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1 **Potential processes leading to winter reddening of young Douglas-fir *Pseudotsuga menseizii* in Europe.**

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15

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37 **Key message**

38 Winter reddening of young Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco), triggered by large thermal  
39 fluctuations in late winter, is a critical problem for European forestry. A literature review identified certain climatic  
40 conditions that are characteristic of 'reddening' years, including warm daily temperatures, high daily temperature  
41 amplitude, low relative humidity, moderate wind speeds, as well as the occurrence of freeze-thaw cycles with cold  
42 night temperatures.

43 By describing the triggering environmental and stand factors, we propose three hypotheses for the physiological  
44 processes leading to winter reddening, namely (i) hydraulic failure due to winter drought stress, (ii) photo-oxidative  
45 stress in shade-acclimated trees, and (iii) early cold deacclimation during warm periods.

46 i) Low soil temperature, by reducing root water uptake, combined with anticyclonic conditions, by increasing  
47 water losses, can induce hydraulic failure in the xylem. Hydraulic failure may be further accelerated by  
48 night frosts.

49 ii) Winter reddening can occur when low temperature and high irradiance coincide, disrupting photostasis.  
50 Overwhelming of winter photo-protection may lead to photodamage and subsequent reddening.

51 iii) Warm periods, by inducing cold deacclimation, make trees susceptible to frost damage.

52 Finally, the three processes may interact under atypical anticyclonic conditions in late winter (e.g. cold or dry soils,  
53 warm days, high irradiance and/or freezing nights). Indeed, trees under water stress would develop a higher  
54 sensitivity to freezing night and photooxidative stress. We therefore proposed mitigation actions to avoid exposing  
55 trees to stressful conditions based on e.g. stand characteristics, understorey vegetation and planting.

56

57 **Keywords:** Cold deacclimation, freezing, hydraulic failure, photo-oxidative stress, *Pseudotsuga menziesii*

## 58 1. Introduction

59 Forest productivity and tree survival are significantly affected by biotic and abiotic disturbances. Summer  
60 drought stress which is often combined with hot spells, can lead to leaf browning and/or shedding, compromising  
61 long-term tree survival (Allen *et al.* 2010). In conifers, severe and prolonged water deficits in summer can also  
62 lead to partial or complete crown browning (Drénou and Rosa 2014). However, a change in needle colour, from  
63 green to red, has also been observed outside the summer season *i.e.* during late winter - early spring in Montana  
64 forests (Hedgcock 1912). During spring 2012, 250,000 ha of forest in Northwestern Ontario were affected by  
65 needle browning, of which 190,000 ha were severely affected, *i.e.*, 25% to 100% of the trees were damaged (Man  
66 *et al.* 2013). In France, the occurrence of winter needle browning in mountainous areas has increased dramatically  
67 in recent decades and now occurs almost every three years, according to the French department for the forest health  
68 (DSF, pers. comm.).

69 Winter needle browning has been observed in many conifer species such as balsam fir *Abies balsamea* (L.)  
70 Mill. and black spruce *Picea mariana* (Mill.) BSP (Cayford *et al.* 1959; Man *et al.* 2013; 2009), white spruce *Picea*  
71 *glauca* (Moench) Voss (Cayford *et al.* 1959; Man *et al.* 2013), jack pine *Pinus banksiana* Lamb. (Man *et al.* 2013),  
72 Sitka spruce *Picea sitchensis* (Bong.) Carr. (Redfern *et al.* 1987), Douglas-fir *Pseudotsuga menziesii* (Mirb.)  
73 Franco (Hedgcock 1912; Malmqvist *et al.* 2018; McMinn and Funk 1970; Nicolescu 2020), Silver fir *Abies alba*  
74 Mill. (Robakowski *et al.* 2021) and locations (Japan, North America, Sweden, Norway, France, Belgium,  
75 Switzerland). Different phenomena, occurring in late winter/early spring, could lead to winter browning: red belt  
76 (Bella and Navrati 1987; Henson 1952), winter burn (Maple *et al.* 1975), winter freezing damages (Man *et al.*  
77 2013), winter reddening (Hughes 2011), frost damages (Christersson and Fircks 1990), late spring frost (Man *et*  
78 *al.* 2013), winter drought (Hart *et al.* 2017), frost-drought (Tranquillini 1982) or winter desiccation (Christersson  
79 and Fircks 1990; Sakai 1970). Needle discolouration is not a highly specific symptom *i.e.* orange or red needles  
80 do not necessarily indicate serious and irreversible damage leading to tree death. Needle discolouration may be a  
81 temporary visual symptom which may disappear with increasing air temperature or resumption of growth (Steyn  
82 *et al.* 2002).

83 Depending on the type of damage, three patterns of needle browning can be distinguished: red belt, spring frost  
84 damage and winter reddening. In Scandinavia and western North America, red belt affects different tree cohorts,  
85 from seedlings to mature trees. The damage appears as a narrow red band at given elevations along slopes  
86 (Hedgcock 1912; Jalkanen 1993; Venn 1993). The red belt is mainly caused by Chinook winds, which are  
87 characterised by warm, dry air in conjunction with limited water uptake. Mature stands of Douglas-fir, lodgepole

88 pine *Pinus contorta* Douglas and ponderosa pine *Pinus ponderosa* Douglas are mainly affected. In 1909, 16,000  
89 hectares of trees died in Montana (Hedgcock 1912) and, in 2009 1,100 hectares in Alberta (Flowers 2009). Spring  
90 frost damage, or false spring, refers to direct frost injury to elongating buds, stems, newly emerging shoots and  
91 foliage that occurs after bud break (Reich 1990; Chamberlain *et al.* 2019). False springs happen after plants have  
92 been exposed to mild temperatures in late winter. Mild temperatures, by accelerating the release of ecodormancy,  
93 make buds highly vulnerable to freezing temperatures (Charrier *et al.* 2015a; 2018a). Frost damage is mainly  
94 observed on annual shoots of Douglas-fir, which lose turgor and turn brown when the temperature rises after  
95 freezing events (Malmqvist *et al.* 2018). Another pattern of winter injury includes winter burn, winter browning,  
96 winter reddening, winter drought and desiccation stress, which cause needle colour change before budbreak. Such  
97 damage has been observed in North America on jack pine, balsam fir, white spruce and black spruce (Man *et al.*  
98 2013; Ontario 190, 000 ha with severe damage *i.e.*, more than 50% of damaged trees), Scandinavia and central  
99 Europe (eg. on Douglas-fir and Scots pine). Such a damage pattern will be referred to as winter reddening in this  
100 paper.

101 In recent decades, winter reddening has been observed mainly in young stands, resulting in significant mortality  
102 and the need for replanting in severely affected stands. This raises critical issues for forest managers in their  
103 replanting strategy. To identify the current knowledge gaps, we aimed to characterize the risk of winter reddening  
104 through the different risk components: hazard, exposure and vulnerability (Bréda and Peiffer 2014). Although  
105 some abiotic and individual factors have been identified, the aetiology of winter physiological reddening is still  
106 not clearly understood, preventing foresters from developing mitigation measures.

107 Douglas-fir, due to its wide adaptability to planting sites, rapid growth, and high wood yield, has been  
108 extensively planted throughout Europe, particularly in France, where plantations increased from 330,000 hectares  
109 in 1993 to 415,000 hectares in 2021 (Nicolescu *et al.* 2023). Over the last few decades, the number of young  
110 Douglas-fir plantations has increased, leading to an increase in observations of winter reddening in France (DSF,  
111 pers. comm.), Belgium (Walloon observatory of forest health) and Switzerland (Swiss Federal Research Institute,  
112 WSL), among others. Therefore, this opinion piece will mainly focus on the winter reddening phenomenon in  
113 Douglas-fir. We will first describe the symptoms and triggering environmental and stand factors. We will then  
114 propose three hypotheses detailing the physiological processes that can lead to winter reddening.

## 115 **2. Symptoms of winter reddening**

116 Winter reddening is a gradual process during which the colour of needles changes from glaucous green to  
117 orange and ultimately to red (Fig. 1; Baubet and Goudet 2015; Solberg 1993; Venn 1993). Red discolouration is

118 visible in early spring before budbreak (Cayford *et al.* 1959; Malmqvist *et al.* 2018; Man *et al.* 2013; McMinn and  
119 Funk 1970). Young needle cohorts (1 or 2 years old for an average lifespan of 3 years) are affected earlier than  
120 older ones (Venn 1993; Redfern *et al.* 1987; Solberg 1993). The reddening process begins at the tip of the needle  
121 and extends to the base and along the branch eventually reaching the trunk. In extremely severe cases, the buds  
122 dry out and the bark necroses (Bella and Navrati 1987; Sakai 1970; Solberg 1993).

123 At tree level, the upper segment of the crown is usually more damaged than the lower one, resulting in a  
124 gradient from red to green from top to bottom (Fig. 2). A common pattern is a multi-coloured crown: red at the  
125 top, glaucous green – orange in the middle and green in the lower part of the crown. Branches covered by snow  
126 and/or understorey vegetation usually remain green (Hedgcock 1912; MacHattie 1963). During the following  
127 growing season, most of the affected whorls in, and above, the red fraction die, although the red needles remain  
128 on the branch until the middle of the growing season (Pourtet 1949; McMinn and Funk 1970).

129 Needle mortality on affected trees can reach 100% (DSF – dataset; Man 2009; 2013; Goudet 2009). Different  
130 patterns of reddening (*i.e.* completely red, red crown and green base, or, less frequently, green crown and red base)  
131 are observed in different stands and even within an affected stand. Individuals close to openings in the stand, on  
132 edges created by nearby clearcuts, windthrow, or in a relative isolation are more likely to be affected (Cayford *et*  
133 *al.* 1959; Redfern *et al.* 1987), although not systematically (Fig. 3).

134 Winter reddening mainly affects young trees, up to 20 years-old and 8 m tall (Malmqvist *et al.* 2018; Man *et*  
135 *al.* 2009; 2013; Nicolescu 2020). When only the upper part of the crown is damaged, trees display a reduced  
136 growth, with an unbalanced architecture leading to tree decline. The reduction in growth is proportional to the  
137 amount of red needles (Bella and Navrati 1987; McMinn and Funk 1970; Redfern *et al.* 1987). In lodgepole pine,  
138 the length of terminal buds formed in the following growing season is reduced by 25% after winter reddening  
139 (Bella and Navrati 1987). The reduced growth of affected trees delays the time of canopy closure and, in addition  
140 to the death of some individuals, reduces the overall density of the stand. Remaining trees are therefore more  
141 exposed to additional stress events (*e.g.* high winds, irradiance and/or daily thermal amplitude). The delayed  
142 growth of affected trees raises forest management issues due to increased stand heterogeneity. Although affected  
143 trees can recover normal physiological function after a winter reddening event, their growth rarely return to pre-  
144 stressed levels. Following winter reddening, 60 to 100% of severely damaged trees died within two years  
145 (Malmqvist *et al.* 2018). The mortality rate of slightly damaged trees was between 20% and 60% four years later.  
146 When most of the buds are dead and more than 60% of the needles are red, a steady decline in physiological

147 functions is observed until complete decay. For balsam fir and black spruce, overall survival after six growing  
148 seasons was also around 70% of the affected trees (Man *et al.* 2013).

