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Clonal variation and damage dynamics in Norway spruce: Towards the selection of climate-resilient genotypes

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Abstract

Climate change is expected to intensify abiotic and biotic stressors in European forests, making the selection of tree genotypes less susceptible to damage a critical priority for sustainable forestry. We evaluated long-term clonal variation in damage susceptibility and growth performance of Norway spruce (*Picea abies* (L.) Karst.) in three clonal plantations (aged 50 to 59 years) located in Latvia. More than 2,100 trees representing 20–80 vegetatively propagated clones per site were evaluated. Data on tree growth (height, diameter), green crown ratio, survival, and multiple types of stem damage – stem cracks, bark beetle (*Ips typographus*) infestation, and cervid browsing damage – were collected during two inventories, 4–9 years apart.

Clonal differences were statistically significant ($p < 0.05$) for tree diameter and stem crack incidence in all plantations (8–23% of trees affected). Bark beetle damage reached up to 9% of trees and showed clonal variation in one plantation. On average, the length of cracks on the stem was 0.6–1.9 m, depending on the plantation. Survival between inventories exceeded 89% overall but differed among clones in relation to damage incidence. Fast-growing trees tended to have more cracks, but at the clone level, there was no consistent trade-off between productivity and damage incidence. Green crown ratio, a key trait reflecting tree architecture, was significantly associated with damage resistance: trees with a live crown ratio ≥ 70% had markedly lower incidence of cracks and bark beetle attacks.

Several clones combined high growth (up to 26% above plantation mean) with low damage occurrence. These results demonstrate significant and consistent clonal differences and support the feasibility of selecting productive and stem-damage-resistant genotypes for use under uncertain future climate conditions. In practice, maintaining or selecting crown types that retain ≥ 70% green crown may represent a viable strategy – from both a genetic and silvicultural perspective – for reducing the risk of trunk damage and increasing the climate resilience of spruce plantations.

Keywords: tree breeding; clonal forestry; climate-smart forestry; bark beetle damage; stem cracks; cervid browsing damage

Introduction

Norway spruce (*Picea abies* (L.) Karst.) is one of the most widespread and economically important conifers in Europe (Szymański 2007, Jansson et al. 2013, Westin and Haapanen 2013). Its valuable timber and suitability for plantation forestry have led to extensive planting even beyond its natural range (Honkaniemi et al. 2020). It gained its popularity due to comparatively easy management and growth potential compared to Scots pine (*Pinus sylvestris* L.). Spruce has lower browsing pressure than pine and needs less weed control in the first years after establishment (Ruņģis et al. 2019). However, spruce's tolerance limits are increasingly tested by climate change. Its shallow root system restricts access to deep soil moisture, making mature spruce prone to drought stress and windthrow (Vitali et al. 2017). As a result, storms and droughts have frequently triggered severe bark beetle infestations with pronounced ecological and economic impacts (Kärvemo et al. 2023). In recent decades, disturbances caused by severe storms and prolonged summer droughts have led to catastrophic outbreaks of *Ips typographus*, which have seriously affected Norway spruce in Europe (Senf and Seidl 2018). Consequently, breeding for climate-resilient spruce genotypes remains a high priority in the Baltic and Scandinavian countries to sustain spruce timber production.

Stem cracks if one of the risks appearing after the juvenile stage. Cracks severely degrade timber quality and create entry points for fungi (Vasiliauskas et al. 2001). Late-summer drought is widely regarded as a primary cause of these radial cracks. Under drought conditions, xylem tension in the trunk can exceed the mechanical strength of cell walls, causing cracking (Grabner et al. 2006). In

addition to moisture stress, silvicultural factors influence cracking. Trees planted at wide spacing on fertile soils tend to grow rapidly and develop wide annual rings; these large trees are especially prone to cracks (Persson 1994b). Genetic factors also play a role: crack incidence varies among provenances and clones (Persson 1994a, Vasiliauskas et al. 2001, Zeltiņš et al. 2016). Therefore, screening of genotypes less prone to stem cracking is important for the economic future of the species, but relatively little research has been devoted to this issue.

Beyond cracking, drought stress weakens tree defences (e.g. resin flow), increasing vulnerability to bark beetle attack (Marini et al. 2017, Netherer et al. 2019). The tree's crown condition and architecture can also influence stress susceptibility: trees with a larger live crown typically maintain better water status, whereas those with diminished crowns may experience higher stress. Korolyova et al. (2022) found that larger-diameter spruces were more susceptible to beetle infestation, whereas trees with more extensive green crowns tended to survive better. In our study, we quantify both abiotic (stem cracks) and biotic (bark beetle and deer) damage in spruce clonal plantations, and examine how these relate to tree size, green crown proportion, and genotype.

This study aims to understand the factors and mechanisms underlying the occurrence and development of stem defects and biotic damage in mature Norway spruce clones. Specifically, we analyse how tree growth characteristics (diameter, height, green crown ratio), previous damage, and genetic (clonal) differences influence the probability and severity of stem cracks and bark beetle injuries in three clonal plantations in Latvia. By linking these damage patterns to tree characteristics and genotype, we seek to identify clones that combine high productivity with reduced susceptibility to stress-related defects, thereby supporting the selection of robust material for Norway spruce breeding and deployment under changing climatic conditions.

Materials and methods

Study site

The trial sites are located in a temperate region with a humid continental climate (approx. 55.6°–58.1°N, 20.9°–28.2°E), characterised by moderately cold winters and mild summers. The average annual temperature ranges from 5.5°C to 7.5°C, and precipitation totals approximately 600–850 mm per year, with rainfall peaking in late summer (LVĢMC 2020). These climatic conditions provide a suitable context for assessing stress-induced damage in Norway spruce in the temperate climate of Northern Europe.

Data were collected in 2023 in three Norway spruce clonal plantations in Latvia: Jurģi, Druvēni, and Valgums (Figure 1). Planting distances were 5 × 5 m in Druvēni and Valgums, and 5 × 7 m in Jurģi. All plantations were originally intended as seed orchards and established using

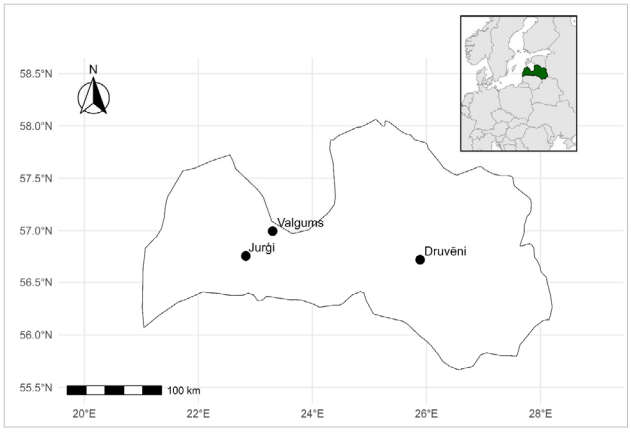

Figure 1. Geographic location of the assessed Norway spruce clonal plantations in Latvia

vegetatively propagated (grafted) clones derived from previously selected plus trees of local origin (from stands in forest district where the respective plantation was located). At the time of the second assessment, plantation age ranged from 50 to 59 years (Table 1). The previous assessment took place 4 to 9 years earlier, depending on the plantation.

Each plantation contained between 20 and 80 clones, planted in randomly distributed single-tree plots. For each tree, height and diameter at breast height (DBH) were measured during both inventories. The height of the lowest living green branch was measured only during the first inventory. The length of the green crown was calculated as the difference between the tree and the lowest living green branch height, and the green crown ratio was estimated as the proportion of green crown length relative to total tree height. Tree survival between the inventories was also recorded at the individual level, excluding trees that were intentionally felled. Additionally, presence of stem cracks (number and length), damage caused by bark beetles (*Ips typographus* L.), cervid bark stripping, resin exudation, and other visible biotic and abiotic damage were noted.

