

# Root growth of different oak provenances in two soils under drought stress and air warming conditions

**Journal Article****Author(s):**

Kuster, Thomas M.; Arend, Matthias; Günthardt-Goerg, Madeleine S.; Schulin, R.

**Publication date:**

2013-08

**Permanent link:**

<https://doi.org/10.3929/ethz-b-000059409>

**Rights / license:**

[In Copyright - Non-Commercial Use Permitted](#)

**Originally published in:**

Plant and Soil 369(1-2), <https://doi.org/10.1007/s11104-012-1541-8>

# Root growth of different oak provenances in two soils under drought stress and air warming conditions

Thomas M. Kuster · Matthias Arend ·  
Madeleine S. Günthardt-Goerg · Rainer Schulin

Received: 4 September 2012 / Accepted: 21 November 2012 / Published online: 6 December 2012  
© Springer Science+Business Media Dordrecht 2012

## Abstract

**Background and aims** Oaks are considered to be drought- and thermo-tolerant tree species. Nevertheless, species and provenances may differ in their ecological requirements. We hypothesised that (i) provenances from xeric sites are better adapted to drought than those from more humid sites, (ii) oaks direct root growth towards resource-rich layers, and (iii) air-warming promotes root growth.

**Methods** To test different provenances of *Quercus robur*, *Q. petraea* and *Q. pubescens*, we conducted a model ecosystem experiment with young trees, grown on acidic and calcareous soil, subjected to drought, air warming, the combination of warming and drought, and a control.

**Results** The results were only in partial agreement with the first hypothesis. As expected the provenances originating from drier sites produced more biomass than those from more humid sites under drought conditions. Surprisingly, however, they reacted more

sensitive to water limiting conditions, as they produced also substantially more biomass under well-watered conditions. The drought treatment reduced root mass substantially in the upper soil. In agreement with the second hypothesis this led to a shift in the centre of root mass to lower depth, where water was still more available than closer to the soil surface. In contrast to the third hypothesis, the air-warming treatment, which was very mild however compared to climate change scenarios, had no significant effects on root growth.

**Conclusions** Given that the provenances from drier sites showed more biomass loss at water limiting conditions than provenances from more humid sites, it remains questionable whether provenances from drier sites are better suited for a future climate.

**Keywords** Climate change · Fine root · Root mass distribution · Root:shoot ratio · *Quercus robur* · *Quercus petraea* · *Quercus pubescens*

---

Responsible Editor: Alain Pierret.

---

T. M. Kuster (✉) · M. Arend · M. S. Günthardt-Goerg  
Swiss Federal Research Institute WSL,  
Zürcherstr. 111,  
8903 Birmensdorf, Switzerland  
e-mail: thomaskuster@gmx.ch

T. M. Kuster · R. Schulin  
Institute of Terrestrial Ecosystems ITES, ETH Zürich,  
Universitätstrasse 16,  
8092 Zürich, Switzerland

## Introduction

Climate change scenarios of the IPCC predict generally increasing temperatures and changing precipitation patterns all over the world (IPCC 2007). According to IPCC Scenario A2, for example, mean summer temperatures will increase by 3.2 to 4.8 °C until the end of this century in central Europe, while summer precipitation will decrease by 21 to 28 % (CH2011 2011). Moreover, periods with extreme

weather conditions are expected to become more frequent than today (IPCC 2007; Schär et al. 2004). This implies that drought and heat resistance will become important for tree survival, in particular together with additional stress by competition with other trees for light, water and nutrients.

Oaks are known to be drought-tolerant among European forest trees (Landolt and Bäumler 2010; Ellenberg et al. 2010). They are therefore considered promising candidates to replace beech (*Fagus sylvatica*), spruce (*Picea abies*) or even the also drought-tolerant Scots Pine (*Pinus sylvestris*) on warm and dry sites in future central European forestry (Leuschner et al. 2001; Wohlgemuth 2006; Friedrichs et al. 2009; Scharnweber et al. 2011). Besides a xeromorphic leaf structure and the ability to rapidly resume assimilation after drought periods (Kubiske and Abrams 1993; Galle et al. 2007; Arend et al. 2012), oaks show root growth patterns that make them particularly well adapted to temporal and spatial variability in soil water and nutrient availability. A common response of oaks to reduced soil water availability is the shift of assimilate allocation from above- to belowground growth, thereby increasing the ability of the root system to exploit water and nutrient resources in the soil and reducing transpirational water losses (Thomas and Gausling 2000; Broadmeadow and Jackson 2000; Joslin et al. 2000; Gieger and Thomas 2002; Fotelli et al. 2000; Thomas 2000a). In many other tree species, including whitebeam (*Sorbus aria*), ash (*Fraxinus excelsior*) and beech, the root:shoot or root:leaf ratio was found to respond less to drought conditions compared to oaks (Broadmeadow and Jackson 2000; Thomas 2000a). Furthermore, plant species are able to respond to uneven vertical distribution of water resources and nutrients by enhancing root proliferation in zones where the limiting resources are most available, as for example shown for oak root growth by Callaway (1990). Again this capacity seems to be particularly pronounced in oaks, in contrast for example to spruce and beech, as shown for nutrient availability by Göransson et al. (2006). Comparing the influence of water and nutrient availability on vertical root growth allocation in *Quercus petraea*, Thomas (2000b) reported that nutrients, especially N, were more important than water availability.