### 149 **3. Factors affecting the risk of winter reddening**

150 Based on the observations recorded by the DSF in France between 1989 and 2019 (Frame 1) analysed through  
151 a risk management approach, we identified three groups of factors involved in the risk of winter reddening:  
152 meteorological hazard, exposure, and tree vulnerability (Kron 2005; Bréda and Peiffer 2014; Charrier *et al.* 2015a).  
153 Hazard is the probability of occurrence of one or more natural disturbances during a given period and over a  
154 defined spatial extent (mainly meteorological events such as high daily thermal amplitudes in February). Exposure  
155 reflects how the subject, regardless of its level of organisation (*e.g.* individual tree or stand), experiences the  
156 hazard. Several factors are related to exposure such as topography, soil properties, position in the stand, forest  
157 management. Finally, vulnerability is the predisposition to be adversely affected by the hazard and therefore  
158 depends on its intrinsic characteristics (*e.g.* age, acclimation state, provenance).

#### 159 *3.1 Meteorological hazard*

160 Winter reddening is observed during late winter and early spring before growth resumption. Two different  
161 types of meteorological events were observed before winter reddening events.

162 In some cases, a period of anticyclonic weather is sufficient to induce damages in symptomatic years (years in  
163 which winter reddening is observed). Anticyclonic events are mainly characterized by a period of warm daytime  
164 and low nighttime temperature, large thermal amplitude, strong wind, and high irradiance (Pourtet 1949; Henson  
165 1952; Baubet and Goudet 2015; Malmqvist *et al.* 2018). The occurrence of warm and dry weather in late winter  
166 usually occurs when the soil is still cold or even frozen (Cayford *et al.* 1952). The concomitance of frozen soil and  
167 warm temperatures for several hours, *i.e.* up to 17°C on southern, sun-exposed, slopes, induces winter damages  
168 (Sakai 1970). In April-May, high light irradiance (*ca.* 2 000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  PPFD) combined with freezing  
169 temperatures induced photodamage in *Abies mariessi* Mast. (Yamazaki *et al.* 2007).

170 Winter reddening damage can also be observed when a mild period is preceded and followed by a cold period  
171 with negative temperatures and several freeze-thaw cycles (Man *et al.* 2009; 2013; Malmqvist 2018; Redfern *et*  
172 *al.* 1987). Two weeks of warm daytime temperature (20 to 25°C) followed by a period of normal daytime  
173 temperature with freezing nights (down to -22°C) induced severe damages on conifers (Redfern *et al.* 1984; Man  
174 *et al.* 2013). Winter damages have been also observed when the temperature in January was warmer than usual  
175 (2.9 to 4.7°C above normal) and colder in February (minimum temperature of -30°C; Kamp and Worrall 1990).

176 Thus, in late winter, relatively warm and dry conditions, combined or not with a cold spell, are predisposing factors  
177 for winter reddening.

### 178 *3.2 Exposure*

179 Meteorological factors are not the only drivers of winter reddening, as there is a high degree of variability  
180 between and within stands. Indeed, site-related factors are crucial, as winter reddening has been observed several  
181 times on the same plot (Venn 1993). In France, winter reddening is mainly observed in hills and low mountain  
182 (500-900 m a.s.l.; Fig. 4A), corresponding to about 70% of the Douglas-fir stands. Damage was more frequent on  
183 the northern than on the southern slopes in France (Fig. 4B). In winter, temperatures on southern slopes are  
184 typically higher than those on northern slopes. This is because southern slopes receive approximately eight times  
185 more daily irradiance than northern slopes (Lhotellier 2005). Additionally, the snow cover on southern slopes  
186 melts earlier than on flat lands or northern slopes and the soil temperature can quickly return to positive values  
187 (Morén and Perttu 1994).

188 Stands located on ridges, upper slopes and flat areas are more affected by winter reddening whereas almost no  
189 winter reddening is observed on lower slopes and in basins (Fig. 4C). Cold temperature does not seem to be a  
190 direct factor, as northern slopes do not systematically suffer from winter reddening, and lower slopes and basins  
191 can be exposed to colder temperatures than ridges in mid-winter during thermal inversions. Exposure to strong  
192 winds on ridges and upper slopes may be a more important factor than temperature on southern slopes (Morén and  
193 Perttu 1994). Indeed, trees that experience winter reddening on southern slopes are more often located on ridges  
194 and upper slopes whereas on northern slopes they are more frequently in lower slopes and flat lands.

195 At stand level, trees on the edge display larger damage than those located in the centre of the stand. Trees on  
196 the edges are exposed to higher irradiance, wind and temperature fluctuations than those in the core of the stand  
197 (Hiratsuka and Zalasky 1993; Stoutjesdijk and Barkman 2015). Recent clear-cuts in the stand exacerbate the  
198 intensity of winter reddening, by exposing shade-acclimated trees to higher exposure to light, wind and temperature  
199 extremes (Sagar and Waterhouse 2010). The presence of perennial understorey plants reduces frost damage  
200 (Aussenac 2000; Petritan *et al.* 2011). Perennial understorey plants (*e.g.* brooms, shrubs) also mitigate damage by  
201 reducing light intensity, buffering nighttime temperatures, reducing the number of freeze-thaw cycles and limiting  
202 warm daytime temperatures. The temperature difference between a clear-cut and a dense stand of Norway spruce  
203 seedlings was positive for the maximum and mean temperature (+ 4.5°C and + 0.7°C, respectively) and negative  
204 for the minimum temperature (-2.1°C) at 0.4 m above the ground (Langvall 2010). Thus, clearcutting increases  
205 the maximum temperature and decreases the minimum temperature encountered by the trees, exposing them to



206 larger daily thermal variations. Exposure to greater variations in meteorological parameters appears to be an  
207 aggravating factor for winter reddening.

### 208 *3.3 Vulnerability*

209 Factors related to tree exposure explain a significant part of the observed reddening, but at the individual level  
210 some factors related to the intrinsic vulnerability of the tree are also important. Winter reddening was mainly  
211 observed on young trees, up to 20 years old (Fig. 5). At the juvenile stage, trees are usually exposed to harsher  
212 conditions than crowns of mature trees. Colder leaf temperature than the surrounding air is generally observed in  
213 early morning (Johnson *et al.*, 2011). Such a leaf temperature depression is likely to promote ice formation even  
214 when air temperatures are above freezing. Additionally, young trees with a reduced root system explore a limited  
215 volume of soil, which limits the amount of water they can access. The shallow distribution of the root system  
216 renders it more exposed to freezing temperature. Frost damage to the root system leads to reduced growth and  
217 yellowing of needles in the following growing season by affecting water supply and mineral nutrition (Jalkanen  
218 1990; Cox and Zhu 2003). Freezing injury to Douglas-fir seedling roots may be triggered by delayed autumn cold  
219 acclimation (Malmqvist *et al.* 2018).

220 Instances where all Douglas-fir trees in a stand are affected are rare (refer to the previous section on symptoms  
221 for additional information). This implies that not all young trees are equally sensitive to winter reddening. In 2014,  
222 in 41 stands exhibiting winter reddening, 75% of symptomatic trees showed root system abnormalities: taproot  
223 malformation or superficial distribution of fine roots (Baubet and Goudet 2015). By reducing water and nutrient  
224 uptake, root system anomalies weaken trees, making them vulnerable to winter damage. As trees grow, the canopy  
225 closes and the variability of microclimatic parameters such as irradiance, wind and temperature are reduced.  
226 Finally, it is unclear whether the age of the tree corresponds to the vulnerability or the exposure component, as in  
227 a mature stand the crowns maintain a buffered environment that limits exposure to the identified stress factors  
228 (temperature, light, wind).

229 In recent decades, Douglas-fir has exhibited an earlier budburst of approximately five days per decade in France  
230 (Bastien 2020). Earlier date of budburst increases the probability of late-freezing events, resulting in higher frost  
231 damages due to early cold deacclimation (Chamberlain and Wolkovich 2021; Mura *et al.* 2022). Among the  
232 various provenances growing in France, California has the earliest bud burst, occurring 20 days before the others  
233 (Bastien *et al.* 2021). To prevent spring damages, other provenances with later date of budburst should be planted,  
234 such as Washington 2 and Luzette, especially under warm and highly fluctuating conditions (Bastien 2020).



#### 235 **4. Putative physiological background of winter reddening**

236 Based on the above observations, the physiological perturbations involved in the development of winter  
237 reddening in trees are most likely related to three potential processes: (i) hydraulic failure due to winter  
238 drought stress, (ii) photo-oxidative stress in shade-acclimated trees or (iii) early cold deacclimation  
239 during warm periods. The following section describes the sequence of physiological events that can lead  
240 to winter reddening by these different processes, bearing in mind that separate processes may also  
241 interact in the development of reddening.

##### *4.1 Winter hydraulic failure*

242 Winter reddening occurs under specific conditions such as low nighttime temperatures, mild daytime  
243 temperatures, cold or frozen soil, high irradiance and moderate to strong wind speed (Sakai 1970; Herrick and  
244 Friedland 1991; Malmqvist *et al.* 2018). The relatively warm conditions during the daytime maintain transpiration,  
245 which may not be adequately compensated by water uptake by the root system because the soil is cold or frozen,  
246 a typical pattern of winter drought (Tranquillini 1982).

##### *4.1.1 Low soil temperature reduces root water uptake*

247 A typical pattern of dehydration in autumn and rehydration in spring is observed in plants, under the control of  
248 soil temperature (Charrier *et al.* 2013a; Charrier & Améglio, 2023). At temperatures below 8°C, root water uptake  
249 is strongly limited (Améglio *et al.* 2002; Mellander *et al.* 2006). The entry point of water into plants is through  
250 the symplastic pathway as the apoplastic pathway is interrupted by barriers in roots such as the one created by exo-  
251 and endodermal Casparian bands in the endoderm (Lee *et al.* 2005). In symplastic pathway, water molecules pass  
252 through the plasma membrane whose permeability is mainly driven by the channel aperture of aquaporins (Lee *et*  
253 *al.* 2012). Low soil temperature affects aquaporin synthesis, but also their three-dimensional conformation which  
254 is constrained by the rigidity of acyl groups at low temperature (Ranganathan *et al.* 2016). If transpiration is  
255 maintained, the subsequent water deficit also increases the resistance to water flow by increasing the viscosity of  
256 the cytoplasm due to more concentrated intracellular sap (Améglio *et al.* 1990).

