

Pruning revisited – effect of pruning season on wood discoloration and occlusion in four temperate broadleaved tree species

Anna Lund*, Anna Levinsson, Johan Östberg and Björn Wiström

Swedish University of Agricultural Sciences, Department of Landscape Architecture, Planning and Management, Box 190, 234 22 Lomma, Sweden

*Corresponding author Tel: +46 40-41 50 00; Email: anna.lund@slu.se

Received 6 May 2022

Pruning is a necessary part of tree management both in silvicultural systems and in urban forestry. For the wood industry's production of high-quality timber, as well as for the urban forest's risk reduction and ecosystem services enhancements, it is essential that the pruning is accurately implemented. This study aimed to determine the effect of pruning season on discoloration amount and occlusion rate in four broadleaved tree species. In 2014, 84 trees were pruned in January, May and September. Six years later, the 252 samples from the three pruning points per tree were collected and analysed. 'Common oak (*Quercus robur* L.)' and 'small-leaved lime (*Tilia cordata* Mill.)' showed least discoloration when pruned in January, 'wild cherry (*Prunus avium* L.)' showed least discoloration when pruned in September and 'Norway maple (*Acer platanoides* L.)' did not show any significant differences. All species occluded fastest when pruned in January, but at different rates. Common oak occluded 84 per cent of the samples, Norway maple 42 per cent, small-leaved lime 32 per cent and wild cherry 13 per cent. In summary, the pruning month affected discoloration amounts and occlusion rates of the tested tree species in varied ways. Our research suggests an important knowledge gap regarding optimal species-specific pruning times and underlying reasons for different reactions to pruning.

Introduction

Pruning is an important part of tree management in both forestry and urban contexts. Trees in silvicultural systems are pruned to attain high-quality timber, and in turn higher economic return (O'Hara, 2007; Hemery *et al.*, 2008; Oosterbaan *et al.*, 2008). In urban environments, pruning is considered necessary to ensure low risk of damage, sufficient space and maintained or improved aesthetic values (Dujesiefken *et al.*, 2005; James *et al.*, 2006). However, despite its importance, the knowledge of *when* to prune is an understudied topic.

Trees react to pruning cuts internally by chemical reactions in the wood, encapsulating discoloration, and externally by callus wood forming over the cut, also called occlusion (Shigo and Marx, 1977). The discoloured wood develops from the cutting surface, resulting in decreased economic value in high-quality timber (Oosterbaan *et al.*, 2008). Discoloration may also develop into decay, leading to increased likelihood of failure and reduced tree vitality (Dujesiefken *et al.*, 2005). Discoloured wood can be caused by either internal cell changes or by bacteria, fungi or algae (Smith, 2006; Schmidt, 2006a), and these different causes often coexist. The external occlusion was described through the Compartmentalization of Decay in Trees model by Shigo and Marx (1977). 'Decay' was later exchanged for 'Dysfunction' since it is a more inclusive term (Smith, 2012). Time of pruning, as well as

cut size and cut type, have been found to affect the amount of discoloration and occlusion rate when pruning (Pietzarka, 2016).

For decades, as seen in arboriculture (Pietzarka, 2016) and silviculture textbooks (Falck, 2014), there has been an assumption that it is preferable to prune trees during the growing season after leaf formation and before leaf senescence, an assumption that most likely gained large influence through Shigo's (1991) *Modern Arboriculture*. Shigo's argumentation departs from Priestley's (1970) work, with the so-called 'Askenasy Potential Energy Curve' departing from studies by Akenasy (1877a; Askenasy, 1877b; Askenasy, 1877c) on 'wild cherry (*Prunus avium* L.)'. In the Askenasy Potential Energy Curve, it is conceptualized that the energy levels decrease at leaf formation, increase when the leaves are formed and stays high during the vegetation period, leading to the practical assumption that pruning is suitable during the trees' active period with high energy levels (Shigo, 1991). Hiron's (2012) questions the generalizability of the Akenasy curve for guiding pruning since it originates from studies of only one species. Hoch *et al.* (2003), who studied non-structural carbohydrates (NSCs) in 10 different tree species, found that newly formed leaves generally become carbon sources at an early developmental stage, implying that the time of deep energy reduction during leaf formation assumed by the Askenasy curve might be very

Handling Editor: Dr. Somidh Saha

© The Author(s) 2023. Published by Oxford University Press on behalf of Institute of Chartered Foresters.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

short, or not as deep as assumed. Hoch *et al.* (2003) also studied wild cherry and found it to look similar to the Askenasy curve, but in general, broadleaved tree species had an increase of NSC in branch wood at the time of bud break, whereas NSC in stem wood had no significant decrease. New leaves and shoots seem to primarily use new, not stored, carbohydrates to develop (Hoch *et al.*, 2003).

Occlusion of pruning cuts is simplified a two-sided process with the cambium at the cut 'pushing' out new wood over it and radial growth adding new wood outside, 'rolling' in over the cut (e.g. Falk, 2014). Several studies within silviculture (e.g. Hein and Spiecker, 2007; Sheppard *et al.*, 2016) have therefore focused on the relation between radial growth and pruning since radial (diameter by breast height (DBH)) growth can be controlled by thinning (e.g. Spiecker, 2006). However, only a few former studies focus on statistical testing of species-specific pruning month and its relation to discoloration and occlusion. Niemistö *et al.* (2019) found 'silver birch (*Betula pendula* Roth)' to occlude fastest when pruned in spring, March to June. A similar study with 'red alder (*Alnus rubra* Bong.)' found the occlusion rate to be fastest when pruning was performed in spring/summer, May to June, and in autumn, September (DeBell *et al.*, 2006). Dujesiefken *et al.* (2005) injured 'common beech (*Fagus sylvatica* L.)', common oak and 'northern red oak (*Quercus rubra* L.)' in their study and found the occlusion rate to be fastest in spring and autumn, April and October, respectively. Another study pruned 'sycamore maple (*Acer pseudoplatanus* L.)' during its dormant season and found no significant differences in occlusion rate between December, January, February and March (Fini *et al.*, 2013). Dănescu *et al.* (2015) found a significant difference between sycamore maple and 'European ash (*Fraxinus excelsior* L.)'. The latter occluded slightly faster than the former, but with no difference in season of pruning.

The least discoloration was found when silver birch were pruned in early autumn, late August (Niemistö *et al.*, 2019). Common oak and northern red oak showed least discoloration in winter and spring, February and April respectively, and common beech showed no significant results in discoloration between months, except for in December when the discoloration was greatest (Dujesiefken *et al.*, 2005). Sycamore maple and European ash had no significant differences in terms of discoloration, neither between seasons, nor between species (Dănescu *et al.*, 2015). The same was observed for 'sandalwood (*Santalum album* L.)' (Burgess *et al.*, 2018). Grabosky and Gilman (2007) did not study pruning month but found no significant difference in discoloration between 'live oak (*Quercus virginiana* Mill.)' and 'shumard oak (*Quercus shumardii* Buckley)' when pruned in spring, April.

A limited number of studies have focused on the relationship between pruning season and discoloration and occlusion, and only a few broadleaved tree species from different genera have been examined. Consequently, the question whether an ideal pruning month exists is not fully answered. Based on this, the aim of this study was to increase the knowledge of pruning time optimum to support tree managers' decision-making. The objective was to examine the relationship between amount of discoloration, occlusion rate and pruning month in four different broadleaved tree species. The research question was, 'Which is the most suitable season of the year to prune broadleaved

trees, when aiming for fast occlusion and minimal amount of discoloration?'

Materials and methods

Materials and experimental set up

The study was set up in 2014 in southern Sweden (55.39°N; 13.04°E) at the Swedish University of Agricultural Sciences in the Alnarp landscape laboratory. This is located on former agricultural land with loamy glacial till and fine sand deposits, average pH 7.1 and uniform nitrogen level across the site (0.005 mg g dw⁻¹) (Bubi, 2009; Wiström and Nielsen, 2014).

The study included four native species: 'wild cherry (*P. avium* L.)', 'common oak (*Quercus robur* L.)', 'Norway maple (*Acer platanoides* L.)' and 'small-leaved lime (*Tilia cordata* Mill.)', selected based on the following criteria (Table 1): utilized in urban settings (Sjöman *et al.*, 2012), forest industry interest (Oosterbaan *et al.*, 2008), different wood anatomy (Baas and Schweingruber, 1987; Schoch *et al.*, 2004; Pigott, 2012; Crivellaro and Schweingruber, 2013; Richter and Dallwitz, 2019) and assumed compartmentalization ability (Schmidt, 2006b; Gilman, 2012).

Norway maple (0.27 ha) and small-leaved lime (0.25 ha) grew in pure stands planted in 1994, and wild cherry and common oak grew in a mixed stand (0.5 ha) planted in 1998. For the study, 84 trees – 21 trees per species – were randomly selected among dominant and co-dominant trees in the stands and ID-marked. We thinned the mixed stand in the winter of 2014–2015, to achieve similar density to the other stands; from ~6000 to ~3600 trees/ha (Table 2).

