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

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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°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 (Kozlowski 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 CO₂

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

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841 Captions of figures

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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.