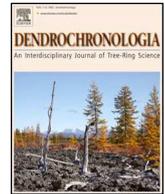




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Original article

Provenance selection and site conditions determine growth performance of pedunculate oak

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ABSTRACT

Forests of the future need to cope with adverse climatic conditions, in particular drought, to ensure forest stability and productivity. Given the usually long rotation period of forests, forest managers need to select appropriate, i.e. productive and climate-change resilient tree species and/or provenances, to lower tree-mortality risks and sustain current wood production rates at the end of the 21st century. A frequent means of assessing which provenances of a given species are adapted to anticipated climate conditions is common garden experiments, where trees from different provenances are planted under similar climate conditions. However, in this context soil conditions also play an important role, since they govern how climate translates into plant-available water and hence plant's ability to cope with extreme drought events. Here, we examine the effects of soil conditions on pedunculate oak (*Quercus robur* L.), by studying 10 different Dutch oak provenances that were planted in three provenance trials on different soil types in 1988 in the Netherlands. Using dendroecological methods, we quantified provenance-specific productivity and assessed provenance- and site-specific growth patterns. Our results indicated clear differences in productivity among provenances as well as soil-type specific growth patterns. Consequently, our study highlights the importance of incorporating soil characteristics when evaluating the growth performance of provenances within common garden experiments.

1. Introduction

The selection of appropriate tree-species and provenances for forest regeneration at a given site has always been an important aspect of forest management. On the one hand, species and provenance selection relates to the overall wood production and the quality of harvested timber, which varies in dependence of site conditions and selected forest reproductive material. On the other hand, it is based on the ability of trees to cope with prevailing climatic conditions thereby minimizing risks associated with tree die-back (Klisz et al., 2019; Konnert et al., 2015). In terms of climatic changes projected for the 21st century, climate resilience of afforested trees is gaining increasing attention (Buras and Menzel, 2019; Walentowski et al., 2017; Zang et al., 2014). This is because higher temperatures in combination with lower plant water availability already today cause drought stress and enhanced tree die-back of specific species at their distributional margins (Allen et al., 2015, 2010; Bigler et al., 2006; Buras et al., 2018; Buras and Menzel, 2019; Cailleret et al., 2017; Choat et al., 2018; Walentowski et al., 2017; Zang et al., 2014). In this context, the relative

longevity of trees (several decades to few centuries) in combination with the relatively high pace of projected climatic changes (1–4 °C within the 21st century; IPCC, 2018) poses challenges for forest managers. That is, in terms of forest rejuvenation managers need to select those species and provenances that are able to cope with the range of projected climate extremes to ensure forest stability and productivity over several decades.

In the past, productivity, wood quality, and resistance to diseases have been the main criteria for selection of suitable forest reproductive material. Given the reasons outlined above adaptation to climate change is becoming increasingly important for species (Aubin et al., 2016; Huang et al., 2017), clone (Dalla-Salda et al., 2009), and provenance selection (Akalusi and Bourque, 2018; Jensen, 2000; Klisz et al., 2019; Montwé et al., 2015; Taeger et al., 2013). For assessing adaptation potential, long-term common garden experiments such as those established by IUFRO in the 1970ies (Kleinschmit and Bastien, 1992) and by the beech network in the 1990ies were found to be valuable to study long-term growth performance and reaction to extreme drought events by means of tree-ring research (Evans et al., 2018;

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George et al., 2019; Housset et al., 2018; Huang et al., 2017; Martinez-Meier et al., 2008; Robson et al., 2018). Tree-ring research in the context of provenance trials has been conducted on economically relevant conifer species such as Norway spruce (Klisz et al., 2019), different pine species (Gray et al., 2016; Taeger et al., 2013), and Douglas fir (Carl et al., 2017; Sergent et al., 2014) as well as the widespread broad leaved species of European beech (Eilmann et al., 2014) and various oak species (Arend et al., 2011). These studies largely focused on the effect of provenance origin on growth performance under increasingly drier conditions (Sáenz-Romero et al., 2017).

Complementary to this, several studies have indicated a significant role of site and soil conditions regarding the performance and resilience of tree species. For instance, Lévesque et al. (2013) compared the drought response of five conifer species growing at xeric vs. mesic sites, to find a species- and site-specific response of trees to water shortage depending on soil conditions. Rehschuh et al. (2017) found an increased drought susceptibility and lower productivity of Norway spruce growing on well-drained, sandy soils in comparison to silty soils. These results emphasize the large relevance of local site conditions which together with species- and provenance-plasticity influence on-site tree growth (Du et al., 2018; Sáenz-Romero et al., 2017). In addition, Sergent et al. (2014) reported site conditions to affect the recovery of Douglas fir after extreme drought. Thus, soil conditions and hydrology at the planting site appear as an important factor for species and provenance selection.

Several studies reported pedunculate oak (*Quercus robur* L.) to be a drought and heat tolerant tree species in Europe (Rubio-Cuadrado et al., 2018; Vitasse et al., 2019) because of its xeromorphic leaf structure and effective stomatal control (Kuster et al., 2014, 2013). In addition, during drought pedunculate oak is able to quickly allocate resources in belowground growth to exploit soil-water and nutrients while simultaneously reducing water loss through transpiration (Thomas and Gausling, 2000). However, other studies have reported drought-induced mortality of pedunculate oak, partly in combination with biotic agents (Andersson et al., 2011; Denman et al., 2018, 2014; Drobyshev et al., 2007; Levanič et al., 2011; Thomas et al., 2002) and a decline at its southern distributional margins (Urli et al., 2015). Given these contrasting findings, it is yet uncertain to which degree pedunculate oak may be a promising candidate for climate resilient forestry. A possible influencing factor affecting the drought susceptibility of pedunculate oak may be related to hydromorphic site conditions which was reported to affect root growth and may increase susceptibility to droughts (Thomas et al., 2002).

