

Long-term effects of increment coring on Norway spruce mortality

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Abstract: Increment coring of trees is a standard method in dendrochronology, wood anatomy, forest ecology, and forestry. However, increment coring is an invasive method that may result in tree decay and decreased physical stability of the cored tree. The long-term effects of coring on tree mortality are poorly understood for any tree species because long-term data sets are rare. We present results from a 40-year study on the effects of coring on tree mortality in a near-primary Norway spruce (*Picea abies* (L.) Karst.) forest in the Swiss Alps (forest reserve Scatlè). In 1965–1966, 551 trees with a diameter at breast height ≥ 8 cm were cored within a 5.9 ha plot. Following a reassessment of the plot in 2006, we compared the mortality rates of the 551 trees cored in 1965 with those of similar trees from the uncored control group, i.e., trees that were similar in size (diameter at breast height), vitality, and forest layer class. Neither nonparametric tests nor logistic regression models indicate a significant influence of coring on tree mortality. Our results suggest that increment coring does not influence the mortality rate of *P. abies* within the study region. Additional studies in different environments and on different tree species are needed to evaluate the generality of our findings.

Résumé : Le carottage des arbres est une méthode standard en dendrochronologie, anatomie du bois, écologie forestière et foresterie. Cependant, le carottage est une méthode invasive qui peut entraîner de la carie chez les arbres et réduire la stabilité physique des arbres qui ont été carottés. Les effets à long terme du carottage sur la mortalité des arbres sont peu connus, peu importe l'espèce, parce que les données à long terme sont rares. Nous présentons les résultats d'une étude d'une durée de 40 ans qui porte sur les effets du carottage sur la mortalité des arbres dans une forêt presque primaire d'épicéa commun (*Picea abies* (L.) Karst.) située dans les Alpes suisses (réserve forestière de Scatlè). En 1965–1966, 551 arbres avec un diamètre à hauteur de poitrine ≥ 8 cm ont été carottés à l'intérieur d'une parcelle de 5,9 ha. À la suite d'une réévaluation de la parcelle en 2006, nous avons comparé le taux de mortalité des 551 arbres carottés en 1965 avec celui d'arbres semblables dans un groupe témoin d'arbres non carottés, c'est-à-dire des arbres dont le diamètre à hauteur de poitrine, la vigueur et la classe de couche forestière étaient semblables. Ni les tests non paramétriques, ni les modèles de régression logistique n'indiquent une influence significative du carottage sur la mortalité des arbres. Nos résultats indiquent que le carottage n'a pas d'influence sur le taux de mortalité de *P. abies* dans la zone d'étude. D'autres études, dans différents milieux et sur différentes espèces d'arbres sont nécessaires pour généraliser nos résultats.

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Introduction

Increment coring of trees is a standard method in dendrochronology, wood anatomy, forest ecology, and forestry (Schweingruber 1996; Grissino-Mayer 2003). The information gained from cores about tree growth, age, and wood structure and composition is used for a wide array of investigations that cover (but are not limited to) tree-ring based reconstructions of past climates (Cook et al. 2007), fire history (Swetnam 1993), and insect outbreaks (Rolland et al. 2001) as well as ecophysiological studies of xylem anatomy (Fonti

et al. 2010) and the modelling of forest dynamic processes (Wunder et al. 2008a).

However, the method of increment coring is invasive and leads to injury of the cored tree (Eckstein and Dujesiefken 1999), which may have several impacts: first, agents of decay such as fungi may enter the tree via the drilling hole and start or accelerate the decay process (e.g., Hart and Wargo 1965), second, the drilling may decrease the physical stability of (smaller) trees (e.g., Jaeger 1970), and finally, a defense reaction is induced, i.e., the building of barrier zones with (autochthonous) fungicides during the compartmentalization

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process (e.g., Shigo 1984). The latter process entails a cost, as assimilates are distracted from the carbon pool of the tree, i.e., they cannot be used for other processes such as height and radial growth, growth of fine roots, or fructification. These effects may vary highly among tree species and taxonomic groups and with the condition of the tree (vitality and size), size of the increment core, season of coring, and treatment of the drilling hole (Eckstein and Dujesiefken 1999).

Research on the effects of increment coring can be split into two broad categories: first, tree injury analyses that deal with the immediate consequences of coring (e.g., discoloration or wound reaction) and second, tree mortality analyses that deal with the ultimate consequence of injuries, i.e., the death of the tree. Tree injury analyses suggest the following general trend of susceptibility to coring: sensitivity increases from conifers to ring porous to diffuse porous species (Jaeger 1970). Tree mortality analyses have been rarely performed due to the lack of appropriate data sets, i.e., individual-based, long-term assessments of the fate of cored versus uncored trees. To our knowledge, the only study published is from van Mantgem and Stephenson (2004) who found no difference in tree mortality rates of 825 cored and 525 uncored white fir (*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.) and 104 cored and 66 uncored red fir (*Abies magnifica* A. Murray) trees in the Sierra Nevada of California, as measured during 12 years of annual inventories after the coring event.

The temporal extent of both tree injury and mortality analyses ranges from 2 years to a maximum of 15 years after the coring event, with most studies addressing the tree condition 10 (or less) years after coring (e.g., Meyer and Hayward 1936; Campbell 1939; Toole and Gammage 1959) and only few studies covering an observation period up to 15 years. Interestingly, damage may decrease over time; for example, Lenz and Oswald (1971) noted a decreasing “damage rate” from 6 to 12 years after coring for Norway spruce (*Picea abies* (L.) Karst.), reporting that fungal growth was increasingly inhibited. However, even a 15-year period is still relatively short compared with the longevity of (most) analysed tree species, and thus, the long-term effects of coring on tree vitality are largely unknown.