In comparison to water and nutrient availability, rapid variations in soil temperature are of importance only very near to the soil surface, while in deeper soil

layers only seasonal fluctuations are still felt. Generally, root growth requires a minimum soil temperature between 0 and 5 °C (Kozłowski et al. 1991). Above this threshold root growth increases with soil temperature, until a maximum growth rate is reached at 20 to 25 °C, as for example reported for *Q. robur* and *Q. petraea* (Lyr and Garbe 1995; Lyr 1996).

Different oak species and provenances may vary considerably in temperature sensitivity, drought stress tolerance and adaptability of root growth to changing conditions. For example, *Q. robur* was generally found less drought tolerant than *Q. petraea* and *Q. pubescens* (Arend et al. 2012; Günthardt-Goerg et al. 2012), but to be more flexible in adapting to changing soil water conditions (Landolt and Bäumler 2010). Provenances from xeric sites generally appeared to be better adapted to enhanced temperatures and low water availability than provenances from more humid sites (Jensen and Hansen 2010; Bruschi 2010).

Effects of warming, drought and nutrient availability on root growth in oaks have mostly been studied independently of each other, whereas interactions between these factors are less well known. Based on the literature presented above, we hypothesised that (i) oak provenances from xeric sites produce more root mass under drought conditions than those from more humid sites, (ii) oaks grow roots at higher density in water- and nutrient-rich than in water- and nutrient-poor layers, and (iii) air-warming promotes root growth. To test these hypotheses we conducted a full-factorial model ecosystem experiment in which various provenances of young *Quercus robur*, *Q. petraea* and *Q. pubescens* trees were grown on two different soils and subjected to drought and air-warming treatments.

## Material and methods

### Study site & experimental design

The experiment was performed in the model ecosystem facility of the Swiss Federal Research Institute WSL, Birmensdorf, Switzerland (47°21'48" N, 8°27'23" E, 545 m a.s.l.). A detailed description of the experimental design is given in Kuster et al. (2012a). Briefly, the facility consists of 16 hexagonal chambers of 3 m height and a surface area of 6 m<sup>2</sup> each. Using a Latin square design, one of the following four

treatments was applied in four replicates from spring 2007 to October 2009: air warming (AW), drought (D), the combination of air warming and drought (AWD), and control (CO). Each chamber is split below ground into two 1.5 m deep concrete-walled lysimeters, filled in spring 2005 with a 0.5 m drainage packing, composed of 3 layers of pure quartz gravel of decreasing grain size (from bottom to top), and a 1 m soil layer on top of this drainage layer. In one lysimeter of each chamber the soil consisted of two layers of acidic loamy sand taken from a Haplic Alisol (pH 4.0, subsoil 0.15–1.00 m, topsoil 0–0.15 m), while in the other lysimeter it consisted of a single layer of calcareous sandy loam taken from a Calcaric Fluvisol (pH 6.9). Further properties and nutrient concentrations of the two soils, both of which originated from mixed oak forests, are presented in Kuster et al. (2012a) and in Kuster et al. (2012b). In spring 2006, the same set of two-year-old saplings of *Quercus robur*, *Q. petraea* and *Q. pubescens* was randomly planted on all lysimeters and grown with sufficient water supply at

ambient air temperature during the growing season of 2006 (Arend et al. 2011). For each species, provenances from 4 different oak stands in Switzerland and Italy were selected. Each provenance was represented by two saplings on each lysimeter (statistical unit=oak provenance,  $n=8$ ), leading to a total number of 768 trees (4 climatic treatments, 2 soils, 12 provenances nested in 3 species, 8 replications). The sites were different for all 12 provenances (Table 1). For each species, one site of origin was located in the Swiss Jura, a second in southern Switzerland and a third in a region where the respective species is most abundant in Switzerland (Günthardt-Goerg et al. 2012). The fourth site was chosen for *Q. robur* and *Q. petraea* in the Swiss Plateau and for *Q. pubescens* in Northern Italy. To indicate soil humidity conditions at these sites during the growing season (May to September), water balances are given in Table 1, representing the differences between precipitation and potential evapotranspiration after Primault (1981). The smaller this difference is at a given site, the more limiting is water for growth; a

**Table 1** Location of the origins of the oak provenances, each with the average climate conditions (1981–2010) at nearby SwissMeteo WMO weather stations during the growing season

(May to September). Water balance data=precipitation - potential evapotranspiration after Primault (1981)