Table 1. Overview of the assessed Norway spruce clonal plantations in Latvia

Plantation	Assessment age, years	Planting density	Number of studied clones
Jurģi	52; 56	5 × 7 m	80
Druvēni	50; 59	5 × 5 m	21
Valgums	50; 59	5 × 5 m	20

Data analysis

Statistical analyses were conducted in R, version 4.3.3 (R Core Team 2024). To assess the effects of different predictors on tree traits and damage occurrence, analytical models were fitted separately for each plantation. Linear models (lm) were used for continuous traits, such as stem crack length, and generalised linear models (glm) with a binomial distribution were applied for binary outcomes,

including stem cracks, bark beetle damage, cervid browsing damage, and survival. The predictor variables included clone, tree height and DBH from both inventories, and green crown ratio. Model results were interpreted at $p < 0.05$.

Clonal means and their 95% confidence intervals were calculated using the emmeans package (Lenth 2016). In addition, the Pearson correlation analysis was used to examine relationships among clonal means of growth and damage traits. Graphical summaries were created using ggplot2 and other tidyverse tools where appropriate (Wickham et al. 2019).

Results

Across the three analysed plantations in 2023 – Jurģi, Druvēni, and Valgums – bark beetle damage by *Ips typographus* was recorded in 5%, 9%, and 3% of trees, respectively (Table 2). In Jurģi, this represents a rise from 3% beetle damage observed in 2019. No *I. typographus* damage was recorded at the Valgums and Druvēni site in the early 2014 assessment. In Jurģi, the probability of bark beetle damage in 2023 was significantly affected by green crown ratio ($\chi^2 = 15.4$, $p < 0.001$), previous bark beetle damage ($\chi^2 = 27.8$, $p < 0.001$), DBH ($\chi^2 = 4.305$, $p = 0.038$), and clone ($\chi^2 = 135.6$, $p < 0.001$). In Valgums, tree height in 2014 showed a weak but significant link with subsequent bark beetle damage ($\chi^2 = 3.94$, $p = 0.047$), whereas for Druvēni, no significant predictors were found ($p > 0.05$). Full model statistics for all response variables and plantations are provided in Supplementary Table S1.

Stem cracks were most frequent in Jurģi (23%), followed by Druvēni (13%) and Valgums (8%). Crack incidence increased in Jurģi from 15% in 2019 to 23% in 2023, while none had been recorded in Druvēni and Valgums during their earlier assessments. Stem crack occurrence in Jurģi was significantly influenced by green crown ratio ($\chi^2 = 8.0$, $p = 0.005$), tree dimensions (height and DBH; $\chi^2 \geq 8.01$, $p \leq 0.005$), previous cracking ($\chi^2 = 142.8$, $p < 0.001$), and clone ($\chi^2 = 2.54$, $p < 0.001$). In Druvēni, crack probability was linked to crown ratio ($\chi^2 = 7.99$, $p = 0.005$) and clone ($\chi^2 = 35.7$, $p < 0.001$), whereas in Valgums it was associated with tree height and DBH ($\chi^2 \geq 6.5$, $p \leq 0.01$), and clone ($\chi^2 = 56.7$, $p < 0.001$). Mean crack length (where present) was longest in Jurģi (1.8 m), followed by Valgums (1.4 m) and Druvēni (0.6 m) (Table 2). Cracks longer in 2019 tended to shrink over time, whereas shorter ones extended further (Figure 2), resulting in a relatively stable average length over time.

Cervid (bark stripping) damage increased notably in Jurģi (from 14% in 2019 to 24% in 2023), appeared minimally in Valgums (from 0% to 3%), and decreased in Druvēni (from 14% to 7%). In Jurģi, cervid browsing damage was significantly related to green crown ratio ($\chi^2 = 10.25$, $p = 0.001$), height and DBH ($\chi^2 \geq 31.5$, $p < 0.001$), previous damage ($\chi^2 = 158.5$, $p < 0.001$), and clone ($\chi^2 = 137.3$, $p < 0.001$). In Druvēni, only previous cervid browsing damage had a significant effect ($\chi^2 = 4.68$, $p = 0.031$), while in Valgums, crown ratio ($\chi^2 = 11.8$, $p = 0.001$), and tree size ($\chi^2 \geq 5.87$, $p \leq 0.015$) were important predictors.

Across all plantations, the green crown ratio consistently influenced the occurrence of damage ($p < 0.05$). Trees with lower crown ratios were more likely to exhibit stem cracks and bark beetle attacks (Figure 3). In Jurģi, larger tree diameter was significantly associated with crack probability (Figure 3), while trees with higher green crown ratio tended to have shorter cracks.

In Druvēni, a more pronounced link was observed between crack frequency and lower green crown ratio, while crack length showed the opposite trend (Figure 4). In Valgums, tree height was the only factor significantly associated with both the likelihood of bark beetle infestation and the likelihood of stem cracks (Figure 5).

Resin exudation was closely related to other types of damage and tree attributes. In Jurģi, it was significantly affected by crown ratio ($\chi^2 = 10.2$, $p = 0.001$), prior resin exudation ($\chi^2 = 45.7$, $p < 0.001$), all recorded damage types ($\chi^2 \geq 9.94$, $p \leq 0.001$), and clone ($\chi^2 = 198.6$, $p < 0.001$). In Valgums, resin exudation was associated with bark beetle ($\chi^2 = 5.02$, $p = 0.026$) and cervid browsing damage ($\chi^2 = 44.01$, $p < 0.001$), whereas in Druvēni it was linked

Table 2. Summary statistics of the studied clonal Norway spruce trials in Latvia

Trial	Jurģi				Druvēni				Valgums			
Year	2019		2023		2014		2023		2014		2023	
Number of trees, N	1623		1520		286		203		475		430	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Height (m)	20.5	3.23	23.4	3.24	25.1	2.27	28.2	2.33	21	3.3	25.6	3.03
Diameter at breast height (cm)	35.8	7.7	38.1	7.64	36.31	5.44	39.6	5.63	35	9.25	39.3	10.02
Green crown ratio	0.81	0.12	-	-	0.75	0.09	-	-	0.81	0.13	-	-
Survival between inventories	0.93				0.91				0.89			
Incidence of stem cracks	0.15	-	0.23	-	0.00	-	0.13	-	0.00	-	0.08	-
Length of stem cracks (m)	1.8	1.92	1.9	1.96	-	-	0.6	0.42	-	-	1.4	1.10
Incidence of bark beetle damage	0.03	-	0.05	-	0.00	-	0.09	-	0.00	-	0.03	-
Incidence of cervid browsing damage	0.14	-	0.24	-	0.14	-	0.07	-	0.00	-	0.03	-
Incidence of resin exudation	0.11	-	0.46	-	0.05	-	0.22	-	0.00	-	0.11	-

Note: SD is the standard deviation

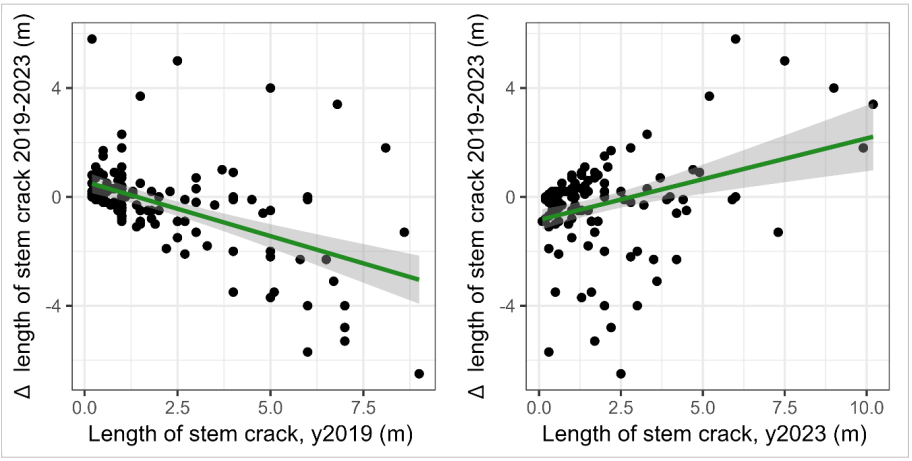

Figure 2. Relationship between the difference in length of the stem crack (Δ length of the stem crack) and length of the stem crack during the first (2019) and second (2023) assessments in plantation Jurģi

Black points represent individual trees; the dark green line represents the mean tendency with 95 % confidence interval (grey area).

