1   **Short term survival and crown rebuilding of European broadleaf tree species following**
2   **a severe ice storm**

3

4   Dušan Roženberger, Jakob Pavlin, Thomas A. Nagel

5

6   D. Roženberger, T.A. Nagel, Department of Forestry and Renewable Forest Resources,

7   Biotechnical Faculty, University of Ljubljana, Večna pot 83, 1000 Ljubljana, Slovenia.

8

9   J. Pavlin, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague,

10   Kamýcká 129, Praha 6–Suchbát, Prague, 16521, Czech Republic.

11

12   Corresponding author: D. Roženberger, e-mail: dusan.rozenberger@bf.uni-lj.si, telephone:

13   +38613203536, fax: +3861 257 11 69

Abstract

Ice storms cause widespread damage to forests in many temperate regions, leaving behind many live trees with severe crown damage. Following a severe ice storm in 2014 that damaged forests across Slovenia, we examined how tree-level attributes influenced survival and crown rebuilding three growing seasons after the storm. Field sampling was carried out in four mature stands dominated by native broadleaf species. Of the 763 sampled trees, the annual mortality rate following the storm was 2.2%, and nearly all of the trees that died experienced > 75% crown removal. Oak (*Quercus petraea*) and chestnut (*Castanea sativa*) had higher rates of mortality than beech (*Fagus sylvatica*) and maple (*Acer pseudoplatanus*). Mixed models found that survival significantly increased with tree diameter and decreased with increasing crown damage. Although we observed sprouting across all the dominant species, maple, oak, and chestnut showed a more vigorous response compared to beech, and maple had the fastest sprout growth. Model results showed that sprout density and length increased with level of crown damage. The results indicate that these broadleaf forests are resilient to severe ice damage. Consequently, hasty salvage cutting of trees with canopy damage should be avoided, as many individuals with over 75% crown damage are likely to survive and recover.

Key words: disturbance, epicormic branches, mortality, resilience, sprouting

Introduction

Ice storms are common disturbance agents in temperate forests of the northern hemisphere, and occasionally cause severe damage over large regions (Brommit et al. 2004; Darwin et al. 2004; Duguay et al. 2001; Nagel et al. 2016; Turcotte et al. 2012; Zhou et al. 2011). Compared to the damage patterns that result from other common disturbance agents in temperate forests, particularly uprooted or snapped trees caused by windthrow, ice storms typically result in damage patterns characterized by a large proportion of trees with highly damaged crowns (Nyland et al. 2016). Both the survival and crown rebuilding capacity of severely damaged trees are key components of forest recovery following severe ice storms. Understanding interspecific differences in survival and crown rebuilding are necessary for both predicting future forest composition and making informed management decisions. Without this knowledge, salvage logging efforts can unnecessarily remove damaged trees that would otherwise survive (Bragg et al. 2003; Nyland et al. 2016).

Only a few studies, nearly all of which were based in North America, have quantified the response of crown damaged trees to severe ice storms in temperate forest regions. Mortality rates reported in these studies indicate strong variation among species and severity of crown loss. For example, in a study that tracked tree survival over a 15 year period, Shortle et al. (2003, 2014) documented high rates of mortality for *Betula papyrifera* (77% of trees with > 50% crown loss died), while late-successional species with severe crown damage, such as *Acer* and *Fraxinus*, had between 94 and 100% survival rates. In mixed broadleaf forests dominated by *Acer saccharum*, Nyland et al. (2016) found between 3% and 8% of trees died during a 10-year monitoring period; of all the trees that died during the study, 98% experienced greater than or equal to 50% crown loss. In a 6-year study, Turcotte et al. (2012)

found that larger trees with higher levels of crown loss were associated with increased mortality, and that *Quercus* species had significantly higher mortality rates than *Acer* species. In a long-term study that tracked mortality over 20 years, Deschenes et al. (2019) found the highest mortality rates for *Ostrya* and *Fagus*, particularly for trees with high crown loss, and lower rates for *Acer*, *Tilia*, and *Tsuga*.

Post disturbance survival of trees with severe crown damage is likely related to their ability to rebuild their crowns (Shortle et al. 2003). Following injury to crowns, tree species resprout from epicormic structures along the main stem and from branches within the crown. The capacity for epicormic branching is largely a function of a given tree. For example, many broadleaved trees develop epicormic branches after crown injury, but few conifers have this capacity. Furthermore, the number of shoots that develop, their growth, and their persistence depend on many additional factors, such as crown class, tree height, damage severity, and light conditions (Kraemer and Nyland 2010; Nyland et al. 2016). Studies of crown rebuilding following ice storm damage in North America indicate notable differences among species (Duguay et al. 2001; Nyland et al. 2016; Shortle et al. 2003; Turcotte et al. 2012). In general, these studies report moderate to vigorous sprouting for species of *Fraxinus*, *Acer*, *Quercus*, and *Prunus*, and a lower capacity to resprout for *Fagus*, *Betula*, and *Populus*.

