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Raunkiær's oaks: mortality and growth among old oaks in a Danish deer park

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ABSTRACT
We evaluate the growth and mortality of veteran oaks studied by C. Raunkiær in a game park in Denmark in 1933. Raunkiær mapped 664 oaks, of which 329 healthy looking oaks had their girth measured (average girth of 318 cm). Mortality decreased with increasing circumference and was estimated to be 0.426% per year. The healthy-looking trees in 1933 had even lower mortality (0.211% per year). There was no difference in mortality between naturally recruited oaks and those planted in the 1830s. These mortality estimates were lower than in previous reports of oaks, veteran trees and large tropical trees, presumably because these oaks were in a non-crowded, non-forested situation. When girth was measured after 50 growing seasons, they had grown an average of 1.33 cm per year. However, the growth rate of these initially healthy trees was highly variable and could be partially explained by the initial tree size. Taking this into account, statistical models suggest that a 300 cm circumference oak in 1933, measured at breast height (130 cm), would have grown 1.28 cm per year in circumference, corresponding to radial growth of 0.20 cm per year and basal area increment of 71.0 cm^2 per year.

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KEYWORDS
Quercus robur; Denmark; death; veteran trees

Introduction

> "Som Kampestenen fast,
> Med løvrige Grene
> Og knudret Knort og Knast,
> Der eensom staaer paa Sletten,
> For hver en Storm et Rov,
> Den sidste ædle Levning
> Af en stormægtig Skov."
> "Hjortens Flugt". Ch. Winther 1855,[1]

Veteran trees have special biological, historical, cultural and aesthetic values (Gibbons et al. 2008; Lindenmayer and Laurance 2017). They can be keystone organisms in different types of landscapes, providing critical habitat for many species (Thor et al. 2010; Altman et al. 2016; Edman et al. 2016). In addition, larger trees store more carbon than smaller ones (Stephenson et al. 2014; Norby et al. 2024), so they can play an important role in carbon storage and dynamics. For forest ecology and biodiversity conservation, knowledge of recruitment, mortality and growth rates of veteran trees is critical for making predictions and informed long-term management decisions (e.g. Johansson et al. 2013).

In northern Europe, large oaks dominate among veteran trees due to their long lifespan and large size (Skarpaas et al. 2017). Oaks, and *Quercus robur* in particular, can survive for many centuries (Drobyshev and Niklasson 2010). As they age, oaks develop cavities with wood mould and a bark that is suitable for specialised lichens (Lättman et al. 2009; Bergman et al. 2012; Milberg et al. 2016). In other words, multiple ecological niches develop with age, making veteran oaks a keystone in the places where they grow.

Unfortunately, veteran oaks tend to be few and far between, making them difficult to study. In addition, events leading to mortality or recruitment of new veteran trees are slow to develop in long-lived individuals (e.g. Andersson et al. 2011). As a result, there is a lack of information on the factors that determine the future availability of veteran oaks.

Two key features for understanding oak population dynamics are the "recruitment" of new veteran oaks and their mortality. Growth rate data, either from boring or repeated circumference measurements, can be used to calculate the future "recruitment" of large trees into an oak population, given the presence and size distribution of sub-veteran oaks. Mortality, however, is a more difficult variable to estimate because of the low rates, the rarity of large oaks, and the long follow-up required. Attempts have been made to estimate oak mortality, and Drobyshev et al. (2008) reviewed published studies and other available data to estimate mortality in *Quercus robur*. The vast majority of the datasets were on trees younger than 150 years, with only four studies/datasets with an average age of over 200 years; the mean mortality rate across these four studies was 1.01%/year ($N = 977$), an estimate with a wide confidence interval (0.47; 2.02%/year). This estimate has been used in subsequent studies of oak dynamics (e.g. Drobyshev et al. 2008; Johansson et al. 2013). The review of oak mortality data (Drobyshev et al. 2008) and others (Rohner et al. 2012) also showed that mortality was higher in younger than in older trees, and higher in high-density than in low-density forests. This leads to the hypothesis that

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veteran oaks in open situations, such as grazed areas, may have the lowest mortality of all oaks.

In the present study, we estimated the mortality of large oaks over a 50-year period in a deer park, originally sampled by Ch. Raunkiær in 1933. Some of the oaks were measured for girth and we calculated the growth rate for them.