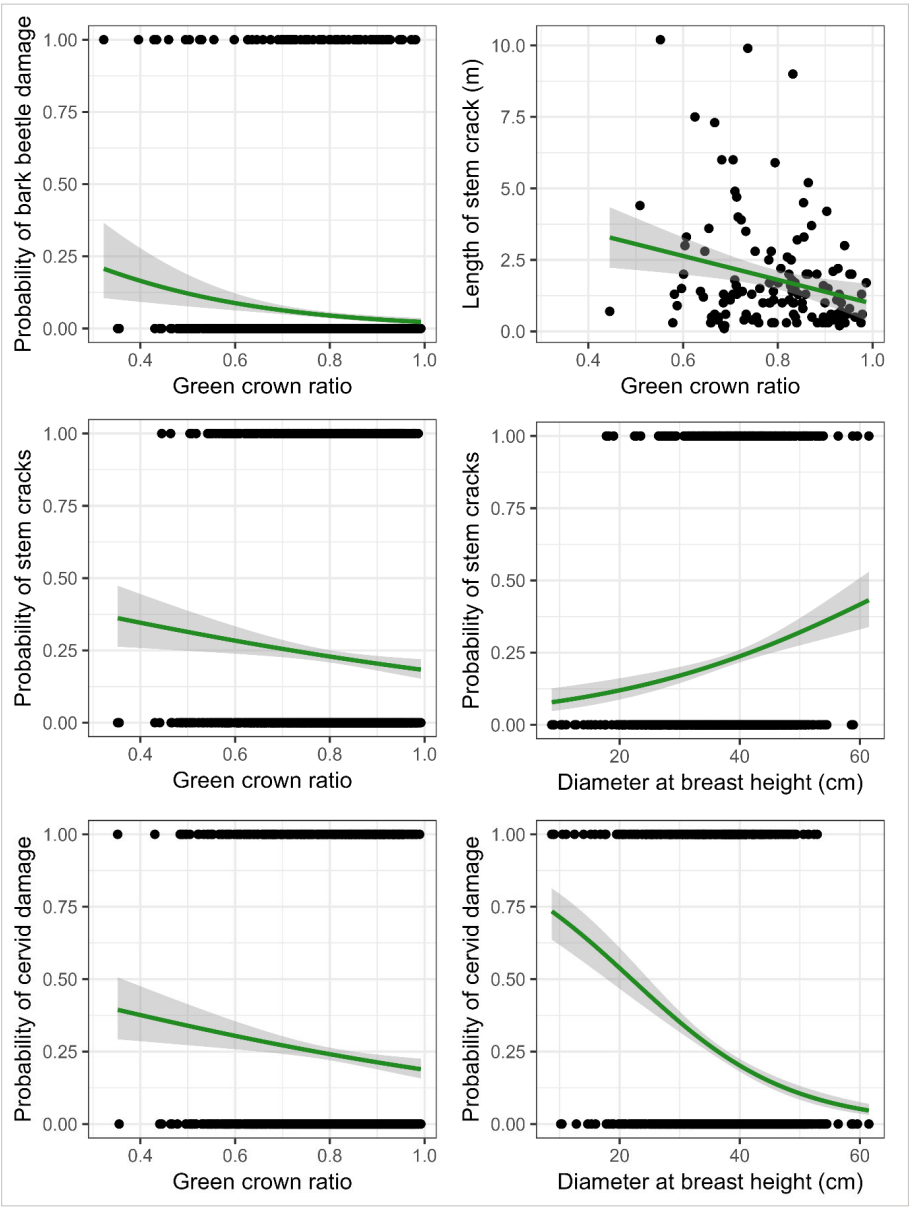

Figure 3. Relationships between stem damage probability and significant predictor variables ($p < 0.05$) in the Jurģi plantation

Black points represent individual trees; the dark green line shows the mean trend with a 95% confidence interval (shaded grey area).

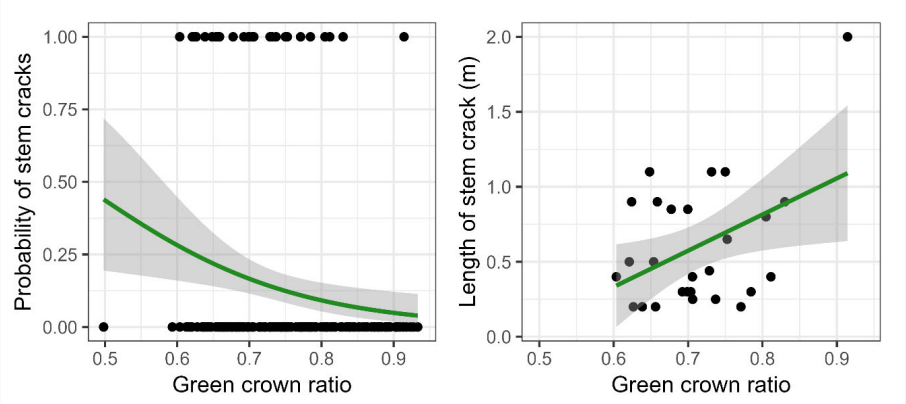

Figure 4. Relationships between stem damage probability and significant predictor variables ($p < 0.05$) in the Druvēni plantation

Black points represent individual trees; the dark green line shows the mean trend with a 95% confidence interval (shaded grey area).

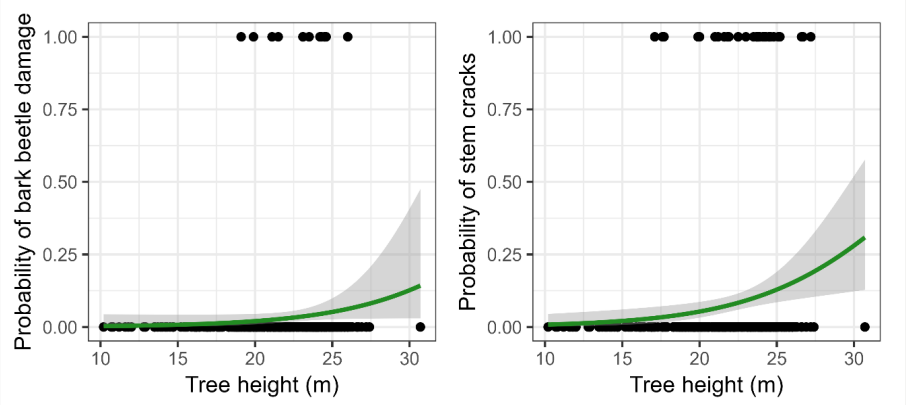

Figure 5. Relationships between stem damage probability and significant predictor variables ($p < 0.05$) in the Valgums plantation

Black points represent individual trees; the dark green line shows the mean trend with a 95% confidence interval (shaded grey area).

to cervid browsing damage in both inventories ($\chi^2 \geq 8.4$, $p \leq 0.004$).

Tree survival between inventories, excluding felled trees, was significantly related to the incidence of damage. In Jurģi, survival was lower for trees with bark beetle damage ($\chi^2 = 7.1$, $p = 0.008$), while in Druvēni it was reduced by cervid browsing damage ($\chi^2 = 8.3$, $p = 0.004$). In Jurģi, survival probability was higher for larger trees without bark beetle damage (Figure 6).

Clonal mean correlation analyses revealed moderate to strong temporal consistency in both growth and stem damage traits between inventories ($r \geq 0.65$). In Jurģi, bark beetle damage in 2023 demonstrated a moderate positive association with resin exudation ($r = 0.35$) and a moderate negative association with survival ($r = –0.51$). Clonal mean resin production was strongly correlated with cervid browsing damage ($r = 0.70$) and with crack length ($r = 0.46$), indicating coordinated stress responses. Cervid browsing damage decreased with increasing tree size, showing weak but significant negative correlations with DBH in both 2019 ($r = –0.27$) and 2023 ($r = –0.30$), and with height in 2023 ($r = –0.23$). A lower green crown ratio in 2019 was associated with greater damage from bark beetles ($r = –0.35$) and cervid browsing ($r = –0.30$) in 2023, as well as longer cracks already visible in 2019 ($r = –0.38$). Crack incidence and length showed high consistency across years, with strong clonal mean correlations from 2019 to 2023 ($r = 0.65$ and 0.74, respectively) (Figure 7).