In 2014, a severe ice storm caused widespread damage to forests across the northern Dinaric mountain range in Slovenia and Croatia. Previous work documented the immediate damage patterns to trees and stands (Nagel et al. 2016). The goal of this study was to examine the tree level response in relation to survival and crown rebuilding three growing seasons after the storm. Specifically, we examined how various tree-level attributes, such as species, diameter, neighborhood competition, and crown loss, influenced survival and crown rebuilding. We

discuss how the results compare with similar studies, and provide forest management guidelines for stands damaged by ice storms based on our findings.

Methods

Study area

The study was conducted between late fall 2016 and early spring 2017, three growing seasons after the February 2014 ice storm. Field sampling was carried out in four study sites (Roznik, Oblakov gozd, Tolmin, and Laze) located in central and western Slovenia (Figure 1). Stand selection was based on the following criteria: ice storm damage was characterized by severe crown damage (based on the plot data from this study, 51% of all trees had > 75% crown damage), as opposed to immediate mortality due to uprooting or bole snapping, which was common in some stands on steep slopes (Nagel et al. 2016); stands were dominated by native broadleaf species that are both ecologically and economically important across the temperate zone of Europe; the canopy layer was comprised of mature trees around 80-120 years old; and trees with severe crown damage were not salvage logged. Observations during the ice storm suggest that ice thickness was around 5 cm in the selected stands, although ice thickness may have reached 8 cm in some locations (Sinjur et al. 2014). The study sites covered a compositional gradient of mixed broadleaf forests, and were dominated by either sessile oak (*Quercus petraea* (Matt.) Liebl; hereafter oak) or European beech (*Fagus sylvatica* L.; hereafter beech). Research plots were located on gentle to moderate slopes with shallow soils and diverse bedrock, including limestone, sandstone, and other marine sedimentary rocks (flysch). The elevation among the stands was between 350 and 600 m (Table 1). Annual average temperatures range between 9-11°C. The precipitation on the

research locations varies from around 1500 mm in the central part to around 2000 mm in the more western part of the country.

Field methods

We established several parallel transects running along the slope contour in each stand. The beginning of the first transect was located with a random point at one end of the stand, and additional transects were placed parallel to the first, separated by approximately 50 m. Plotless sampling points were spaced systematically along transects, with at least 30 m between points depending on the length of the transects, until 20 sampling points were established at each site. The 10 closest trees to the sampling point and that survived the immediate impact of the ice storm were recorded. Sampling was done in late fall and early spring, when we could still see damaged crowns, but when enough leaves were still on the trees in the fall, or were starting to flush in the spring, such that it was easy to distinguish dead trees from live trees. Trees that uprooted and snapped below the base of the crown were presumed dead and not included; field observations indicated that nearly all stems that snapped below the crown were dead at the time of sampling, even if they indicated some signs of initial sprouting. In some cases, we recorded the closest 12 trees to increase the sample of less dominant species. In total, 763 trees > 10 cm diameter at breast height (DBH) were sampled. Although a number of species were encountered across the sites, the analyses presented here focus on the four most dominant broadleaf species distributed across the sites, namely, beech, oak, sycamore maple (*Acer pseudoplatanus* L.; hereafter maple) and sweet chestnut (*Castanea sativa* M.; hereafter chestnut). For each tree we recorded the species, DBH, height, height to crown base, surrounding stand basal area using an angle gauge (basal area factor $k=2$) and the angle count sampling method (Bitterlich 1948), status (dead or

alive), and crown damage level. Crown damage was visually estimated using a simple ordinal scale with three levels: 1) undamaged or < 25% crown damage; 2) 25-75% crown damage; 3) and > 75% crown damage. Dead trees often showed evidence of initial sprouting, but had died by the time of sampling three growing seasons after the ice storm. Slope angle and aspect were measured on each plot.

Epicormic sprouting was estimated separately for the main bole and the crown. This was done to determine if a given species responded to ice damage with both types of sprouting, and also because bole sprouting reduces timber quality, which has implications for post-ice storm management. For each category, we visually classified trees into three classes: 1) no sprouting; 2) moderate sprouting (sparse sprouts located in the bole or crown with up to 5 sprouts per m of bole); 3) vigorous sprouting (dense sprouting with greater than 5 sprouts per m of bole). To further quantify bole sprouting, we counted the total number of sprouts on one completely visible side of the main bole for each tree. For optimal visibility of the bole and crown, these counts were systematically done uphill in the direction of the slope aspect for each tree. To assess species-specific growth rates of sprouts, we estimated the length (to the nearest 20 cm) of the 3 longest bole and 3 longest crown sprouts not growing from the same sprout cluster for each tree using 8 × 42 power binoculars. A clearly marked meter stick was placed on the tree bole to aid the visual estimates of sprout lengths. While we acknowledge that this measure is a rough estimate, we felt it was sufficient to identify general patterns of sprout growth rates among tree species.