So far studies reported clear differences in productivity between provenances of pedunculate oak, however without assessing effects of differing soil conditions on provenance performance (Arend et al., 2011; Jensen, 2000, 1993; Jensen and Hansen, 2008; Kuster et al., 2014). Consequently, we yet lack a comprehensive understanding on how differing soil conditions may affect the performance of various pedunculate oak provenances. Moreover, more knowledge is needed on how soil conditions may modify the response of oak provenances to climatic factors and extreme drought events such as the European droughts of 2003 and 2018 (Buras et al., 2020; Ciais et al., 2005).

To deepen our knowledge with respect to the influence of soil conditions on wood production and climate-resilience of pedunculate oak provenances, we here investigate the performance of ten *Q. robur* provenances planted in the Netherlands in the late 1980s at three different sites representative of contrasting soil conditions (i.e. clay vs. sand). We hypothesize, that (I) soil conditions and (II) provenances influence a) productivity and b) inter-annual growth patterns.

2. Materials and methods

2.1. Trial description

Ten Dutch provenances of pedunculate oak (*Quercus robur* L.) were

Table 1

Selected provenances from the Netherlands (FOREMATIS, 2018).

Provenance number	Sel. code	Provenance name	Provenance code
1	222	Duiven-02	NL.S.1.2.13-02
2	230	Beek en Donk-01	NL.S.3.3.33-01
3	233	Helmond-01 North	NL.S.3.3.29-01
4	234	Helmond-01 South	NL.S.3.3.29-01
5	236	Nuenen-02	NL.T.3.3.10-02
6	240	Princenhage-02	NL.S.3.2.10-02
7	244	Hapert-01	NL.T.3.3.07-01
8	245	Oirschot-02	NL.S.3.3.05-02
9	250	Bocholtz-01	NL.S.3.6.06-01
10	256	Helvoirt-02	NL.S.3.3.20-02

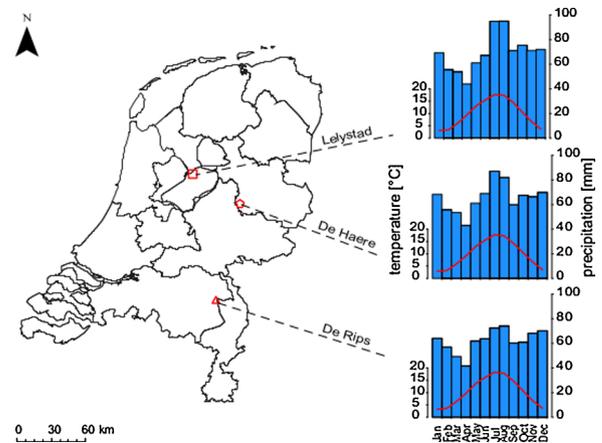


Fig. 1. Location of the study sites in the Netherlands (map to the left) along with their Walter-Lieth climate diagrams (right).

selected and investigated in three provenance trials (Table 1). The trials were located in De Rips, De Haere, and Lelystad in the Netherlands (Fig. 1). The selected provenances are all listed in the Dutch List of recommended varieties and provenances of trees (www.rassenlijstbomen.nl) and registered in the European Forest Reproductive Material Information System (FOREMATIS, 2018; <https://ec.europa.eu/forematis>) which were selected for forestry purposes based on characteristics like stem form, branching habit, presence of forks, epicormics and spiral grain (Kranenborg and de Vries, 1999). Since all considered provenances originate from the Netherlands, they represent more or less similar climate origins. All investigated provenance trials were established in 1988 using 120 two-year-old seedlings per provenance and site. Seedlings were evenly planted in six randomized blocks with 1.5×1.5 m spacing between individual trees.

All sites are characterized by a maritime climate with mean temperatures of roughly 10 °C and annual precipitation sums of 690 mm, 743 mm, and 774 mm in De Rips, De Haere, and Lelystad, respectively. For each site, climate data from the closest climate station (Volkel, Heino, and Lelystad, respectively) were downloaded from KNMI. Corresponding Walter-Lieth climate diagrams are depicted in Fig. 1.

Soil and groundwater properties of the three trials differ (Table 2, Fig. 2). 'De Rips' is located on a gleyic sandy soil which is developed in flushed cover sands on sandy fluvial deposits. The topsoil is disturbed by human activity to a depth of 40–50 cm (probably a 'plaggen' layer). The texture is sand to slightly loamy sand (moderately fine to fine in the topsoil and somewhat coarser in the subsoils). Locally the profiles have disturbed podzolic layers (B-horizons). pH is around 4 in the topsoil and around 5 in the subsoil. Among the three sites, De Rips is characterized by lowest groundwater levels (Fig. 2). The soil of the trial in 'De Haere' is situated in fine to moderately fine cover sands. The weakly developed soil is well drained, poor in nutrients and has a pH of around 4 in the topsoil and around 5 in the subsoil. Groundwater levels are between the

Table 2
Soil properties of the provenance trials.

