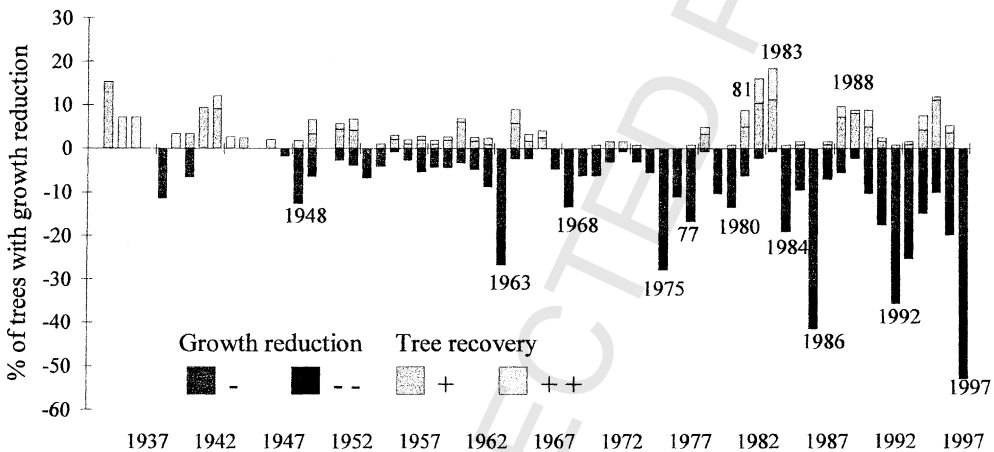


Fig. 7. Percentages of trees with extreme growth changes (since 1933), in an uninfested Norway spruce natural forest (located in Isère), and in an Ardèche plantation heavily infested by *Dendroctonus micans*, showing growth reduction and recovery phases.

533 our study. Precipitation influence was also found to be
 534 positive at this Polish site, during the previous year
 535 from April to August ($n - 1$), in winter and during the
 536 current spring (from March to May [n]). In an other
 537 humid spruce forest located in the Valley of Gónra
 538 Wisla (Piersciec, Poland), Feliksik et al. (1994) also
 539 observed a positive role for rainfall in June and July
 540 (n), whereas the temperature effect was positive from
 541 March to May (n). Desplanque et al. (1998) also

reported positive correlations with May to July precipi-
 542 tation in spruce forests in the French Alps, but they
 543 were restricted to low elevation sites. Similarly, spruce
 544 roots are known to be strongly influenced by precipi-
 545 tation (41% of explained variance), and their growth
 546 favoured by high rainfall especially during April,
 547 June–July and September (Krause and Eckstein,
 548 1994). Norway spruce was also affected by drought
 549 in the Jura mountains (Badot et al., 1990).
 550

551 Petitcolas (1993) also found in 8 subalpine spruce
552 forests in the French Alps (in the Tarentaise, the
553 Maurienne, and the Belledonne massifs) a positive
554 influence of high summer temperature from May (n) to
555 July (n), with opposite effects during August ($n - 1$).
556 Such results were consistent with ours. However, in
557 Petitcolas's study (1993) the precipitation only played
558 a minor part (because of higher elevation sites), but a
559 positive link with tree growth was also observed in
560 August ($n - 1$).

561 As we observed, June and July (n) high air tem-
562 peratures were also found to have a positive influence
563 in the Babia Gora subalpine spruce forests in the
564 western Carpathians (southern Poland) according to
565 Bednarz et al. (1997). A similar influence of May–
566 June–July (n) high temperature was also reported in
567 Poland by Feliksik (1972) in the Tatra mountains, and
568 by Sander et al. (1995) in Czechoslovakia (in Labe
569 valley), especially on northern exposures. Spruce trees
570 growing in Tyrol (Austria) were also correlated with
571 June–July (n) temperatures (Eckstein and Aniol,
572 1980). Thus, such positive response to summer tem-
573 perature was probably a general characteristic of high
574 elevation, subalpine, north facing and cold spruce
575 stands (Desplanque et al., 1998). It was not observed
576 for spruce growing at lower elevations as in Seyde
577 (Germany) (Wimmer and Grabner, 1997), and was
578 observed only at high elevation in the Italian Tyrol by
579 Hüsken (1994), as in Cortina d'Ampezzo (Urbinati
580 et al., 1996) or in Trentino, with a positive correlation
581 with April to July (n) temperatures (Brugnoli and
582 Gandolfo, 1991).