Data analysis

For each species, we calculated the annual mortality rate (m), using the following formula (Sheil and May 1996):

$$m = (1 - (N_r/N_t)^{1/t}) \times 100$$

where N_r is the number of live trees at the end of the study, N_t is the initial number of trees prior to the ice storm and t is the number of years that passed until mortality was recorded (in our case 3 years).

Generalized linear mixed models (GLMM) using the Laplace approximation method (Raudenbush et al. 2000) were used to model the probability of survival (coded 0 for dead and 1 for alive) as a function of the categorical predictor *species*, continuous predictors *DBH*, and *crown damage* (we treated the 3 ordinal crown damage categories as numeric in the model). The collinearity of predictor variables was also examined (all variance inflation factor values were around 1). Sampling point and study site were used as random factors, with sampling point nested inside study site.

Differences in epicormic sprouting intensity among tree species were investigated using a Chi-Square Test of independence. Generalized linear mixed models were also used to examine tree sprouting. Average bole sprout length, average crown sprout length, and average number of bole sprouts per m of a bole were used as response variables (rv). The probability distribution that best fit all three response variables was lognormal. Therefore, the penalized quasiliikelihood parameter estimation approach was used (Bolker et al. 2009; Wolfinger and Oconnell 1993). We built a separate model for every response variable using the following general form:

$$rv \sim DBH + \text{basal area} + \text{crown damage} + \text{tree species}, \sim 1 \mid \text{study site/sampling point}$$

In the starting model the following predictor variables were used: *DBH*, *basal area* and *crown damage* as continuous variables and *tree species* as a categorical variable. For the latter, maple was used as a reference level due its strong reaction to damage. The numeric and ordinal factor *crown damage* was treated as a continuous variable to allow better quantification of the relationship with the response variable. We included variables that reflect the potential differences in the population resulting from variability between the hierarchical levels in the sampling design as random effects. These were *sampling point* and *study site*, with sampling point nested inside study site. A stepwise approach was used to remove predictors according to the test results. The final version of the model is presented in the results. Confidence intervals of parameters were examined and sets of graphical summaries were analyzed for validation purposes (Robinson and Hamann 2011). All statistical analyses were performed using R using the package lme4 and MASS (R Development Core Team 2013).

Results

Crown damage

Severe crown damage (> 75% crown loss) was the most common crown damage category among all the trees recorded in the study, while trees with < 25% crown loss were less frequent (Table 2). Regarding individual species, oak had the largest proportion of stems in the severe damage class (69%), followed by chestnut (59%), beech (52%) and maple (45%). The different crown damage classes were relatively evenly distributed across tree diameter classes (Figure 2). For example, trees with moderate and severe crown loss were recorded in nearly all diameter classes for each species. Given that there was a sufficient number of trees

representing the range of diameter and crown damage classes for each species, the dataset was appropriate for further analyses regarding the influence of these key drivers on survival and crown rebuilding.

Mortality

The average annual mortality rate during the 3 growing seasons following the ice storm was 2.2% for all species combined (Table 2). Oak had the highest mortality rate (4.4%), followed by chestnut (3.8%), while mortality rates were notably lower for beech (0.9%) and maple (0.6%). All of the trees that died, except one chestnut tree, had > 75% crown damage. It is worth noting, however, that 57% of the surviving trees also experienced > 75% crown damage.

The GLMM analysis found that DBH and crown damage were significant predictors of survival (Table 3). Survival increased with DBH and decreased with increasing crown damage. Tree species did not have an important influence on survival.

Resprouting

The visual estimate of sprout density indicated that boles sprouted more vigorously compared to crowns (Figure 3). There were also notable differences among species. For example, vigorous bole sprouting was observed for 51% of maple, 44% of chestnut, 26% of oak and 13% of beech trees ($\chi^2(6, N = 763) = 77, p = 0.000$), while vigorous crown sprouting was observed for 33% of maple and less than 10% of the remaining tree species ($\chi^2(6, N = 763) = 56, p = 0.000$). Over all tree species, the average number of bole sprouts per m of bole was

1.03 (SD 1.30), and the maximum of 10.68, three growing seasons after the storm. The average annual growth over all tree species was higher for bole sprouts (26 cm) compared to crown sprouts (20 cm), but note that these are estimates to the nearest 20 cm. On average, annual bole sprout growth was 62 cm for maple, 41 cm for chestnut, 22 cm for oak, and 18 cm for beech. Average annual crown sprout growth was 51 cm for maple, 26 cm for chestnut, 16 cm for beech, and 15 cm for oak.