Trial	Dominant soiltype (soil reference base FAO)	Sub-domi-nant	Depth Hydro-morphic properties cm below surface	Depth	Texture			Particle size sand (µm)	Free Calcium content * class	pH (indicator strips) **
					clay %	silt	sand			
Lelystad	Gleyic fluvisol	-	10–15	0–20	16–20	50–70	10–30	90–110	2	6.0–6.5
				40–60	7–10	15–40	50–70	90–110	2–3	6.5–7.0
				80–100	10–12	40–50	38–50	90–110	3	8.0–8.3
De Haere	Umbric Arenosol	Dystric Arenosol	55–90	0–20	2–4	8–12	85–90	110–120	1	3.8–4.4
				40–60	2–4	8–12	85–90	110–140	1	4.6–5.1
				80–100	3–4	10–17	80–90	120–140	1	4.8–5.5
De Rips	Umbric Arenosol	Umbric Spodosol	65–85	0–20			>90	130	1	3.6–4.3
				40–60			>90	130–150	1	4.5–5.2
				80–100			>90	140–185	1	4.8–5.5

* = non calcareous (1); slightly calcareous (2); strongly calcareous (3) **pH is comparable with pH(KCl).

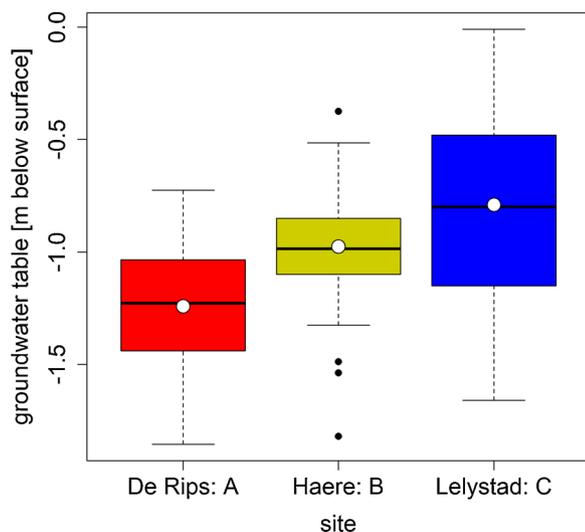


Fig. 2. Groundwater values measured at De Rips, De Haere, and Lelystad during the period 1972–2017. White dots indicate the corresponding site means. Capital letters on the x-axis refer to assignment according to pairwise Wilcoxon rank-sum test. Colour-code: red = De Rips, yellow = Haere, blue = Lelystad.

other two sites (Fig. 2). The trial ‘Lelystad’ is located on moderately to well drained young marine deposits with a topsoil of silt loam on a loamy subsoil. The soil is nutrient and calcium rich due to a high percentage of shell fragments. Its pH (KCl) is 6–6.5 in the topsoil and more than 7.5 in the subsoil. Lelystad has the highest groundwater table (Fig. 2). Groundwater data in close proximity to each of the sites were provided by the Dutch Organisation for applied scientific research (<https://www.dinoloket.nl/>).

2.2. Fieldwork, sample preparation, and tree-ring measurements

In November 2016, we selected 10 trees per provenance evenly spread over the provenance trial. We aimed at reducing the variation possibly introduced by competition by selecting dominant or co-dominant trees. To avoid overestimation of the level of increment by edge effects, trees growing close to a forest road or edge were excluded. We generally collected and measured one increment core at 50 cm stem height per tree. Moreover, we measured tree height (Nikon Forestry pro) and diameter at coring height (50 cm, in the following DCH), from which we eventually computed stem volume (see below).

The cores were glued to wooden sample holders and prepared by using a core microtome (WSL, Switzerland). Earlywood and latewood widths were measured separately and combined to ring width (RW) using a combination of a Lintab digital positioning table and the software TSAP-Win (both Rinntech, Germany). Single ring-width series

were cross-dated and – next to the individual tree analyses (see section 2.3) – averaged into respectively ten provenance chronologies per trial.

For our analyses, we used two different tree-ring parameters, i.e. cumulative basal areas (cBA) and detrended ring-width (RW) indices. To obtain cBA, we first computed basal area increments (BAI) using ring-width measurements and DCH within the function `bai.out` in the ‘`dplr`’ package (Bunn, 2008). BAI better represent actual growth since they account for the successive narrowing of tree-rings with increasing stem size. From BAI we computed cBA time series, by integrating BAI from the pith to each respective year. Moreover, as an approximation of total stem volume and thus timber produced over the period of the trial, we multiplied the basal area of 2018 (as derived from DCH) with tree height. Furthermore, RW-series were detrended using the residuals of an autoregressive model (aka pre-whitening) and resulted in so-called ring-width indices (RWI). Thus, while cBA reflects productivity over time, RWI series emphasize the year-to-year variations of tree growth as a reaction to environmental conditions.

2.3. Statistical analyses

To test the hypotheses related to a) we pooled the data according to hypotheses. That is to test for hypothesis Ia, data were pooled according to sites, while they were pooled according to provenances to test for hypothesis II a. Measured and computed features related to tree stature and productivity were compared among sites and per site among provenances (Ia and IIa, shown in section 3.1.). The significance of observed differences was tested using pairwise Wilcoxon rank sum test (p-value adjustment using the ‘Holm’-method) to account for partial non-normal distribution of the data. To visualize growth performance over time, we pooled cBA series per site and for each site per provenance and plotted the corresponding master chronologies, i.e. time series representative of the mean cBA of a corresponding group of trees (site or provenance).