Material & methods

Background

Christen Christensen Raunkiær (1860–1938) was a Danish botanist and pioneer of plant ecology famous for his system of "lifeforms" (Raunkiær 1905), and his ambition to quantify phenomena in nature (e.g. Raunkiær 1912). After early retirement from a professorship in botany at the University of Copenhagen in 1923, he continued with a wide range of research projects, some of which were published by J.H. Schultz Forlag in København, under the title "Botaniske Studier" (in total 5 issues and 16 articles published 1934–1937, all in Danish and authored by Raunkiær). One article reported a study of old oaks in a deer park north of Copenhagen (Raunkiær 1934). Raunkiær's aim was to measure circumference of large oaks in order to calculate their growth rate when visited again in the future. From such growth rates, he believed we could better estimate the age of veteran oaks, but how remains unclear (Holten 1998).

In the winter of 1984, one of us (KC) happened to come across this report while working for the manager of the deer park where the study had been conducted, and was given the opportunity to revisit Raunkiær's oaks after 50 growing seasons.

The study site

Dyrehaven, also called Jægersborg Dyrehave, north of Copenhagen, can trace its history as a deer park back several centuries. The practice of reserving land where deer were fenced in and kept for hunting has a long tradition in Europe (Birrell 1992; Ahrland 2011; Liddiard 2019; Olsson 2022). At high stocking densities, tree recruitment in deer parks has often been low, resulting in an open landscape with scattered trees or groups of trees.

A map of the area made during the siege of Copenhagen in 1658–1660 shows mainly open land to the west of today's Dyrehaven and forests in the east and south with the text "dass Königs Thiergarten" (the kings deerpark) ("Accurata delineatio Castrorum Suecicorum, ut et Haffniæ, Regni Daniæ Metropolis"; p. 846 in von Pufendorf 1696). It is likely that extensive felling and culling of deer and domestic animals took place during the siege, and it has been suggested that many of today's oaks were recruited in the years after the siege (Möller 1938; Nielsen and Frederiksen 1973).

In 1670, an area of 1500 hectares was fenced off and the farmers were evicted. Since then, it has remained a deer park. In 1844 it was decided that Dyrehaven should be excluded from forestry and instead be used as a "lystskov", a forest for recreation (Flor 1941). Today, located on the northern outskirts of Copenhagen, it is a popular recreational area of about 11 km^2 with a mixed population of fallow, red and sika deer. As a result, Dyrehaven has long been subject to deer grazing and browsing and has been excluded from forestry, with only a few plantations and the occasional removal of dead trees or trees deemed unsafe for the public.

In 1934 Raunkiær described Dyrehaven as follows: "As long as the present balance between deer and trees is maintained, it is a dying forest that is slowly being transformed into open grassland". The oaks he studied are described as naturally recruited. Exceptions were some oaks planted around 1830.

Today, oaks are a prominent feature of Dyrehaven and large and famous trees have been measured on several occasions. The age of the ten largest oaks in 1989 (girth at 130 cm height: 7.50–10.4 m) was estimated to be between 350 and 1000 years (Holten 1998). One of Raunkiær's oaks fell in 2008 and turned out to have 380 year rings, suggesting that it was established in 1628.[2]

Methods used by Raunkiær in 1933

Raunkiær had a long-term interest in Dyrehaven (e.g. Raunkiaer 1932, 1933), and he set out to map all oaks. During this work he defined a total of 35 oak groups, with in total about 2000 oaks. In 1933, he selected 17 of the oak groups for measurements, and made detailed maps of them (Raunkiær 1934). These groups ranged in size from 18 to 68 oaks, with occasional other tree species. On the maps, Raunkiær (1934) shows the location of the oaks – both living and dead – in relation to roads, a railway and various topographical features. To further aid in re-locating the trees, he also describes (for example, oak 9 in the Fort group is described as "Free-standing, large, with a wide canopy. Stem is leaning towards east"). Also, 27 oaks are shown in photographs (Raunkiær 1934).

Although Raunkiær noted all the oaks on the maps, he selected a subset for girth measurement (Raunkiær 1934; about half of the oaks in each group were selected). The oaks measured were healthy-looking and preferably had a regular trunk shape (to increase the accuracy of the measurements). Some prominent trees, due to size or location, were included despite having an irregular trunk.

Unusually, his preferred measuring height was 150 cm (rather than the 130 cm now commonly used). Furthermore, if the trunk was irregularly shaped at this height, he would choose a different height (between 70 and 170 cm).

Raunkiær's method in 1933 was to first determine the compass direction where the ground was flattest. The measurement height was then determined from a point 75 cm from the trunk. In total, five circumference measurements were taken, with the tape measure being removed and reattached around the tree each time. In the report, the average is given as well as the largest deviation from the average, together with the height and direction of the measurement (Raunkiær 1934).