In addition to their short temporal extent, most of these studies are based on a relatively small number of trees. For the tree injury analyses, the number of trees per species ranged from 2 to 112, with most studies focusing on fewer than 25 trees (e.g., Hepting et al. 1949; Laflamme 1979; Weber and Mattheck 2006). Only Vuokila (1976), Hart and Wargo (1965), and Lenz and Oswald (1971) used more trees per species (up to 86, 100, and 142, respectively). For the only tree mortality study (van Mantgem and Stephenson 2004), the sample sizes were much larger (see above).

Here, we analyse long-term tree mortality using a unique data set comprising a >40 year observational period and a large sample size of 1102 *P. abies* trees. We assess the fate of 551 trees cored in 1965–1966 in a near-primary forest of the Swiss Alps with a control group consisting of 551 uncored trees, which are similar in size, vitality, and forest layer class as the cored trees. We perform a comparative analysis of long-term mortality rates to address our main research question: does increment coring affect tree mortality?

Methods

Study site

We used data from the Swiss forest reserve network, currently maintained jointly by the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL Birmensdorf), ETH Zurich, and the Federal Office for the Environment (FOEN). The network was initiated in the late 1940s to observe in a representative way the long-term dynamics of unmanaged, near-natural forests in Switzerland (Leibundgut 1957). The former Institute of Silviculture (ETH Zurich) directed the successive expansion of the network until 2004. It now comprises 49 forest reserves measured during repeated inventories at intervals of approximately 5–15 years.

Tree-ring information was originally considered as a constitutive part of the methodology applied in the forest reserve network (Leibundgut 1959). However, only few forest reserves experienced relatively intensive coring campaigns, among them the most pristine Swiss forests Derborence (Leibundgut 1959), Scatlè (Hillgarter 1971), and Bödmeren (Horat et al. 2005). Here, we focus on Scatlè, since the coring occurred more than 40 years ago and detailed documentation of this coring campaign is available.

Scatlè is a *P. abies* forest located near Brigels (46°47'26"N, 9°02'50"E) in the Vorderrhein Valley of the Swiss Alps and comprises approximately 9 ha of pristine forest (Hillgarter 1971) from the upper montane (1580 m above sea level) to the krummholz zone (2015 m above sea level). The forest is characterized by a mosaic-like structure of different successional stages and is considered as one of the very few (near-) primary forests in Switzerland: pollen records demonstrate the absence of anthropogenic disturbances since the 13th century (Kral and Mayer 1969). Since 1911, the forest has been protected by a state law, and in 1965, the first forest inventory took place.

Sample size

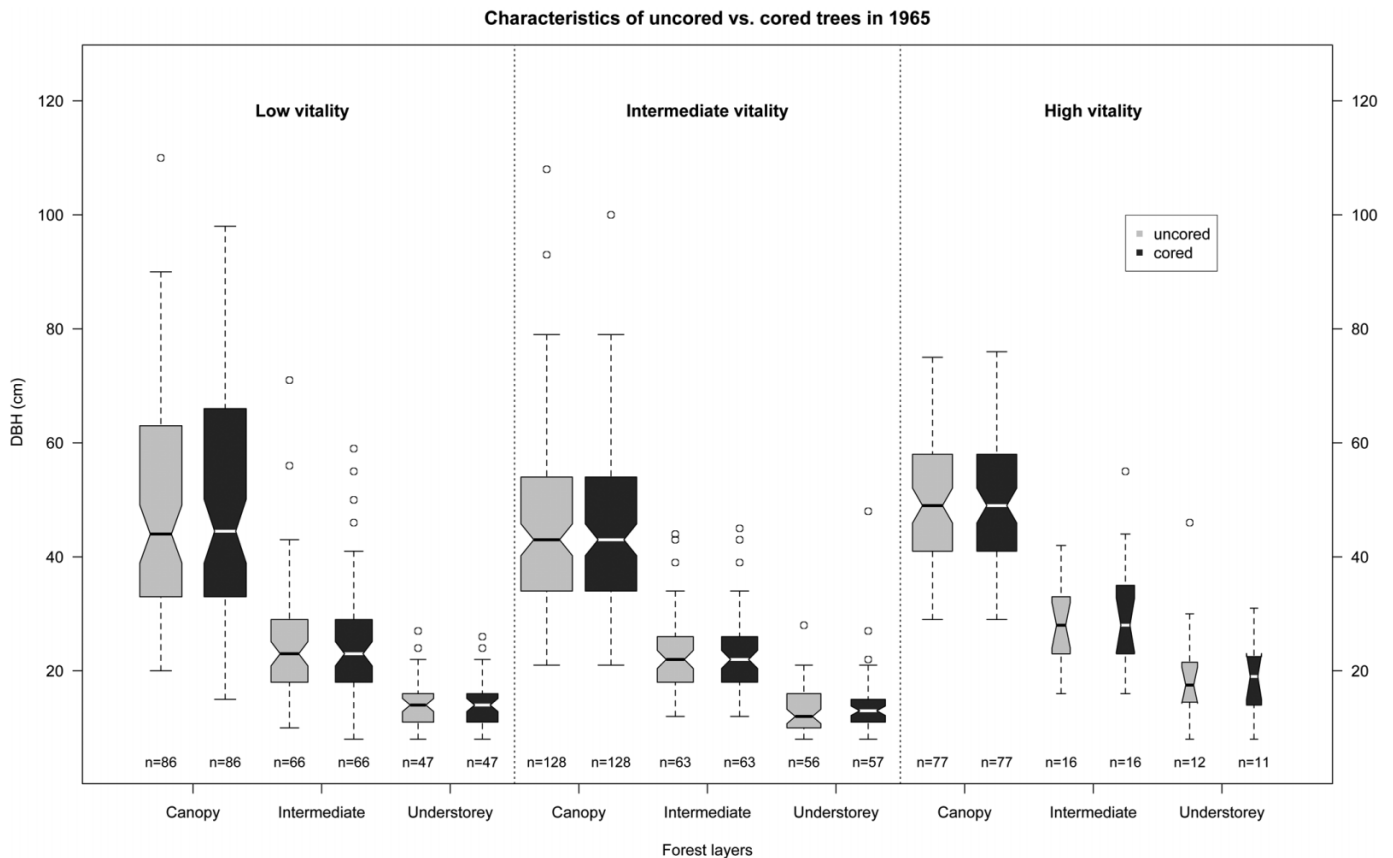
We used data from Hillgarter (1971) who installed two large, adjacent long-term inventory plots within the lower half of the Scatlè forest reserve comprising 3.23 ha (1587–1686 m above sea level) and 2.68 ha (1687–1786 m above sea level), respectively.