The GLMM analysis indicated that significant predictor variables influenced sprouting density and growth rate in varied ways (Table 4). DBH had a negative influence on the number of bole sprouts per m of bole, while sprout density increased with increasing crown damage. Compared to maple, which was selected as a reference level for the categorical factor *tree species*, the density of sprouts was higher for chestnut and oak, and lower for beech. With regard to sprout growth rates, basal area of the surrounding stand had a negative influence and crown damage a positive influence on the average length of bole sprouts. Average bole sprouts lengths were smaller for beech and oak compared to maple. For crown sprout length, the model found that average sprout length increased with increasing DBH and crown damage level. With regard to species, the length of crown sprouts was shorter for chestnut, beech, and oak compared to maple.

Discussion

For trees that experienced crown damage during the 2014 ice storm, the overall mortality rate was relatively low during the three years following the storm, particularly considering that a large proportion of trees in our sample experienced greater than 75% crown loss. The overall annual mortality rate of 2.2% in our study region is more than double the rates reported for managed forests in central Europe, which are generally less than 1% (Etzold et al. 2019;

Neumann et al. 2017), but is consistent with mortality rates of ice-damaged trees reported in the North American literature. Following the 1998 ice storm in Canada, (Deschênes et al. 2019) report an annual mortality rate of 2.3% in a mixed-species old-growth forest 2-6 years after the storm. Based on the data reported by (Turcotte et al. 2012), annual mortality rates across all tree species were 4% during the first 3 years and 2.9% over 6 years following an ice storm in mixed-broadleaf forests in Ohio. In mixed broadleaf stands in New York, Nyland et al. (2016) found that between 3% and 8% of all trees died within 10 years of the 1998 ice storm, which would roughly equate to even lower annual rates compared to the studies listed previously. It is worth highlighting that mortality from ice damaged trees can remain higher than background rates for decades after the storm event (Deschênes et al. 2019), such that the three year period observed in our study may not reflect the long-term effects of the storm.

The results show a clear positive relationship between the level of crown damage and the likelihood of mortality, which is consistent with other ice storm studies (Deschênes et al. 2019; Nyland et al. 2016; Proulx and Greene 2001; Shortle et al. 2014; Shortle et al. 2003; Turcotte et al. 2012; Whitney and Johnson 1984). Nearly all the trees that died in our study had more than 75% of crown damage. It is nevertheless remarkable that 57% of the trees that had more than 75% of crown damage were still alive three years after the storm. This and other studies indicate that while short-term mortality rates for trees with severe crown damage are notably higher than for lightly or undamaged trees, trees with severe crown damage, especially those with good initial tree vigor, have a remarkable capacity to survive this damage (Nyland et al. 2016; Shortle et al. 2014; Turcotte et al. 2012).

Although species identify was not a significant predictor of survival in the GLMM analysis, the mortality rates for oak and chestnut were higher than for beech and maple, which is generally consistent with North America literature. For example, Turcotte et al. (2012) found higher rates of mortality for *Quercus alba* and *Q. rubra* compared to species of

285 *Acer*, and both Nyland et al. (2016) and Deschenes et al. (2019) report relatively low
286 mortality rates for *Acer saccharum* following ice storm damage. Given that oak and beech are
287 often codominant across lower elevation mountain forests in the study region, recurring ice
288 storms could favor beech dominance and hinder ongoing silvicultural efforts to increase oak,
289 which is favored for both economic reasons and climate change adaptation (Mette et al. 2013;
290 Scharnweber et al. 2011).

291   We observed a strong sprouting response across the dominant species, which may also
292 explain the relatively low mortality rates for heavily damaged individuals. Our visual
293 estimate indicated that sprouting intensity tended to be stronger on boles than in crowns
294 across the four dominant species, yet this estimate should be treated with caution because we
295 did not quantify the density of sprouts in the crown. We found a consistent positive
296 relationship between crown damage and bole sprout density, bole sprout length, and crown
297 sprout length, which is consistent with the study by Brommit et al. (2004), who recorded
298 crown resprouting in mixed broadleaf trees following ice storm damage in Canada. We also
299 found that larger trees tended to have more rapid sprout growth rates, but a lower density of
300 bole sprouts compared to smaller trees. This is partly consistent with literature on epicormic
301 sprouting, which suggests that less vigorous trees, such as those in intermediate or suppressed
302 crown positions, are more likely to produce epicormic sprouts (Meier et al. 2012). We also
303 found that bole sprout lengths were negatively influenced by the basal area of surrounding
304 trees. We suspect that this is related to sunlight, whereby stems that were more sun-exposed
305 (i.e. fewer neighboring trees due to direct storm mortality) had higher bole sprout growth
306 rates, which is consistent with the literature on epicormic sprouting (Meier et al. 2012).