Experiment initiation and pruning

The experiment started in 2014, when the treatments took place. We pruned every tree on each of the three pruning occasions; winter: January (28 January 2014), late spring: May (08 May 2014) and early autumn: September (04 September 2014), which resulted in three cuts per tree at the end of the year (Table 3). The months were selected to represent pruning on dormant trees in the winter (January), leaf-flush (May) and the latter part of the active period (September), where the last one is considered ideal in many pruning textbooks (e.g. Pietzarka, 2016). We adopted a balanced randomization for the relative height between pruning occasions. The lowest branch alive was identified as starting point for selection of branches to cut, together with at least two other suitable branches above that (i.e. not too close to each other). Seven trees per species were then selected randomly and cut starting with the lowest branch, seven from the first above that (middle branch) and seven above that (highest branch). We continued to prune seven trees per relative height for each tree species and date (Table 3), in other words 21 pruning cuts/species/pruning occasion, 63 pruning cuts/species and 252 pruning cuts in total.

We pruned the branches with a pole saw, using natural target pruning as the method, i.e. cutting right outside the branch collar (ANSI, 2017; O'Hara, 2007; SIS, 2020). We recorded the height of the pruned branches using a measuring pole to be able to later identify which knots were pruned on which occasion (Table 4). Branch angle and pruning cut length were measured

Table 1 Selection criteria of species included in the study. 1: Baas and Schweingruber 1987; Richter and Dallwitz, 2009; Schoch et al., 2004, 2: Baas and Schweingruber 1987; Richter and Dallwitz, 2009; Schoch et al., 2004; Crivellaro and Schweingruber, 2013, 3: Baas and Schweingruber 1987; Schoch et al., 2004; Pigott 2012, 4: Gilman 2012; Schmidt 2006a.

Species	<i>Acer platanoides</i>	<i>Prunus avium</i>	<i>Quercus robur</i>	<i>Tilia cordata</i>
Wood anatomy	Diffuse porous ¹	Diffuse porous ²	Ring porous ¹	Semi-ring porous ³
Compartmentalization ability⁴	Weak	Weak	Strong	Strong
Other characteristics	Pre-leaf flowering	Pre-leaf flowering		

Table 2 Stand and tree attributes; stand density and DBH for each species.

Species	<i>Acer platanoides</i>	<i>Prunus avium</i>	<i>Quercus robur</i>	<i>Tilia cordata</i>
Stand density, trees/ha	2600	3600	3600	3100
2020 mean DBH, SD (cm)	13.93, 2.57	11.94, 1.92	14.66, 2.55	17.50, 3.18

Table 3 Schematic table visualizing the number of trees pruned on each occasion and the relative height for each species. The letters represent the relative height of the branches, H = highest branch, M = middle branch and L = lowest branch.

TreeID	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
January	L	H	L	M	M	H	H	H	M	H	L	M	L	M	L	L	H	M	H	L	M
May	M	M	M	L	H	M	M	L	L	L	H	L	M	H	H	M	L	H	L	H	H
September	H	L	H	H	L	L	L	M	H	M	M	H	H	L	M	H	M	L	M	M	L

Table 4 Branch attributes for each species. Branch angle, pruning cut length and pruning height in mm.

	Min	Mean	Max	SD
<i>Acer platanoides</i>				
Branch angle	19.02	40.39	55.85	7.65
Pruning cut length	14.17	47.97	101.25	17.55
Pruning height	215.00	393.70	654.00	102.50
<i>Prunus avium</i>				
Branch angle	23.23	48.46	72.21	9.19
Pruning cut length	11.14	33.09	97.76	14.07
Pruning height	105.00	449.00	720.00	114.99
<i>Quercus robur</i>				
Branch angle	19.52	45.20	75.89	13.03
Pruning cut length	14.13	42.50	111.51	21.04
Pruning height	50.00	436.00	633.00	150.57
<i>Tilia cordata</i>				
Branch angle	19.41	42.11	79.52	12.11
Pruning cut length	25.14	55.97	128.52	21.02
Pruning height	168.00	382.30	607.00	101.92

using ImageJ after felling (Table 4). The pruning cut length is the diameter of the pruning cut measured in the longitudinal direction, visualized in Figure 2. Pruning height represents the height of the branch pruned, measured from the ground up.

Sample harvesting and preparation

Six years later, in January 2020, we revisited the stands. A professional arborist felled the trees with a chain saw and split the stems into sections. The pruning wounds from 2014 were thereby

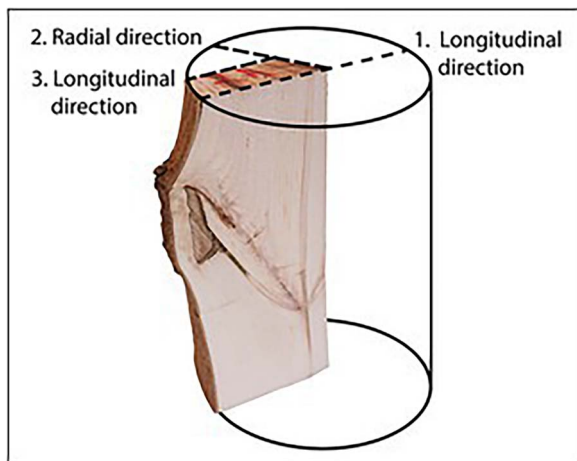


Figure 1 Illustration of how the sections were sawed to expose the pruning knot.

cut free 10 cm above and 20 cm below the knot, resulting in 30 cm long sections as described by Dănescu *et al.* (2015) and Qin *et al.* (2019). We marked the sections with the ID-number and a letter, H, M or L, representing the relative height of the cuts.

To expose the insides of the pruning knots, we split the sections with a band saw in a longitudinal direction at the centre of the knot and pith (Figure 1). A radial and another longitudinal cut attained smaller, equally thick samples.

The samples were dried in a drying cabinet at 35°C for 96 h (Thermo Scientific Heratherm Advanced Protocol Oven, Heratherm OGS400). We sanded the samples using a bench belt sander and 40 grit sanding paper to achieve the exact angle between pith and knot, and 120 grit sanding paper was used to polish and reinforce the wood patterns. The samples were cleaned from sawdust using an air compressor.

Five samples were destroyed due to poor foresight during the initial pruning, as knots were located too close together to allow correct angle cuts. In addition, while checking for distinct pruning cuts, we found 10 samples that were not the 2014 cuts, but had naturally died or were broken branches. These 10 samples were also discarded. Due to these shortcomings, 237 samples were included in the analysis. Total samples per species were Norway maple: 56, small-leaved lime: 62, wild cherry: 61 and common oak: 58.

Analysis of samples

We divided the analyses into two phases. The first phase focused on discoloration and the second phase focused on occlusion.

We scanned the samples using EPSON Perfection V800 Photo, and the software Silverfast 8.0. The image settings were 1200 ppi, A4 format and saved as TIFF files. We analysed the images with the software ImageJ (ImageJ 1.52a) where a calibration was made and saved as a macro to maintain the same calibration for all images. The measurements taken with ImageJ are represented in Table 5 and Figure 2.

We sanded the samples again with a finer sandpaper, up to 800 grit, to refine the wood structure and enhance the year rings. We determined which year the samples fully occluded

using a stereomicroscope. We then scanned them and took new measurements using ImageJ to measure non-occluded length for each year and thereby attain the occlusion rate per year. Since the trees were pruned in January, May and September, then felled all at once in January 6 years later, they had different amounts of time to react by occlusion and discoloration. By determining exactly which year the samples fully occluded, we obtained more information on how many growing seasons the samples needed to fully occlude.

Statistics

Statistical overview

All models and statistical analyses were performed in the statistical program R (R version 3.6.1) (R Core Team, 2019) with the software RStudio (RStudio Team, 2019) (Version 1.2.5019) using the following functional libraries: lme4 (Bates *et al.*, 2015), lmerTest (Kuznetsova *et al.*, 2017), emmeans (Lenth *et al.*, 2019), multcompView (Graves *et al.*, 2019), ggplot2 (Wickham, 2016), dplyr (Wickham *et al.*, 2020), gt (Iannone *et al.*, 2020) and MuMIn (Bartoń, 2022), with a significance level of 0.05.

Modelling approach

Four different response variables were modelled separately as mixed models: discoloration, occlusion rate, radial rate and occlusion probability, as presented in each section below. The experiment has a hierarchical structure with repeated measurement within trees, often referred to as split-plot design without blocks. This hierarchical structure was regarded in the statistical models by nesting the species under the tree in the random part of the models.