583 Similarly, in Switzerland Lingg (1986) found a
584 positive influence of May to August (n) temperature
585 at high elevation, especially in June (n). Drought
586 sensitivity (in June and July ($n - 1$)) was observed
587 there only at low elevation (Lingg, 1986), as observed
588 by Desplanque et al. (1998) in France, or by Kienast
589 et al. (1987) who reported positive responses to May
590 temperature and precipitation in June (n) in two low
591 elevation sites in the Swiss Jura (at 1180 and 1500 m,
592 in moist sites).

593 Therefore, spruce trees planted in the Ardèche
594 shared with other natural *Picea abies* forests located
595 at high elevations a general sensitivity to summer air
596 temperature during ring formation (Desplanque et al.,
597 1998; Petitcolas, 1993). However, the influence of
598 unfavourable water balance during the previous sum-

599 mer was rarely observed in other studies (Desplanque
600 et al., 1998), except at low altitude. Consequently, the
601 spruces growing at the Ardèche sites presented both
602 the common “subalpine spruce behavior” that char-
603 acterized a dependence of high altitude trees to low
604 temperatures, and the drought sensitivity, that usually
605 characterized low altitude forests. Such features were
606 probably due to the Ardèche local climate, that com-
607 bined both cold temperatures and severe summer
608 drought.

609 However, it was difficult to know exactly if changes
610 observed in tree responses to climate in the infested
611 forest were a consequence of bark beetle attack, or a
612 cause that favoured *Dendroctonus micans* by lowering
613 *Picea abies* health. Cold spring and dry summer may
614 have acted in synergy to facilitate infestation, as
615 described for scolytid outbreaks triggered by drought
616 (Joly, 1977), during the 1976 drought year, for
617 instance.

5. Conclusions 618

619 In many Norway spruce plantations located in the
620 Ardèche (France), *Picea abies* suffered from *Den-*
621 *droctonus micans* infestation. This bark boring beetle
622 attacked apparently healthy trees, leading to extensive
623 forest diebacks. In a heavily infested forest, that was
624 subsequently cleared by foresters, a dendroecological
625 investigation was carried out in order to understand
626 this phenomenon. Our main objectives were to date
627 the first tree infestations, to compare radial tree growth
628 in infested and uninfested sites, and analyse tree-ring
629 and monthly climate relationships. A comparison of
630 infested and healthy trees was also achieved in order to
631 examine if such relationships might be altered by
632 insect outbreaks, and hence to determine if extreme
633 climatic phenomena might interact with insects
634 attacks.

635 As already observed for some other *Dendroctonus*
636 species, such as *D. rufipennis* (Lindgren and Lewis,
637 1997; Veblen et al., 1991), dendrochronological meth-
638 ods proved to be efficient for a posteriori study of *D.*
639 *micans* outbreaks.

640 Infested trees reacted to insect attacks by exuding
641 copious resin flow through the holes bored in their
642 bark, and showing a decreased sap flow due to sap-
643 wood destruction by larvae feeding when the attacks

644 succeeded. Therefore, such infestations induced visi-
645 ble features in wood structure, that appeared very
646 suitable for dendrochronology. Thus, in most cases
647 a radial growth reduction was noticeable after tree
648 infestation. However, such insect related growth
649 reductions were often comparable to those produced
650 by extreme climatic events, such as summer drought.
651 In a first analysis, the correct discrimination between
652 these two phenomena might be difficult. However, two
653 additional features facilitated this task. First, all the
654 pointer years attributed to climate were synchronous
655 among trees growing in the same stand, and even
656 among several spruce forests located in different
657 regions. In contrast to this, insect effects were not
658 synchronous, and of course absent in uninfested
659 spruce forests. Secondly, growth reductions induced
660 by climatic stress were followed by a more or less
661 rapid tree recovery (in most cases, 1 or 2 years later),
662 whereas the abrupt growth changes associated with
663 *Dendroctonus micans* infestations were never found to
664 be followed by tree recovery. A progressive spruce
665 dieback was observed, extending over a 10–15-year
666 period, with only narrow rings formed after attacks
667 because of the larval feeding effects that could last for
668 several years.