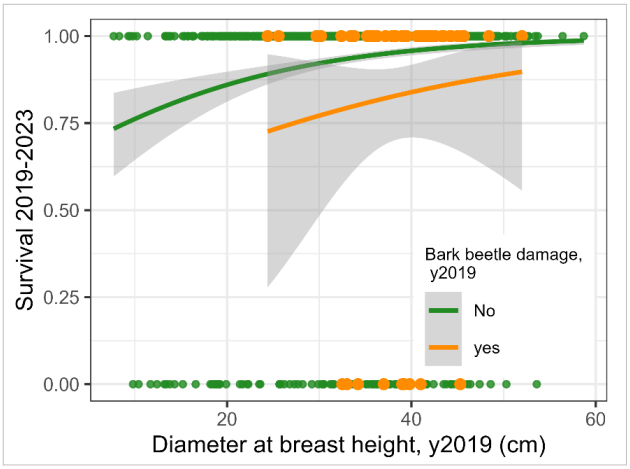

Figure 6. Relationship between tree diameter at breast height in 2019 and survival probability (2019–2023) in the Jurģi plantation, stratified by bark beetle damage status

Green and orange lines represent trees without and with bark beetle damage, respectively. Shaded areas indicate 95% confidence intervals.

In Druvēni, bark beetle damage in 2023 was positively correlated with resin exudation ($r = 0.47$) and negatively with survival ($r = –0.60$). Earlier indicators were predictive: higher resin levels in 2014 were associated with more cracks in 2023 ($r = 0.65$) and reduced survival ($r = –0.55$). Clonal means of cervid browsing damage and resin content were already correlated in 2014 ($r = 0.51$), and early cervid browsing damage was associated with poorer subsequent

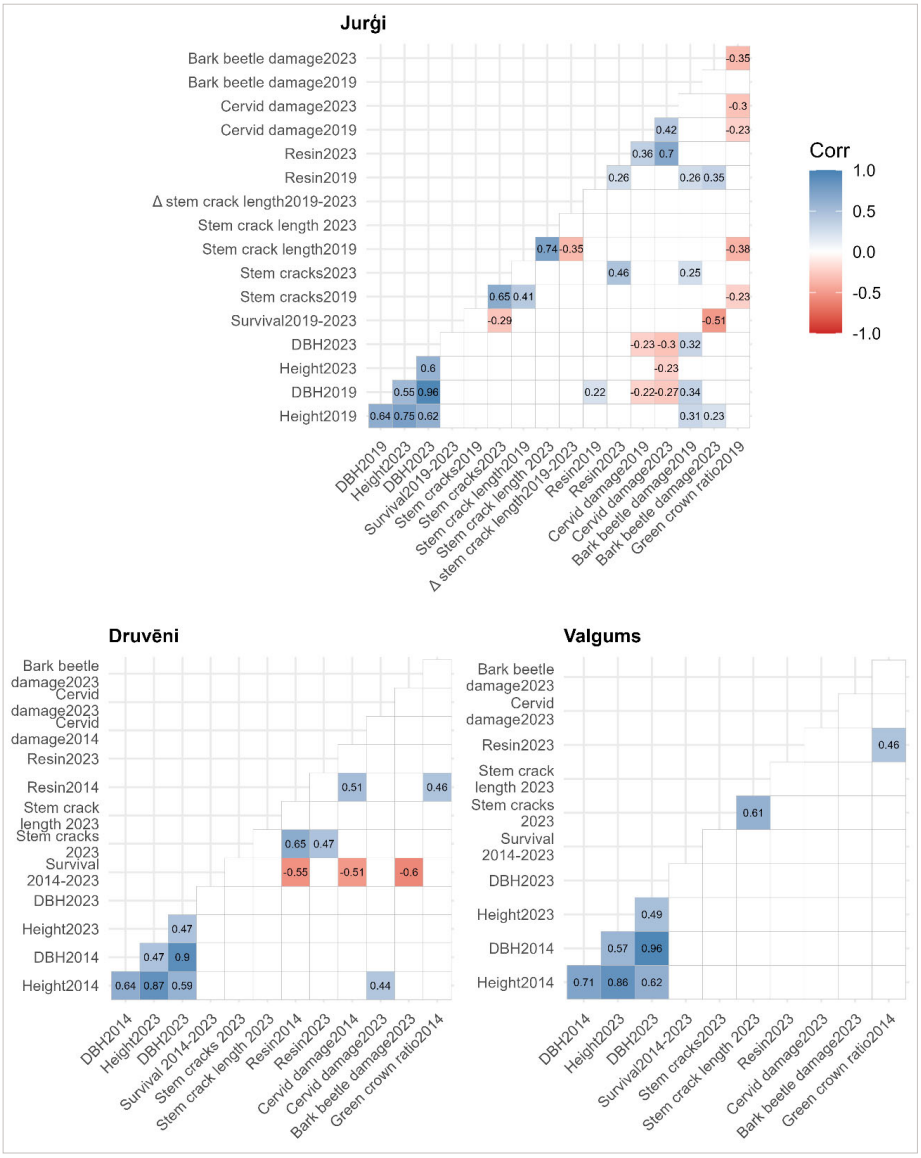

Figure 7. Clonal mean correlations in the studied trials

Only statistically significant ($p \leq 0.05$) correlations are shown.

survival ($r = –0.51$). Tree height in 2014 was moderately correlated with later cervid browsing damage ($r = 0.44$). The green crown ratio in 2014 was positively related to resin production ($r = 0.46$), but not directly associated with later damage outcomes (Figure 7).

At Valgums, stem crack incidence in 2023 was moderately correlated with crack length ($r = 0.61$). The crown ratio measured in 2014 showed no clear relationship with damage variables (Figure 7).

For DBH and stem crack formation, clonal differences were statistically significant in all plantations ($p < 0.05$). Clones significantly influenced bark beetle damage, crack length, and survival only in Jurģi. Clonal differences in cervid browsing damage were significant in Jurģi (second assessment) and Druvēni (first assessment). The green crown ratio differed among clones in Jurģi and Valgums ($p < 0.05$) but not in Druvēni.

Discussion

Damage patterns and tree-level predictors

Our findings confirmed that both environmental stress and genetic factors shape spruce stem defects. The overall crack incidence (8–23% of trees in the second survey) was comparable to other observations in fast-growing spruce stands. Previous studies reported 22–31% cracking under similar conditions (Napola and Napola 2014, Zeltiņš et al. 2018) and lower rates (2–7%) under Swedish conditions (Persson 1994b). Thus, our data fit within the range observed for mature spruce. Similar cracking phenomena have also been reported in larch. For instance, *Larix decidua*, *L. kaempferi* and their hybrids develop longitudinal stem cracks already at a younger age than Norway spruce, typically during periods of rapid juvenile growth. These cracks have been linked to fast diameter increment and drought

stress, particularly in open or thinned stands (Pâques et al. 2023). Such parallels indicate that cracking in conifers reflects a general growth-stress response.

Bark beetle damage remained relatively low (< 10%) at most sites. This is typical for plantations outside major outbreak periods; severe attacks affecting a significant proportion of trees are usually associated with extreme disturbances such as severe storms or droughts (Marini et al. 2017). We documented differences in the incidence of cervid browsing damage between the sites and over time: thus, in Jurģi, the proportion of damaged trees increased from 14% in 2019 to 24% in 2023, whereas in Druvēni, there was a decrease from 14% to 7% over similar period. These trends likely reflect differences in local deer pressure, as well as the changing vulnerability of trees as they grow. Deer usually target younger or thinner-barked trees for stripping (Månsson et al. 2013); consistent with this, we found that cervid browsing damage was significantly negatively correlated with tree size in Jurģi (Figure 3) – smaller-diameter trees were more likely to be damaged.