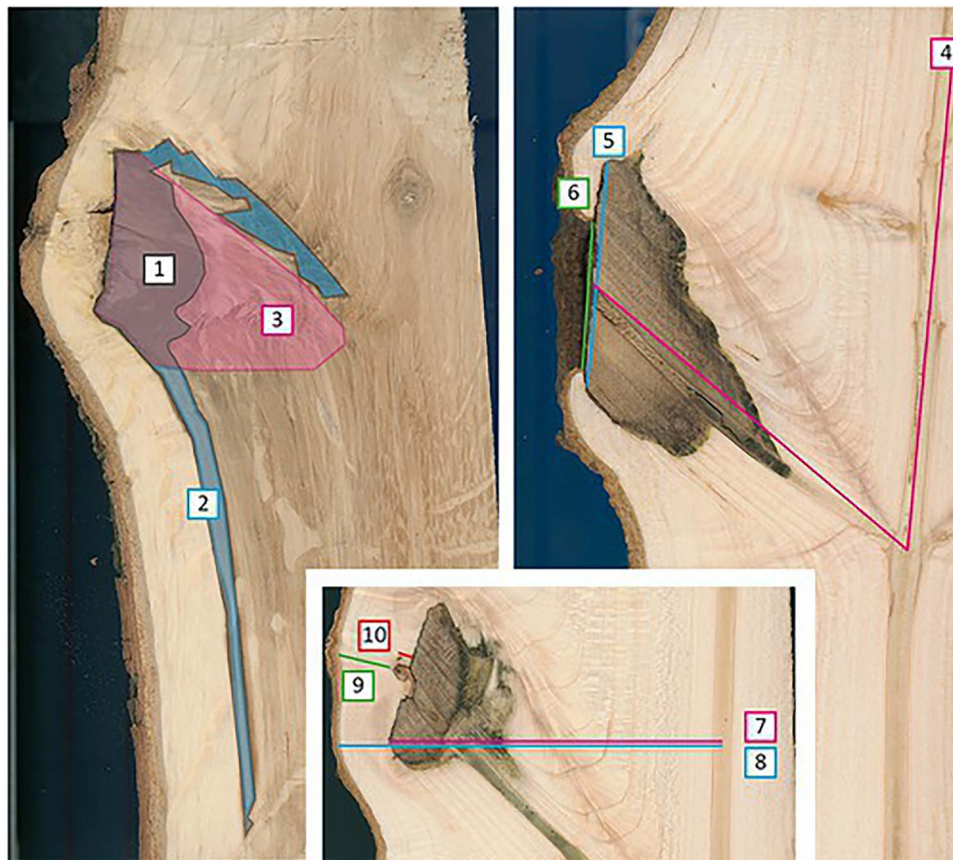
For all the models, the main experimental variables, i.e. species (4 levels) and month (3 levels), including their interactions, were first included as the fixed part of the model and tested using ANOVA Type III with Kenward-Roger approximation for the degrees of freedom. Then individual covariates of relevance based on earlier research were included one by one to safeguard against multicollinearity and overfitting. This gives the following base equation for all the general linear models tested and corresponding generalized linear model with logit as a link function:

$$y_{ijk} = \alpha_i + \tau_j + (\alpha\tau)_{ij} + \delta_{ik} + \text{covariates} + \varepsilon_{ijk}, i = 1, \dots, 4, j = 1, 2, 3, k = 1, \dots, 21$$

Covariates tested for inclusion in the final models were pruning cut length ($M=44.9$ mm, $SD=20.37$), aspect ratio ($M=0.33$, $SD=0.16$), branch departure angle ($M=44.1$, $SD=11.1$) and height of the pruning cut above ground ($M=415.3$ cm, $SD=121.7$), all which have shown correlation to discoloration and occlusion in other studies (Eisner *et al.*, 2002; Sheppard *et al.*, 2016; Wang *et al.*, 2016; Niemistö *et al.*, 2019; Qin *et al.*, 2019). The covariates were evaluated for their significance using ANOVA Type III test with Kenward-Roger approximation. The different models were compared against each other using Akaike's Information Criteria (AIC) values as a measure

Table 5 Measurements taken in ImageJ; the numbers correspond to those in Figure 2.

Nr	Name	Description	Unit
1	Area 1	Total discoloration.	mm ²
2	Area 2	Discoloration outside the branch area.	mm ²
3	Area 3	Estimated branch area inside the stem.	mm ²
4	Branch departure angle	Angle between the stems' direction and along the branch, from pith to branch cut.	°
5	Length of pruning cut	The diameter of the pruned branch.	mm
6	Length, not occluded	The diameter of the pruned branch that was not occluded.	mm
7	Stem radius 1	Stem radius 2014, length from pith to pruning cut. This was made to backtrack the radius of the samples when pruned.	mm
8	Stem radius 2	Stem radius 2020, length from pith to bark. Represented the radius of samples when felled.	mm
9	Defect free wood	Defect free wood outside knot, measured between pruning cut and bark.	mm
10	Defect wood	Defect wood outside knot, measured between pruning cut and bark.	mm

**Figure 2** Image describing the measurements taken in ImageJ; the numbers correspond to those in Table 5.

of model parsimony and one final model was selected for each of the response variables. Post hoc tests for the final models were performed using estimated marginal means and Tukey's method for multiple comparisons. Model validation, including assumptions of linearity, independence, normality and homoscedasticity, was performed by plotting the residuals of the models.

Discoloration

Since the trees were pruned at different times but were felled on the same date, the reaction time differs between samples pruned in January, May and September. Since it is not possible to determine the exact discoloration change over time, and thus adjust the values per individual year, the discoloration area was

Table 6 ANOVA table for (log) discoloration per growth season of species, months, pruning cut length and the interaction of species and month.

	Sum Sq	Mean Sq	Num DF	Den DF	F-value	P-value
Species	35.984	11.995	3	82.683	53.8056	<0.001
Month	3.063	1.531	2	154.302	6.8698	0.001
Pruning cut length	44.191	44.191	1	217.533	198.2378	<0.001
Species:Month	9.685	1.614	6	151.227	7.2413	<0.001

divided by 5 growing seasons for September and 6 for January and May to give an average discoloration area per year since pruning. This average was used as response for the discoloration model. Using the exact number of total months from pruning to felling instead as correction for this did not affect the main results from the models. The response was log-transformed to fulfil the model assumptions. This gave the following linear mixed-effect model (function lmer) with discoloration (Area 1) per growth season log transformed as response:

$$\text{discoloration}_{ijk} = \alpha_i + \tau_j + (\alpha\tau)_{ij} + \delta_{ik} + \text{covariate} + \varepsilon_{ijk}, i = 1, \dots, 4, j = 1, 2, 3, k = 1, \dots, 21$$

Occlusion rate

As the number of years before occlusion between the samples differs, the observation window of occlusion length (i.e. total distance occluded of the pruning cut) varies between the different samples. This results in an unbalanced and sparse data structure if trying to analyse the data per individual year. To enable one joint model for the occlusion rate, the total occluded length was divided by the numbers of growing seasons before occlusion. For samples not occluded, these were divided by 5 growing seasons for September and 6 growing season for January and May, following the same approaches as for the discoloration. This gave the following linear mixed-effect model (function lmer) with occlusion rate as response:

$$\text{occlusion rate}_{ijk} = \alpha_i + \tau_j + (\alpha\tau)_{ij} + \delta_{ik} + \text{covariate} + \varepsilon_{ijk}, i = 1, \dots, 4, j = 1, 2, 3, k = 1, \dots, 21$$

Radial rate

Occlusion of pruning cuts happens both through the cambium 'pushing' out new wood over the cut and through radial growth adding new wood, 'rolling' in over the cut. Therefore, also the radial growth rate at the pruning cut was modelled as complement to the occlusion rate. Response for the radial rate was calculated as the stem radius in 2020 subtracted by the stem radius in 2014 (Table 5) divided by number of growth season observed (see section above). This gave the following linear mixed-effect model (function lmer) with radial rate as response:

$$\text{radial rate}_{ijk} = \alpha_i + \tau_j + (\alpha\tau)_{ij} + \delta_{ik} + \text{covariate} + \varepsilon_{ijk}, i = 1, \dots, 4, j = 1, 2, 3, k = 1, \dots, 21$$

Occlusion probability

As the September cuts have had less time to grow and occlude, we used an observation window of five growing seasons for the probability of occlusion model. Thus, the binary outcome if the pruning cut had occluded fully or not after five growing season was used as the response variable using a binomial generalized mixed-effect model with logit as a link function. The main fixed effects were species and month, including test of their interaction. Interaction was non-significant and dropped to aid model convergence and fit. Covariate in the final model was pruning cut length as an integer to aid computation of predicted probabilities. The use of pruning cutting length without decimals did not affect the main results of the model. Additional to visual evaluation of residuals-plots, we also tested for over-dispersion. This resulted in the following final generalized linear mixed-effect model (function glmer with logit function) with probability of occlusion after five growing seasons as response:

$$\text{logit}(p_{ijk}) = \alpha_i + \tau_j + \delta_{ik} + \text{covariate} + \varepsilon_{ijk}, i = 1, \dots, 4, j = 1, 2, 3, k = 1, \dots, 21$$

Results

Discoloration

The effect of pruning month, species and their interaction on discoloration per growing season were all significant (Table 6). Pruning cut length gave the best model fit (Table 7) with a significant effect and had a clear positive relationship for all species and pruning months (Figure 3).