669 Precise outbreak dating was possible, especially
670 when the tree section was cut near enough to the level
671 of one hole in the bark. In such situations, specific
672 characteristics were clearly visible in the wood. Both
673 missing rings around the hole (but not on the other
674 sides of the trunk), and crescent-shaped resin patches
675 between two consecutive tree-rings produced clear
676 evidences for an insect attack. Abrupt growth reduc-
677 tion began immediately after these signs, providing an
678 indirect and additional confirmation of *D. micans*
679 successful attack during a given year, that therefore
680 could successfully be dated. Thus, the oldest attack
681 that was possible to date with dendrochronology
682 occurred 20 years before tree felling, in 1979, whereas
683 *D. micans* was recorded in that region by foresters
684 only in 1984, after it reached a sufficient population
685 level and was present since 1977 in the Mézenc area,
686 5 km away from the study site.

687 Most years with synchronous extreme narrow rings
688 were common to uninfested spruce stands, even in
689 other regions, and therefore induced by climatic
690 events. However, the intensity of such pointer years
691 gradually increased after 1980 in the infested site,

692 because of progressive tree weakening. The tree die-
693 back extended during the last 20 years, and no spruce
694 recovery was observed.

695 Our results demonstrate that entire stand felling
696 was the only suitable solution in such a situation. In
697 some cases, the introduction of *Rhizophagus grandis*
698 Gyll., the main natural enemy of *Dendroctonus*
699 *micans*, was used as a pest control method (Lempé-
700 rière, 1992).

701 The years with abrupt radial growth reductions
702 observed in the infested stand such as 1948, 1980,
703 1984 or 1992 were cold years, with summer frosts,
704 whereas 1986 was characterized by summer drought.
705 In the Ardèche plantations, Norway spruce was there-
706 fore affected by both cold years and by hot and dry
707 summers.

708 These results were confirmed by the tree-ring and
709 monthly climate relationship analysis. It showed that
710 infested *Picea abies* growth was reduced by three
711 main limiting factors: (1) excessively low minimum
712 temperature during most parts of the year prior to ring
713 formation; (2) higher than average maximum tem-
714 perature during the current spring and summer; and (3)
715 dry periods in winter, spring and summer.

716 In other words, the climate in the Ardèche region
717 with cold winters and summer drought, especially in
718 July, appeared to be unsuitable for optimal and sus-
719 tained spruce growth. The basal area growth curves
720 confirmed that a rapid inflection appeared when trees
721 reached 30–40 years, whereas spruce growth in natural
722 stands was sustained over longer periods, usually with
723 inflections only after 150 years.

724 Even-aged plantations of trees with reduced
725 genetic variability outside the natural distribution area
726 of the tree have often led to enhanced insect attacks
727 (Schvester, 1985). Spruce trees in the Ardèche con-
728 firmed this general rule. The type of soil could influ-
729 ence insect performance, as already observed for the
730 white pine weevil (*Pissodes strobi*) infestation on
731 *Picea abies* (Lavallée et al., 1996). To avoid *Den-*
732 *droctonus micans* attacks on spruce, eventually fol-
733 lowed by other pathogens (Wilson et al., 1998), it
734 would be better to avoid replanting *Picea abies* in the
735 Ardèche, especially on volcanic and cryptopodzolic
736 soils with poor water reserves that enhanced the
737 effects of summer drought.

738 However, the spruce plantations of this previously
739 afforested area were not dedicated to timber produc-

740 tion but to the protection of soil and the control of
741 erosion.

742 Our results revealed a negative combined effect of
743 altitude, soil, climate and insect impacts on spruce
744 development in this area.

745 Since the forest managers have to face this new
746 situation, new silvicultural practices must integrate the
747 management of infested and dead wood matter. *Den-*
748 *droctonus micans* can be regarded as a major candi-
749 date for sustaining biodiversity because of the
750 presence of associated organisms such as other arthro-
751 pods, birds and fungi (Lempérière et al., 2004).

752 The replacement of spruce by indigenous tree or
753 shrub species might also be an alternative to the
754 practice of planting Norway spruce. In Eastern Eur-
755 ope, pine also suffers from the bark beetle attacks
756 (Voolma, 1994), but pine or spruce prone to infestation
757 may be replaced here by the silver fir (*Abies alba*), as
758 done by foresters on our study site. Larch (*Larix*
759 *decidua*) has also been used for reforestation in that
760 region.

761 Uncited reference

762 Guiot et al. (1982).

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