Across all sites, the green crown ratio was found to be the strongest predictor of damage. Trees retaining ≥ 70% of their height in live crown showed fewer cracks, beetle attacks, and cervid injuries than those with small crowns (Figures 3 and 4). Bark beetle damage was relatively limited in absolute terms (5–9% of trees in 2023, depending on site; Table 2), but it was non-random and showed clear associations with crown characteristics. Jakuš et al. (2011) reported that in a severe bark beetle outbreak, survivors had longer, denser crowns (more shaded boles) than killed trees. Baier (1996) likewise found fewer beetle attacks on spruces with greater crown length. This is supported by the large European outbreak study by Korolyova et al. (2022), who found that spruce survival probability rose steeply with increasing crown length. A larger live crown likely improves whole-tree water status, sustains carbohydrate reserves, and supports resin production – all factors known to deter beetles and limit xylem tension that can trigger cracking (Grabner et al. 2006). Because green crown ratio is at least partially heritable and can be modified by silviculture (Isik and Isik 1999, Lowell et al. 2014), it may represent a practical target trait for both breeding and plantation management aimed at increasing climate change resilience.

Nevertheless, the relationships between growth and damage highlight potential trade-offs for climate-smart forestry. Although wider spacing reduces belowground competition and often results in higher live-to-crown ratio (Sharma et al. 2017), we found that the fastest-growing and largest trees tend to crack more frequently and are damaged by bark beetles to a greater extent. The Jurģi plantation, with higher crack rates, had the lowest stocking density, implying wider spacing and faster growth. Persson (1994b) similarly noted that widely spaced, vigorously growing trees on fertile sites are most prone to stem crack. The mechanism is thought to involve higher cambial stress in rings of wide growth combined with summer moisture deficits, when late-summer drought conditions can create high xylem tension, causing cell walls to fracture and radial cracks to form (Grabner et al. 2006). The interaction between drought and bark beetle infestation is well studied: acute drought stress is known to predispose *P. abies* to infestation (Netherer et al. 2019). Korolyova et al. (2022) found that larger-diameter trees were more susceptible to beetle colonisation, perhaps because they stand out to dispersing beetles or allocate proportionally less carbon to defence.

However, the differences in tree spacing in the studied plantations were relatively small, not allowing examination of any patterns related to initial density (Table 1). A dense stand (initially 1.5 × 2 m spacing) in a Latvian provenance trial still suffered high crack rates (Zeltiņš et al. 2018), implying that spacing alone is not the sole cause. A Finnish study showed that severe cracks can be observed across the entire range of tree diameters (Napola and Napola 2014). Instead, local site conditions (e.g. fertility, drought history) appear to play a major role. In our study, it is important to distinguish different levels of organisation: at the individual tree level, larger diameter clearly promoted cracking in the low-density stand, whereas at the clone level (comparing mean values per clone), we found no consistent trade-off between growth and cracking (more on this below). Forest management recommendations generally favour moderate thinning to encourage continuous growth, maintain spruce resilience in drought conditions and, consequently, reduce the risk of mortality from bark beetles (Bernal et al. 2023). Our observations imply that adaptive management aimed at maintaining a live crown ratio of ~ 0.7 can reduce stem defects regardless of genotype.

Over time, we observed partial healing of the longest cracks and growth of smaller cracks (Figure 2), a pattern also reported by Persson (1994b). This suggests physiological recovery in older trees (larger cracks sealing over) while new cracks emerge in other trees. For the Druvēni plantation, a weak positive correlation between green crown ratio and crack length was unmasked at the clonal level (Figure 7), but given the low overall crack incidence, this pattern should be treated with caution.

Genetic variation and climate-resilient breeding

We found significant genetic (clonal) variation in diameter growth in all three plantations and, notably, also in stem crack incidence, with certain clones showing consistently low crack incidence (Figure 8). This finding aligns with previous studies reporting genotype-dependent variation in stem cracking (Persson 1994b, Vasiliauskas et al. 2001), suggesting that certain clones inherently possess wood or growth characteristics that predispose them to damage. Although the clones studied were grafted, grafting itself is unlikely to be the cause of cracking. Previous Latvian studies have reported similar cracking for spruce seedlings in progeny and provenance trials (Zeltiņš et al.

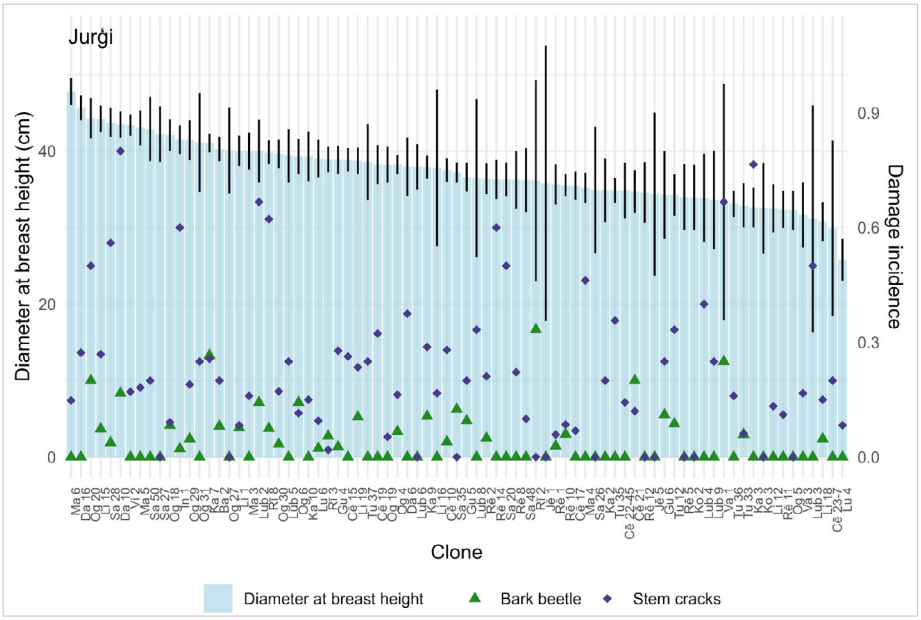

Figure 8. Clonal mean diameter at breast height (primary *y* axis) and incidence of bark beetle damage and stem cracks (secondary *y* axis) in the trial Jurģi

Black whiskers denote 95% confidence intervals for diameter at breast height.

2016, 2018), and in our material cracks typically started above the graft union.

We also observed potential clonal differences in susceptibility to biotic damage. Variation between clones in bark beetle damage and cervid browsing damage was detected in at least one location in each case, suggesting a genetic basis for resistance. Although overall incidence was low and site-dependent (Table 2), clone identity significantly influenced beetle damage, crack length, and survival in some trials (e.g. Jurģi), consistent with earlier findings of genotype-based variation in defence traits (Persson 1994b, Katrevics et al. 2019). Resin exudation, recorded as visible stem flow, offered additional insight: at the clonal mean level, resin output was positively correlated with bark beetle damage ($r \approx 0.35$–0.47), cervid bark-stripping ($r \approx 0.70$), and crack length ($r \approx 0.46$) (Figure 7). These patterns suggest that resin flow was largely reactive – clones experiencing more wounding produced more resin – rather than indicative of constitutive resistance (Krokene et al. 2008). In fact, clones with higher resin often had greater damage, and resin levels were negatively associated with survival ($r \approx -0.5$ to -0.6) in some sites. While resin remains a key defence component, our findings underscore the need to distinguish between induced and inherent resistance when selecting for resilience.

In the context of climate change, our findings have clear implications for Norway spruce management. Increases in the frequency of summer heatwaves and droughts will likely increase the risk of stem cracking, as water stress is a known trigger (Cameron 2019). Concurrently, rising temperatures and disturbance-driven insect outbreaks are expected to intensify bark beetle pressure across Europe (Singh et al. 2024). In light of these trends, deploying genetically resilient planting material is increasingly important. Our results support a climate-adaptive breeding strategy that prioritises not only growth and wood quality but also resistance to abiotic and biotic stress. This aligns with existing breeding goals in the Baltic Sea region, where climatic change resilience is already a key focus (Keskitalo et al. 2016, Matisons et al. 2021, 2024, Ray et al. 2022). The clonal control over stem cracking provides a basis for selecting and propagating damage-resistant genotypes in breeding programmes. Given the negative impact of cracks on wood quality and decay resistance (Vasiliauskas et al. 2001), incorporating crack resistance into selection criteria can help improve timber value without compromising productivity. We recommend that stem crack resistance – and potentially traits related to crown architecture, such as the ability to maintain a high green crown ratio – be incorporated into selection criteria. These traits may serve as indirect indicators of drought or pest tolerance.