257 The sensitivity of root water uptake to low soil temperature may be further limited by the distribution of the  
258 root system in superficial soil layers (*e.g.*, young plants or those with an unbalanced root system conformation;  
259 Cox and Zhu 2003; Lopushinsky and Kaufmann 1984). Soil temperature in the superficial layers exhibits overall  
260 larger thermal fluctuations and can reach damaging freezing temperature. A shallow root system is therefore more  
261 at risk due to an increased exposure to frost damage (Jalkanen 1990). Finally, if part of the root system is damaged,  
262 root water uptake is further limited (Malmqvist *et al.* 2018). Although cold limitation of water uptake is more  
263

264 likely on northern slopes, a deficit in soil water content can have a similar effect on southern slopes, if winter  
265 precipitations are limited.

#### 266 **4.1.2 Anticyclonic conditions can exacerbate water losses**

267 Warm daytime temperatures, high light intensity and dry air induce higher needle transpiration rates. Although,  
268 under drought stress, water loss by needles is limited by stomatal closure, non-controlled fluxes through leaky  
269 stomata, leaf cuticle or bark can further increase plant water deficit (Duursma *et al.* 2019). During winter, stomatal  
270 control may not be as effective as during the growing season (Zweifel *et al.* 2007). Changes in the lipid composition  
271 of the plasma membrane may alter the efficiency of guard cells to regulate stomatal opening (Ruelland *et al.* 2009).

272 Water losses can be enhanced by short-term thermal fluctuations for the organ above the snow cover or the  
273 understorey vegetation. Warm periods may suddenly release the inhibition of stomatal responsiveness to cold  
274 temperature, resulting in enhanced water losses and a drop in xylem water potential. When a critical threshold is  
275 reached, a bubble is formed in the sap and propagates to adjacent xylem conduits by air-seeding (Cochard *et al.*  
276 1992; 2006). Air-filled vessels do no longer contribute to the transfer of water to the needles, increasing further  
277 needle dehydration and ultimately leading to drought-induced reddening (Cochard *et al.* 2009). Finally, the  
278 concomitance of cold soil temperature with warm air temperature is likely to induce winter drought by limiting  
279 root water uptake whereas water losses are enhanced. Although some conifer species can resist to such seasonal  
280 stress, even under harsh conditions (Chang *et al.* 2021; Charrier *et al.* 2017), the sensitivity of Douglas-fir to  
281 maintain its hydraulic integrity by preventing water losses may explain why this species would be more vulnerable  
282 to winter reddening than other species.

#### 283 **4.1.3 Interaction between nighttime freezing events and daytime passive water losses.**

284 Night temperatures below  $-2^{\circ}\text{C}$  can induce freezing of sap around a nucleus in xylem elements, resulting in the  
285 formation of air bubbles in the frozen sap (Zimmermann, 1964; Špulák and Balcar 2013; Charra-Vaskou *et al.*,  
286 2023). As night freezing events appears to be a key parameter in triggering winter reddening, a significant decrease  
287 in xylem water potential at the solid-liquid interface is expected, although it may not be low enough to induce  
288 bubble expansion and embolism formation (Charrier *et al.*, 2015b). However, in dehydrated samples, ice  
289 nucleation occurs in the xylem at colder temperatures than in saturated branches (Lintunen *et al.* 2013). The water  
290 potential generated at the solid-liquid interface is temperature dependent ( $-1.18\text{MPa}\cdot\text{K}^{-1}$ ; Rajashekar *et al.* 1983)  
291 and induces greater water fluxes towards ice nucleation sites under pre-existing water stress (Ball *et al.* 2006;  
292 Charra-Vaskou *et al.* 2016). Indeed, a dehydrated xylem would be more vulnerable to the formation and  
293 propagation of gas bubbles in xylem conduits (Sperry *et al.* 1992; Mayr and Charra-Vaskou. 2007; Charrier *et al.*

294 2014; 2015b). Successive freeze-thaw cycles promote air seeding and bubble expansion from conduit to conduit  
295 in dehydrated trees (Charrier *et al.* 2015b; Charra-Vaskou *et al.* 2023).

296 *In natura*, ice nucleation usually occurs at the basal part of the branch, which can draw liquid sap from the  
297 distal part towards the basal part, creating a water potential gradient (Charrier *et al.* 2017). At tree level, the  
298 temperature at the base is more constant so the base remains frozen for a longer time than the upper crown which  
299 is exposed to more freeze-thaw cycles (Mayr *et al.* 2003). Needle tissue experience severe water stress after several  
300 days of freezing, even under negligible transpiration (Kozłowski 2012). Furthermore, younger and distal twigs  
301 tend to dehydrate more rapidly than older parts (Lemoine *et al.* 1999). This may be due to their lower relative  
302 water content and cuticular resistance to water loss (Herrick and Friedland 1991). Under severe water deficit,  
303 chlorophyll a may be degraded, resulting in a colour change of the needle from green to red-brown. (Guadagno *et*  
304 *al.* 2017). Water stress is more pronounced in younger shoots, causing Douglas-fir needles to gradually dehydrate  
305 from the top to the base of the tree, resulting in the coloration pattern from the crown to the base.

#### 306 **4.1.4 How to induce experimental winter hydraulic failure in young Douglas-fir?**

307 To test the effects of cold soil on plant water relations, a differential conditioning with cold soil and warm air  
308 temperature would induce winter drought by limiting water uptake while transpiration is maintained (Lopushinsky  
309 and Kaufman 1984; Wang and Hoch 2022). New insights into the physiological behaviour of Douglas-fir under  
310 such conditions would be provided by measuring stomatal conductance, water status and hydraulic conductivity  
311 along the soil-plant-atmosphere continuum as well as growth resumption. A complementary experiment could test  
312 the effects of freeze-thaw cycles to amplify winter drought and increase the rate of hydraulic failure in the xylem  
313 by exposing single branches or part of the crown to successive freeze-thaw cycles.

### 314 **4.2 Photo-oxidative stress**

315 Winter reddening may occur when low temperature and high irradiance coincide, disturbing the photostasis  
316 *i.e.*, the energy balance between the photo-physical (from the electron chain transport) and photochemical  
317 processes that transform light and the metabolic sinks that consume the energy (Calvin-Benson cycle and related  
318 primary metabolism; Öquist and Huner 2003; Ensminger *et al.* 2006). In response to changing irradiance, plants  
319 can rapidly engage or disengage dissipatory pathways, which facilitates sustained thermal energy dissipation.

#### 320 **4.2.1 Low temperatures and high irradiance imbalance photostasis**

321 Low temperature reduces the rate of electron transport, by decreasing membrane fluidity and the rates of  
322 enzymatic reactions involved in the Calvin-Benson cycle, whereas high irradiance enhances photochemistry  
323 (Hüner *et al.* 1998; Yamazaki *et al.* 2007). If there is an imbalance in the energy flow between the rapid,  
324 temperature-insensitive reactions of photochemistry and the slow, temperature-dependent reactions of CO<sub>2</sub>

325 reduction, the capacity to modulate this balance may be overwhelmed (Ensminger *et al.* 2006). Thus, a potential  
326 energy imbalance is induced by the down-regulation of the biochemical reactions of the Calvin-Benson cycle by  
327 low temperature that cannot be compensated by heat dissipation.

#### 328 **4.2.2 Excess light energy and induction of a photo-oxidative stress**

329 Excess light is transferred to the ever-present oxygen (Ledford & Niyogi, 2005), resulting in the formation of  
330 reactive oxygen species (ROS). More specifically, singlet electrons can generate ROS, resulting in photo-oxidative  
331 damage to the photosynthetic apparatus (Soitamo *et al.* 2008; Ruelland *et al.* 2009; Yun *et al.* 2010). ROS are  
332 known to induce damages to thylakoid membranes (Levitt 1980), to alter the conformation of proteins associated  
333 with photosystems (Ogren and Oquist 1985; Gamon and Pearcy 1990; Zwiazek *et al.* 2001; Dellerio *et al.* 2016),  
334 and to degrade PS2 reaction centres *via* lipid peroxidation and chlorophyll bleaching (Yamazaki *et al.* 2007). In  
335 some cases, ROS may lead to cell and leaf death (Suzuki and Mittler 2006; Petrov *et al.* 2015). To prevent the  
336 accumulation of ROS, plants have developed photo-protective processes by enhancing alternative energy  
337 dissipation pathways (Demmig-Adams *et al.*, 1996, Adams *et al.*, 2006).

#### 338 **4.2.3 Winter protective processes to limit photo-oxidative stress**

339 During the dormant period, the photosynthetic capacity of the Douglas-fir is significantly reduced due to a  
340 decrease in the sink demand for photo-assimilates (Adams *et al.* 2006; Öquist and Huner, 2003). Faced with a  
341 down-regulation of the photosynthetic capacity and the saturation of photochemistry, evergreen conifers have  
342 evolved protective processes to dissipate the excess energy (Chang *et al.* 2021; Gillies and Vidaver 1990;  
343 Yamazaki 2003).

344 Photoprotection is mainly provided by the thermal energy dissipation, whereby excess energy absorbed by  
345 chlorophyll is safely dissipated as heat rather than being transferred to oxygen, resulting in ROS production. Non-  
346 photochemical quenching (NPQ) dissipate excess energy not used in photosynthesis as heat either through antenna  
347 quenching via the xanthophyll cycle (Demmig-Adams *et al.* 2014) or reaction center quenching through PSII  
348 charge recombination (Hüner *et al.* 2012). Under the conditions that trigger reddening, this ability may be  
349 overwhelmed by a combination of cold temperatures and relatively high irradiance. This protective mechanism is  
350 key in winter, as the pool of xanthophyll cycle carotenoids is higher than in summer in the needles of the Douglas-  
351 fir (Adams *et al.* 2004). Other secondary protective processes include structural adaptations through the  
352 rearrangement of the light harvesting complexes, the degradation of PSII reaction centres (Ottander *et al.* 1995) or  
353 cyclic electron transport around PSI, which acts as an alternative electron sink (Ivanov *et al.* 2001).

354 **4.2.4 Overwhelming of the photoprotection mechanism may result in photodamage and subsequent reddening.**

355 When environmental stress increases (frozen/cold soil, freezing day/night temperatures and high irradiance),  
356 the efficiency of the photoprotective mechanism decreases (Gillies and Vidaver 1990) by altering the biophysical  
357 properties of the thylakoid membrane and limiting the function of the xanthophyll cycle (Zhang *et al.* 2016). Long-  
358 lasted photoinhibition due to the combination of high irradiance and low temperature may induce permanent  
359 damages to PSII and needle discoloration (Robakowski, 2011), with the uncontrolled production and accumulation  
360 of ROS (Suzuki and Mittler 2006; Petrov *et al.* 2015). When photo-damages occurs, repairing processes involve  
361 photoprotective proteins and enzymes, such as the D1 protein to maintain photochemistry (Aro *et al.* 1993;  
362 Ottander *et al.* 1995).