The pairwise comparison of estimated means revealed both interspecies and intraspecies differences in the amount of discoloration between the different pruning occasions (Figure 4). For Norway maple (*Acer*), there was no difference between the three pruning occasions. Pruning wild cherry (*Prunus*) in September led to significantly less discoloration than pruning in May. Pruning common oak (*Quercus*) in January led to significantly less discoloration than pruning in either of the two other months. Pruning small-leaved lime (*Tilia*) in January led to significantly less discoloration than pruning in September. For Norway maple, there were no significant differences in discoloration between pruning months, both common oak and small-leaved lime had least discoloration in January, and wild cherry in September.

Occlusion rate

There was a significant effect of species ($F_3; 82.5 = 16.06$, $P < 0.001$), month ($F_2; 157.1 = 5.96$, $P < 0.01$) and pruning cut

Table 7 AIC values and marginal R^2 for the different covariates tested in modelling of Discoloration, Occlusion rate, Radial Rate and Occlusion Probability. The covariate with lowest AIC was chosen for the final model.

Covariate in model	Discoloration model		Occlusion rate model		Radial rate model		Occlusion probability model	
	AIC	R^2_{mar}	AIC	R^2_{mar}	AIC	R^2_{mar}	AIC	R^2_{mar}
Aspect ratio	447.5	0.356	1387.2	0.343	692.65	0.279	242.3	0.348
Branch angle	487.4	0.244	1411.1	0.294	702.99	0.259	245.1	0.342
Pruning cut length	355.4	0.585	1380.0	0.369	697.54	0.276	240.1	0.358
Height of cut	495.0	0.222	1411.8	0.292	703.11	0.259	249.1	0.318
Without covariate	496.0	0.213	1409.8	0.293	701.28	0.261	248.4	0.312

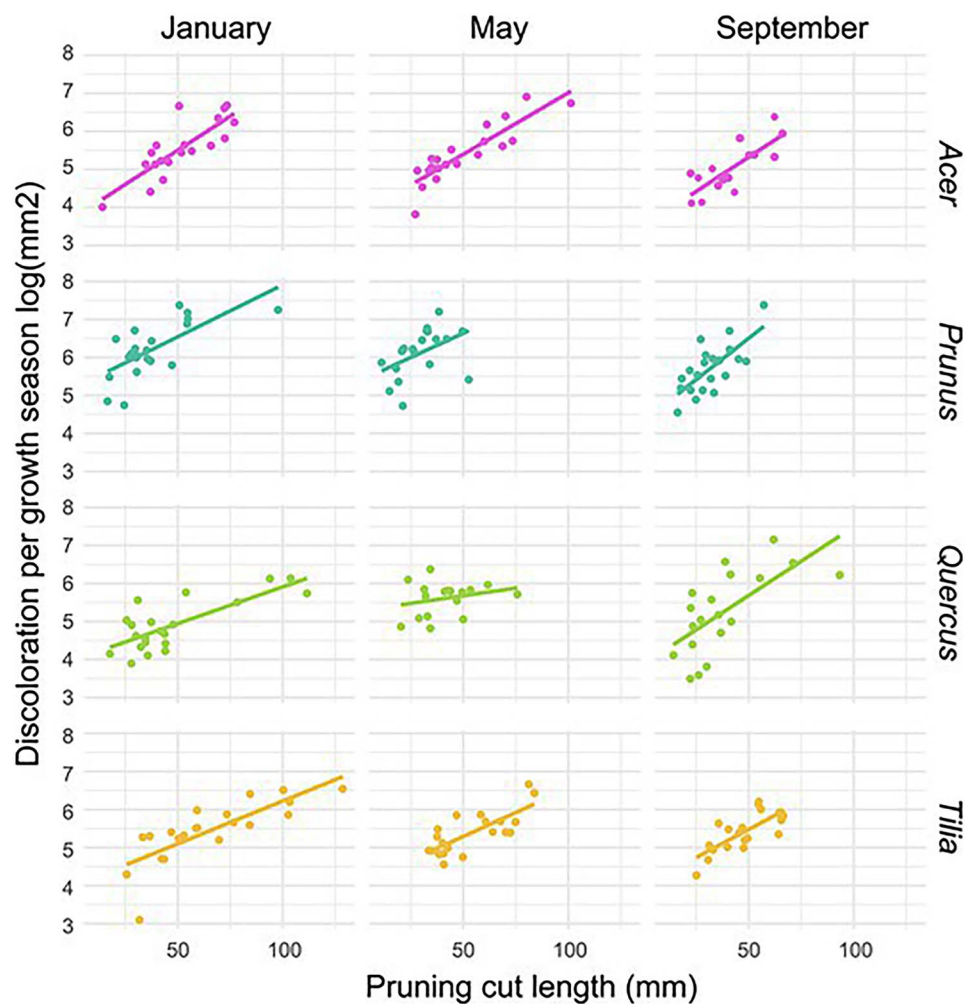


Figure 3 Discoloration by species and pruning month per growth season. Plot visualizing the relationship between pruning cut length (mm) and total discoloration per growth season $\log[(\text{mm}^2)]$ for each pruning month and species.

length ($F_{1; 226.0} = 31.82$, $P < 0.001$) on occlusion rate per growth season. No interaction effects were found and pruning cut length as covariate gave the lowest AIC value (Table 7). January cuts occluded significantly faster per growing season (7.3 mm, 95 per cent CI (confidence interval) [6.3–8.2]) than cuts in May

(5.9 mm, 95 per cent CI [4.8–6.9]) and September (5.2 mm, 95 per cent CI [4.2–6.3]). Common oak occluded significantly faster per year (10.5 mm, 95 per cent CI [9.0–12.1]) than Norway maple (5.8 mm, 95 per cent CI [4.2–7.3]), wild cherry (4.1 mm, 95 per cent CI [2.6–5.7]) and small-leaved lime (4.0 mm, 95 per

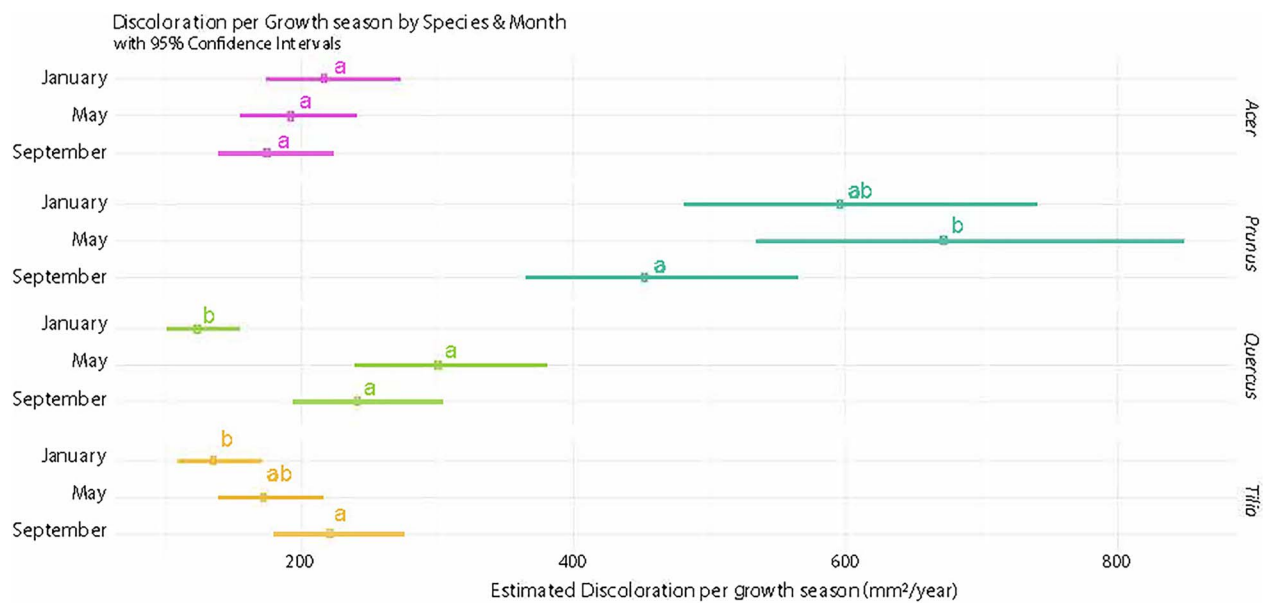


Figure 4 Discoloration per growth season by species and month. Estimated discoloration per growth season (mm²/year). The letters represent significant difference between pruning months within the species.

cent CI [2.5–5.6]) irrespective of pruning month. When plotting the occlusion rate year wise (data not shown), the pattern with January having the highest rate was evident for all years except the last, most likely due to the fact that more of them already had occluded then. There was also a marked drop of occlusion in the extremely dry summer of 2018.