In order to explore site- and provenance specific tree-growth patterns (hypotheses Ib and IIb, shown in section 3.2.), we used Principal Component Gradient Analyses (PCGA, Buras et al., 2016) on the basis of RWI. PCGA relies on the loadings of the first two principal components of an ordinary PCA. Each pair of loadings represents one single time series. If the first two PCs explain a fair amount (> 0.5) of the overall variance of the data, the similarity of the corresponding loadings among series directly reflects similarity of growth patterns (for further details and examples see Buras et al., 2016). Here, we used detrended data to emphasize on high-frequency growth variations, which represent the annual change of growth as a reaction to environmental conditions. PCGA was first applied to the provenance chronologies over all sites and then to the single individual tree-series for each site separately. On the basis of provenance chronologies over all sites, PCGA will explore whether site-specific growth patterns prevail (Ib). In contrast, the analyses based on single series per site will explore whether

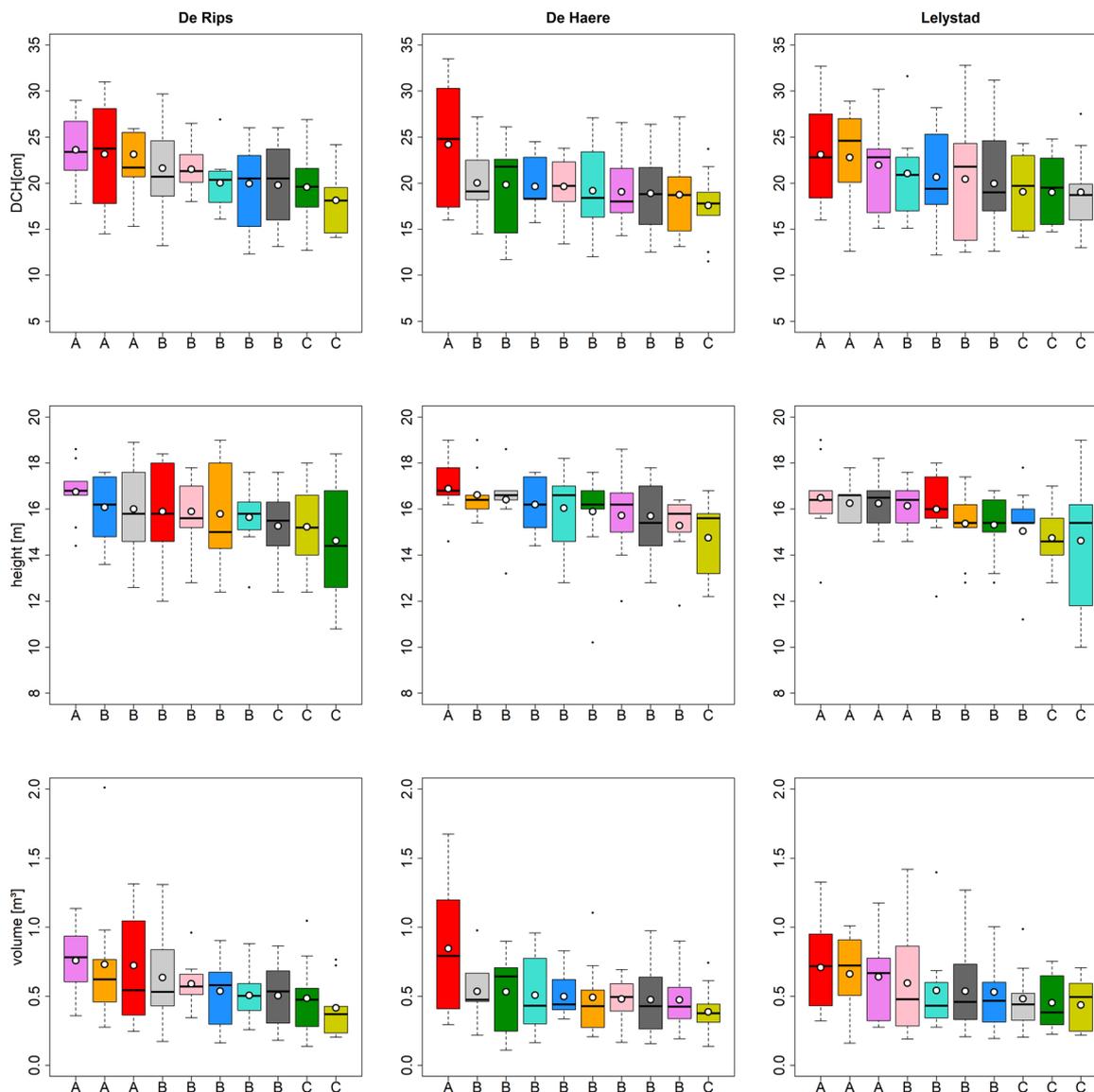


Fig. 3. DCH (top panels), height (mid panels), and stem volume (bottom panels) for De Rips (left), De Haere (mid), and Lelystad (right) pooled by provenances. Boxes were sorted according to their provenance-specific mean value in descending order from left to right. White dots indicate the corresponding provenance means. Capital letters on the x-axis refer to assignment according to pairwise Wilcoxon rank-sum test. Colour-code: light grey = 222, red = 230, blue = 233, yellow = 234, pink = 236, orange = 240, turquoise = 244, green = 245, violet = 250, dark grey = 256 (common names of these selections are depicted in Table 1).