363 Winter reddening usually initiates on the youngest needles, from the top to the base of the branch. In the case  
364 of Norway spruce, the current year's needles has a lower ratio of xanthophyll and alpha-tocopherol to chlorophyll  
365 (Tegischer *et al.* 2002). Alpha-tocopherol being the main lipophilic antioxidant (Fryer 1992), the potential  
366 photoprotection of the current year's needles is reduced compared to the previous year's needles (Tegischer *et al.*  
367 2002). The upper crown of a Douglas-fir, which bears younger needles and is more exposed to high irradiance and  
368 low temperature, is thus more susceptible to photo-oxidative stress. Mature trees have a higher proportion of older  
369 needles, which are generally better protected than the younger ones, by a higher concentration of the xanthophyll  
370 pool and antioxidants (Tegischer *et al.* 2002). Older trees are therefore less vulnerable to photooxidative stress  
371 than seedlings and young trees.

372 Needles that have been acclimated to full light conditions have a four to five times larger xanthophyll pool than  
373 shade-developed needles (Adams and Demmig-Adams 1994). After clearcutting, young trees that were acclimated  
374 to shade conditions are suddenly exposed to high irradiance and may be exposed to photo-oxidative stress and  
375 reddening (Adams and Demmig-Adams 1994).

376 Although many evergreen species are able to down-regulate photosynthesis during winter, Douglas-fir  
377 maintains photosynthesis under favourable conditions. From October to March, photosynthesis can account for up  
378 to 30% of annual net assimilation at the branch level (Guehl *et al.* 1985; Choisnel *et al.* 1990). Douglas-fir is  
379 probably more vulnerable to winter reddening than other conifer species because of its ability to maintain the  
380 integrity of the photosynthetic apparatus during winter. Although this ability enables a rapid resuming of  
381 photosynthesis as soon as temperature and irradiance become favorable, when the photosystem is saturated but  
382 temperature low, photo-oxidative stress is to be expected.

383 **4.2.5 How to induce experimental photo-oxidative stress in young Douglas-fir?**

384 To characterize the risk of photo-oxidative stress in young trees through their contents in xanthophyll,  
385 carotenoid, lutein and antioxidants, seedlings may be exposed to different treatments that combine high irradiance  
386 and chilling temperature.

387 **4.3 Early cold deacclimation**

388 During the winter season, trees transiently increase their tolerance to freezing temperatures through the process  
389 of cold acclimation / deacclimation. Cold acclimation is induced by cold temperatures in autumn, while cold  
390 deacclimation is induced by warm temperatures in late winter to early spring (Charrier *et al.* 2011; 2015a).  
391 Anticyclonic conditions or a period of mild temperature in late winter may increase the vulnerability to the  
392 following cold spell, by inducing cold deacclimation before budbreak (Man *et al.* 2009).

393 **4.3.1 Warm spell induces Douglas-fir cold deacclimation**

394 In Douglas-fir, the period of maximal cold hardiness usually occurs in December before trees deacclimate to  
395 cold under the control of environmental factors (Stevenson *et al.* 1999). Cold deacclimation is mainly driven by  
396 mild/warm air temperature rather than water availability, day length or light intensity (Driessche 1969; Kalberer  
397 *et al.* 2006; Charrier *et al.* 2018a). In Douglas-fir, air temperature above +5°C induces cold deacclimation, after  
398 endodormancy is released (Bailey and Harrington 2006). Short periods of warm temperature can induce cold  
399 deacclimation in *Picea rubens* (*i.e.* 45 hours at 15°C or 18 hours at 24°C; DeHayes *et al.* 1990). Over a longer  
400 period, warm temperature promotes the resumption of growth. A significant increase in water content is observed  
401 in buds and in other living tissues, before bud break, as growing tissues require higher water content to reach the  
402 cell turgor necessary for cell enlargement (Pagter *et al.* 2011; Charrier *et al.* 2013a).

403 Cold acclimation is induced, at the cellular level, by a decrease in water content and an increase in various  
404 compounds such as soluble carbohydrates, raffinose family oligosaccharides (Charrier *et al.* 2013b; Baffoin *et al.*  
405 2021; Deslauriers *et al.* 2021). Cold deacclimation is associated with significant changes in cell and tissue water  
406 relations, as well as carbohydrate metabolism, which can be affected by temperature-induced changes in  
407 respiratory metabolism (Pagter and Arora 2012; Charrier *et al.* 2018b). The depletion of cryoprotectants induced  
408 by warm temperatures, using rapid metabolic pathways, cannot be reversed quickly and at low energy cost  
409 (Kalberer *et al.* 2006). Deacclimation is therefore much faster than reacclimation, taking several days or weeks  
410 (*e.g.* 10 to 20 days in *Picea rubens*; Strimbeck *et al.* 1995) to return to previous levels of frost hardiness. Following  
411 a warm period, trees are therefore vulnerable to a sudden drop in temperature.

#### 412 **4.3.2 Frost damages can lead to winter reddening**

413 The use of cumulative growing degree days (GDD) since 1 January is a relevant proxy of ontogenic  
414 development during ecodormancy and concomitant cold deacclimation, regardless of the date of endodormancy  
415 release (Man *et al.* 2009). In 2007 in Northeastern Ontario, trees reached critical values of 100 GDD a week earlier  
416 than during the 1981-2007 period. The occurrence of extremely cold nights at this period induced severe winter  
417 freezing injuries on conifer trees (Man *et al.* 2009). Freezing events occurring before budbreak affect more severely  
418 young trees of different sizes and species over large areas than after budbreak (Man *et al.* 2009). Colder conditions  
419 (eg. on norther slopes) would decrease the vulnerability of living cells but increase the exposure to frost hazard,  
420 compared to southern slopes.

421 In Douglas-fir, the provenances that exhibit earlier dormancy release and growth initiation are more vulnerable  
422 to frost damages (Stevenson *et al.* 1999). Usually, late freezing events mainly damage buds and needles (Tinus *et*  
423 *al.* 2000), which are more sensitive than stems (Burr *et al.* 1986). Late freezing events, commonly referred to as  
424 false springs, occur close to the time of bud break and cause frost injury when exposure to cold temperatures  
425 exceeds the frost hardiness of the plant (Mura *et al.* 2022). However, frost damage can also be observed on the  
426 cambium, affecting the timing and the pattern of secondary growth resumption, noticeable by a frost ring along  
427 the growth ring chronology (Glerum and Farrar 1966). In this case, the new ring formation and consequently the  
428 restoration of hydraulic conductivity may be limited by the cambium damage, increasing the dehydration of the  
429 needles, which may turn red.

430 Frost injury depends not only on frost hardiness but also on the duration and intensity of the frost event, the  
431 number of freeze-thaw cycles and the rate of cooling and thawing (Charrier *et al.* 2015a). The upper part of the  
432 crown is usually exposed to lower temperatures and tends to be more severely affected with killed buds (Redfern  
433 *et al.* 1987; Kamp and Worrall 1990). Young Douglas-fir saplings, less than 2 m tall, are at high risk as their upper  
434 part is exposed to cold air (Morén and Perttu 1994). Perennial understorey plants can act as a shelter and protect  
435 the seedling from very low temperatures. Thus, frost causes cellular damage to the upper parts of the trees, which  
436 can impact the photosynthetic apparatus and degrade chlorophyll a. As a result, needles, which are particularly  
437 vulnerable to cold, may change colour from green to red.

#### 438 **4.3.3 How to experimentally induce frost damages in young Douglas-fir?**

439 To test this hypothesis, young saplings or isolated branches of Douglas-fir could be stored at different  
440 temperature after endodormancy release in late winter to build deacclimation curves (Man *et al.* 2017). The whole  
441 plant or individual branches can also be exposed to different types of freezing events (intensity, duration) in a  
442 controlled environment at varying levels of cold hardiness to clarify the damaging process (Man *et al.* 2021). The



443 objective would be to induce localized damage to needles and/or cambium. Needle colour and the resumption of  
444 primary and secondary growth after exposure to a stress condition could shed light on the relevance of this  
445 mechanism.

#### 446 *4.4 Potential interaction between physiological stresses*

447 The three processes described above, namely winter hydraulic failure, photo-oxidative stress, and early  
448 cold deacclimation, are not necessarily mutually exclusive. For instance, freezing nighttime temperature combined  
449 with high irradiance and warm daytime temperature can trigger the formation of freeze-thaw induced embolism in  
450 pre-stressed trees. Additionally, frost damage to the cambium can prevent the restoration of hydraulic function.  
451 Another interaction between stomatal closure, induced by either water stress or low temperature, and  
452 photosynthetic carbon assimilation would primarily maintain the hydration status of the tree. This would occur at  
453 the cost of photo-oxidative stress in the needles under high light. The variation in vulnerability between young and  
454 mature trees indicates that either ontogenic changes are taking place in the upper crown, where more stressful  
455 conditions are present, such as lower temperatures, higher wind speeds, and greater irradiance, or the vertical  
456 growth of the root system enables mature trees to escape drought stress during the winter season. Although winter  
457 drought due to low soil temperature is observed in *P. abies* with only minor consequences at the photo-oxidative  
458 and hydraulic levels (Day *et al.* 1991; Delucia 1986; Charrier *et al.* 2017), Douglas-fir could be highly sensitive  
459 to this stress. The differences could lie in the maintenance of photosynthesis and stomatal regulation, or the ability  
460 to limit air seeding during freeze-thaw cycles.

### 461 **5. Conclusion**

462 Under atypical anticyclonic conditions in late winter, Douglas-fir trees may experience winter reddening due  
463 to various abiotic factors. The interaction between warm/dry and cold temperatures can make trees vulnerable to  
464 stress at the cellular and hydraulic level.

465 Cold soil or soil water deficit can reduce root uptake, leading to a drop in water potential and subsequent  
466 stomatal closure. Clear nights and freezing events, combined with warm, sunny days, can affect stomatal  
467 regulation, damage living cells, promote the biosynthesis of photoprotective pigments and alter water flow within  
468 the crown of the tree. A hydraulic gradient can cause dehydration of the apexes, diameter contraction, and a drop  
469 in water potential. This can result in massive embolism in the most exposed parts of the tree, such as the top of the  
470 tree, while the base remains frozen for longer. The reduced water content of the needles may result in chlorophyll  
471 degradation and the emergence of secondary pigments. Although whole crown reddening is usually irreversible,  
472 moderate colouration may disappear with increasing air temperature and resumption of growth in spring,

473 suggesting that this symptom is related to the photoprotective response. To confirm the mechanism of reddening,  
474 measurements of the changes in diameter, water potential, hydraulic conductivity should be taken at various  
475 heights in the crown to demonstrate the presence of a hydraulic gradient. Finally, to demonstrate the loss of  
476 stomatal regulation, gas exchange measurements and residual transpiration should be measured before and after  
477 one or more freeze-thaw cycles, in combination with pigment extraction.