Radial rate

There was a significant effect of species ($F_{3; 79.1} = 8.32, P < 0.001$) and month ($F_{2; 157.1} = 11.78, P < 0.001$) on radial rate per growing season. Both pruning cut length and aspect ratio ($F_{1; 210.2} = 10.96, P < 0.01$) had significant effects but aspect ratio gave a lower AIC value (Table 7). There was a small interaction effect ($F_{6; 149.7} = 2.46, P < 0.05$), with small-leaved lime having relatively lower values for September than other species. Looking at the main effects, January (2.5 mm, 95 per cent CI [2.2–2.7]) had a significantly higher radial rate than May (2.1 mm, 95 per cent CI [1.8–2.3]) and September (1.8 mm, 95 per cent CI [1.5–2.1]). Small-leaved lime (2.7 mm, 95 per cent CI [2.3–3.1]) had the fastest rate followed by common oak (2.4 mm, 95 per cent CI [2.0–2.8]), wild cherry (1.8 mm, 95 per cent CI [1.4–2.2]) and Norway maple (1.5 mm, 95 per cent CI [1.1–1.9]). Small-leaved lime was significantly faster than Norway maple and Wild cherry, the latter was also significantly slower than common oak.

Occlusion probability

At the time of harvest, 42 per cent of the samples were fully occluded, but the proportion differed amongst species. Wild cherry occluded 13 per cent of the samples, small-leaved lime 32 per cent of the samples, Norway maple 42 per cent of the samples and common oak 84 per cent of the samples.

Probability of full occlusion after five growing seasons included no significant interactions, and species, pruning month and pruning cut length all had a significant effect (Table 8) with pruning cut length as the covariate giving the lowest AIC value (Table 7). Common oak had the highest probability and wild cherry the lowest probability to occlude, regardless of pruning month (Figure 5, Table 8). January had a higher probability of occlusion (Figure 5), with no marked differences between May and September.

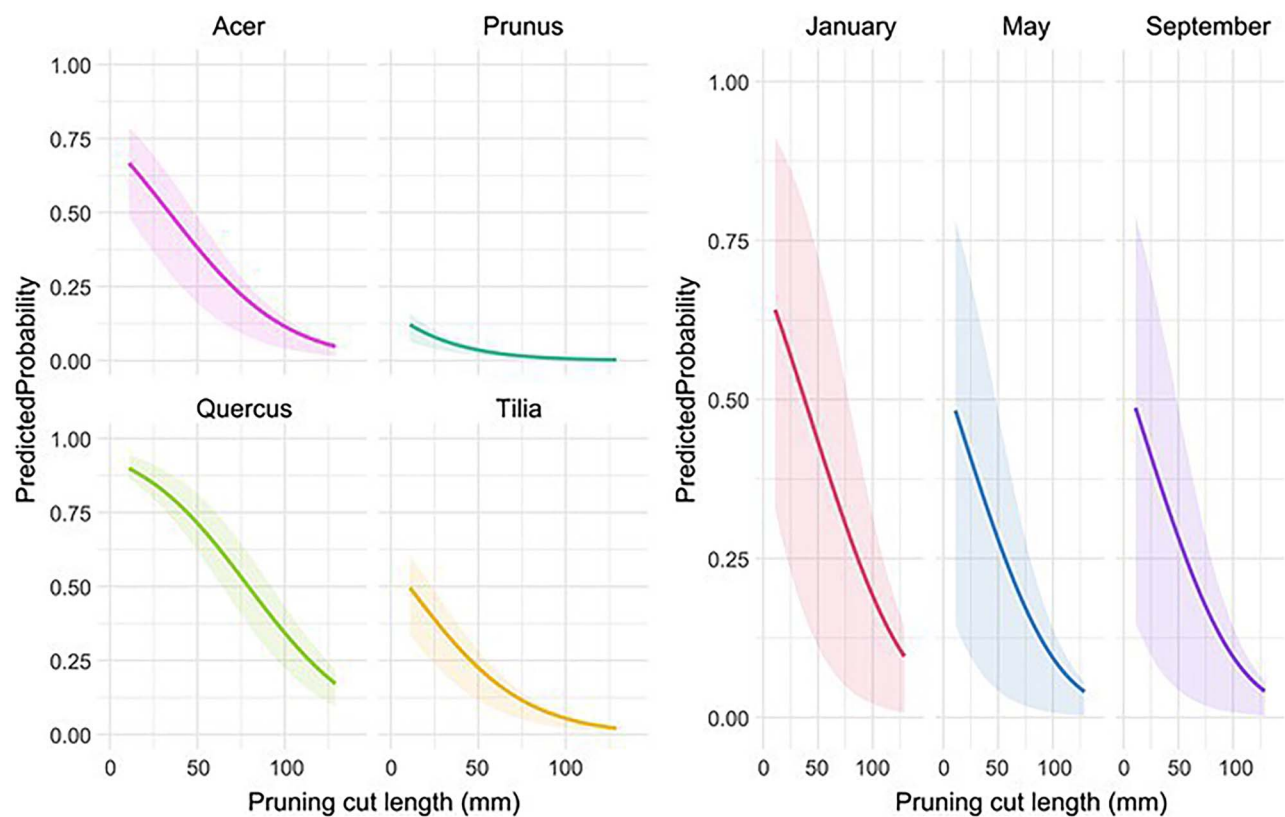
The relationship between probability of occlusion by month and pruning cut length was evident, as well as for species (Figure 5). This implies that the same pruning cut length made in January compared with May or September and/or on different species will have different probabilities to become occluded within a certain timeframe, although irrespective of this, a large cut increases the time until occlusion under all examined circumstances.

Discussion

Pruning is necessary in both silviculture and urban forestry, but is related to negative consequences. Discoloration of the wood surrounding the cutting locations can become a problem in both timber production in terms of less valuable wood, and in urban forestry in terms of reduced vitality and increased damage risks. Minimizing these negative effects of pruning is therefore of high importance. For decades there has been a qualified guess that it is best to prune during the growing season. This is likely based on Shigos' work (1991) and the idea that the energy levels of the trees, or NSCs, determine when it is best to prune. This assumption is still widespread despite the related research-based knowledge being very limited. To our knowledge, this study is the first to statistically test more than two species from several genera concerning discoloration and occlusion and the relationship to pruning season.

Table 8 Generalized linear mixed model fit by maximum likelihood (Laplace approximation). Summary of fixed effects for the hierarchical mixed binomial model of occlusion. Norway maple is used as reference level (Species) and January for the pruning occasion (Month).

	Estimate	Std. Error	z value	P-value
(Intercept)	1.845	0.754	2.446	0.014
SpeciesPrunus	-2.973	0.748	-3.971	<0.001
SpeciesQuercus	1.640	0.594	2.758	0.005
SpeciesTilia	-0.851	0.584	-1.456	0.145
MonthMay	-1.042	0.460	-2.266	0.023
MonthSeptember	-1.017	0.468	-2.173	0.029
CutLength	-0.034	0.011	-3.062	0.002
Random effects				
Groups	Name	Variance	Std.Dev.	
Tree:Species	(Intercept)	0.02368	0.1539	
Residual		0.22292	0.4721	

**Figure 5** Left panel: predicted probability of occlusion by species and pruning cut length (mm) with confidence band of lower and upper quartiles. Right panel: predicted probability of occlusion by pruning month and pruning cut length (mm) with confidence band of lower and upper quartiles.

The best pruning season, regarding both occlusion and discoloration, clearly differed between species. This confirms what previous studies have shown (Dujesiefken *et al.*, 2005; DeBell *et al.*, 2006; Fini *et al.*, 2013; Dănescu *et al.*, 2015; Burgess *et al.*, 2018; Niemistö *et al.*, 2019). In our study, the amount of discoloration also varied between the species. Several authors have emphasized the interspecies variation in capacity to prevent spreading of discoloration. Morris *et al.* (2019) argues that species-specific variation in production and composition of secondary

metabolites is important for the reaction of a tree to pruning, since secondary metabolites largely function as a defence system. Barry *et al.* (2000) describes the amount and distribution of phenols and suberins, moisture content, mineral content and pH-value as important aspects in compartmentalization. Baum and Schwarze (2002) agree that these chemical compounds are important for the defence system, and that there is a variation between species. Furthermore, Boddy's (2001) theory of latent propagules and fungi composition, supported by Sieber (2007)

and Parfitt *et al.* (2010), and the role of stress (Boddy, 2021) could explain why tree species developed different amount of discoloration. If tree species have different amounts of host-specific fungi this could affect discoloration amount. However, to verify this, the life cycle of the latent fungi, as well as outside pathogens, would need examination in depth. As an example, for wild cherry, it has been proposed to avoid off-season pruning, since the fungal silver leaf disease *Chondrostereum purpureum* produces most spores during the autumn and winter (Savill and Wise, 2019).