Within these plots, every tree with a diameter at breast height (DBH) ≥ 8 cm (measured at 1.5 m) was permanently marked in 1965 using a tree-specific identification that was engraved on a metal plate and nailed to the tree base. Tree species, DBH, forest layer (understorey, intermediate, canopy), and vitality (low, intermediate, high) were recorded (Leibundgut 1956). This resulted in individual-based information for 2454 live trees.

Hillgarter (1971) cored 619 live *P. abies* trees in summer and autumn 1965–1966, i.e., approximately a quarter of all living trees. Trees were randomly selected comprising trees of different tree size (DBH), vitality, and forest layer class. One core per tree was extracted at 1.3 m height using a Swedish standard corer. Cores were taken from the upslope part of the stem (i.e., reaction wood was avoided) and the drilling holes were sealed by injecting a standard tree wound dressing without fungicides.

The cores were measured using an Eklund measuring stage where tree identification and ring widths were printed on pa-

Fig. 1. DBH versus *Picea abies* tree vitality and forest layer position in 1965: reduced data set with balanced sample size between uncored trees ($n = 551$) and cored trees ($n = 551$). Box widths are proportional to the square roots of the number of observations in the groups (R Development Core Team 2011).



per rolls. Most of the printed rolls were archived for the last 40 years, while the physical increment cores were lost (J.-F. Matter, personal communication).

We compared the mortality rates of the cored versus uncored trees between 1965–1966 and 2006, i.e., more than 40 years after the coring event. We did not use any of the trees cored during other, more recent dendrochronological analyses at Scatël: a total of 81 trees cored by Götz (2001) and Bigler and Bugmann (2003) were subtracted from the abovementioned 2454 trees leading to a data set comprising 2373 trees, i.e., 551 cored and 1822 uncored trees.

Statistical analysis

To get an unbiased comparison of the mortality rates of cored and uncored trees, the tree characteristics (e.g., size) of the cored (treatment) and uncored (control) group should be as similar as possible. Even though a random selection of the cored trees was intended in 1965 (Hillgarter 1971), the treatment group and the control group of the original data set exhibited different characteristics in 1965: (i) the DBH distributions of cored versus uncored trees differ significantly (two-sample Kolmogorov–Smirnov test, $p = 0.003$), with the cored trees being somewhat larger than their uncored counterparts (Appendix A, Figs. A1 and A2), and (ii) the sampling design is unbalanced, i.e., the proportion of cored trees is not constant among tree subgroups of different classes of

vitality and forest layers, ranging from approximately 16% (canopy trees of intermediate vitality) to approximately 44% (understorey trees of intermediate vitality). These biases of the coring campaign in 1965 may at least partly be attributed to an (unconscious) preferential selection of slightly larger and also more vital trees for coring, especially in the understorey.

To overcome these limitations, we selected for each of the 551 cored trees the “most similar” counterpart tree from the uncored trees ($n = 1822$), leading to a new reduced set of uncored trees ($n = 551$). The selection criterion for the “most similar” trees was the Mahalanobis distance (Mahalanobis 1936) based on tree size, vitality, and forest layer class. This procedure led to very similar characteristics of both cored and uncored trees and an almost perfectly balanced data set (Fig. 1).

To test for significant effects of coring on tree mortality, we used the nonparametric χ^2 test with Yates’ continuity correction for small sample sizes (Yates 1934). This conservative test allowed for a 2×2 comparison of tree treatment (cored versus uncored) in 1965–1966 and tree status (dead, live) in 2006. The χ^2 test was also applied separately to trees of different vitality classes in 1965 (low, intermediate, high) and trees of different forest layer classes in 1965 (understorey, intermediate, canopy).

We calculated a set of logistic regression models with tree

Table 1. Effect of coring on tree mortality of cored and uncored *Picea abies* between 1965–1966 and 2006.