Raunkiær included 32 oaks, divided among two groups, which had been planted around 1830.

Raunkiær conducted the fieldwork from August 12 to 30 1933, with one measurement on October 9 (Raunkiær 1934).

Notable irregularities in Raunkiær's report include the mention that trees planted in 1737 (Grams plantage) were included, but no such data are presented. Furthermore, Raunkiær mentions that a map had been made for each of the 35 oak groups he had identified in Dyrehaven; but in the report he chose to present only 17 oak groups for which high-quality maps were made. We do not know if the maps of the remaining 18 oak groups still exist today.

Methods used in 1984

The unique opportunity left by Raunkiær's data was to estimate the mortality of large oaks in open landscapes and, as he intended, to estimate the growth rate of such trees.

In some oak groups, it was time-consuming to relocate the trees on Raunkiær's maps, especially where there were several dead trees and where dead trees had been removed.

Multiple girth measurements, as performed by Raunkiær, were time-consuming, but were not considered necessary given the small deviations in measurements noted by Raunkiær (1934) and recorded in the field in 1984. Instead, most trees were measured twice, and the average was used.

Another addition to the methods was a custom-made tool that was used to ensure the target height 75 cm from the tree.

The fieldwork was carried out in February and March 1984, 50 growing seasons after Raunkiær.

Note that Raunkiær's oaks were also measured in 1993, but these measurements seem to be lost. A published report contains data for 22 trees (Meulengracht-Madsen 1999). These measurements have not been included in the present study.

Analyses

Growth was measured in the field as increase in girth per year. In addition, radial growth per year was calculated because many studies report ring width (which is equivalent to radial growth,, assuming a tree's bark thickness is relatively constant over the time period). Finally, we also calculated basal area increase as this is sometimes a preferred measure of growth (West 1980), again assuming no increase in bark thickness over the 50 years.

Since growth is likely to be affected by the size of the tree and possibly the height at which the girth measurements were taken, the growth variables – girth, radial and basal area growth – were subjected to GLM (generalised linear model. log link; normal distribution) with tree girth in 1933 and the height at which measurement was taken as independent variables.

To assess whether mortality was affected by tree circumference in 1933, a GLM (binomial; logit link) was run including the 329 oaks measured in that year.

We also used GLM (binomial; logit link) to evaluate the planted and naturally regenerated oaks, using only trees from the two sites where trees had been planted. These sites had 53 surviving trees and 14 that had died. All GLM were conducted with the software Statistica 13 (TIBCO Software Inc. http://statistica.io).

Finally, annual mortality was calculated as:

$$annual\ mortality\ rate = 1 - (C/N_0)^{1/y} \qquad (1)$$

where C is the number of living trees in 1984, N_0 original number of living trees in 1933, y the number of growth seasons between samplings.

Confidence intervals were calculated by generating 1000 data points from a binomial distribution reflecting the number of initial trees and the percentage of survival. For each of the 1000 data points, a mortality rate was calculated and the 2.5%–97.5% percentiles were used as the 95% confidence interval.

Results

Mortality

Using all the 641 living oaks mapped in 1933, the annual mortality was 0.426% year^{-1} ($CI_{95\%}$: 0.354; 0.501). The trees in 1933 consisted of two groups: those selected for measurement and considered healthy, and the remaining trees that were of unknown health status. Mortality was lower among the healthy oaks (0.211% year^{-1}, $CI_{95\%}$: 0.145; 0.280), than among t oaks with unknown health status (0.681% year^{-1}, $CI_{95\%}$ 0.541; 0.821).

Among the 329 trees for which circumference was measured in 1933, mortality was less likely with increasing tree circumference (binomial GLM, $p = 0.02234$; oddsratio (OR) 3.636, CI 2.353, 5.619).

On the other hand, there was no difference between trees planted in two oak groups around 1830 and older trees naturally recruited within the same groups (binomial GLM, $p = 0.31440$; OR 1.869, CI 0.553, 6.323).

Growth rate

Of the 296 oaks measured in 1933 and still alive in 1983, circumference had increased by an average 1.34 cm year^{-1} (SD 0.530), radial growth by 0.21 cm (0.084) and basal area by 82.0 cm^2 per year (61.13). However, these data were skewed, and all were sensitive to the initial size of the tree, and in the case of basal area, to the height at which circumference was measured. Consequently, for more valid estimates of growth, we used the models (Table 1) to predict the growth of a tree 300 cm in circumference in 1933 and measured at 130 cm height. For such an oak, circumference would increase by 1.28 cm per year (prediction interval: 0.700; 2.34), radial growth by 0.20 cm per year (0.111; 0.373), and basal area 71.0 cm^2 per year (39.10; 128.79).