Wild cherry developed significantly more discoloration than the other species, which supports the idea that species have various inherent abilities to compartmentalize (Morris *et al.*, 2019). Customizing timing of pruning to each species in an urban setting is of course time consuming and somewhat inefficient from a management perspective, at least over the short-term. However, the results might indicate that the right timing for pruning is more important in some species, as some have a higher general tendency to develop discoloration. The *Prunus* genus is popular both in horticultural contexts and as a timber. Reducing risk of failure in urban settings, as well as producing as high amounts of quality wood as possible, is desirable. It is, however, unclear whether it is possible to generalize this finding to include an entire genus. As wild cherry seemed to be the weakest compartmentalizer in this study, it might have the highest positive effect to customize time of pruning for species comparable to wild cherry. Our results suggest that pruning of cherry in early autumn, September, was most favourable. Hoch *et al.* (2003) studied energy levels in trees and found that wild cherry had a non-significant decrease of NSCs before bud break. Hiron (2012) reasons, because of this, that pruning should be done with caution for pre-leaf flowering species. However, both Hoch *et al.* (2003) and Martínez-Vilalta *et al.* (2016) have stated that NSC depletion is rare, which suggests that NSC concentration is not a reliable parameter for decisions in pruning management (Hiron, 2012). Our other pre-leaf flowering species – Norway maple – showed no significant differences in discoloration over the season. The season of pruning thus seems irrelevant with respect to discoloration for this species, despite its pre-leaf flowering timing. Dănescu *et al.* (2015) found the same result for sycamore maple. Furthermore, Norway maple displayed no indication that spring pruning and sap exudation had any negative effects on occlusion or discoloration. This confirms previous statements (Shigo, 1991; Gilman, 2012); however, in an urban context, sap exudation might be an aesthetic disadvantage that perhaps needs to be considered.

Small-leaved lime developed significantly less discoloration when pruned in winter, January, than in early autumn, September, and common oak developed significantly less discoloration when pruned in winter, January, than in the rest of the seasons studied. Dujesiefken *et al.* (2005) found a contradicting result when common oak was wounded by drilling, having least discoloration when drilled in spring, April and states that trees should not be pruned during the winter season. The different methods, drilling stems or pruning branches, the smaller unbalanced size of their data set, or their statistical analysis that did not account for different lengths of reaction time from wounding to analysis, might be the reason for these conflicting results. The results of small-leaved lime and common oak are rather surprising,

since trees are believed to react less and slower during the dormant season (Dujesiefken *et al.*, 2016). In contrast to our results, Hiron (2012) discusses the results of Hoch *et al.* (2003) and reasons that based on the indicated but non-significant decrease of NSC in the beginning of the year in common oak, ring-porous species should be pruned with caution at this time. Based on the results of this and the study of Hoch *et al.* (2003), NSC does not seem to have a large effect on discoloration. However, we have no information on the occurrence of fungal spores at our experimental site. Levels of spores in the air are in general low during the winter, which might have made the winter-pruning favourable for these species, even more so if there would be a high amount of specialized fungi species that infect oak or lime in our area. Furthermore, we have not investigated what caused the discoloration of our samples. Although it commonly develops from mix of abiotic and biotic stresses, we cannot exclude that the higher amounts of discoloration found in the samples from the September pruning in the species could be an effect of high amounts of specialized spores during that time. Boddy (2001, 2021) argues that wood anatomy affects how fungi spread. However, there is no apparent correlation between wood anatomy, discoloration and pruning month in this study, since the diffuse porous Norway maple showed similar results to the ring-porous oak. Moreover, the Norway maple in the present study showed little similarities to the results reported from the studies of the diffuse porous species silver birch (Niemistö *et al.*, 2019) and red alder (DeBell *et al.*, 2006).

One possible study limitation, noted while sanding the samples, was that in some cases within a few millimetres, the discoloured area changed drastically. Although we deem our precision to be in line with the methods described by Dănescu *et al.* (2015) and Qin *et al.* (2019), there is clear risk for errors when comparing with other study designs. This needs to be addressed in future studies by adapting measuring protocols in line with Dănescu *et al.* (2015). A future study that would measure the changes in discoloration when sanding would be interesting to attain knowledge about this method uncertainty.

There was a positive relationship between discoloration amount and occlusion rate and pruning cut length, which confirms findings from earlier studies (e.g. Grabosky and Gilman, 2007; Nicolescu *et al.*, 2013; Niemistö *et al.*, 2019; Qin *et al.*, 2019). Consequently, the necessity of minimizing pruning cut sizes for managers seems clear, irrespective of species or the pruning month.

Appropriate pruning season according to occlusion held unexpected results. Pruning cuts performed in winter, January, occluded fastest for all species. Furthermore, the suitable pruning month according to occlusion and according to discoloration differed. Our study found common oak to occlude fastest when pruned in winter, which contradicts Dujesiefken *et al.* (2005) who found common oak to occlude fastest when wounded by drilling in spring, April. As mentioned above, the conflicting results might be because of different methods. Also, the proportion of fully occluded samples and occlusion rate per year varied widely among the species. Common oak and Norway maple occluded their first samples already after 1 year, while small-leaved lime and wild cherry occluded their first samples after 3 years. What caused this delay is unknown. These species showed lower occlusion rates per year, but only slightly lower than Norway maple.

A possible limitation is the field trial's location, or rather the good growing conditions at the location. Trees growing in stands with fertile soil have a quite different upbringing than in more xeric forests or urban environments with multiple stress factors (Sieghardt *et al.*, 2005; Tello *et al.*, 2005). The environmental differences could possibly give different outcomes in terms of occlusion rate, as indicated by the decline in occlusion during the extremely dry summer of 2018. Another aspect to highlight is the age of the trees we studied. We examined young trees, that is, 16 and 20 years when pruning took place. These trees probably reacted faster to pruning than it might have been the case for older trees, since overall vitality usually is higher in young trees. However, both in silviculture and urban forestry, pruning in early stages is recommended to increase wood quality (O'Hara, 2007; Sheppard *et al.*, 2016) and support good structure for street and park trees (Gilman, 2012). The stands pruned in the study represent the phase where pruning is often advised to accelerate the natural pruning and create a branch free trunk faster, followed or in tandem with thinning to promote the crown diameter of the pruned crop trees (Falk, 2014; Spiecker, 2006). Providing more growing space to the tree crown through thinning increases the radial growth of the tree and is central for occlusion of the pruning cut (Hein, 2008; Hein and Spiecker, 2007; Sheppard *et al.*, 2016). Here it is interesting that although both occlusion rate and radial rate were fastest for all species in January, some of the species had relative faster occlusion rate than radial rate and vice versa. Norway maple had a relative fast occlusion rate but a slow radial rate, whereas we observed the opposite for small-leaved lime. Accelerating occlusion through thinning therefore might be more effective for some species than others. Ideally spacing should be experimentally controlled and give insight in how thinning affects the occlusion. We did not control spacing in this study. However, since pruning season is nested within the trees, the overall season effect should not be affected, but of course limits the interpretation in relations to spacing and thinning. The stands used in the study had unequal density when the trial started, but the mixed stand was thinned the second year to resemble the density of the other stands. The thinning did not affect the main result of pruning season due to the nested structure of the experiment. Our results confirm this, since the species in the thinned stand, common oak and wild cherry, had such different results regarding both occlusion and discoloration. Although the forester can accelerate occlusion through thinning to give higher radial increment of the crop trees, the urban tree manager often works with already free growing trees and can only support radial increment by reducing growth stress through actions such as watering or mulching/fertilization.

The statistical models included the varying reaction time with regard to pruning month, something previous studies often lacked. However, this also meant using average values and rates meaning that compensating for the different climatic conditions for different growth seasons was not possible. With a larger sample size than available in this study, more complex models could include weather data.

Conclusion

The results of our study show that discoloration amount and occlusion rate differ between species in relation to season of pruning. The reason for this is unknown but could be connected

to wood anatomy, fungi composition and the species-specific chemical production and composition. The result clearly goes against the common idea in many pruning textbooks that there is one optimal season of pruning for all species.

Common oak and small-leaved lime both had significantly less discoloration and faster occlusion rate when pruned in January, which contradicts previous studies. Similarly, Norway maple had no significant differences in discoloration amount but occluded fastest when pruned in January. Wild cherry showed scattered results, which indicates the complexity when aiming to come with clear recommendations on pruning months. Least discoloration in wild cherry was seen in pruning cuts conducted in September, but the fastest occlusion was seen in January. Our recommendation is that pruning should primarily aim to reduce the amount of discoloration, since this is what causes an increased likelihood of failure and thereby might affect the trees potential risk in an urban environment and lower wood quality in production. Although it might be too complex for managers in an urban context to customize pruning time for every tree species, since species variety is often very high, it might be relevant for species that risk high amounts of discoloration, such as wild cherry. The management in wood production might be easier to adjust for monocultures, but more complicated for mixed stands including minority species as crop trees (Spiecker, 2006). Larger pruning cuts increase discoloration amount and occlusion rate, therefore minimizing pruning cuts is of great importance irrespective of pruning month (e.g. Grabosky and Gilman, 2007; Nicolescu *et al.*, 2013; Niemistö *et al.*, 2019; Qin *et al.*, 2019).