provenance-specific growth patterns prevail at each site (Iib). We coloured the resulting loadings according to categories, i.e. sites or provenances. By doing so, the existence of possible site- or provenance-specific growth patterns is visualized by a corresponding clustering of loading colours (see e.g. Buras et al., 2018, 2016; Rehschuh et al., 2017 or the Dendroschool video tutorial on PCGA: <https://dendroschool.org/multivariate-statistics-in-tree-ring-analyses-coming-soon/>). Initially we also explored commonly computed climate-growth relationships. However, since the overlap period of tree-ring and climate data only spans 26 years (1990–2015) and tree-ring data mostly represent juvenile growth of trees which to a large degree is governed by competition for light (and not climate) we refrained from interpreting these correlations, particularly since they did not indicate clear results. All analyses were performed in R (R foundation for statistical computing, Vienna, 2019).

3. Results

3.1. Tree features and absolute growth (Ia, Iia)

Tree features varied significantly among sites (Ia). While De Haere was characterized by significantly lower diameter at coring height (DCH), it expressed significantly higher tree height in comparison to the other two sites, which in combination resulted in significantly lower stem volume (Fig. S1). We also observed significantly different tree features among provenances (IIa). Particularly provenance 2 (i.e. selection 230, see Table 1; red in Fig. 3) protruded through relatively high productivity measures in all sites, while selection 234 (yellow in Fig. 3) performed comparably poor. With regard to cumulative basal area series (cBA), De Rips provenances on average showed a relatively higher productivity. Comparing cBA among provenances confirmed the superior performance of selection 230 (Fig. 4).

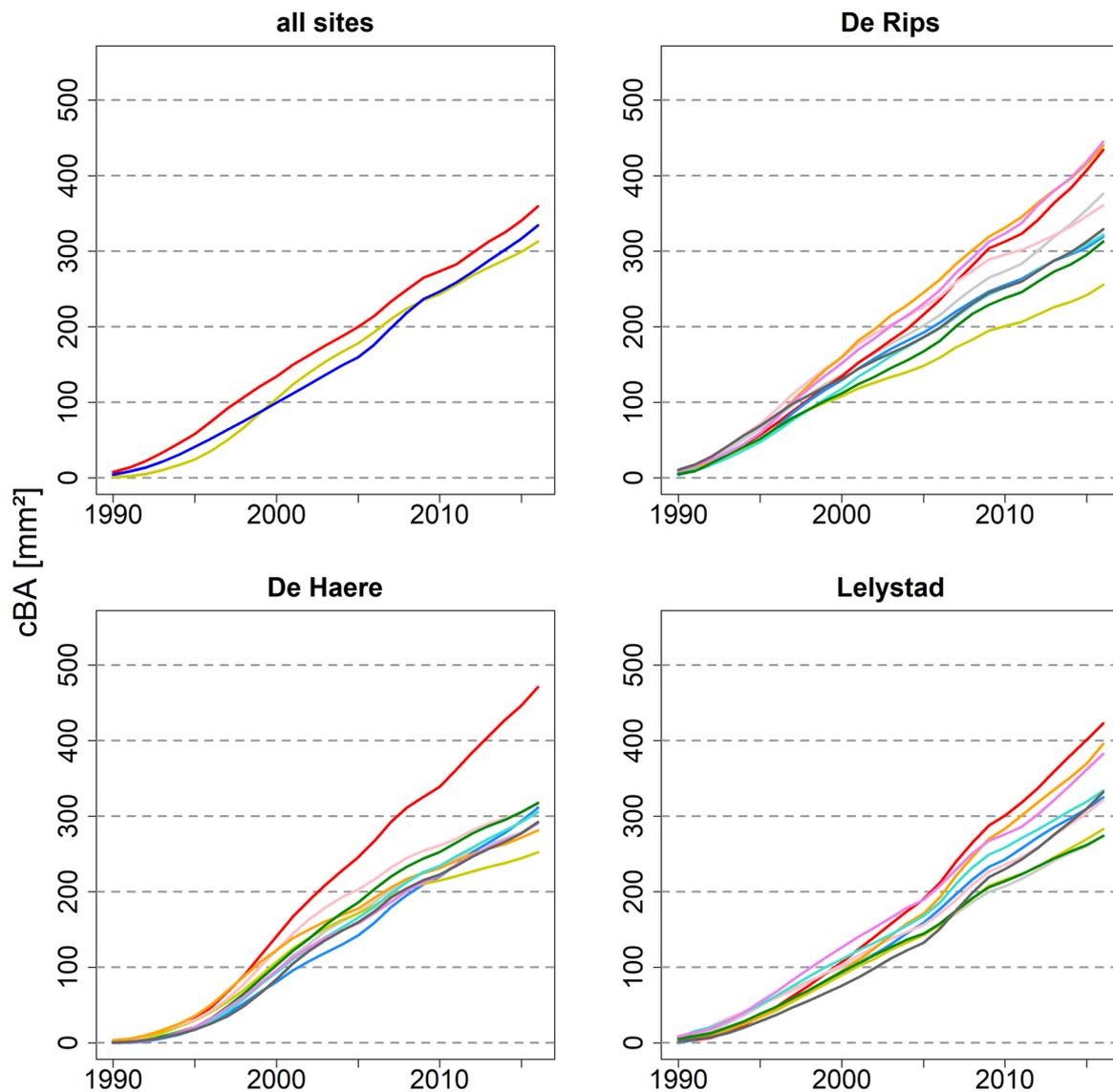


Fig. 4. Cumulative basal area (cBA), site chronologies (top left), and provenance chronologies per site (top right and bottom panels). Colour-code for site chronologies: red = De Rips, yellow = De Haere, blue = Lelystad. Colour-code for provenance chronologies: light grey = 222, red = 230, blue = 233, yellow = 234, pink = 236, orange = 240, turquoise = 244, green = 245, violet = 250, dark grey = 256.