478 All provenances are potentially exposed to reddening, but phenological traits exhibiting intraspecific variability  
479 such as the dates of bud burst in relation to cold deacclimation, may amplify winter reddening. To minimize the  
480 risk, forest managers must focus on three key points: selecting local factors at the massif scale, maintaining a forest  
481 atmosphere in the stand, and promoting a regular root system at the tree scale.

482 Douglas-fir is at a higher risk of reddening if it is located between 400 and 800m asl, on the top of north-facing  
483 slopes, ridges, or flatlands. In high-risk locations, saplings can be protected by placing them under shelter.  
484 Additionally, selecting perennial understorey vegetation, such as broom, or keeping small shrubs can protect young  
485 trees from large fluctuations in environmental factors such as light, temperature, and wind. Finally, when planting  
486 a new stand, it is important to take care to allow the tree to develop its root system evenly and to avoid rough  
487 planting. Finally, this raises questions about the sustainability of the silvo-industrial system. The system promotes  
488 clear-cutting and relatively invasive replanting, which may have negative impacts on the environment. To  
489 minimize the risk of reddening, it is recommended to adopt an approach that is more respectful of natural balances.  
490 This can be achieved by allowing natural regeneration without undue stress on the root system and by maintaining  
491 a forest atmosphere through accompanying vegetation that buffers the abrupt shocks of the weather.

492 Frame 1. Observation database of the French Forest Health Department.

493 The data collected by the Forest Health Department's observer correspondents using standard forms (DRAAF  
494 1997; 2010; Ministère de l'Agriculture, de l'Agroalimentaire et de la Forêt 2009) in mainland France, in regions  
495 where Douglas-fir is present and affected by the physiological reddening phenomenon between 1989 and 2019  
496 (Fig. 6). Although the provenances are not always known, the Luzette provenance accounts for around 80% of the  
497 resource. The various information reported concerns the date of observation, the location of the plot, its altitude,  
498 surface area, age, type of forest (public/private), stand type, dominant species, species affected by the health  
499 problem, percentage of stems affected and degree of severity (scale from 0 to 4). The presentation of site factors  
500 linked to reddening (Fig. 4 and 5) focuses on observations between January and May, to ensure that summer  
501 reddening data are not included in the analysis. Geographical and topological information, such as altitude,  
502 exposure and topology, was added using the Geoportail (<https://www.geoportail.gouv.fr>) and Google Earth  
503 (<https://earth.google.com>) portals.

504

- 506 Adams, W.W., B. Demmig-Adams, A.S. Verhoeven, et D. H. Barker. 1995. « Photoinhibition” During Winter  
507 Stress: Involvement of Sustained Xanthophyll Cycle-Dependent Energy Dissipation ». *Functional Plant Biology*  
508 22 (2): 261–76. <https://doi.org/10.1071/pp9950261>.
- 509 Adams, W.W., C. Ryan Zarter, V. Ebbert, B. Demmig-Adams. 2004. « Photoprotective Strategies of  
510 Overwintering Evergreens ». *BioScience*, 54 (1): 41–49, [https://doi.org/10.1641/0006-3568\(2004\)054\[0041:PSOOE\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0041:PSOOE]2.0.CO;2)
- 511 Adams, W.W., C.R. Zarter, K.E. Mueh, V. Amiard, B. Demmig-Adams. 2006. « Energy dissipation and  
512 photoinhibition: a continuum of photoprotection ». *Photoprotection, photoinhibition, gene regulation, and  
513 environment. Advances in photosynthesis and respiration*, (21): 49–64
- 514 Allen, C., A. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Venetier, et T. Kitzberger. 2010. « A  
515 Global Overview of Drought and Heat-Induced Tree Mortality Reveals Emerging Climate Change Risks for  
516 Forests ». *Forest Ecology and Management* 259 (4): 660–84. <https://doi.org/10.1016/j.foreco.2009.09.001>.
- 517 Améglio, T., C. Bodet, A. Lacoïnte, et H. Cochard. 2002. « Winter Embolism, Mechanisms of Xylem Hydraulic  
518 Conductivity Recovery and Springtime Growth Patterns in Walnut and Peach Trees ». *Tree Physiology* 22 (17):  
519 1211–20. <https://doi.org/10.1093/treephys/22.17.1211>.
- 520 Améglio, T., J. Morizet, P. Cruziat, et M. Martignac. 1990. « The Effects of Root Temperature on Water Flux,  
521 Potential and Root Resistance in Sunflower ». *Agronomie* 10 (4): 331.
- 522 Aro, EM, I. Virgin, B. Andersson. 1993. « Photoinhibition of photosystem II. Inactivation, protein damage and  
523 turnover ». *Biochimica et Biophysica Acta* 1143: 113–134.
- 524 Aussenac, G. 2000. « Interactions between Forest Stands and Microclimate: Ecophysiological Aspects and  
525 Consequences for Silviculture ». *Annals of Forest Science* 57 (3): 287–301.  
526 <https://doi.org/10.1051/forest:2000119>.
- 527 Baffoin, R., G. Charrier, A-E. Bouchardon, M. Bonhomme, T. Améglio, et A. Lacoïnte. 2021. « Seasonal Changes  
528 in Carbohydrates and Water Content Predict Dynamics of Frost Hardiness in Various Temperate Tree Species ». *Tree Physiology* 41 (9): 1583. <https://doi.org/10.1093/treephys/tpab033>.
- 529 Bailey, J.D., et C. A. Harrington. 2006. « Temperature Regulation of Bud-Burst Phenology within and among  
530 Years in a Young Douglas-Fir (*Pseudotsuga Menziesii*) plantation in Western Washington, USA ». *Tree  
531 Physiology* 26 (4): 421–30. <https://doi.org/10.1093/treephys/26.4.421>.
- 532 Ball, M.C., M.J. Canny, C.X. Huang, J.J.G. Egerton, et J. Wolfe. 2006. « Freeze/Thaw-Induced Embolism  
533 Depends on Nadir Temperature: The Heterogeneous Hydration Hypothesis ». *Plant, Cell & Environment* 29 (5):  
534 729–45. <https://doi.org/10.1111/j.1365-3040.2005.01426.x>.
- 535 Bastien, J-C. 2020. « Potential of Douglas-fir under climate change ». In *Douglas-Fir - an Option for Europe*,  
536 *Édité Par Valeriu-Norocel Nicolescu 11:5*. What Science Can Tell Us. European Forest Institute.  
537 <https://doi.org/10.36333/wsctu11>.
- 538 Baubet, O., et M. Goudet. 2015. « Enquête sur le rougissement physiologique du douglas dans le Massif central ».  
539 *Bilan de la santé des forêts en*.  
540 [https://agriculture.gouv.fr/sites/minagri/files/article\\_rougissement\\_physiologique.pdf](https://agriculture.gouv.fr/sites/minagri/files/article_rougissement_physiologique.pdf).
- 541 Bella, I.E., et S. Navrati. 1987. « Growth Losses from Winter Drying (Red Belt Damage) in Lodgepole Pine Stands  
542 on the East Slopes of the Rockies in Alberta ». <https://cdnscepub.com/doi/abs/10.1139/x87-199>.
- 543 Bréda, N., et M. Peiffer. 2014. « Vulnerability to Forest Decline in a Context of Climate Changes: New Prospects  
544 about an Old Question in Forest Ecology ». *Annals of Forest Science* 71 (6): 627–31.  
545 <https://doi.org/10.1007/s13595-014-0411-3>.
- 546 Burr, K.E., R.W. Tinus, S.J. Wallner, R.M. King. 1986. « Comparison of Four Cold Hardiness Tests on Three  
547 Western Conifers ». In *Proceedings of the Combined Western Forest Nursery Council and Intermountain  
548 Nursery Association Meeting* (pp. 87–95).
- 549 Cayford, J.H., M.P.H. Wheaton, V. Hildahl, et L.D. Nairn. 1959. « Injury to Trees from Winter Drying and Frost  
550 in Manitoba and Saskatchewan in 1958 ». *The Forestry Chronicle* 35 (4): 282–90.  
551 <https://doi.org/10.5558/tfc35282-4>.
- 552 Chamberlain, C.J., et E. M. Wolkovich. 2021. « Late Spring Freezes Coupled with Warming Winters Alter  
553 Temperate Tree Phenology and Growth ». *New Phytologist* 231 (3): 987–95. <https://doi.org/10.1111/nph.17416>.
- 554 Chang, C. Y-Y., K. Bräutigam, N. P.A. Hüner, et I. Ensminger. 2021. « Champions of Winter Survival: Cold  
555 Acclimation and Molecular Regulation of Cold Hardiness in Evergreen Conifers ». *New Phytologist* 229 (2):  
556 675–91. <https://doi.org/10.1111/nph.16904>.
- 557 Charra-Vaskou, K., E. Badel, G. Charrier, A. Ponomarenko, M. Bonhomme, Loïc Foucat, Stefan Mayr, et Thierry  
558 Améglio. 2016. « Cavitation and Water Fluxes Driven by Ice Water Potential in Juglans Regia during Freeze–  
559 Thaw Cycles ». *Journal of Experimental Botany* 67 (3): 739–50. <https://doi.org/10.1093/jxb/erv486>.
- 560 Charra-Vaskou, K., A. Lintunen, T. Améglio, E. Badel, H. Cochard, S. Mayr, Y. Salmon, H. Suhonen, M. Van  
561 Rooij, et G. Charrier. 2023. « Xylem Embolism and Bubble Formation during Freezing Suggest Complex

564 Dynamics of Pressure in *Betula Pendula* Stems » *Journal of Experimental Botany* 74 (18): 5840-53.  
565 <https://doi.org/10.1093/jxb/erad275>.

566 Charrier, G., & Améglio, T. (2023). Dynamic modeling of stem water content during the dormant period in walnut  
567 trees. *Tree Physiology*, tpad128.

568 Charrier, G., M. Bonhomme, A. Lacoïnte, et T. Améglio. 2011. « Are Budburst Dates, Dormancy and Cold  
569 Acclimation in Walnut Trees (*Juglans Regia* L.) under Mainly Genotypic or Environmental Control? »  
570 *International Journal of Biometeorology* 55 (6): 763-74. <https://doi.org/10.1007/s00484-011-0470-1>.

571 Charrier, G., Poirier, M., Bonhomme, M., Lacoïnte, A., & Améglio, T. (2013). Frost hardiness in walnut trees  
572 (*Juglans regia* L.): how to link physiology and modelling?. *Tree Physiology*, 33(11), 1229-1241.  
573 <https://doi.org/10.1093/treephys/tpt090>

574 Charrier, G., H. Cochard, et T. Améglio. 2013a. « Evaluation of the Impact of Frost Resistances on Potential  
575 Altitudinal Limit of Trees ». *Tree Physiology* 33 (9): 891-902. <https://doi.org/10.1093/treephys/tpt062>.