Overall, the models showed that circumferential and radial growth increased with circumference, while basal area was also affected by the height at which circumference was measured (Table 1).

Discussion

Mortality

Our results support the hypothesis that larger/older oaks in open environments exhibit low mortality rates. This is consistent with several studies of other tree species where mortality decreases with size or age (e.g. Monserud and Sterba 1999;

Table 1. GLM results of three model where growth was predicted by tree circumference in 1933 and measurement height.

		Estimate	Lower CL	Upper CL	*p*
Circumference (cm/year)	Intercept	−0.10494	−0.40276	0.19287	0.48979
	Height (cm)	−0.00162	−0.00333	0.00008	0.06228
	Circumference (cm)	0.00188	0.00159	0.00216	0.00000
Radial growth (cm/year)	Intercept	−1.94282	−2.24064	−1.64500	0.00000
	Height (cm)	−0.00162	−0.00333	0.00008	0.06228
	Circumference (cm)	0.00188	0.00159	0.00216	0.00000
Basal area (cm^2/year)	Intercept	3.39132	3.08888	3.69376	0.00000
	Height (cm)	−0.00217	−0.00378	−0.00056	0.00841
	Circumference (cm)	0.00384	0.00356	0.00412	0.00000

Eid and Tuhus 2001; Shifley et al. 2006; Luo and Chen 2011; Thomas et al. 2013). Our study estimated mortality, over a 50-year period, among 641 veteran oaks in a deer park to be only 0.426% year^{-1}, lower than our current best estimate of 1.01% year^{-1} (Drobyshev et al. 2008). Mortality among healthy-looking trees in 1933 was even lower. Thus, it is likely that our current view of dynamics of large oaks (Drobyshev et al. 2008; Johansson et al. 2013) is overly pessimistic.

Finally, it should be emphasized that our results were obtained from oaks in open environments and are not transferable to forested situations where growth is hindered by shading and mortality higher (Drobyshev et al. 2008; Petersson et al. 2019; Brunet and Larsson 2022).

Growth rate

Our growth rate estimates of veteran oaks were in good agreement with a number of previous studies: A 50 year follow-up of oaks with >500 cm circumference in 1953, from nearby Scania, recorded an average circumference increase of 1.33 cm year^{-1} (Blomberg and Red 2003), compared to our 1.34 cm year^{-1}. Median annual ring width in 70 old oaks trees in southern Sweden was 0.13 cm (Drobyshev and Niklasson 2010), and from southcentral Sweden (Östergötland), about 500 km north of the current study, was 0.14 cm on average (Andersson et al. 2011). These slightly lower estimates than in the current study (0.20 cm; n.b. estimated from circumference growth), were not unexpected, given the milder Danish climate with a longer growing season.

Our finding that the growth rate of veteran oaks is highly variable also confirms previous studies (Drobyshev and Niklasson 2010). Apart from edaphic factors, tree health is probably the most important factor (e.g. Shifley et al. 2006, Levanič et al. 2011; Andersson et al. 2011). In our study, most of the oaks measured in 1933 showed vigorous growth since then.

The consensus on growth of veteran trees is that it decreases with age (Fay 2002; Lindenmayer and Laurance 2017; but see Sheil et al. 2017 for a different view). In the case of Raunkiær's oaks, however, we were unable to calculate growth based on tree volume, but it is clear that other indicators of growth, such as girth increase, ring width and basal area, remained high in this cohort of veteran trees.

In conclusion, Raunkiær's cohort of veteran oaks clearly demonstrates a lower mortality rate than previously expected for such trees. This has implication for studies with rather pessimistic views on the dynamics of old oaks. Further studies of mortality and growth rates of veteran oaks and their stand conditions would be welcometo improve estimates and understanding of the cases of death.

Notes

1. "like the Battle Stone fixed but
   with leafy branches
   and the gnarled Knotted stick of twigs
   It stands alone on the plain
   For every storm a robbery,
   The last noble Relic
   Of a once mighty forest".
   Winther wrote "The Stag's flight" in a house adjacent to Dyrehaven 1854 (Friis 1961).
2. Klaus Waage Sørensen, in letter 2024, oak 34 in the Skovrider group.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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