Complementary silvicultural practices are also essential. Even well-selected clones require management that maintains crown health and avoids excessive stand density. Co-opted genetic selection and adaptive silviculture can help maintain spruce productivity under increasing climate stress by reducing trunk cracking and susceptibility to *Ips typographus* attack.

Importantly, we found no evidence of a trade-off between growth and damage resistance. Several clones, including Ma 5, Ma 6 and Vi 2 in Jurģi (Figure 8), and No. 1 and No. 41 in Druvēni, combined above-average growth (average diameter 10–26% larger) with low levels of stem cracking and pest damage. This supports the view that high productivity and stress resilience can co-occur, consistent with Zeltiņš et al. (2018), and confirms the feasibility of breeding climate-resilient Norway spruce. With careful selection and deployment, such genotypes can help secure the species' role in future forestry under increasingly extreme environmental conditions.

Conclusions

This study demonstrates substantial clonal variation in both growth and susceptibility to stem damage in mature Norway spruce plantations. Significant differences among clones were observed for diameter growth and stem crack incidence in all three sites, with several clones (e.g. Ma 5, Ma 6, and Vi 2 in Jurģi, and No. 1 and No. 41 in Druvēni), combining high productivity (up to 26% above plantation mean DBH) with low levels of damage. These genotypes represent strong candidates for breeding and deployment under climate-adaptive forestry strategies.

Importantly, no consistent trade-off was found between growth and damage incidence at the clonal level, indicating that it is possible to select for both high productivity and stress resilience. Stem crack dynamics showed partial healing of longer cracks and extension of shorter ones, suggesting a stable long-term average crack length in older stands.

Crown architecture emerged as a key factor in damage resistance. Trees with a green crown ratio ≥ 70% had significantly lower probabilities of stem cracks and biotic damage. This highlights the importance of managing stand structure to maintain vigorous crown development.

Overall, our findings support a combined approach to climate-resilient spruce forestry: selecting genetically superior, damage-tolerant clones and applying silvicultural practices that sustain crown health and reduce stress. Together, these measures can help mitigate risks associated with cracking and *Ips typographus* infestation, while maintaining long-term productivity and wood quality under changing climate conditions.

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References

Baier, P. 1996. Defence reactions of Norway spruce (*Picea abies* Karst.) to controlled attacks of *Ips typographus* (L.) (Col., Scolytidae) in relation to tree parameters. *Journal of Applied Entomology* 120(1–5): 587–593; https://doi.org/10.1111/J.1439-0418.1996.TB01656.X.

Bernal, A.A., Kane, J.M., Knapp, E.E. and Zald, H.S.J. 2023. Tree resistance to drought and bark beetle-associated mortality following thinning and prescribed fire treatments. *Forest Ecology and Management* 530: 120758; https://doi.org/10.1016/J.FORECO.2022.120758.

Cameron, A.D. 2019. Mitigating the risk of drought-induced stem cracks in conifers in a changing climate. *Scandinavian Journal of Forest Research* 34(8): 667–672; https://doi.org/10.1080/02827581.2019.1692900.

Grabner, M., Cherubini, P., Rozenberg, P. and Hannrup, B. 2006. Summer drought and low earlywood density induce intra-annual radial cracks in conifers. *Scandinavian Journal of Forest Research* 21(2): 151–157; https://doi.org/10.1080/02827580600642100.

Honkaniemi, J., Rammer, W. and Seidl, R. 2020. Norway spruce at the trailing edge: the effect of landscape configuration and composition on climate resilience. *Landscape Ecology* 35(3): 591–606; https://doi.org/10.1007/S10980-019-00964-Y/FIGURES/5.

Isik, K. and Isik, F. 1999. Genetic variation in *Pinus brutia* Ten. in Turkey. *Silvae Genetica* 48(6): 293.

Jakuš, R., Edwards-Jonášová, M., Cudlín, P., Blaženec, M., Ježík, M., Havlíček, F. and Moravec, I. 2011. Characteristics of Norway spruce trees (*Picea abies*) surviving a spruce bark beetle (*Ips typographus* L.) outbreak. *Trees – Structure and Function* 25(6): 965–973; https://doi.org/10.1007/S00468-011-0571-9/TABLES/2.

Jansson, G., Danusevičius, D., Grotehusman, H., Kowalczyk, J., Krajmerova, D., Skrøppa, T. and Wolf, H. 2013. Norway Spruce (*Picea abies* (L.) H.Karst.). In: Pâques, L. (Ed.) Forest Tree Breeding in Europe. Managing Forest Ecosystems. Springer, Dordrecht, Vol. 25, p. 123–176; https://doi.org/10.1007/978-94-007-6146-9_3.

Kärvemo, S., Huo, L., Öhrn, P., Lindberg, E. and Persson, H.J. 2023. Different triggers, different stories: Bark-beetle infestation patterns after storm and drought-induced outbreaks. *Forest Ecology and Management* 545: 121255; https://doi.org/10.1016/J.FORECO.2023.121255.

Katrevics, J., Kapostins, R., Bickovskis, K. and Jansons, A. 2019. Influence of initial density on inventory parameters of unthinned Norway spruce stands. In: Raupelienė, A. (Ed.) Proceedings of the 9th International Scientific Conference "Rural Development 2019", Kaunas, Lithuania, September 26–28, 2019. Kaunas: VDU, p. 273–277; https://doi.org/10.15544/RD.2019.032.

Keskitalo, E.C.H., Bergh, J., Felton, A., Björkman, C., Berlin, M., Axelsson, P., Ring, E., Ågren, A., Roberge, J.M., Klapwijk, M.J. and Boberg, J. 2016. Adaptation to Climate Change in Swedish Forestry. *Forests* 7(2): 28; https://doi.org/10.3390/F7020028.

Korolyova, N., Buechling, A., Ďuračiová, R., Zabihi, K., Turčáni, M., Svoboda, M., Bláha, J., Swarts, K., Poláček, M., Hradecký, J., Červenka, J., Němčák, P., Schlyter, F. and Jakuš, R. 2022. The Last Trees Standing: Climate modulates tree survival factors during a prolonged bark beetle outbreak in Europe. *Agricultural and Forest Meteorology* 322: 109025; https://doi.org/10.1016/J.AGRFORMET.2022.109025.

Krokene, P., Nagy, N.E. and Krekling, T. 2008. Traumatic Resin Ducts and Polyphenolic Parenchyma Cells in Conifers. In: Schaller, A. (Ed.) Induced Plant Resistance to Herbivory. Springer, Dordrecht, p. 147–169; https://doi.org/10.1007/978-1-4020-8182-8_7.

Lenth, R.V. 2016. Least-Squares Means: The R Package lsmeans. *Journal of Statistical Software* 69(1): 1–33; https://doi.org/10.18637/jss.v069.i01.

Lowell, E.C., Maguire, D.A., Briggs, D.G., Turnblom, E.C., Jayawickrama, K.J.S. and Bryce, J. 2014. Effects of silviculture and genetics on branch/knot attributes of coastal Pacific Northwest Douglas-fir and implications for wood quality – a synthesis. *Forests* 5(7): 1717–1736; https://doi.org/10.3390/F5071717.

LVĢMC. 2020. Latvijas klimats [Climate of Latvia]. Klimata Portāls, Latvijas Vides, ģeoloģijas un meteoroloģijas centrs. *URL*: https://klimats.meteo.lv/klimats_latvija/latvijas_klimatiskais_raksturojums/ (in Latvian).