576 Charrier, G., I. Chuine M. Bonhomme, et T. Améglio. (2018a). Assessing frost damages using dynamic models in  
577 walnut trees: exposure rather than vulnerability controls frost risks. *Plant, Cell & Environment*, 41(5), 1008-  
578 1021. <https://doi.org/10.1111/pce.12935>

579 Charrier, G., A. Lacoïnte, et T. Améglio. 2018b. « Dynamic Modeling of Carbon Metabolism During the Dormant  
580 Period Accurately Predicts the Changes in Frost Hardiness in Walnut Trees *Juglans Regia* L ». *Frontiers in Plant  
581 Science* 9: 1746. <https://doi.org/10.3389/fpls.2018.01746>.

582 Charrier, G., J. Ngao, M. Saudreau, et T. Améglio. 2015a. « Effects of Environmental Factors and Management  
583 Practices on Microclimate, Winter Physiology, and Frost Resistance in Trees ». *Frontiers in Plant Science* 6.  
584 <https://doi.org/10.3389/fpls.2015.00259>.

585 Charrier, G., M. Nolf, G. Leitinger, K. Charra-Vaskou, A. Losso, U. Tappeiner, T. Améglio, et S. Mayr. 2017.  
586 « Monitoring of Freezing Dynamics in Trees: A Simple Phase Shift Causes Complexity ». *Plant Physiology* 173  
587 (4): 2196-2207. <https://doi.org/10.1104/pp.16.01815>.

588 Charrier, G., M. Pramsöhler, K. Charra-Vaskou, M. Saudreau, T. Améglio, G. Neuner, et S. Mayr. 2015b.  
589 « Ultrasonic Emissions during Ice Nucleation and Propagation in Plant Xylem ». *New Phytologist* 207 (3): 570  
590 78. <https://doi.org/10.1111/nph.13361>.

591 Choïsnel, E., V. Jacq, JM. Guehl, et G. Aussenac. 1990. « Simulation de la variabilité de la photosynthèse hivernale  
592 du douglas (*Pseudotsuga menziesii* Mirb) dans les conditions climatiques françaises ». *Annales des Sciences  
593 Forestières* 47 (5): 495-508. <https://doi.org/10.1051/forest:19900507>.

594 Christersson, L. et Fircks, H.V. 1990. « Frost and Winter Dessication as Stress Factors ». *Ser. Botanica*, n° No. 29:  
595 13-19.

596 Cochard, H., P. Cruziat, M.T. Tyree. 1992. « Use of positive pressures to establish vulnerability curves: further  
597 support for the air-seeding hypothesis and implications for pressure-volume analysis ». *Plant physiology*, 100(1),  
598 205-209

599 Cochard, H. 2006. « Cavitation in Trees ». *Comptes Rendus Physique, Nucleation* 7 (9): 1018-26.  
600 <https://doi.org/10.1016/j.crhy.2006.10.012>.

601 Cochard, H., T. Hölttä, S. Herbette, S. Delzon, et M. Mencuccini. 2009. « New Insights into the Mechanisms of  
602 Water-Stress-Induced Cavitation in Conifers ». *Plant Physiology* 151 (2): 949-54.  
603 <https://doi.org/10.1104/pp.109.138305>.

604 Cox, R.M., et X. B. Zhu. 2003. « Effects of Simulated Thaw on Xylem Cavitation, Residual Embolism, Spring  
605 Dieback and Shoot Growth in Yellow Birch ». *Tree Physiology* 23 (9): 615-24.  
606 <https://doi.org/10.1093/treephys/23.9.615>.

607 Day, T.A., S.A. Heckathorn, et E.H. DeLucia. 1991. « Limitations of Photosynthesis in *Pinus Taeda* L. (Loblolly  
608 Pine) at Low Soil Temperatures ». *Plant Physiology* 96 (4): 1246-54. <https://doi.org/10.1104/pp.96.4.1246>.

609 DeHayes, D.H., C.E. Waite, et M.A. Ingle. 1990. « Storage Temperature and Duration Influence Cold Tolerance  
610 of Red Spruce Foliage ». *Forest Science* 36 (4): 1153-58. <https://doi.org/10.1093/forestscience/36.4.1153>.

611 Dellero, Y., M. Jossier, J. Schmitz, V.G. Maurino, M. Hodges. 2016. « Photorespiratory glycolate-glyoxylate  
612 metabolism ». *Journal of Experimental Botany*, 67(10), 3041-3052.

613 DeLucia, E.H. 1986. « Effect of Low Root Temperature on Net Photosynthesis, Stomatal Conductance and  
614 Carbohydrate Concentration in Engelmann Spruce (*Picea Engelmannii* Parry Ex Engelm.) Seedlings ». *Tree  
615 physiology*, 2(1-2-3), 143-154

616 Demmig-Adams, B., S-C. Koh, C.M. Cohu, O. Muller, JJ. Stewart, et W.W. Adams. 2014. « Non-Photochemical  
617 Fluorescence Quenching in Contrasting Plant Species and Environments ». In *Non-photochemical quenching  
618 and energy dissipation in plants*, 531-552. [https://doi.org/10.1007/978-94-017-9032-1\\_24](https://doi.org/10.1007/978-94-017-9032-1_24).

619 Deslauriers, A., L. Garcia, G. Charrier, V. Buttò, A. Pichette, M. Paré, C. Drénou, et J. Rosa. 2021. « Cold  
620 Acclimation and Deacclimation in Wild Blueberry: Direct and Indirect Influence of Environmental Factors and  
621 Non-Structural Carbohydrates ». *Agricultural and Forest Meteorology*, 301-302, 108349.  
622 <https://doi.org/10.1016/j.agrformet.2021.108349>.



623 Driessche, R. Van Den. 1969. « Influence of Moisture Supply, Temperature, and Light on Frost-Hardiness  
624 Changes in Douglas-Fir Seedlings ». *Canadian Journal of Botany* 47 (11): 1765-72. <https://doi.org/10.1139/b69-254>.  
625  
626 Duursma, R.A., C.J. Blackman, R. Lopéz, N.K. Martin-StPaul, H. Cochard, et B.E. Medlyn. 2019. « On the  
627 Minimum Leaf Conductance: Its Role in Models of Plant Water Use, and Ecological and Environmental  
628 Controls ». *New Phytologist* 221 (2): 693-705. <https://doi.org/10.1111/nph.15395>.  
629 Ensminger, I., D. Sveshnikov, D. A. Campbell, C. Funk, .... & G. Öquist. 2004. Intermittent low temperatures  
630 constrain spring recovery of photosynthesis in boreal Scots pine forests. *Global Change Biology*, 10(6), 995-  
631 1008.  
632 Ensminger, I., F. Busch, et N. P.A. Hüner. 2006. « Photostasis and Cold Acclimation: Sensing Low Temperature  
633 through Photosynthesis ». *Physiologia Plantarum* 126 (1): 28-44. <https://doi.org/10.1111/j.1399-3054.2006.00627.x>.  
634  
635 Fryer, M.J. 1992. « The Antioxidant Effects of Thylakoid Vitamin E ( $\alpha$ -Tocopherol) ». *Plant Cell Environ* 15:  
636 381-92.  
637 Gamon, J.A., et R. W. Pearcy. 1990b. « Photoinhibition in *Vitis Californica*: Interactive Effects of Sunlight,  
638 Temperature and Water Status ». *Plant, Cell & Environment* 13 (3): 267-75. <https://doi.org/10.1111/j.1365-3040.1990.tb01311.x>.  
639  
640 Gillies, S.L., et W. Vidaver. 1990. « Resistance to Photodamage in Evergreen Conifers ». *Physiologia Plantarum*,  
641 80 (1): 148-53. <https://doi.org/10.1111/j.1399-3054.1990.tb04389.x>.  
642 Glerum, C., et J. L. Farrar. 1966. « Frost Ring Formation in the Stems of Some Coniferous Species ». *Canadian*  
643 *Journal of Botany* 44 (7): 879-86. <https://doi.org/10.1139/b66-103>.  
644 Guadagno, C. R., B.E. Ewers, H.N. Speckman, T.L. Aston, B.J. Huhn, S.B. DeVore, J.T. Ladwig, R.N. Strawn, et  
645 C. Weinig. 2017. « Dead or Alive? Using Membrane Failure and Chlorophyll a Fluorescence to Predict Plant  
646 Mortality from Drought ». *Plant Physiology* 175 (1): 223-34. <https://doi.org/10.1104/pp.16.00581>.  
647 Guehl, J.M., B. Clerc, et J.M. Desjeunes. 1985. « Etude comparée des potentialités hivernales d'assimilation  
648 carbonée de trois conifères de la zone tempérée (*Pseudotsuga menziesii* Mirb. *Abies alba* Mill. et *Picea excelsa*  
649 Link.) ». *Annales des Sciences Forestières* 42 (1): 23-38. <https://doi.org/10.1051/forest:19850102>.  
650 Hart, S.J., T.T. Veblen, D. Schneider, et N.P. Molotch. 2017. « Summer and Winter Drought Drive the Initiation  
651 and Spread of Spruce Beetle Outbreak ». *Ecology* 98 (10): 2698-270.  
652 Hedgcock, G.G. 1912. « Winter-killing and Smelter-injury in the Forest of Montana ». *Torrey*, 12(2), 25-30.  
653 Henson, W.R. 1952. « Chinook Winds and Red Belt Injury to Lodgepole Pine in the Rocky Mountain Parks Area  
654 of Canada ». *The Forestry Chronicle* 28 (1): 62-64. <https://doi.org/10.5558/tfc28062-1>.  
655 Herrick, G.T., et A. J. Friedland. 1991. « Winter Desiccation and Injury of Subalpine Red Spruce ». *Tree*  
656 *Physiology* 8 (1): 23-36. <https://doi.org/10.1093/treephys/8.1.23>.  
657 Hiratsuka, Y., et Zalasky, H. 1993. « Frost and other climate-related damage of forest trees in the prairie  
658 provinces ».  
659 Hughes, N.M. 2011. « Winter Leaf Reddening in 'Evergreen' Species: Minireview ». *New Phytologist* 190 (3):  
660 573-81. <https://doi.org/10.1111/j.1469-8137.2011.03662.x>.  
661 Hüner, N.P., G. Öquist, F. Sarhan. 1998. « Energy Balance and Acclimation to Light and Cold ». *Trends Plant Sci.*  
662 3, 224-230  
663 Hüner, N. P., R. Bode, K. Dahal, L. Hollis, D. Rosso, M. Krol, and A.G. Ivanov. 2012. Chloroplast redox imbalance  
664 governs phenotypic plasticity: the "grand design of photosynthesis" revisited. *Frontiers in Plant Science*, 3, 255.  
665 Ivanov, A.G., P.V. Sane, Y. Zeinalov, G. Malmberg, P. Gardeström, N.P. Hüner, et G. Öquist. 2001a.  
666 « Photosynthetic Electron Transport Adjustments in Overwintering Scots Pine (*Pinus Sylvestris* L.) ». *Planta*  
667 213 (4): 575-85. <https://doi.org/10.1007/s004250100522>.  
668 Jalkanen R. 1990. « Root cold stress causing a premature yellowing of oldest Scots pines needles ». In *Recent*  
669 *research on foliage diseases*, 34-37.  
670 Johnson, D. M., McCulloh, K. A., & Reinhardt, K. (2011). The earliest stages of tree growth: development,  
671 physiology and impacts of microclimate. Size- and age-related changes in tree structure and function, 65-87.  
672 [https://doi.org/10.1007/978-94-007-1242-3\\_3](https://doi.org/10.1007/978-94-007-1242-3_3)  
673 Kalberer, S.R., M. Wisniewski, et R. Arora. 2006. « Deacclimation and Reacclimation of Cold-Hardy Plants:  
674 Current Understanding and Emerging Concepts ». *Plant Science* 171 (1): 3-16.  
675 <https://doi.org/10.1016/j.plantsci.2006.02.013>.  
676 Kamp, B. J. Van Der, et J. Worrall. 1990. « An Unusual Case of Winter Bud Damage in British Columbia Interior  
677 Conifers ». *Canadian Journal of Forest Research* 20 (10): 1640-47. <https://doi.org/10.1139/x90-217>.  
678 Kozłowski, T.T. 2012. *Soil Water Measurement, Plant Responses, and Breeding for Drought Resistance*. Vol 4.  
679 Elsevier.  
680 Kron, W. 2005. « Flood Risk = Hazard • Values • Vulnerability ». *Water International* 30 (1): 58-68.  
681 <https://doi.org/10.1080/02508060508691837>.