Data set	Cored, 1965–1966 (<i>n</i>)	Uncored, 1965–1966 (<i>n</i>)	Proportion cored, 1965–1966 (%)	Dead (cored), 2006 (%)	Dead (uncored), 2006 (%)	χ^2	<i>p</i>
All trees	551	551	50.0	43.2	46.8	1.324	0.250
Subset vitality (1965)							
High	104	105	49.8	28.8	33.7	0.304	0.581
Intermediate	248	247	50.1	38.7	42.7	0.740	0.390
Low	199	199	50.0	56.3	58.8	0.165	0.685
Subset forest layers (1965)							
Canopy	291	291	50.0	39.5	42.3	0.348	0.555
Intermediate	145	145	50.0	49.7	48.3	0.014	0.906
Understorey	115	115	50.0	44.3	56.5	2.939	0.086

Note: Bold indicates the group with the highest mortality (cored versus uncored). χ^2 tests with Yates' continuity correction for significant difference between the two groups.

condition (dead, live) in 2006 as the response variable and all possible combinations of the following explanatory variables as measured in 1965: treatment (cored versus uncored), tree size (DBH), vitality class (low, intermediate, high), and forest layer class (understorey, intermediate, canopy) as well as the most meaningful interactions (treatment \times tree size, treatment \times vitality, treatment \times forest layer). We transformed the variable tree size (DBH) using transformations of different flexibility: either an ordinary log transformation or a restricted cubic spline (rcs) transformation with three knots (Harrell 2001). Applying rcs's allows for a flexible nonlinear relationship between tree size and the survival probabilities to be fitted (see also Wunder et al. 2007, 2008b). The log and rcs transformations eventually defined the model types, referred to here as the rigid "log model" (Model I) and the flexible "rcs model" (Model II). For each type, the best-fitting model was selected from the pool of candidate models using the Akaike information criterion (Burnham and Anderson 1998). Model performance was assessed using the area under the receiver operating characteristic curve (AUC) (Fielding and Bell 1997).

To assess the impact of core length on tree mortality, we estimated the total core length for a given tree in 1965 by adding up all individual tree-ring width measurements of that tree. To achieve a rough estimate of the coring impact in 1965, this absolute core length was divided by the tree's DBH in 1965. For example, a coring impact of 0.5 corresponds to a core that reached exactly the geometrical centre of the tree. We performed two-sided Wilcoxon rank sum tests between the coring impact (in 1965) of dead and live trees (in 2006). We excluded all tree-ring width measurements containing manually introduced coded numbers whose meaning was not reconstructable. Thus, the impact analysis was ultimately based on 392 trees with reliable tree-ring information (out of the 551 cored trees analysed here).

All analyses were performed using R, a language and environment for statistical computing (R version 2.12.2; R Development Core Team 2011). The optimal pairing of cored versus uncored trees was performed using the "optmatch" package (R-package version 0.7-1; Hansen and Klopfer 2006); rcs's were fitted using the "Design" package (R-package version 2.3-0; Harrell 2009). For visualizations, we used the "plotrix" package (Lemon 2006).

Results

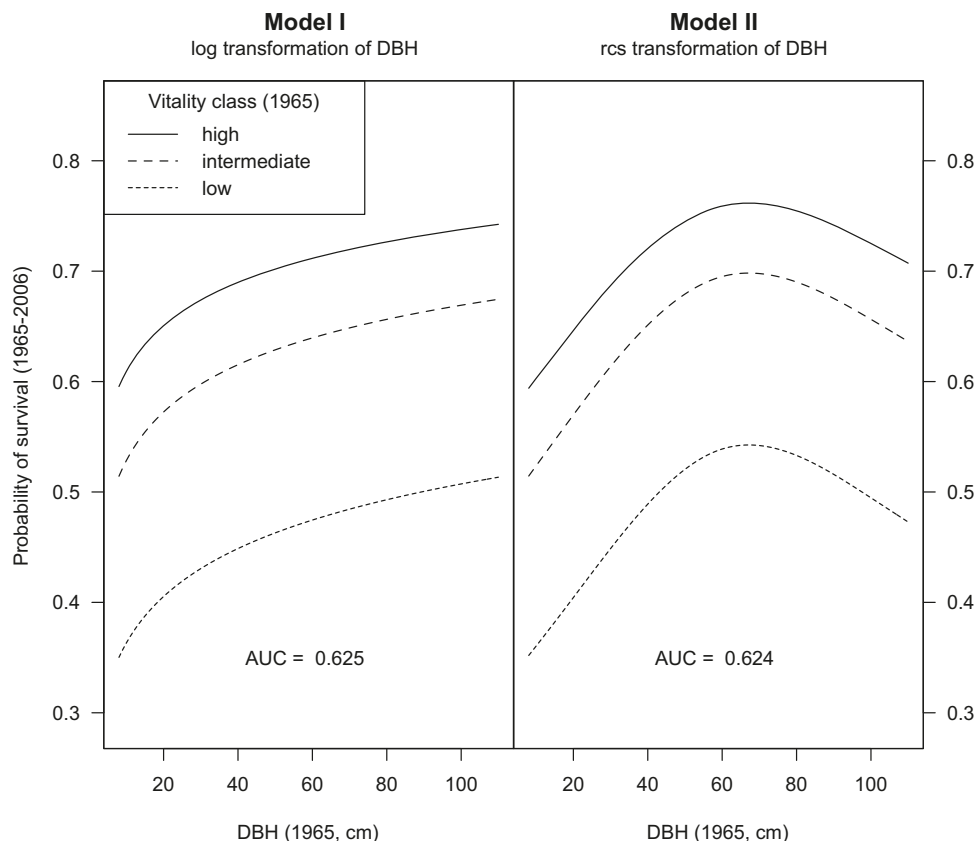
Tree mortality of cored versus uncored trees

We found no significant difference between mortality rates of cored versus uncored trees: for both groups, nearly half of all analysed trees alive in 1965 had died by 2006, resulting in an average annual mortality rate of approximately 2% (Table 1). Trees of the two groups exhibited a similar development of mortality rates and tree vitality over time (results not shown).