3.2. Site- and provenance specific growth patterns (Ib, IIb)

PCGA clearly indicated site-specific tree-growth patterns (Ib). That is, an obvious separation according to the sites occurred along the second principal component which explained 10 percent of the overall variance (Fig. 5). The corresponding site chronologies featured differing growth patterns, but surprisingly none of the RWI-chronologies expressed a growth depression during the extreme summer drought of 2003 (Fig. 6). However, in 2010 De Rips and Lelystad featured a strong growth depression due to a severe late frost damage followed by growth recovery in 2011 (see also Fig. S2). In contrast to site chronologies, PCGA of provenance chronologies per site did not indicate any provenance-specific growth patterns (IIb, Fig. 7).

4. Discussion

The presented results support hypotheses Ia, Ib, and IIa and falsify IIb. That is, productivity varied systematically among soil conditions (Ia), with De Haere expressing lowest basal areas, DCH-values, stem volumes, and cBA (Figs. 3–4 and S1). Regarding growth variability (Ib), PCGA clearly separated Lelystad – the site with high clay contents in the

soil – from the two sandy sites (Fig. 5). Per site, provenances varied significantly regarding productivity (IIa, Figs. 3–4) but no provenance-specific growth patterns were detected (IIb, Fig. 7).

4.1. Oak productivity is determined by site conditions and provenance

Productivity of oak significantly varied among sites, i.e. seemed to be governed by soil conditions and water availability since climate conditions were rather similar across sites. Yet, the observed differences were relatively small. De Haere expressed the lowest basal areas and stem volumes, but largest tree heights (Figs. 3–4 and S1). This finding is likely related to nutrient-poor conditions at the sandy site De Haere. The better water availability in comparison to De Rips, caused by a higher groundwater table (Fig. 2) may explain the observation of taller trees at this site (Klein et al., 2015). Overall, the mean height growth of 15.6 m (Lelystad) to 15.9 m (De Haere) after 30 years across sites is high (Jansen et al., 2018) and shows that all oak provenances can cope well with different soil types and hydrologic conditions in the Netherlands.

Our analyses show clear effects regarding provenances on tree productivity. Considering stem volume, we found that the provenances

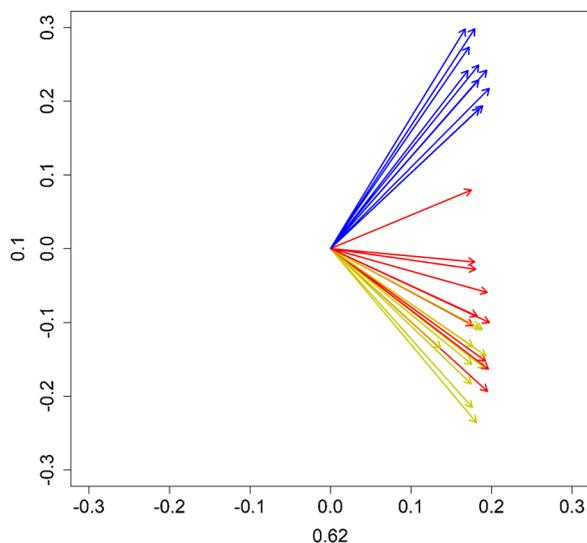


Fig. 5. PCGA loadings coloured according to sites. The values on the x- and y-axis indicate the amount of variance explained by the first and second principal component, respectively. Colour-code: red = De Rips, yellow = De Haere, blue = Lelystad.

Beek en Donk-01, Nuenen-02, and Princehage-02 (selections 230, 236, and 240) were performing best in both Lelystad and in De Rips with Beek and Donk-01 (230) performing best also in de Haere. Helmond-01 (234) performed poor at all sites and Oirschot-02 (245) performed poor at Lelystad and in De Rips. In De Haere, nine out of the ten provenances grew less compared to Lelystad or De Rips. Only the provenance Beek en Donk-01 (selection 230) showed comparably high growth in all three sites. Although differences between provenances were generally small, some provenances are obviously able to cope with a wide range of site conditions while keeping a high production level. These provenances are of particular interest for foresters, especially if they have few epicormics, no spiral grain, and contain a high number of straight stems (Kranenborg and de Vries, 1999). We want to stress that we here only considered the performance of Dutch provenances. If including non-native provenances whose origins feature different climatic conditions than the Netherlands, the differences among provenances regarding productivity might be higher.