682 Langvall, O. 2010. « Interactions between Near-Ground Temperature and Radiation, Silvicultural Treatments and  
683 Frost Damage to Norway Spruce Seedlings ». Phd thesis.

684 Ledford, H. K., and K.K. Niyogi. 2005. Singlet oxygen and photo-oxidative stress management in plants and algae.  
685 *Plant, Cell & Environment*, 28(8), 1037-1045. <https://doi.org/10.1111/j.1365-3040.2005.01374.x>

686 Lee, S.H., G.C. Chung, Ji Y. Jang, S.J. Ahn, et J.J. Zwiazek. 2012. « Overexpression of PIP2;5 Aquaporin  
687 Alleviates Effects of Low Root Temperature on Cell Hydraulic Conductivity and Growth in Arabidopsis ». *Plant*  
688 *Physiology* 159 (1): 479 88. <https://doi.org/10.1104/pp.112.194506>.

689 Lee, S.H., G.C. Chung, et E. Steudle. 2005. « Gating of Aquaporins by Low Temperature in Roots of Chilling-  
690 Sensitive Cucumber and Chilling-Tolerant Figleaf Gourd ». *Journal of Experimental Botany* 56 (413): 985 95.  
691 <https://doi.org/10.1093/jxb/eri092>.

692 Lemoine, D., A. Granier, et H. Cochard. 1999. « Mechanism of Freeze-Induced Embolism in *Fagus Sylvatica* L »  
693 *Trees* 13 (4): 206 10. <https://doi.org/10.1007/PL00009751>.

694 Levitt, J. 1980. « Responses of Plants to Environmental Stress ». In Responses of Plants to Environmental Stress,  
695 2nd éd. Vol. 1. Chilling, freezing, and high temperature stress. Physiological Ecology series. Academic Press,  
696 New York, p. 497 pp <https://www.cabdirect.org/cabdirect/abstract/19802605739>.

697 Lhotellier, R. 2005. « Spatialisation des températures en zone de montagne alpine » ». <http://www.theses.fr/2005GRE10201>.

698

699 Lintunen, A., T. Hölttä, et M. Kulmala. 2013. « Anatomical Regulation of Ice Nucleation and Cavitation Helps  
700 Trees to Survive Freezing and Drought Stress ». *Scientific Reports* 3 (1): 2031.  
701 <https://doi.org/10.1038/srep02031>.

702 Lopushinsky, W., et M.R. Kaufmann. 1984. « Effects of Cold Soil on Water Relations and Spring Growth of  
703 Douglas-Fir Seedlings ». *Forest Science* 30 (3): 628 34. <https://doi.org/10.1093/forestscience/30.3.628>.

704 MacHattie, L.B. 1963. « Winter injury of Lodgepole pine foliage ». *Weather* 18 (10): 301 7.  
705 <https://doi.org/10.1002/j.1477-8696.1963.tb05148.x>.

706 Malmqvist, C., K. Wallertz, et U. Johansson. 2018. « Survival, Early Growth and Impact of Damage by Late-  
707 Spring Frost and Winter Desiccation on Douglas-Fir Seedlings in Southern Sweden ». *New Forests* 49 (6): 723  
708 36. <https://doi.org/10.1007/s11056-018-9635-7>.

709 Man, R., S. Colombo, G. Kayahara, S. Duckett, R. Velasquez, et Q. Dang. 2013. « A Case of Extensive Conifer  
710 Needle Browning in Northwestern Ontario in 2012: Winter Drying or Freezing Damage? » *The Forestry*  
711 *Chronicle* 89 (05): 675 80. <https://doi.org/10.5558/tfc2013-120>.

712 Man, R., G. Kayahara, Q. Dang, et J. Rice. 2009. « A Case of Severe Frost Damage Prior to Budbreak in Young  
713 Conifers in Northeastern Ontario: Consequence of Climate Change? » *The Forestry Chronicle* 85 (3): 453 62.  
714 <https://doi.org/10.5558/tfc85453-3>.

715 Man, R., P. Lu, and Q.L. Dang. 2021. « Cold tolerance of black spruce, white spruce, jack pine, and lodgepole  
716 pine seedlings at different stages of spring dehardening. » *New Forests* (52): 317-328.

717 Man, R., P. Lu, and Q.L. Dang. 2017. « Cold hardiness of white spruce, black spruce, jack pine, and lodgepole  
718 pine needles during dehardening ». *Canadian Journal of Forest Research* (47): 1116-1122.

719 Maple, W.R. 1975. « Mortality of Longleaf Pine Seedlings Following a Winter Burn against Brown-Spot Needle  
720 Blight ». *Forest Service*, Southern Forest Experiment Station: U.S. Department of Agriculture.

721 Mayr, S., et K. Charra-Vaskou. 2007. « Winter at the Alpine Timberline Causes Complex Within-Tree Patterns of  
722 Water Potential and Embolism in *Picea Abies* ». *Physiologia Plantarum* 131 (1): 131 39.  
723 <https://doi.org/10.1111/j.1399-3054.2007.00942.x>.

724 Mayr, S., A. Gruber, et H. Bauer. 2003. « Repeated Freeze–Thaw Cycles Induce Embolism in Drought Stressed  
725 Conifers (Norway Spruce, Stone Pine) ». *Planta* 217 (3): 436-41. <https://doi.org/10.1007/s00425-003-0997-4>.

726 McMinn, R.G., et A. Funk. 1970. « Unusual Drought Symptoms in Douglas-Fir ». *Canadian Journal of Botany*  
727 48 (12): 2123 27. <https://doi.org/10.1139/b70-307>.

728 Mellander, P-E., M. Stähli, D. Gustafsson, et K. Bishop. 2006. « Modelling the Effect of Low Soil Temperatures  
729 on Transpiration by Scots Pine ». *Hydrological Processes* 20 (9): 1929 44. <https://doi.org/10.1002/hyp.6045>.

730 Morén, A-S., et K.L. Perttu. 1994. « Regional Temperature and Radiation Indices and Their Adjustment To  
731 Horizontal and Inclined Forest Land ». *Studia Forestalia Suecica*.

732 Mura, C., V. Buttò, R. Silvestro, A. Deslauriers, G. Charrier, P. Raymond. 2022. « The Early Bud Gets the Cold:  
733 Diverging Spring Phenology Drives Exposure to Late Frost in a *Picea Mariana* [(Mill.) BSP] Common Garden ». <https://doi.org/10.1111/pp1.13798>.

734

735 Nicolescu, V.N. 2020. « Douglas-Fir Ecology ». In *Douglas-Fir - an Option for Europe*, 11:5. What Science Can  
736 Tell Us. European Forest Institute. <https://doi.org/10.36333/wscu11>.

737 Nicolescu, V-N., W.L. Mason, J-C. Bastien, T. Vor, K. Petkova, V. Podrázský, et M. Ďodan. 2023. « Douglas-Fir  
738 (*Pseudotsuga Menziesii* (Mirb.) Franco) in Europe: An Overview of Management Practices ». *Journal of*  
739 *Forestry Research*. <https://doi.org/10.1007/s11676-023-01607-4>.



740 Ogren, E., et G. Oquist. 1985. « Effects of Drought on Photosynthesis, Chlorophyll Fluorescence and  
741 Photoinhibition Susceptibility in Intact Willow Leaves ». *Planta* 166 (3): 380–88.  
742 <https://doi.org/10.1007/BF00401176>.

743 Öquist, G., et N. P. A. Hüner. 2003. « Photosynthesis of Overwintering Evergreen Plants ». *Annual Review of Plant*  
744 *Biology* 54 (1): 329–55. <https://doi.org/10.1146/annurev.arplant.54.072402.115741>.

745 Ottander, C., D. Campbell, G. Öquist. 1995. Seasonal changes in photosystem II organisation and pigment  
746 composition in *Pinus sylvestris*. *Planta* 197: 176–183.

747 Pagter, M., et R. Arora. 2012. « Winter Survival and Deacclimation of Perennials under Warming Climate:  
748 Physiological Perspectives ». *Physiologia Plantarum* 147. <https://doi.org/10.1111/j.1399-3054.2012.01650.x>.

749 Pagter, M., I. Lefèvre, R. Arora, et J-F. Hausman. 2011. « Quantitative and Qualitative Changes in Carbohydrates  
750 Associated with Spring Deacclimation in Contrasting Hydrangea Species ». *Environmental and Experimental*  
751 *Botany, Responses, Acclimations and Adaptations of Northern Plants to Global Change* 72 (3): 358–67.  
752 <https://doi.org/10.1016/j.envexpbot.2011.02.019>.

753 Petritan, I.C., B. Lüpke, et A.M. Petritan. 2011. « Influence of Shelterwood and Ground Vegetation on Late Spring  
754 Frost Damages of Planted Beech (*Fagus sylvatica*) and Douglas-Fir (*Pseudotsuga Menziesii*) Saplings ». *BALTIC FORESTRY* 17 (2).