The χ^2 tests did not detect any significant effect of coring on tree mortality, i.e., there was no difference in the mortality rates of cored versus uncored trees ($p = 0.250$) (Table 1). This pattern was persistent for subgroups of different vitality and forest layer. Even very small cored trees (8–10 cm DBH) did not show elevated tree mortality rates compared with same-sized uncored trees ($p = 0.243$). Remarkably, cored understorey trees tended to have marginally lower mortality rates than the corresponding uncored trees ($p = 0.086$).

Congruent findings of the effect of coring on tree mortality were also evident from logistic regression models that were used to explain the long-term mortality between 1965–1966 and 2006: the lowest Akaike information criterion values (i.e., better performance) were achieved for models without treatment variable (cored versus uncored), i.e., coring information did not explain the observed mortality pattern. Rather, the best-fitting models contained the explanatory variables tree vitality and tree size (DBH) in 1965, irrespective of the applied DBH transformation (log versus rcs transformation; Appendix A, Tables A1 and A2). In addition, the best-fitting models did not contain an interaction term "treatment \times tree size (DBH)", thus showing that treatment had no statistically significant effect on tree mortality, irrespective of tree size. The log model (Model I) was characterized by a monotonously increasing survival probability with higher vitality class and increasing tree size. The rcs model (Model II) also showed increasing survival probabilities with higher tree vitality class but a more complex effect of tree size: survival probabilities increased with size up to a peak at approximately 65 cm DBH; beyond that, they started to decline with size (Fig. 2). The performance of both models was almost the same, with the log model achieving an AUC of 0.625 and the rcs model an AUC of 0.624.

Fig. 2. Modelled survival probabilities for *Picea abies* trees of different size. Best-fitting models are shown for two DBH transformations of different flexibility: log transformation (Model I) and rcs transformation (Model II).



Impact of core length

Relative core length (in relation to the DBH) had no influence on tree mortality in 2006 (two-sided Wilcoxon rank sum test, $p = 0.571$), nor did it significantly affect tree vitality in 2006 (Fig. 3). Most of the cores covered about one third of a tree's DBH, i.e., only a small portion reached the geometrical centre. Two extreme values were recorded, with one core comprising about two thirds of the DBH (tree alive in 2006) and the other core covering the entire DBH (dead in 2006). Canopy trees experienced a lower coring impact as compared with trees of the other layers.

Discussion

Impact of increment coring on tree mortality

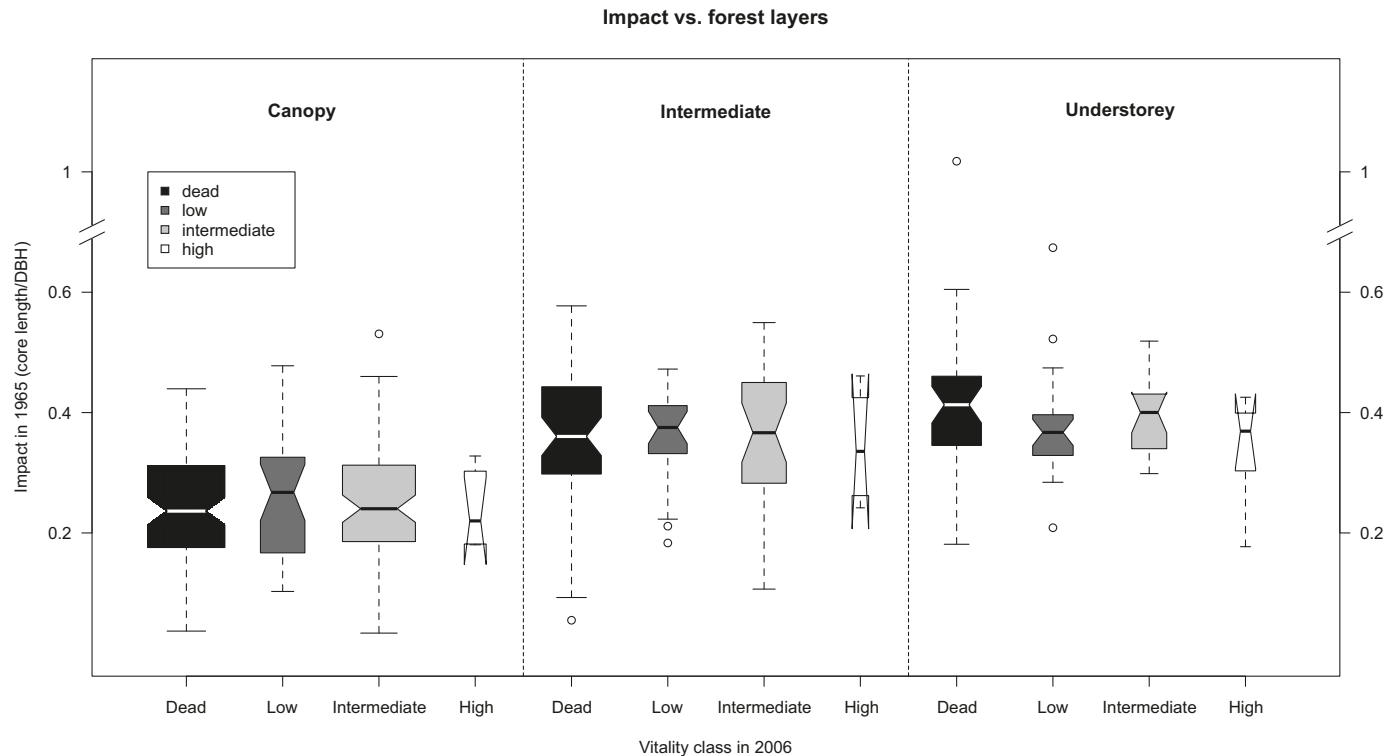
We found no evidence for elevated tree mortality of cored trees more than 40 years after the coring campaign. These results are in line with the only large-scale mortality study of cored trees by van Mantgem and Stephenson (2004) who rejected a negative impact of coring on tree mortality. Our estimated annual mortality rates of approximately 2% are higher than in an unmanaged *P. abies* dominated forest in the Italian Alps (0.8% for *P. abies* >7.5 cm DBH; Castagneri et al. 2010) or boreal *P. abies* dominated forests (0.6% for *P. abies* averaged over all diameters; Fraver et al. 2008). The high mortality rate at Scatlè may be explained by the regionally dry years of 1983 and 1985–1986 (J.-F. Matter, personal communication): the inventory period covering these years (1977–1989) is characterized by a fairly high annualized