307   Although we found that a very high proportion of ice-damaged trees resprouted, there
308 were notable differences among species in their capacity to resprout. Maple, chestnut, and
309 oak had a high capacity for bole sprouting compared to beech (Figure 4). While all four

species showed a moderate capacity to resprout from damaged crown branches, maple had the highest proportion of vigorous crown resprouting, and also had the fastest sprout growth rates, which together led to rapid rebuilding of damaged crowns. Some of these sprouting patterns are supported by the literature on epicormic branching. For example, the number of axillary buds that potentially develop into epicormic sprouts was found to be 5 times greater in *Q. petraea* compared to *F. sylvatica* (Fontaine et al. 2002; Colin et al. 2012). However, much less is known about epicormic sprouting in *A. pseudoplatanus* (Hein et al. 2008), although our results indicate this species has a strong capacity to resprout. The sprouting responses observed here are also generally consistent with North American literature, which often report more vigorous sprouting for species of *Acer* and *Quercus*, and notably lower sprouting capacity for *Fagus grandifolia* (Brommit et al. 2004; Duguay et al. 2001; Nyland et al. 2016; Turcotte et al. 2012).

One aspect of forest recovery that was not dealt with in our research, but may be important for long term management of damaged stands, includes the long-term influence of severe crown damage on wood quality of surviving trees. Severely damaged trees may have a high incidence of rotten wood due to pathogens that entered broken branches. This is partly supported by the N. America literature ((Hopkin et al. 2001; Kraemer and Nyland 2010; Nyland et al. 2016; Shortle et al. 2003), but few studies have followed the long term effects of ice storm damage on wood decay. Indeed, both the high density of epicormic sprouts on the main bole of some species and the potential for wood decay will likely affect tree grade and quality of boles. For example, as few as five sprouts on a five meter bole, as well as resulting defects caused by epicormic branches, have been found to substantially reduce log and lumber grade for *Quercus* (Meadows and Burkhardt 2001).

Both the survival and crown rebuilding capacity of severely damaged trees are key components of forest resilience following severe ice storms. According to results of this

study, mixed broadleaf forests in Central Europe are resilient to severe ice storm damage. Consequently, hasty salvage cutting of trees with severe canopy damage should be avoided, as many individuals with over 75% crown damage are likely to survive and recover, at least in the short term. Even if severely damaged trees ultimately die prematurely, they may provide a useful source of seed or partial shade for the recovering forests. Managers might choose to selectively remove heavily damaged trees that have high-value bole wood to avoid the effects of potential decay and epicormic sprouting if left in the stand. Reduced salvage activities will also help to limit damage to the boles of surviving trees and to advance regeneration, both of which are important for rapid forest recovery.

Acknowledgements

This research was supported by the Slovenian Research Agency, Research Programme P4-0059 and by the research project V4-1124 financed by the Ministry of Agriculture, forestry and food. Partial support was also provided by the Pahernik foundation. We thank the undergraduate students from the University of Ljubljana, Anže Martin Pintar, Jaime Torres Albert, Kristina Sever, Liza Stančič and Maruša Nahtigal for help with field work. Finally, we thank three anonymous reviewers for helping to improve an earlier version of this manuscript.