Månsson, J., Jarnemo, A., Månsson, J. and Jarnemo, A. 2013. Bark-stripping on Norway spruce by red deer in Sweden: level of damage and relation to tree characteristics. *Scandinavian Journal of Forest Research* 28(2): 117–125; https://doi.org/10.1080/02827581.2012.701323.

Marini, L., Økland, B., Jönsson, A.M., Bentz, B., Carroll, A., Forster, B., Grégoire, J.C., Hurling, R., Nageleisen, L.M., Netherer, S., Ravn, H.P., Weed, A. and Schroeder, M. 2017. Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. *Ecography* 40(12): 1426–1435; https://doi.org/10.1111/ECOG.02769.

Matisons, R., Schneck, V., Jansone, D., Bāders, E., Dubra, S., Zeltiņš, P. and Jansons, Ā. 2021. South-eastern Baltic provenances of Scots pine show heritable weather-growth relationships. *Forests* 12(8): 1101; https://doi.org/10.3390/F12081101/S1.

Matisons, R., Zeltiņš, P., Kāpostiņš, R., Ozoliņš, K. and Jansons, Ā. 2024. Productivity of local Norway spruce clones relates to weather sensitivity of height increment in the eastern Baltic region. *Dendrochronologia* 85: 126187; https://doi.org/10.1016/j.dendro.2024.126187.

Napola, M. and Napola, J. 2014. Observations and results of stem damages in the experimental Norway spruce plantations. *Working Papers of the Finnish Forest Research* 296: 51 (in Finnish).

Netherer, S., Panassiti, B., Pennerstorfer, J. and Matthews, B. 2019. Acute Drought Is an Important Driver of Bark Beetle Infestation in Austrian Norway Spruce Stands. *Frontiers in Forests and Global Change* 2: 465067; https://doi.org/10.3389/FFGC.2019.00039/BIBTEX.

Pâques, L.E., Millier, F. and Veisse, D. 2023. Longitudinal stem cracks in larch: what makes trees vulnerable? *New Forests* 54: 813–832; https://doi.org/10.1007/s11056-022-09942-w.

Persson, A. 1994a. How genotype and silviculture interact in forming timber properties. *Silva Fennica* 28(4): 275–282.

Persson, A. 1994b. Stem cracks in Norway spruce in southern Scandinavia: causes and consequences. *Annales Des Sciences Forestières* 51(3): 315–327; https://doi.org/10.1051/forest:19940310.

R Core Team. 2024. R: a language and environment for statistical computing, version 4.3.3. R Foundation for Statistical Computing, Vienna, Austria. *URL*: https://www.R-project.org.

Ray, D., Berlin, M., Alia, R., Sanchez, L., Hynynen, J., González-Martinez, S. and Bastien, C. 2022. Transformative changes in tree breeding for resilient forest restoration. *Frontiers in Forests and Global Change* 5: 1005761; https://doi.org/10.3389/ffgc.2022.1005761.

Ruņģis, D.E., Lībiete, Z., Korica, A., Katrevičs, J., Jansons, Ā., Veinberga, I. and Jansons, J. 2019. Genetic diversity and differentiation of even-aged Norway spruce stands in Latvia. *Baltic Forestry* 25(1): 45–51; https://doi.org/10.46490/vol25iss1pp045.

Senf, C. and Seidl, R. 2018. Natural disturbances are spatially diverse but temporally synchronized across temperate forest landscapes in Europe. *Global Change Biology* 24(3): 1201–1211; https://doi.org/10.1111/GCB.13897.

Sharma, R.P., Vacek, Z., Vacek, S., Podrázský, V. and Jansa, V. 2017. Modelling individual tree height to crown base of Norway spruce (*Picea abies* (L.) Karst.) and European beech *(Fagus sylvatica* L.). *PLOS One* 12(10): e0186394; https://doi.org/10.1371/JOURNAL.PONE.0186394.

Singh, V.V., Naseer, A., Mogilicherla, K., Trubin, A., Khodabakhsh, Z., Amit, R., Jakuš, R. and Erbilgin, N. 2024. Understanding bark beetle outbreaks: exploring the impact of changing temperature regimes, droughts, forest structure, and prospects for future forest pest management. *Reviews in Environmental Science and Bio/Technology* 23(2): 257– 290; https://doi.org/10.1007/S11157-024-09692-5.

Szymański, S. 2007. Silviculture of Norway Spruce. In: Tjoelker, M.G., Boratyński, A. and Bugała, W. (Eds.) Biology and Ecology of Norway Spruce. Forestry Sciences. Springer, Dordrecht, Vol. 78, p. 295–307; https://doi.org/10.1007/978-1-4020-4841-8_13.

Vasiliauskas, R., Juška, E., Stenlid, J. and Vasiliauskas, A. 2001. Clonal differences and relations between diameter growth, stem cracks and fungi in a 36-year-old clonal seed orchard of Norway spruce (*Picea abies* (L.) Karst.). *Silvae Genetica* 50(5–6): 227–233.

Vitali, V., Büntgen, U. and Bauhus, J. 2017. Silver fir and Douglas fir are more tolerant to extreme droughts than Norway spruce in south-western Germany. *Global Change Biology* 23(12): 5108–5119; https://doi.org/10.1111/GCB.13774.

Westin, J. and Haapanen, M. 2013. Norway spruce – *Picea abies* (L.) Karst. In: Mullin, T.J. and Lee, S.J. (Eds.) Best practice for tree breeding in Europe. Uppsala: Skogforsk, p. 29–47.

Wickham, H., Averick, M., Bryan, J., Chang, W., Mcgowan, L.D'A., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P. and Yutani, H. 2019. Welcome to the Tidyverse. *Journal of Open Source Software* 4(43): 1686; https://doi.org/10.21105/JOSS.01686.

Zeltiņš, P., Katrevičs, J., Gailis, A., Maaten, T., Bāders, E., Jansons, Ā. 2018. Effect of Stem Diameter, Genetics, and Wood Properties on Stem Cracking in Norway Spruce. *Forests* 9(9): 546; https://doi.org/10.3390/f9090546.

Zeltiņš, P., Katrevičs, J., Gailis, A., Maaten, T., Jansons, J. and Jansons, Ā. 2016. Stem cracks of Norway spruce (*Picea abies* (L.) Karst.) provenances in Western Latvia. *Forestry Studies* 65(1): 57–63; https://doi.org/10.1515/fsmu-2016-0012.

Supplementary Table S1. Results of generalised (glm) and linear (lm) models testing the effects of clone, tree attributes, and previous damage on stem and pest damage occurrence and severity in three Norway spruce clonal plantations in Latvia

Site	Response	Predictor (Inventory year)	df	Test	Statistics	*p*-value
Jurģi	Incidence of bark beetle damage (2023)	Green crown ratio (2019)	1	χ^2	15.431	< 0.001 ***
		Height (2019)	1	χ^2	0.064	0.8
		Height (2023)	1	χ^2	0.077	0.781
		Diameter at breast height (2019)	1	χ^2	2.384	0.123
		Diameter at breast height (2023)	1	χ^2	4.305	0.038 *
		Clone	78	χ^2	135.610	< 0.001 ***

Supplementary Table S1 (continued)