mortality rate of 2.5% (1965–1977: 0.8%, 1989–2006: 1.2%). In addition, the DBH distribution of our sample mimics an inverse J-shaped distribution with a relatively large proportion of small trees that typically experience higher mortality rates (Appendix A, Fig. A1, reduced data set).

Mortality rates for some cored trees (understorey trees of low vitality) tended to be lower than for the corresponding group of uncored trees. Lenz and Oswald (1971) measured a reduction of fungal damage in *P. abies* between 6 and 12 years after the coring event. They speculated about a short time window for the development and expansion of fungi directly after the coring event and subsequent massive tree-induced inhibition of fungal growth. Interestingly, these effects could be observed even though their tree sample was slightly biased towards less healthy trees (to avoid “wasting” of timber; Lenz and Oswald 1971). Unfortunately, the experiment had to be stopped after a storm- and snow-load-induced disturbance occurred in the investigated stands. In the Scatlè forest, at least some cored understorey trees may have gained physical stability from the localized formation of heartwood during the compartmentalization process (Shigo 1984; Smith 1988). However, the observed trend may also be an artefact of the accessibility of cored trees in 1965, i.e., it seems plausible that the least accessible understorey trees were avoided by the field workers, e.g., small trees inside very dense cohorts or on top of rocks that may experience relatively high mortality rates.

Schöpfer (1962) indicated that wood-decaying fungi may be dispersed in forest stands during intensive coring cam-

Fig. 3. Impact of coring for *Picea abies* trees of different forest layers. Box widths are proportional to the square roots of the number of observations in the groups (R Development Core Team 2011).



paigns. At Scatlè, the patterns of tree vitality of cored versus uncored trees are very similar over time (results not shown) and do not exhibit differential behaviour in the aftermath of extreme events that may have led to relatively high mortality rates, e.g., the regionally dry years of 1983 and 1985–1986 (J.-F. Matter, personal communication).

Comparable with the χ^2 tests, no effect of coring on tree mortality could be detected using logistic regression models of different flexibility, i.e., the predicted survival probabilities differ with tree size and vitality but not with treatment (cored versus uncored) (Fig. 3). Both models reflect increasing survival probabilities with increasing DBH due to self-thinning (cf. Franklin et al. 1987). However, only the flexible rcs model was able to capture decreasing survival probabilities for the largest trees, resulting in a U-shaped mortality curve (Monserud and Sterba 1999; Coomes and Allen 2007; Vieilledent et al. 2010). Remarkably, we could not find significant differences in the mortality rates of cored versus uncored small-diameter trees. This indicates that the assumed lower physical stability of (smaller) cored trees (sensu Jaeger 1970) did not affect their mortality rates, at least not for the trees analysed here (≥ 8 cm DBH). It should be kept in mind that the explanatory power of both models is relatively low (AUC = 0.62), corresponding to “average” performance sensu Hosmer and Lemeshow (2000). This indicates that a fairly large number of factors not taken into account here may affect tree mortality. For example, the relatively high proportion of snags (1965: 12% of all trees; Hillgarter 1971) may lead to tree falls that either kill or severely damage otherwise healthy trees (Larson and Franklin 2010).

The coring impact, i.e., relative core length, did not affect tree mortality. This indicates that cores of different relative

length do not shape a specific tree mortality pattern such as higher mortality rates for trees with the largest coring impact. Even though the average core length was about a third of a tree’s diameter, the distance between pith and innermost measured ring (= pith offset) was probably relatively low for most samples due to the intensive formation of compression wood on the downside slope of the stems along the steep slopes of Scatlè forest.