References

- Bitterlich, W. 1948. Die Winkelzahlprobe. Allgemeine Forst-und- Holzwirtschaftliche Zeitung, 59 (1/2): 4-5.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., and White, J.S.S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol **24**(3): 127-135. doi:10.1016/j.tree.2008.10.008.
- Bragg, D.C., Shelton, M.G., and Zeide, B. 2003. Impacts and management implications of ice storms on forests in the southern United States. Forest Ecology and Management **186**(1-3): 99-123. doi:10.1016/S0378-1127(03)00230-5.
- Brommit, A.G., Charbonneau, N., Contreras, T.A., and Fahrig, L. 2004. Crown Loss and Subsequent Branch Sprouting of Forest Trees in Response to a Major Ice Storm. J. Torrey Bot. Soc. **131**(2): 169. doi:10.2307/4126918.
- Colin, F., Sanjines, A., Fortin, M., Bontemps, J.D., and Nicolini, E. 2012. Fagus sylvatica trunk epicormics in relation to primary and secondary growth. Ann Bot-London **110**(5): 995-1005. doi:10.1093/aob/mcs178.
- Darwin, A.T., Ladd, D., Galdins, R., Contreras, T.A., and Fahrig, L. 2004. Response of Forest Understory Vegetation to a Major Ice Storm. J. Torrey Bot. Soc. **131**(1): 45. doi:10.2307/4126927.
- Deschênes, É., Brice, M.-H., and Brisson, J. 2019. Long-term impact of a major ice storm on tree mortality in an old-growth forest. Forest Ecology and Management **448**: 386-394. doi:https://doi.org/10.1016/j.foreco.2019.06.018.
- Duguay, S.M., Arai, K., Hooper, M., and Lechowicz, M.J. 2001. Ice storm damage and early recovery in an old-growth forest. Environmental Monitoring and Assessment **67**(1-2): 97-108. Available from <http://link.springer.com/article/10.1023/A:1006464511158> [accessed 2015/09/14/08:48:01].
- Etzold, S., Zieminska, K., Rohner, B., Bottero, A., Bose, A.K., Ruehr, N.K., Zingg, A., and Rigling, A. 2019. One Century of Forest Monitoring Data in Switzerland Reveals Species- and Site-Specific Trends of Climate-Induced Tree Mortality. Front Plant Sci **10**. doi:Artn 30710.3389/Fpls.2019.00307.
- Fontaine, F., Jarret, P., Druelle, J.L. 2002. Study and monitoring of epicormic buds that produce shoots in sessile oak. Rev. Forest. Française **54**, 337–356.
- Hein, S., Collet, C., Ammer, C., Goff, N.L., Skovsgaard, J.P., and Savill, P. 2008. A review of growth and stand dynamics of Acer pseudoplatanus L. in Europe: implications for silviculture. Forestry: An International Journal of Forest Research **82**(4): 361-385. doi:10.1093/forestry/cpn043.
- Hopkin, A.A., Greifenhagen, S., and Holland, J. 2001. Decay, stains, and beetles in ice-storm-damaged forests: A review. Forest Chron **77**(4): 605-611. doi:10.5558/Tfc77605-4.
- Kraemer, M.J. and Nyland, R.D. 2010. Hardwood crown injuries and rebuilding following ice storms: a literature review. U.S. Department of Agriculture, Forest Service, Northern Research Station NRS **60**.
- Meier, A.R., Saunders, M.R., and Michler, C.H. 2012. Epicormic buds in trees: a review of bud establishment, development and dormancy release. Tree Physiology **32**(5): 565-584. doi:10.1093/treephys/tps040.
- Mette, T., Dolos, K., Meinardus, C., Bräuning, A., Reineking, B., Blaschke, M., Pretzsch, H., Beierkuhnlein, C., Gohlke, A., and Wellstein, C. 2013. Climatic turning point for

- beech and oak under climate change in Central Europe. *Ecosphere* **4**(12): art145. doi:10.1890/ES13-00115.1.
- Meadows, J.S. and Burkhardt, E.C. 2001. Epicormic Branches Affect Lumber Grade and Value in Willow Oak. *Southern Journal of Applied Forestry* **25**(3): 136-141. doi:10.1093/sjaf/25.3.136.
- Nagel, T.A., Firm, D., Rozenbergar, D., and Kobal, M. 2016. Patterns and drivers of ice storm damage in temperate forests of Central Europe [journal article]. *European Journal of Forest Research* **135**(3): 519-530. doi:10.1007/s10342-016-0950-2.
- Neumann, M., Mues, V., Moreno, A., Hasenauer, H., and Seidl, R. 2017. Climate variability drives recent tree mortality in Europe. *Global Change Biology* **23**(11): 4788-4797. doi:10.1111/gcb.13724.
- Nyland, R.D., Dalton, J.L., Allen, D.C., and Bevilacqua, E. 2016. Response of ice-damaged northern hardwood stands in northern New York. *The Forestry Chronicle* **92**(1): 77-89. Available from <http://pubs.cif-ifc.org/doi/abs/10.5558/tfc2016-020> [accessed 2017/02/09/10:56:45].
- Proulx, O.J. and Greene, D.F. 2001. The relationship between ice thickness and northern hardwood tree damage during ice storms. *Canadian Journal of Forest Research* **31**(10): 1758-1767. doi:10.1139/cjfr-31-10-1758.
- R Core Team. 2013. R: a language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org/>.
- Raudenbush, S.W., Yang, M.L., and Yosef, M. 2000. Maximum likelihood for generalized linear models with nested random effects via high-order, multivariate Laplace approximation. *J Comput Graph Stat* **9**(1): 141-157. doi:Doi 10.2307/1390617.
- Robinson, A.P., Hamann, J.D., 2011. *Forest Analytics with R: An Introduction*. Springer, New York.
- Scharnweber, T., Manthey, M., Criegee, C., Bauwe, A., Schröder, C., and Wilmking, M. 2011. Drought matters – Declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. *Forest Ecol Manag* **262**(6): 947-961. doi:<https://doi.org/10.1016/j.foreco.2011.05.026>.
- Sheil, D. and May, R.M. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* **84**(1): 91-100. doi:Doi 10.2307/2261703.
- Shortle, W.C., Smith, K.T., and Dudzik, K.R. 2014. Tree survival 15 years after the ice storm of January 1998. *USDA For. Serv. Res. Pap. NRS-25*: 4.
- Shortle, W.C., Smith, K.T., Dudzik, K.R., and others. 2003. Tree survival and growth following ice storm injury [US For. Serv. Res. Paper NE-723]. 4. Available from http://www.fs.fed.us/ne/newtown_square/publications/research_papers/pdfs/2003/rpn_e723.pdf [accessed 2015/09/14/08:49:25].
- Sinjur, I., Vertačnik, G., Likar, L., Hladnik, V., Miklavčič, I., and Gustinčič, M. 2014. Ice storm in Slovenia in January and February 2014 – Spatial and temporal variability in weather across the dinaric landscapes in Slovenia. *Gozdarski vestnik* **72**(7-8): 299-309.
- Turcotte, R.M., Elliott, T.R., Fajvan, M.A., Park, Y.-L., Snider, D.A., and Tobin, P.C. 2012. Effects of Ice Storm Damage on Hardwood Survival and Growth in Ohio. *Northern Journal of Applied Forestry* **29**(2): 53-59. doi:10.5849/njaf.10-053.
- Whitney, H.E. and Johnson, W.C. 1984. Ice Storms and Forest Succession in Southwestern Virginia. *Bull. Torrey Bot. Club* **111**(4): 429. doi:10.2307/2995892.
- Wolfinger, R. and Oconnell, M. 1993. Generalized Linear Mixed Models - a Pseudo-Likelihood Approach. *J Stat Comput Sim* **48**(3-4): 233-243. doi:Doi 10.1080/00949659308811554.