755 Petrov, V., J. Hille, B. Mueller-Roeber, T.S. Gechev. 2015. « ROS-Mediated Abiotic Stress-Induced Programmed  
756 Cell Death in Plants ». *Frontiers in Plant Science* 6.  
757 <https://www.frontiersin.org/articles/10.3389/fpls.2015.00069>.

758 Pourtet, J. 1949. « Sur divers dommages survenus dans les plantations de Douglas ». *Revue Forestière Française*,  
759 n° 4: 174. <https://doi.org/10.4267/2042/27607>.

760 Rajashekar, C.B., et M. J. Burke. 1996. « Freezing Characteristics of Rigid Plant Tissues (Development of Cell  
761 Tension during Extracellular Freezing) ». *Plant Physiology* 111 (2): 597–603.  
762 <https://doi.org/10.1104/pp.111.2.597>.

763 Ranganathan, K., W. El Kayal, J. E.K. Cooke, et J.J. Zwiazek. 2016. « Responses of Hybrid Aspen Over-  
764 Expressing a PIP2;5 Aquaporin to Low Root Temperature ». *Journal of Plant Physiology* 192 (mars): 98–104.  
765 <https://doi.org/10.1016/j.jplph.2016.02.001>.

766 Redfern, D.B., S.C. Gregory, J.E. Pratt, et G. A. Macaskill. 1987. « Foliage Browning and Shoot Death in Sitka  
767 Spruce and Other Conifers in Northern Britain during Winter 1983-84 ». *Forest Pathology* 17 (3): 166–80.  
768 <https://doi.org/10.1111/j.1439-0329.1987.tb00742.x>.

769 Reich, R.W. 1990. « Causes of Dieback of Douglas-Fir in the Interior of B.C. » Doctoral dissertation, University  
770 of British Columbia.

771 Robakowski, P. 2011. « Photochemical processes in needles of overwintering evergreen conifers. »  
772 *Photochemistry UV/VIS spectroscopy, photochemical reactions and photosynthesis*. Nova Science Publishers,  
773 New York, 333–351.

774 Robakowski, P., Pietrzak, T., Kowalkowski, W., & Małecki, G. 2021. Survival, growth and photochemical  
775 efficiency of silver fir seedlings produced with different technologies. *New Forests* 52: 1055–1077.  
776 <https://doi.org/10.1007/s11056-021-09835-4>.

777 Ruelland, E., M-N. Vaultier, A. Zachowski, et V. Hurry. 2009. « Chapter 2 Cold Signalling and Cold Acclimation  
778 in Plants ». *Advances in Botanical Research* 49 (35): 150. [https://doi.org/10.1016/S0065-2296\(08\)00602-2](https://doi.org/10.1016/S0065-2296(08)00602-2).

779 Sagar, R.M., et M. J. Waterhouse. 2010. « Microclimate Studies in Uniform Shelterwood Systems in the Sub-  
780 Boreal Spruce Zone of Central British Columbia ». Technical Report -. Ministry of Forests and Range, Forest  
781 Science Program, British Columbia. <https://www.cabdirect.org/cabdirect/abstract/20103123297>.

782 Sakai, A. 1970. « Mechanism of Desiccation Damage of Conifers Wintering in Soil-Frozen Areas ». *Ecology* 51  
783 (4): 657–64. <https://doi.org/10.2307/1934045>.

784 Soitamo, A.J., M. Piippo, Y. Allahverdiyeva, N. Battchikova, et E-M. Aro. 2008. « Light Has a Specific Role in  
785 Modulating Arabidopsis Gene Expression at Low Temperature ». *BMC Plant Biology* 8 (1): 13.  
786 <https://doi.org/10.1186/1471-2229-8-13>.

787 Solberg, S. 1993. « Monitoring of Abiotic Forest Diseases in Norway ». In *Extended SNS Meeting in Forest*  
788 *Pathology in Lapland*, 89–93.

789 Sperry, J.S., et J. E.M. Sullivan. 1992. « Xylem Embolism in Response to Freeze-Thaw Cycles and Water Stress  
790 in Ring-Porous, Diffuse-Porous, and Conifer Species 1 ». *Plant Physiology* 100 (2): 605–13.  
791 <https://doi.org/10.1104/pp.100.2.605>.

792 Stevenson, J. F., B. J. Hawkins, J.H. Woods. 1999. « Spring and fall cold hardiness in wild and selected seed  
793 sources of coastal Douglas-fir ». *Silvae Genetica*, 48(1), 29–34.

794 Steyn, W. J., S. J. E. Wand, D. M. Holcroft, G. J. N. P. Jacobs. 2002. « Anthocyanins in vegetative tissues: a  
795 proposed unified function in photoprotection ». *New Phytologist*, 155(3), 349–361.  
796 <https://doi.org/10.1046/j.1469-8137.2002.00482>.

797 Stoutjesdijk, P., et Barkman J.J. 2015. *Microclimate, Vegetation & Fauna*. Brill  
798 <https://doi.org/10.1163/9789004297807>.

799

800 Strimbeck, G.R., D.H. DeHayes, J.B. Shane, G.J. Hawley, et P.G. Schaberg. 1995. « Midwinter Dehardening of  
801 Montane Red Spruce during a Natural Thaw ». *Canadian Journal of Forest Research* 25 (12): 2040-44.  
802 <https://doi.org/10.1139/x95-221>.

803 Suzuki, N., et R. Mittler. 2006. « Reactive Oxygen Species and Temperature Stresses: A Delicate Balance between  
804 Signaling and Destruction ». *Physiologia Plantarum* 126 (1): 45-51. <https://doi.org/10.1111/j.0031-9317.2005.00582.x>.

806 Tegischer, K., M. Tausz, G. Wieser, et D. Grill. 2002. « Tree- and Needle-Age-Dependent Variations in  
807 Antioxidants and Photoprotective Pigments in Norway Spruce Needles at the Alpine Timberline ». *Tree  
808 Physiology* 22 (8): 591-96. <https://doi.org/10.1093/treephys/22.8.591>.

809 Tinus, R.W., K.E. Burr, N. Atzmon, et J. Riov. 2000. « Relationship between Carbohydrate Concentration and  
810 Root Growth Potential in Coniferous Seedlings from Three Climates during Cold Hardening and Dehardening ». *Tree  
811 Physiology* 20 (16): 1097-1104. <https://doi.org/10.1093/treephys/20.16.1097>.

812 Tranquillini, W. 1979. « Climatic Resistance and Damage of Trees at Timberline ». In *Physiological Ecology of  
813 the Alpine Timberline: Tree Existence at High Altitudes with Special Reference to the European Alps*, 91-111.  
814 Ecological Studies. Berlin, Heidelberg: Springer. [https://doi.org/10.1007/978-3-642-67107-4\\_8](https://doi.org/10.1007/978-3-642-67107-4_8).

815 Tranquillini, W. 1982. « Frost-Drought and Its Ecological Significance ». In *Physiological Plant Ecology II: Water  
816 Relations and Carbon Assimilation*, 379-400. Berlin, Heidelberg: Springer.

817 Venn, K. 1993. « Red Belts in Boreal Forests ». In *Extended SNS Meeting in Forest Pathology in Lapland*, 50-54.  
818 Finland: Metsäntutkimuslaitos.

819 Wang, W., et G. Hoch. 2022. « Negative Effects of Low Root Temperatures on Water and Carbon Relations in  
820 Temperate Tree Seedlings Assessed by Dual Isotopic Labelling ». *Tree Physiology* 42 (7): 1311-24.  
821 <https://doi.org/10.1093/treephys/tpac005>.

822 Yamazaki, J.Y., S. Tsuchiya, S. Nagano, et E. Maruta. 2007. « Photoprotective Mechanisms against Winter  
823 Stresses in the Needles of *Abies Mariesii* Grown at the Tree Line on Mt. Norikura in Central Japan ». *Photosynthetica* 45 (4): 547-54. <https://doi.org/10.1007/s11099-007-0094-1>.

824 Yamazaki, K. 2003. « Effects of Pruning and Brush Clearing on Debarking within Damaged Conifer Stands by  
825 Japanese Black Bears ». *Ursus* 14 (1): 94-98.

827 Yun, Mi R., Hye M. Park, Kyo W. Seo, Seung J. Lee, Dong S. Im, et Chi D. Kim. 2010. « 5-Lipoxygenase Plays  
828 an Essential Role in 4-HNE-Enhanced ROS Production in Murine Macrophages via Activation of NADPH  
829 Oxidase ». *Free Radical Research* 44 (7): 742-50. <https://doi.org/10.3109/10715761003758122>.

830 Zhang, A., Zhen-H. Cui, Jia-L. Yu, Zi-L. Hu, R. Ding, Da-M. Ren, et Li-J. Zhang. 2016. « Dissipation of Excess  
831 Excitation Energy of the Needle Leaves in *Pinus* Trees during Cold Winters ». *International Journal of  
832 Biometeorology* 60 (12): 1953-60. <https://doi.org/10.1007/s00484-016-1182-3>.

833 Zweifel, Roman, Kathy Steppe, et Frank J. Sterck. 2007. « Stomatal Regulation by Microclimate and Tree Water  
834 Relations: Interpreting Ecophysiological Field Data with a Hydraulic Plant Model ». *Journal of Experimental  
835 Botany* 58 (8): 2113-31. <https://doi.org/10.1093/jxb/erm050>.

836 Zwiazek, J. J., S. Renault, C. Croser, J. Hansen, E. Beck. 2001. « Biochemical and biophysical changes in relation  
837 to cold hardiness ». *Conifer cold hardiness*, 165-186.

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#### 841 Captions of figures

842  
843 Figure 1: Different stages of a Douglas-fir winter reddening (Livradois-Forez 2022). The colour of needles changes  
844 from glaucous green to orange and finally to red.

845 Figure 2: Douglas-fir affected by winter reddening (Livradois-Forez 2022). The Douglas-fir in the foreground is  
846 entirely red, while the one in the second foreground is in the process of turning red (red crown and green base).

847 Figure 3: Aerial view of a plot of Douglas-fir affected by winter reddening (Livradois-Forez 2022). The red  
848 Douglas-fir are relatively evenly distributed within the plot.

849 Figure 4: Distribution of reddening observations according to several factors. A: Frequency of winter reddening  
850 depending on elevation. B: Frequency of winter reddening depending on azimuth – N: North, E: East, S: South,  
851 W: West - C: Frequency of winter reddening depending on the topography of the Douglas stand with L.slope: Low  
852 slope. Based on DSF data

853 Figure 5: Distribution of reddening observations according to the age of Douglas-fir stands – Based on DSF data

854 Figure 6: Locations of 426 different Douglas-fir stands in France where reddening was observed between 1989  
855 and 2019. The yellow triangles represent plots with reddening from 1989 to 2006. The red triangles represent

856 reddening observations from 2006 to 2019. Triangles surrounded by a circle are Douglas-fir stands with  
857 meteorological data – DSF data.