Tree managers, urban and in forestry, require reliable sources to correctly conduct their work. Results from this study, along with previous ones, demonstrate the variation of species' appropriate pruning month, but further studies to understand the underlying factors are needed to be able to firmly conclude why a certain time of year seems more appropriate for pruning of a certain species.

Seasonal dynamics of NSCs do not seem to determine appropriate pruning month, since it has been shown in several species that there is a constant abundance (Martinez-Vilalta *et al.*, 2016). However, it might be interesting to examine how NSC is affected by pruning and what it means for compartmentalization, since Ramirez *et al.* (2018) found an increase of NSC after pruning in one of the species studied. Being an important, but perhaps neglected, foundation for (Shigo, 1975; 1991) original ideas about pruning seasons, the seasonal dynamics of pest and pathogens might be an important aspect to incorporate in future research to be able to better understand species-specific causes and effects for different pruning months.

Data Availability

The data underlying this article will be shared on reasonable request to the corresponding author.

Acknowledgements

The study set up and sample preparation were possible thanks to Alnarp Landscape Laboratory and the Dendrochronological Laboratory at Alnarp (DELA). Several people have been essential for this project

and we acknowledge their support with initial trial establishment: Anders Busse Nielsen; fieldwork: Blaz Klobucar, Urška Klepec, Erik Svensson, Claes Lööw, technical assistants/dendrochronological methods Igor Drobyshev, Guilherme Pinto and Kent Hansson, analytical support Magnus Löf, Jens Peter Skovsgaard, Jan-Erik Englund and Adam Flöhr. Thank you for contributing!

Conflict of interest statement

None declared.

Funding

The Royal Swedish Academy of Agriculture and Forestry [GFS2019-0052]; and Swedish Research Council Formas [2016-00951]; with additional support from The Swedish Tree Association [56440130]; and Nordisk Fond for Bytræer [56440136].

Author contributions

Anna Lund: Methodology, Investigation, Formal analysis, Data curation, Writing—original draft, Writing—review and editing, Visualization. **Anna Levinsson:** Methodology, Writing—review and editing, Supervision. **Johan Östberg:** Conceptualization, Funding acquisition, Writing—review and editing. **Björn Wiström:** Conceptualization, Funding acquisition, Methodology, Formal analysis, Writing—review and editing, Project administration, Supervision, Visualization.

References

- American National Standards Institute (ANSI) 2017 *American National Standard for Tree Care Operations – Tree, Shrub, and other Woody Plant management – Standard Practices (Pruning)*. ANSI A300 (Part 1) - 2017 Pruning. Tree Care Industry Association, Inc.
- Baas, P. and Schweingruber, F.H. 1987 Ecological trends in the wood anatomy of trees, shrubs and climbers from Europe. *IAWA J.* **8**, 245–274. <https://doi.org/10.1163/22941932-90001053>.
- Barry, K.M., Pearce, R.B. and Mohammed, C.M. 2000 Properties of reaction zones associated with decay from pruning wounds in plantation-grown *Eucalyptus nitens*. *For. Pathol.* **30**, 233–245. <https://doi.org/10.1046/j.1439-0329.2000.00206.x>.
- Bartoń, K. (2022). *MuMin: Multi-Model Inference*. [R package version 1.46.0.] <https://CRAN.R-project.org/package=MuMin>
- Bates, D., Maechler, M., Bolker, B. and Walker, S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Baum, S. and Schwarze, F.W.M.R. 2002 Large-leaved lime (*Tilia platyphyllos*) has a low ability to compartmentalize decay fungi via reaction zone formation. *New Phytol.* **154**, 481–490. <https://doi.org/10.1046/j.1469-8137.2002.00390.x>.
- Boddy, L. 2001 Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse Woody debris. *Ecol. Bull.* **49**, 43–56.
- Boddy, L. 2021 *Fungi and Trees: Their Complex Relationships*. Arboricultural Association.
- Bubi, J.W. 2009 *Created grassland diversity after 12 years of mowing in Southern Sweden*. MSc Thesis in Conservation Biology. University of Nairobi.
- Burgess, T.I., Howard, K., Steel, E. and Barbour, E.L. 2018 To prune or not to prune; pruning induced decay in tropical sandalwood. *For. Ecol. Manag.* **430**, 204–218. <https://doi.org/10.1016/j.foreco.2018.08.009>.
- Crivellaro, A. and Schweingruber, F. H. (2013). *Atlas of Wood, Bark and Pith Anatomy of Eastern Mediterranean Trees and Shrubs with a Special Focus on Cyprus*. Springer Berlin. doi:<https://doi.org/10.1007/978-3-642-37235-3>
- Dănescu, A., Ehring, A., Bauhus, J., Albrecht, A. and Hein, S. 2015 Modelling discoloration and duration of branch occlusion following green pruning in *Acer pseudoplatanus* and *Fraxinus excelsior*. *For. Ecol. Manag.* **335**, 87–98. <https://doi.org/10.1016/j.foreco.2014.09.027>.
- DeBell, D.S., Harrington, C.A., Gartner, B.L. and Singleton, R. 2006 Time and distance to clear wood in pruned red alder saplings. In *Red Alder – A State of Knowledge*. R.L., Deal, C.A., Harrington (eds.). USDA Forest Service - General Technical Report PNW, pp. 103–114.
- Dujesiefken, D., Drenou, C., Oven, P. and Stobbe, H. (2005) Arboricultural practices. In *Urban Forests and Trees: A Reference Book*. C. Konijnendijk, K. Nilsson, T. Randrup and J. Schipperijn (eds). Springer Berlin, pp. 419–441. doi:https://doi.org/10.1007/3-540-27684-X_16
- Dujesiefken, D., Fay, N., De Groot, J.-W. and De Berker, N. 2016 *Trees - A Lifespan Approach Contributions to Arboriculture from European Practitioners*. Fundacja EkoRozwoju.
- Dujesiefken, D., Liese, W., Shortle, W. and Minocha, R. 2005 Response of beech and oaks to wounds made at different times of the year. *Eur. J. For. Res.* **124**, 113–117. <https://doi.org/10.1007/s10342-005-0062-x>.
- Eisner, N.J., Gilman, E. and Grabosky, J. 2002 Branch morphology impacts compartmentalization of pruning wounds. *J. Arboric.* **28**, 99–105. <https://doi.org/10.48044/jauf.2002.013>.
- Falck, J. 2014 *Skogsskötselserien – Stamkvistning*. 2nd edn. Skogsstyrelsen, Jönköping.
- Fini, A., Ferrini, F., Frangi, P., Piatti, R., Faoro, M. and Amoroso, G. 2013 Effect of pruning time on growth, wound closure and physiology of sycamore maple (*Acer pseudoplatanus* L.). *Acta Hort.* **990**, 99–104. <https://doi.org/10.17660/ActaHortic.2013.990.9>.
- Gilman, E.F. 2012 *An Illustrated Guide to Pruning*. 3rd edn. Delmar Cengage Learning.
- Grabosky, J. and Gilman, E. 2007 Response of two oak species to reduction pruning cuts. *Arboricult. Urban For.* **33**, 360–366. <https://doi.org/10.48044/jauf.2007.041>.
- Graves, S., Piepho, H.P., Selzer, L. and Dorai-Raj, S. 2019 *multcompView: Visualizations of Paired Comparisons*, [R package, version 0.1-8].
- Hein, S. 2008 Knot attributes and occlusion of naturally pruned branches of *Fagus sylvatica*. *For. Ecol. Manag.* **256**, 2046–2057. <https://doi.org/10.1016/j.foreco.2008.07.033>.
- Hein, S. and Spiecker, H. 2007 Comparative analysis of occluded branch characteristics for *Fraxinus excelsior* and *Acer pseudoplatanus* with natural and artificial pruning. *Can. J. For. Res.* **37**, 1414–1426. <https://doi.org/10.1139/X06-308>.
- Hemery, G., Spiecker, H., Aldinger, E., Kerr, G., Collet, C. and Bell, S. (2008) COST action E42: growing valuable broadleaved tree species. Final report. <http://www.valbro.uni-freiburg.de/> (accessed on 29 December, 2022).
- Hirons, A. 2012 Straightening out the Askenasy curve. *Arboricult. Urban For.* **38**, 31–32. <https://doi.org/10.48044/jauf.2012.006>.
- Hoch, G., Richter, A. and Körner, C. 2003 Non-structural carbon compounds in temperate forest trees. *Plant Cell Environ.* **26**, 1067–1081. <https://doi.org/10.1046/j.0016-8025.2003.01032.x>.
- Iannone, R., Cheng, J. and Schloerke, B. 2020 *Gt: Easily Create Presentation-Ready Display Tables [R Package]*.
- James, K.R., Haritos, N. and Ades, P.K. 2006 Mechanical stability of trees under dynamic loads. *Am. J. Bot.* **93**, 1522–1530. <https://doi.org/10.3732/ajb.93.10.1522>.