Zhou, B., Gu, L., Ding, Y., Shao, L., Wu, Z., Yang, X., Li, C., Li, Z., Wang, X., Cao, Y., Zeng, B., Yu, M., Wang, M., Wang, S., Sun, H., Duan, A., An, Y., Wang, X., and Kong, W. 2011. The great 2008 Chinese ice storm its socioeconomic-ecological impact and sustainability lessons learned. *Bulletin of The American Meteorological Society* **92**(1): 47+. doi:10.1175/2010BAMS2857.1.

Table 1 Elevation and tree species composition of the four research stands included in the study.

Study site	Roznik	Oblakov gozd	Tolmin	Laze
Elevation	350	350	600	550
Species (%)				
<i>Fagus sylvatica</i>	1	54	51	97
<i>Quercus petraea</i>	43	37	3	-
<i>Acer pseudoplatanus</i>	1	-	14	-
<i>Castanea sativa</i>	28	1	5	-
<i>Picea abies</i>	13	-	1	-
<i>Pinus sylvestris</i>	14	8	0	-
<i>Fraxinus excelsior</i>	-	-	11	-
Other	1	-	15	2
Total basal area (m ² /ha)	22	28	33	33

Table 2 Number of trees (N), crown damage, and annual mortality rates for the dominant tree species.

Tree species	N	Crown damage class			Mortality rate
		< 25%	25-75%	> 75%	%
Oak	190	5 %	26 %	69 %	4.4
Chestnut	118	14 %	27 %	59 %	3.8
Beech	404	8 %	40 %	52 %	0.9
Maple	51	18 %	37 %	45 %	0.7
Total	763				2.2

Table 3 Effects of DBH, crown damage, and tree species on survival of trees after the ice storm.

	Estimate	Std. Error	z value	P (> z)
Intercept	11.23	3.18	3.53	0.0004
DBH	0.05	0.02	3.34	0.0008
Crown damage	-3.20	1.00	-3.20	0.0013
Chestnut	-1.56	1.07	-1.46	0.1455
Beech	0.01	1.07	0.01	0.9924
Oak	-1.86	1.05	-1.76	0.0778

Note: Maple was used as a reference level for the categorical factor tree species.

Table 4 Results of GLMM analyses showing the effects of different variables on bole sprout length, crown sprout length, and number of bole sprouts per m of bole.

Bole sprouts length					
	Value	Std.Error	DF	t-value	p-value
Intercept	0.8811	0.0606	622	14.53	0.0000
Basal area	-0.0038	0.0011	622	-3.56	0.0004
Crown damage	0.0927	0.0131	622	7.06	0.0000
Chestnut	-0.0522	0.0397	622	-1.32	0.1886
Beech	-0.5583	0.0319	622	-17.49	0.0000
Oak	-0.4315	0.0389	622	-11.09	0.0000
Crown sprouts length					
	Value	Std.Error	DF	t-value	p-value
Intercept	0.6880	0.0566	368	12.15	0.0000
DBH	0.0051	0.0007	368	6.64	0.0000
Crown damage	0.0391	0.0142	368	2.74	0.0064
Chestnut	-0.2876	0.0448	368	-6.42	0.0000
Beech	-0.5462	0.0356	368	-15.31	0.0000
Oak	-0.5072	0.0438	368	-11.57	0.0000
Number of bole sprouts per m of bole					
	Value	Std.Error	DF	t-value	p-value
Intercept	0.7840	0.1492	679	5.25	0.0000
DBH	-0.0074	0.0018	679	-4.06	0.0001
Crown damage	0.1046	0.0299	679	3.50	0.0005
Chestnut	0.4663	0.0938	679	4.97	0.0000
Beech	-0.3038	0.0740	679	-4.10	0.0000
Oak	0.3270	0.0945	679	3.46	0.0006

Note: Maple was used as a reference level for categorical factor tree species.