Perspectives

In conclusion, increment coring does not affect mortality of *P. abies* within the study region, and there is strong evidence that the often feared increase in tree mortality rates of cored trees did not occur. Still, a number of questions remain open as follows.

First, it would be worthwhile to focus future studies on the physiological reaction of trees to coring, e.g., the alteration of wood density due to compartmentalization zones, or changes in wood anatomical features such as the formation of resin ducts as a part of the defensive system of the tree.

Second, a generalization of our results to other tree species and environments is not feasible. For example, serious forest diseases may result from the infection of borer wounds if made in a season when trees are highly susceptible, such as with the boring of North American oaks when the beetle vectors of oak wilt are active (Hart and Wargo 1965). Thus, the analysis should be expanded to more tree species and sites to get a more comprehensive picture of the effects of coring on tree mortality. Still, our study adds an important piece of evidence to the debate about the pros and cons of increment coring.

Lastly, our study should contribute to more informed deci-

sion-making by the authorities of national parks and forest reserves whether or not to give permission for increment coring to "access" tree-ring archives for research.

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Appendix A

Tables A1 and A2 and Figs. A1 and A2 appear on the following pages.

Table A1. Model representation of logistic regression models with the lowest AIC (i.e., best performance) for each model type: Model I with log transformation of DBH and Model II with restricted cubic splines (rcs) transformation of DBH.

Model I: log transformation of DBH	Model II: rcs transformation of DBH
Pr{ $Y_i = 1 X_i\} = \frac{1}{1+\exp(-X_i\beta)}$, where Y_i is the status of tree i (dead = 0, alive = 1) and:	
$X_i\beta = -1.741$	$X_i\beta = -0.759$
+0.256 log(DBH)	+0.002 DBH
+0.675 Vit.intermed.	$-7.331 \times 10^{-9} (DBH - 13.0)_+^3$
+1.005 Vit.high	$+1.147 \times 10^{-8} (DBH - 31.0)_+^3$
	$-4.137 \times 10^{-9} (DBH - 62.9)_+^3$
	+0.668 Vit.intermed.
	+0.991 Vit.high
	with $(x)_+ = x$ if $x > 0$, 0 otherwise

Note: The three knots of the rcs model are located at DBH values of 13.0, 31.0, and 62.9 cm. The lowest vitality class (Vit.low) represents the base level; coefficients were fitted for both the intermediate (Vit.intermed.) and highest vitality class (Vit.high).

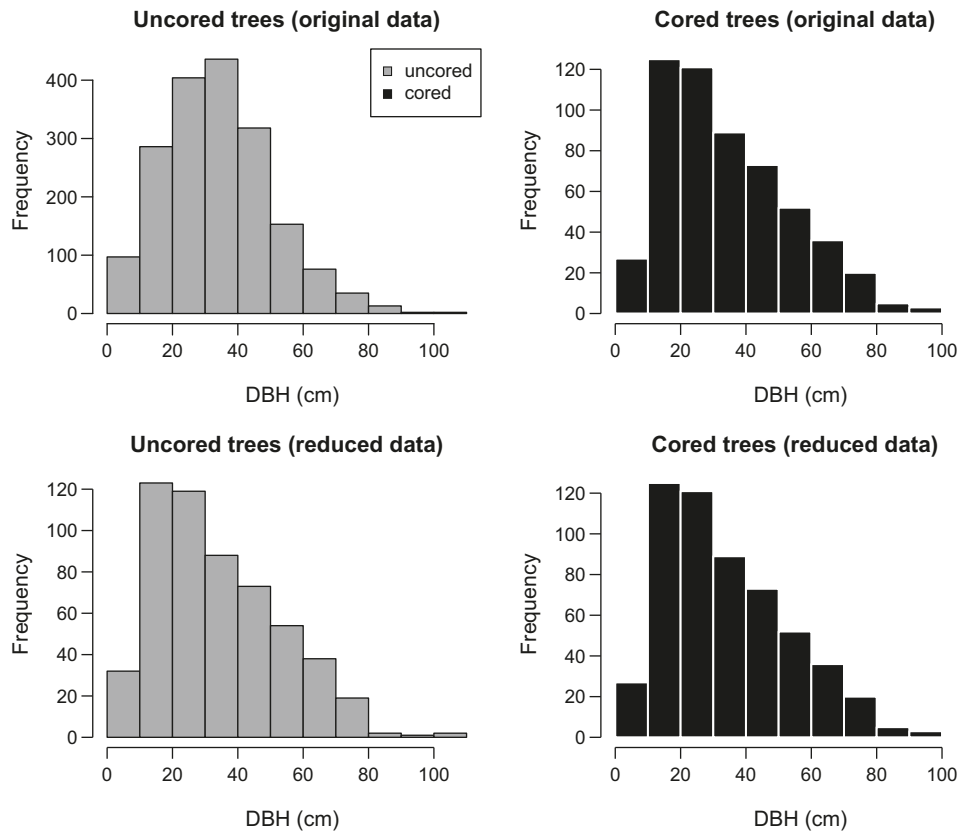
Table A2. Regression coefficients of logistic regression models with the lowest AIC (i.e., best performance) for each model type: Model I with log transformation of DBH and Model II with restricted cubic splines (rcs) transformation of DBH.