Site	Response	Predictor (Inventory year)	df	Test	Statistics	*p*-value
		Incidence of bark beetle damage (2019)	1	χ^2	27.849	< 0.001 ***
	Incidence of stem cracks (2023)	Green crown ratio (2019)	1	χ^2	8.011	0.005 **
		Height (2019)	1	χ^2	15.110	< 0.001 ***
		Height (2023)	1	χ^2	14.675	< 0.001 ***
		Diameter at breast height (2019)	1	χ^2	19.726	< 0.001 ***
		Diameter at breast height (2023)	1	χ^2	24.560	< 0.001 ***
		Clone	78	χ^2	254.680	< 0.001 ***
		Incidence of stem cracks (2019)	1	χ^2	142.780	< 0.001 ***
	Length of stem cracks (2023)	Green crown ratio (2019)	1	F	8.210	0.005 **
		Height (2019)	1	F	1.535	0.218
		Height (2023)	1	F	1.967	0.163
		Diameter at breast height (2019)	1	F	5.049	0.026 *
		Diameter at breast height (2023)	1	F	3.420	0.067
		Clone	37	F	2.639	< 0.001 ***
		Length of stem cracks (2019)	1	F	92.398	< 0.001 ***
	Incidence of cervid browsing damage (2023)	Green crown ratio (2019)	1	χ^2	10.249	0.0014**
		Height (2019)	1	χ^2	31.521	< 0.001 ***
		Height (2023)	1	χ^2	41.877	< 0.001 ***
		Diameter at breast height (2019)	1	χ^2	106.380	< 0.001 ***
		Diameter at breast height (2023)	1	χ^2	93.936	< 0.001 ***
		Clone	78	χ^2	137.270	< 0.001 ***
		Incidence of cervid browsing damage (2019)	1	χ^2	158.510	< 0.001 ***
	Survival 2019-2023	Green crown ratio (2019)	1	χ^2	10.825	0.001 **
		Incidence of bark beetle damage (2019)	1	χ^2	7.092	0.008 **
		Incidence of stem cracks (2019)	1	χ^2	2.261	0.133
		Incidence of cervid browsing damage (2019)	1	χ^2	0.058	0.809
		Incidence of resin exudation (2019)	1	χ^2	2.907	0.088
		Clone	78	χ^2	105.920	0.019 *
	Incidence of resin exudation (2023)	Green crown ratio (2019)	1	χ^2	10.183	0.001 **
		Incidence of resin exudation (2019)	1	χ^2	45.688	< 0.001 ***
		Incidence of bark beetle damage (2019)	1	χ^2	11.118	0.001 ***
		Incidence of bark beetle damage (2023)	1	χ^2	9.937	0.002 **
		Incidence of stem cracks (2019)	1	χ^2	2.696	0.101
		Incidence of stem cracks (2023)	1	χ^2	199.010	< 0.001 ***
		Incidence of cervid browsing damage (2019)	1	χ^2	84.873	< 0.001 ***
		Incidence of cervid browsing damage (2023)	1	χ^2	672.860	< 0.001 ***
		Clone	78	χ^2	198.620	< 0.001 ***
	Green crown ratio (2019)	Height (2019)	1	F	17.933	< 0.001 ***
		Diameter at breast height (2019)	1	F	1.614	0.204
		Clone	78	F	1.608	0.001 ***
	Height (2023)	Clone	78	F	2.932	< 0.001 ***
	Diameter at breast height (2023)	Clone	78	F	6.429	< 0.001 ***
Valgums	Incidence of bark beetle damage (2023)	Green crown ratio (2014)	1	χ^2	0.248	0.619
		Height (2014)	1	χ^2	3.940	0.047 *
		Height (2023)	1	χ^2	3.826	0.051
		Diameter at breast height (2014)	1	χ^2	2.875	0.09
		Diameter at breast height (2023)	1	χ^2	2.409	0.121
		Clone	19	χ^2	20.583	0.36
	Incidence of stem cracks (2023)	Green crown ratio (2014)	1	χ^2	0.853	0.356
		Height (2014)	1	χ^2	9.447	0.002 **
		Height (2023)	1	χ^2	6.653	0.010 **
		Diameter at breast height (2014)	1	χ^2	6.827	0.009 **
		Diameter at breast height (2023)	1	χ^2	6.530	0.011 *
		Clone	19	χ^2	56.742	< 0.001 ***
	Length of stem cracks 2023	Green crown ratio (2014)	1	F	0.163	0.69
		Height (2014)	1	F	2.484	0.125
		Height (2023)	1	F	0.095	0.76
		Diameter at breast height (2014)	1	F	2.498	0.124
		Diameter at breast height (2023)	1	F	2.457	0.127
		Clone	11	F	0.811	0.63
	Incidence of cervid browsing damage (2023)	Green crown ratio (2014)	1	χ^2	11.836	0.001 ***
		Height (2014)	1	χ^2	14.204	< 0.001 ***
		Height (2023)	1	χ^2	5.874	0.015 *
		Diameter at breast height (2014)	1	χ^2	15.210	< 0.001 ***

Supplementary Table S1 (continued)

Site	Response	Predictor (Inventory year)	df	Test	Statistics	*p*-value
		Diameter at breast height (2023)	1	χ^2	11.836	0.001 ***
		Clone	19	χ^2	22.818	0.246
	Survival 2014-2023	Green crown ratio (2014)	1	χ^2	0.208	0.648
		Clone	19	χ^2	25.928	0.132
	Incidence of resin exudation (2023)	Green crown ratio (2014)	1	χ^2	0.153	0.696
		Incidence of bark beetle damage (2023)	1	χ^2	5.018	0.026 *
		Incidence of stem cracks (2023)	1	χ^2	3.423	0.065
		Incidence of cervid browsing damage (2023)	1	χ^2	44.010	< 0.001 ***
		Clone	19	χ^2	0.781	0.731
	Green crown ratio (2014)	Height (2014)	1	F	39.807	< 0.001 ***
		Diameter at breast height (2014)	1	F	52.016	< 0.001 ***
		Clone	19	F	1.869	0.015 *
	Height (2023)	Clone	19	F	0.616	0.895
	Diameter at breast height (2023)	Clone	19	F	4.412	< 0.001 ***
Druvēni	Incidence of bark beetle damage (2023)	Green crown ratio (2014)	1	χ^2	0.002	0.965
		Height (2014)	1	χ^2	1.532	0.216
		Height (2023)	1	χ^2	0.157	0.692
		Diameter at breast height (2014)	1	χ^2	0.285	0.594
		Diameter at breast height (2023)	1	χ^2	1.065	0.302
		Clone	20	χ^2	29.501	0.078
	Incidence of stem cracks (2023)	Green crown ratio (2014)	1	χ^2	7.988	0.005 **
		Height (2014)	1	χ^2	1.794	0.181
		Height (2023)	1	χ^2	2.620	0.106
		Diameter at breast height (2014)	1	χ^2	1.225	0.268
		Diameter at breast height (2023)	1	χ^2	0.565	0.452
		Clone	20	χ^2	35.174	0.019 *
	Length of stem cracks (2023)	Green crown ratio (2014)	1	F	5.557	0.027 *
		Height (2014)	1	F	0.213	0.649
		Height (2023)	1	F	0.500	0.486
		Diameter at breast height (2014)	1	F	0.056	0.814
		Diameter at breast height (2023)	1	F	0.743	0.397
		Clone	20	F	0.426	0.932
	Incidence of cervid browsing damage (2023)	Green crown ratio (2014)	1	χ^2	1.788	0.181
		Height (2014)	1	χ^2	0.286	0.593
		Height (2023)	1	χ^2	0.000	0.991
		Diameter at breast height (2014)	1	χ^2	1.466	0.226
		Diameter at breast height (2023)	1	χ^2	2.969	0.085
		Clone	20	χ^2	24.063	0.24
		Incidence of cervid browsing damage (2014)	1	χ^2	4.680	0.031 *
	Survival 2014–2023	Green crown ratio (2014)	1	χ^2	0.080	0.777
		Incidence of cervid browsing damage (2014)	1	χ^2	8.332	0.004 **
		Incidence of resin exudation (2014)	1	χ^2	0.156	0.693
		Clone	20	χ^2	26.928	0.137
	Incidence of resin exudation (2023)	Green crown ratio (2014)	1	χ^2	1.184	0.277
		Incidence of resin exudation (2014)	1	χ^2	2.360	0.125
		Incidence of bark beetle damage (2023)	1	χ^2	0.256	0.613
		Incidence of stem cracks (2023)	1	χ^2	0.320	0.572
		Incidence of cervid browsing damage (2014)	1	χ^2	8.417	0.004 **
		Incidence of cervid browsing damage (2023)	1	χ^2	46.844	< 0.001 ***
		Clone	20	χ^2	23.308	0.274
	Green crown ratio (2014)	Height (2014)	1	F	1.916	0.167
		Diameter at breast height (2014)	1	F	12.117	< 0.001 ***
		Clone	20	F	1.119	0.33
	Height (2023)	Clone	20	F	6.953	< 0.001 ***
	Diameter at breast height (2023)	Clone	20	F	3.774	< 0.001 ***