Figure 1 Locations of the four stands selected for study. (Map: Slovenia Forest Service, Gal Kušar, June 2016)

Figure 2 Number of trees according to tree species, DBH and crown damage

Figure 3 Bole and crown sprouting intensity according to tree species.

Figure 4 Epicormic sprouting of maple (left) and beech (right) three years after the ice storm.

Table 1 Elevation and tree species composition of the four research stands included in the study.

Study site	Roznik	Oblakov gozd	Tolmin	Laze
Elevation	350	350	600	550
Species (%)				
<i>Fagus sylvatica</i>	1	54	51	97
<i>Quercus petraea</i>	43	37	3	-
<i>Acer pseudoplatanus</i>	1	-	14	-
<i>Castanea sativa</i>	28	1	5	-
<i>Picea abies</i>	13	-	1	-
<i>Pinus sylvestris</i>	14	8	0	-
<i>Fraxinus excelsior</i>	-	-	11	-
Other	1	-	15	2
Total basal area (m ² /ha)	22	28	33	33

Table 2 Number of trees (N), crown damage, and annual mortality rates for the dominant tree species.

Tree species	N	Crown damage class			Mortality rate
		< 25%	25-75%	> 75%	%
Oak	190	5 %	26 %	69 %	4.4
Chestnut	118	14 %	27 %	59 %	3.8
Beech	404	8 %	40 %	52 %	0.9
Maple	51	18 %	37 %	45 %	0.7
Total	763				2.2

Table 3 Effects of DBH, crown damage, and tree species on survival of trees after the ice storm.

	Estimate	Std. Error	z value	P ($> z $)
Intercept	11.23	3.18	3.53	0.0004
DBH	0.05	0.02	3.34	0.0008
Crown damage	-3.20	1.00	-3.20	0.0013
Chestnut	-1.56	1.07	-1.46	0.1455
Beech	0.01	1.07	0.01	0.9924
Oak	-1.86	1.05	-1.76	0.0778

Note: Maple was used as a reference level for the categorical factor tree species.

Table 4 Results of GLMM analyses showing the effects of different variables on bole sprout length, crown sprout length, and number of bole sprouts per m of bole.

Bole sprouts length					
	Value	Std.Error	DF	t-value	p-value
Intercept	0.8811	0.0606	622	14.53	0.0000
Basal area	-0.0038	0.0011	622	-3.56	0.0004
Crown damage	0.0927	0.0131	622	7.06	0.0000
Chestnut	-0.0522	0.0397	622	-1.32	0.1886
Beech	-0.5583	0.0319	622	-17.49	0.0000
Oak	-0.4315	0.0389	622	-11.09	0.0000

Crown sprouts length					
	Value	Std.Error	DF	t-value	p-value
Intercept	0.6880	0.0566	368	12.15	0.0000
DBH	0.0051	0.0007	368	6.64	0.0000
Crown damage	0.0391	0.0142	368	2.74	0.0064
Chestnut	-0.2876	0.0448	368	-6.42	0.0000
Beech	-0.5462	0.0356	368	-15.31	0.0000
Oak	-0.5072	0.0438	368	-11.57	0.0000

Number of bole sprouts per m of bole					
	Value	Std.Error	DF	t-value	p-value
Intercept	0.7840	0.1492	679	5.25	0.0000
DBH	-0.0074	0.0018	679	-4.06	0.0001
Crown damage	0.1046	0.0299	679	3.50	0.0005
Chestnut	0.4663	0.0938	679	4.97	0.0000
Beech	-0.3038	0.0740	679	-4.10	0.0000
Oak	0.3270	0.0945	679	3.46	0.0006

Note: Maple was used as a reference level for categorical factor tree species.

Figure 1 Locations of the four stands selected for study (Map: Slovenia Forest Service, Gal Kušar, June 2016)

178x123mm (600 x 600 DPI)

Figure 2 Number of trees according to tree species, DBH and crown damage

166x149mm (600 x 600 DPI)

Figure 3 Bole and crown sprouting intensity according to tree species.

175x60mm (600 x 600 DPI)

Figure 4 Epicormic sprouting of maple (left) and beech (right) three years after the ice storm.

85x128mm (600 x 600 DPI)