4.2. Soil conditions determine growth patterns

De Haere and De Rips featured more similar soil and groundwater conditions in comparison to Lelystad, which is also reflected in the PCGA that clearly separated Lelystad from the other two sites. Thus, variation in growth patterns seems to be related to site conditions. This finding corroborates other studies which found systematic effects of soil conditions with respect to productivity and climate sensitivity (Lévesque et al., 2013; Rehschuh et al., 2017). In these studies, effects were mainly linked to drought susceptibility, which might also play a role here (higher water permeability in De Rips and de Haere due to the sandy soils). Given the shortness of tree-ring series, climate-RWI correlations however did not provide clear results (and were therefore not shown). Besides, competition among juvenile, even-aged specimens presumably adds substantial noise to climate-growth relationships, which may additionally explain why we could not find clear climate-growth relationships. Given the differing soil texture and groundwater tables among sites, it seems possible, that trees will react differently to prevailing climatic conditions. This may also explain the contrasting reports from the literature with respect to the drought susceptibility of pedunculate oak (Andersson et al., 2011; Drobyshev et al., 2007; Kuster et al., 2014, 2013; Levanič et al., 2011; Rubio-Cuadrado et al., 2018; Thomas and Gausling, 2000; Urli et al., 2015). Besides, biotic agents may play an important role in oak decline (Denman et al., 2018, 2014; Thomas et al., 2002). Contrasting findings in the literature may to some degree be explained by systematically differing soil properties among the study sites, which may translate into a higher drought susceptibility at hydromorphic sites with fluctuating water tables, where root formation of *Q. robur* may be impeded (Copini et al., 2016; Thomas et al., 2002). Moreover, varying plant available water capacities due to differing soil textures among sites may alter trees' drought susceptibility (Lévesque et al., 2013; Rehschuh et al., 2017). In addition, harsher climate conditions as in Urli et al. (2015) may play a role for the drought-susceptibility of pedunculate oak provenances (see also Klisz et al., 2019 regarding Norway spruce). To further test the hypothesis of soil type modifying the drought -susceptibility of pedunculate oak, in-situ plant monitoring and/or longer time-series from provenance trials are needed for assessing to what degree and in which manner soil conditions affect climate sensitivity.

Interestingly, we did not encounter provenance-specific growth patterns as for instance observed by Klisz et al. (2019). These authors reported provenance specific growth patterns to prevail under climate conditions representing the centre of a species distributional range,

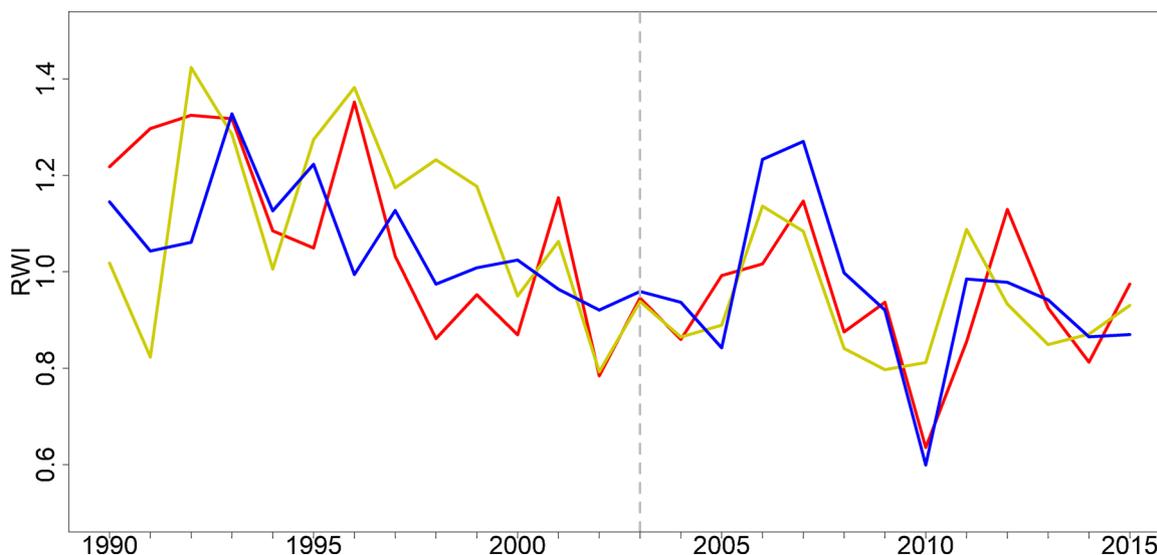


Fig. 6. RWI site chronologies for De Rips (red), De Haere (yellow) and Lelystad (blue). The grey dashed line indicates the year 2003.