Model	Transformation		DBH			Vit.intermed.	Vit.high	
			Intercept	log(DBH)	DBH			DBH'
I	log	Coefficient	-1.7411	0.2563		0.6752	1.0051	
		(±SE)	(±0.6105)	(±0.1072)		(±0.1370)	(±0.1848)	
		<i>p</i>	0.004	0.017		<0.001	<0.001	
II	rcs	Coefficient	-0.7594		0.0019	-0.0018	0.6683	0.9910
		(±SE)	(±0.2322)		(±0.0010)	(±0.0014)	(±0.1372)	(±0.1860)
		<i>p</i>	0.001		0.053	0.192	<0.001	<0.001

Note: Model II (rcs) contains the additional nonlinear term DBH'. The lowest vitality class (Vit.low) represents the base level; coefficients were fitted for both the intermediate (Vit.intermed.) and highest vitality class (Vit.high).

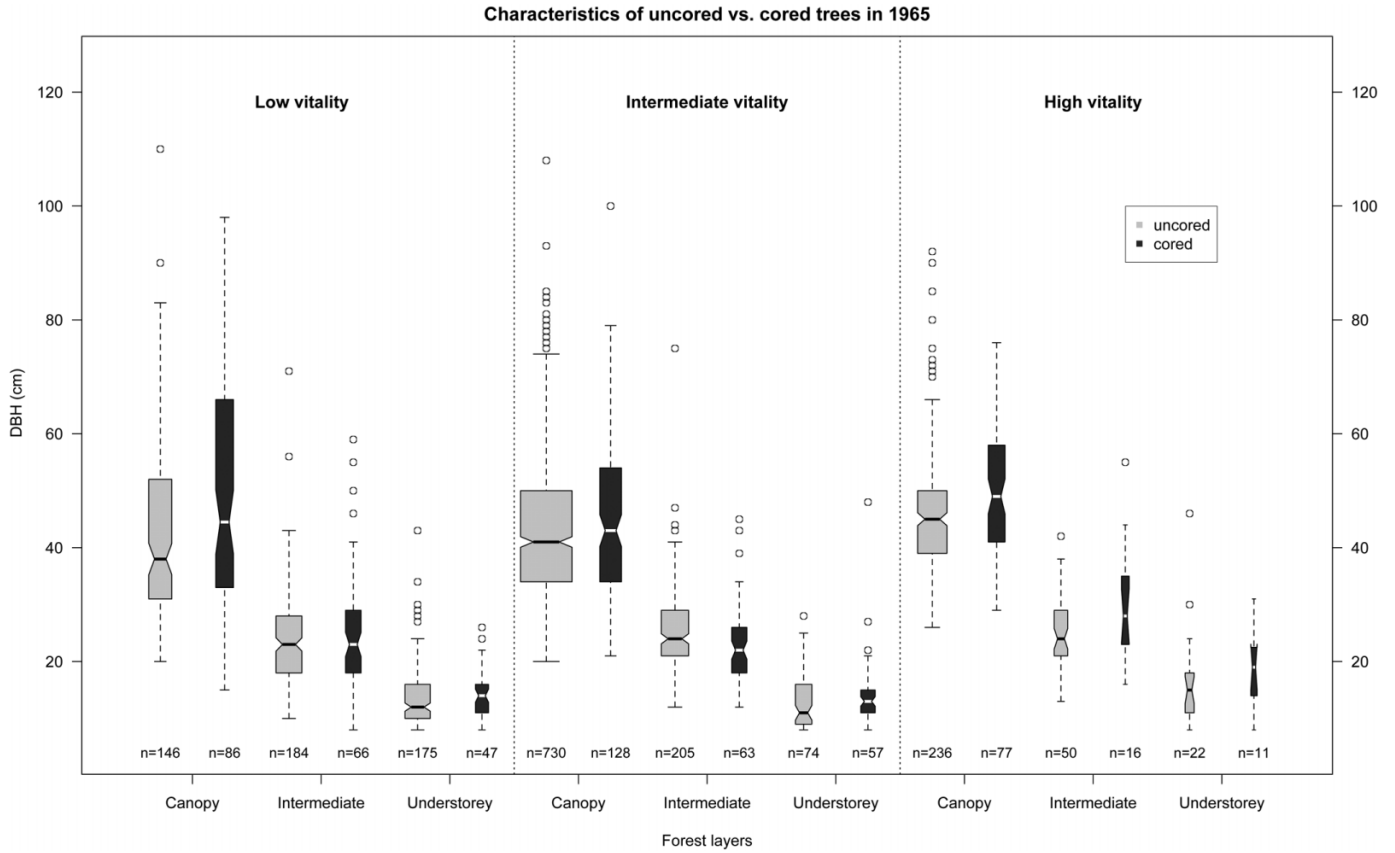
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Fig. A1. DBH distribution of uncored versus cored *Picea abies* trees in 1965: original and reduced data sets with unbalanced and balanced sample sizes between uncored and cored trees. Sample size (original data): $n = 1822$ uncored trees, $n = 551$ cored trees. Sample size (reduced data): $n = 551$ uncored trees, $n = 551$ cored trees.



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Fig. A2. DBH versus *Picea abies* tree vitality and forest layer position in 1965: original data set with unbalanced sample size between uncored trees ($n = 1822$) and cored trees ($n = 551$). Box widths are proportional to the square roots of the number of observations in the groups (R Development Core Team 2011).



Reference

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

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