- Kuznetsova, A., Brockhoff, P. and Christensen, R. 2017 lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* **82**, 1–26. <https://doi.org/10.18637/jss.v082.i13>.
- Lenth, R., Buerkner, P., Herve, M., Love, J., Miguez, F., Riebl, H., et al. 2019 *Emmeans: Estimated Marginal Means, Aka Least-Squares Means*, [R package, version 1.7.1-1].
- Martinez-Vilalta, J., Sala, A., Asensio, D., Galiano, L., Hoch, G., Palacio, S., et al. 2016 Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis. *Ecol. Monogr.* **86**, 495–516. <https://doi.org/10.1002/ecm.1231>.
- Morris, H., Hietala, A.M., Jansen, S., Ribera, J., Rosner, S., Salmeia, K.A., et al. 2019 Using the CODIT model to explain secondary metabolites of xylem in defence systems of temperate trees against decay fungi. *Ann. Bot.* **125**, 701–720. <https://doi.org/10.1093/aob/mcz138>.
- Niculescu, V.-N., Sandi, M. and Păun, M. 2013 Occlusion of pruning wounds on northern red oak (*Quercus rubra*) trees in Romania. *Scand. J. For. Res.* **28**, 340–345. <https://doi.org/10.1080/02827581.2012.747621>.
- Niemistö, P., Kilpeläinen, H. and Heräjärvi, H. 2019 Effect of pruning season and tool on knot occlusion and stem discoloration in *Betula pendula* – situation five years after pruning. *Silva Fennica* **53**, 1–29. <https://doi.org/10.14214/sf.10052>.
- O'Hara, K.L. 2007 Pruning wounds and occlusion: a long-standing conundrum in forestry. *J. For.* **105**, 131–138. <https://escholarship.org/uc/item/2nh227fr>.
- Oosterbaan, A., Hochbichler, E., Valeriu-Norocel, N. and Spiecker, H. 2008 Silvicultural principles, goals and measures in growing valuable broadleaved tree species. *Die Bodenkultur* **60**, 45–51 Corpus ID: 55330436.
- Parfitt, D., Hunt, J., Dockrell, D., Rogers, H.J. and Boddy, L. 2010 Do all trees carry the seeds of their own destruction? PCR reveals numerous wood decay fungi latently present in sapwood of a wide range of angiosperm trees. *Fungal Ecol.* **3**, 338–346. <https://doi.org/10.1016/j.funeco.2010.02.001>.
- Pietzarka, U. 2016 Tree pruning: methods and parameters. In *Urban Tree Management: For the Sustainable Development of Green Cities*. A., Roloff (ed.). John Wiley & Sons, pp. 154–168.
- Pigott, D. 2012 *Lime-Trees and Basswoods: A Biological Monograph of the Genus Tilia*. Cambridge University Press. <https://doi.org/10.1017/CBO9781139033275>.
- Priestley, C.A. 1970 Carbohydrate Storage and Utilization. In *Physiology of Tree Crops*. L.C., Luckwill, C.V., Cutting (eds.). Academic Press, p. 382.
- Qin, G., Hao, J., Yang, J., Li, R. and Yin, G. 2019 Branch occlusion and discoloration under the natural pruning of *Mytilaria laosensis*. *Forests* **10**, 892. <https://doi.org/10.3390/f10100892>.
- R Core Team 2019 R: A Language and Environment for Statistical Computing. In (Version 3.6.1). R Foundation for Statistical Computing.
- Ramirez, J.A., Handa, I.T., Posada, J.M., Delagrangé, S. and Messier, C. 2018 Carbohydrate dynamics in roots, stems, and branches after maintenance pruning in two common urban tree species of North America. *Urban For. Urban Green.* **30**, 24–31. <https://doi.org/10.1016/j.ufug.2018.01.013>.
- Richter, H.G. and Dallwitz, M.J. (2019) *Commercial Timbers: Descriptions, Illustrations, Identification, and Information Retrieval*. In English, French, German, Portuguese, and Spanish. Version: 9th April 2019. delta-intkey.com
- RStudio Team. (2019) *RStudio: Integrated Development Environment for R*. RStudio, URL <http://www.rstudio.com/>
- Savill, P.S. and Wise, R. 2019 *The Silviculture of Trees Used in British Forestry*. 3rd edn. CABI.
- Schmidt, O. (2006a) Wood discoloration. In *Wood and Tree Fungi: Biology, Damage, Protection, and Use*. Springer Berlin, pp. 119–133. doi:https://doi.org/10.1007/3-540-32139-x_6
- Schmidt, O. (2006b) Habitat of wood fungi. In *Wood and Tree Fungi: Biology, Damage, Protection, and Use* Springer Berlin, pp. 161–236. doi:https://doi.org/10.1007/3-540-32139-x_8
- Schoch, W., Heller, I., Schweingruber, F.H. and Kienast, F. (2004) *Wood Anatomy of Central European Species*. Online version: www.woodanatomy.ch
- Sheppard, J., Urmes, M., Morhart, C. and Spiecker, H. 2016 Factors affecting branch wound occlusion and associated decay following pruning – a case study with wild cherry (*Prunus avium* L.). *Ann. Silvicult. Res.* **40**, 133–139. <https://doi.org/10.12899/asr-1193>.
- Shigo, A.L. 1975 Microorganisms isolated from wounds inflicted on red maple, paper birch, American beech, and red oak in winter, summer, and autumn. *Phytopathology* **66**, 559–563. <https://doi.org/10.1094/Phyto-66-559>.
- Shigo, A.L. 1991 *Modern Arboriculture: A Systems Approach to the Care of Trees and their Associates*. Shigo and Trees.
- Shigo, A.L. and Marx, H.G. 1977 *Compartmentalization of Decay in Trees*. Department of Agriculture, Forest Service, U.S.
- Sieber, T.N. 2007 Endophytic fungi in forest trees: are they mutualists? *Fungal Biol. Rev.* **21**, 75–89. <https://doi.org/10.1016/j.fbr.2007.05.004>.
- Sieghardt, M., Mursch-Radlgruber, E., Paoletti, E., Couenberg, E., Dimitrakopoulos, A., Rego, F., Hatzistathis, A. and Randrup, T.B. (2005) The abiotic urban environment: impact of urban growing conditions on urban vegetation. In *Urban Forests and Trees: A Reference Book*. C. Konijnendijk, K. Nilsson, T. Randrup and J. Schipperijn (eds). Springer Berlin, pp. 281–323. doi:https://doi.org/10.1007/3-540-27684-X_12
- Sjöman, H., Östberg, J. and Bühler, O. 2012 Diversity and distribution of the urban tree population in ten major Nordic cities. *Urban For. Urban Green.* **11**, 31–39. <https://doi.org/10.1016/j.ufug.2011.09.004>.
- Smith, K.T. 2006 Compartmentalization today. *Arboricult. J.* **29**, 173–184. <https://doi.org/10.1080/03071375.2006.9747457>.
- Spiecker, H. 2006 Minority tree species – a challenge for multi-purpose forestry. In *Nature Based Forestry in Central Europe: Alternative to Industrial Forestry and Strict Preservation*. J., Diaci (ed.). Studia Forestalia Slovenica, pp. 47–59.
- Swedish Institute for Standards (SIS) 2020 *Tree Care — Processes and Methods for Tree Pruning — Part 2: Requirements for Providers*. Swedish Institute for Standards, pp. SS 990001–SS 990002.
- Tello, M-L., Tomalak, M., Gáper, J., Motta, E. and Mateo-Sagasta, E. (2005) Biotic urban growing conditions — threats, pests and diseases. In *Urban Forests and Trees: A Reference Book*. C. Konijnendijk, K. Nilsson, T. Randrup and J. Schipperijn (eds). Springer Berlin, pp. 325–365. https://doi.org/10.1007/3-540-27684-X_13
- Wang, C.-S., Hein, S., Zhao, Z.-G., Guo, J.-J. and Zeng, J. 2016 Branch occlusion and discoloration of *Betula alnoides* under artificial and natural pruning. *For. Ecol. Manag.* **375**, 200–210. <https://doi.org/10.1016/j.foreco.2016.05.027>.
- Wickham, H. 2016 *ggplot2: Elegant Graphics for Data Analysis*. [R package]. Springer-Verlag.
- Wickham, H., François, R., Henry, L. and Müller, K. 2020 *Dplyr: A Grammar of Data Manipulation*. [R package].
- Wiström, B. and Nielsen, A. 2014 Effects of planting design on planted seedlings and spontaneous vegetation 16 years after establishment of forest edges. *New For.* **45**, 97–117. <https://doi.org/10.1007/s11056-013-9394-4>.