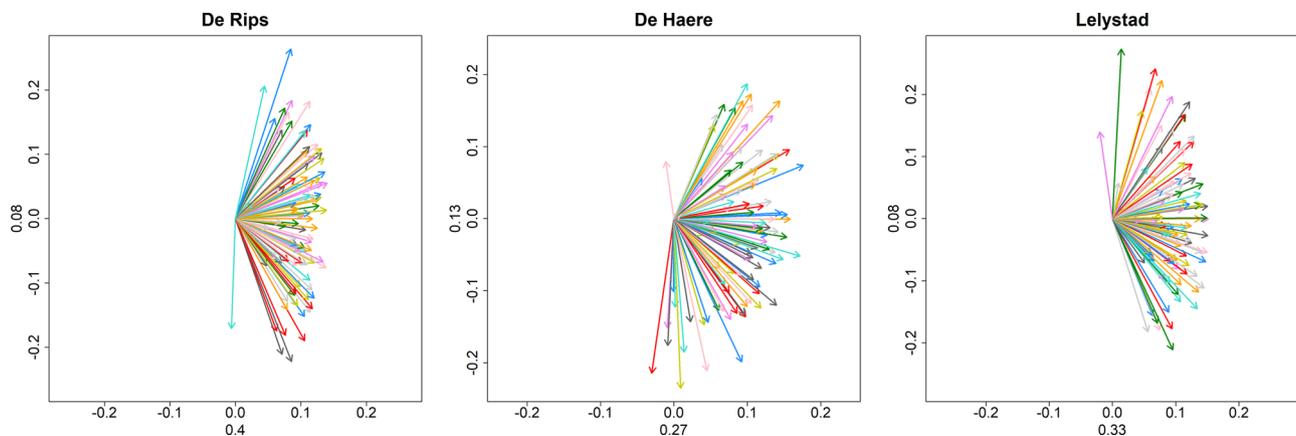


Fig. 7. PCGA loadings coloured according to provenances for De Rips, De Haere, and Lelystad. The values on the x- and y-axis indicate the amount of variance explained by the first and second principal component, respectively. Colour-code: light grey = 222, red = 230, blue = 233, yellow = 234, pink = 236, orange = 240, turquoise = 244, green = 245, violet = 250, dark grey = 256.

while provenance specific differences diminished towards the species range margins (in a climatic context). Since we studied native oak provenances which likely grew in the centre of their distributional range, we would have expected clearer differences among provenances. It seems possible that the juvenile growth of trees – which is largely governed by competition and may vary largely among individual trees – did not allow for identifying provenance-specific growth patterns as observed for Norway spruce (Klisz et al., 2019; Mátyás, 1994). To test this hypothesis further, reassessing the existence of provenance-specific growth patterns for the trees studied here in one or two decades, i.e. when longer time-series of more mature trees are available, seems to be meaningful. In the meantime, existing tree-ring data from provenance trials covering longer periods could be assessed for diminishing provenance-specific growth patterns during the juvenile stage of trees.

4.3. Summer drought of 2003 did not affect radial growth

It is worth to mention that we found no negative effect of the extreme dry summer of 2003 on tree growth for any provenance in all sites (Fig. 6). Also, in the following years (2004–2005) the trees did not feature strong growth decline, i.e. the typical growth patterns of commonly observed legacy effects following drought (Anderegg et al., 2015; Kannenberg et al., 2018; Perkins et al., 2018). For *Quercus petraea*, Leuzinger et al. (2005) found no significant reduction of daily sap flow peak values, although photosynthesis decreased considerably in mid of August during the peak of the drought in 2003. Our findings suggest that isolated summer droughts like in 2003 might induce few problems for oak in the temperate maritime climate in the Netherlands. Also, other studies for central Europe or outside the natural distribution range of oak reported that oak does not significantly reduce ring width in years of drought, although drought legacies appeared to be common (Perkins et al., 2018). Finally, two independent projections of pedunculate oak performance under anticipated climate conditions consistently indicated this species to prevail under future climate conditions (Buras and Menzel, 2019; Huang et al., 2017). We want to stress that the trees in our provenance trials were only 15 years old at the time of the 2003 drought. Therefore, our observation that trees were not affected by the 2003 drought cannot be extrapolated to mature trees, which – given their larger canopies and thus evaporative surface – may have experienced more stress during 2003. However, van der Werf et al. (2007) also reported no extraordinary growth decline for mature pedunculate oak in 2003, which they explained by favourable weather conditions in 2002 and spring 2003. Nonetheless, to clarify how soil conditions may modify the drought resilience of mature pedunculate oak further research is needed.

In contrast to 2003, ring width was significantly reduced in 2010 in

De Rips and Lelystad which might be related to a severe late frost event in May during earlywood vessel formation (see also Copini et al., 2016, 2015). In addition defoliation through winter moth larvae that were highly abundant in the Netherlands in both 2009 and 2010 might have influenced radial growth (Moraal, 2011). Interestingly, the reaction to 2010 differed among provenances in De Rips but not in Lelystad (Fig. S2). This may point at provenance-specific characteristics (e.g. systematically earlier leaf-flush) which may render specific genotypes particularly vulnerable to late-frost events and may be additionally affected by soil-type since Lelystad did not express any differences among provenances as shown earlier for European beech (Arend et al., 2016). However, since in our study only one late-frost event occurred, this hypothesis needs further testing by investigating tree-ring data from provenance trials across different soil types that comprise more late frost events which would allow for assessing whether the observed differences vary systematically across provenances.

5. Conclusions

This study reports clear effects of provenances and soil types on the productivity of pedunculate oak. Moreover, growth patterns were governed by site conditions, i.e. provenances growing on clay-rich soils with high groundwater table showed different growth patterns compared to two sandy sites with relatively low groundwater tables. The observation of a significant effect of soil conditions on productivity and growth variability highlight the importance of incorporating soil information into the evaluation of common garden experiments and may explain the reported varying drought susceptibility of pedunculate oak in the literature. To further address this important topic in the context of climate change, further research is needed on the basis of larger networks of pedunculate oak provenance trials incorporating Southern provenances that currently grow in climates we anticipate to experience in the Netherlands in future. Thereby, more insights into the interaction among climate, soil, and provenance may be obtained which would provide a broader and clearer picture on the drought resilience of pedunculate oak under climate change.

Declaration of Competing Interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.dendro.2020.125705>.

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