Species/ Provenance	Latitude	Longitude	Altitude (m)	Weather station <sup>a</sup>	Precipitation (mm)	Temperature (°C) <sup>c</sup>	Water balance (mm)
<i>Q. robur</i>							
Tägerwilen (T)	47° 38' N	9° 08' E	510	Illhart/ Güttingen	508	15.7	+ 205
Bonfol (B)	47° 28' N	7° 09' E	450	Fahy	515	16.2	+ 232
Hühnenberg (H)	47° 11' N	8° 25' E	398	Cham/ Luzern	631	17.0	+ 385
Magadino (Mi)	46° 09' N	8° 53' E	199	Magadino	975	19.1	+ 686
<i>Q. petraea</i>							
Corcelles (C)	46° 51' N	6° 41' E	550	Yverdon/ <sup>b</sup>	436	16.3	+ 94
Magden (M)	47° 32' N	7° 48' E	308	Arisdorf/ Basel	514	17.1	+ 251
Wädenswil (W)	47° 14' N	8° 38' E	430	Wädenswil	734	16.8	+ 435
Gordevio (G)	46° 12' N	8° 44' E	450	Locarno	1023	18.6	+ 615
<i>Q. pubescens</i>							
Leuk (Lk)	46° 18' N	7° 38' E	720	Sierre/ Visp	268	16.3	- 282
Le Landeron (LL)	47° 04' N	7° 03' E	700	Neuchâtel	456	15.7	+ 7
Promontogno (P)	46° 20' N	9° 33' E	900	Soglio/ Poschiavo	794	14.9	+ 457
Arezzo/Italy (A)	43° 28' N	11° 53' E	296	Molin Bianco	297	not avail.	not avail.

<sup>a</sup> Meteorological network for measuring precipitation is denser than for other parameters, therefore different stations were used to describe the climate conditions: 1st station refers to precipitation measurements, 2nd to temperature and parameters (sunshine, relative air humidity) needed to calculate potential evapotranspiration

<sup>b</sup> Average climate data of the nearby weather stations Payerne, Neuchâtel and Bullet/La Frétaz

<sup>c</sup> Air temperature was adjusted to the altitude of the provenance by  $\pm 0.65$  °C / 100 m

negative water balance indicates conditions where the water losses are higher than water input through precipitation. For the Italian provenance Arezzo no data was available to calculate a water balance.

The air warming treatment consisted in keeping the side-walls less opened than in the control treatment. As a result, day-time air temperatures were 1–2 °C higher than in the control chambers during summer, and topsoil temperatures (at 5 cm depth) increased by 0.5–1 °C. In the drought treatment, irrigation was suspended for several consecutive weeks during the growing seasons, while it was continued in the control treatment. Rainfall was excluded from the chambers during the growing season (April–October) in all treatments by automatically closing roofs, while roofs were left open during the dormant seasons to allow for irrigation by natural precipitation. Compared to the long-term (1961–2009) mean precipitation from April to October at the experimental site, irrigation was reduced by 60 % over the entire growing season of 2007 and by 43 % in 2008 and 2009 in the drought treatment. Detailed information about air and soil temperatures and about the soil water regime are presented by Kuster et al. (2012a).

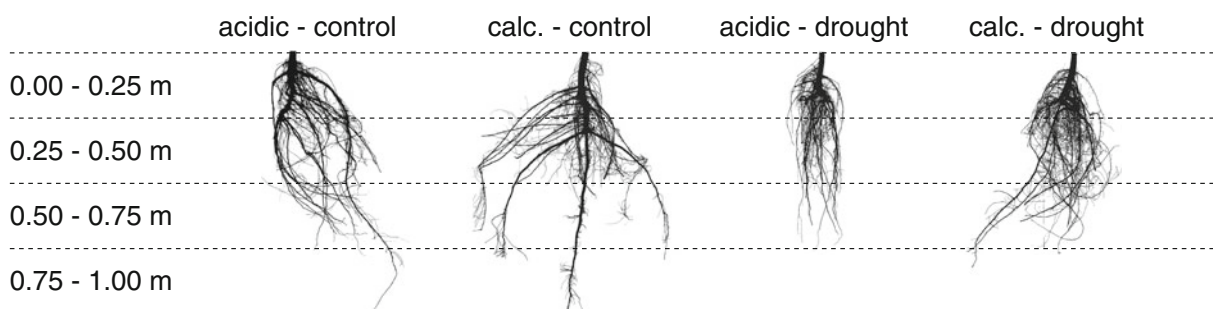
### Biomass sampling

Aboveground biomass (stems, twigs and foliage) was harvested tree by tree at the end of the growing season 2009. Then, 10 soil cores (diameter=0.08 m,  $h=0.22$  m) were taken from each lysimeter soil compartment to sample topsoil fine root density (diameter<2 mm). Thereafter, fine root biomass samples of each lysimeter were pooled for further analysis (statistical unit=soil

type,  $n=4$ , in total 32 fine root samples). After thawing in spring 2010, also all rootstocks were carefully excavated and separated from the soil. Dry mass of all plant parts was determined after drying to constant weight at 65 °C. A picture from each rootstock was taken in front of a white background (see example shown in Fig. 1). The pictures were converted using ImageJ 1.44 h (U.S. National Institutes of Health, Bethesda, Maryland, USA) into black and white images in which black pixels represented root tissue and white pixels the background and analysed for “projected root area” per soil layer using IDL 7.1 (ITT Visual Information Solutions, Boulder, Colorado, USA). These 2D pictures give a representative record of the root distributions over depths. This was confirmed by the finding of a close and approximately linear relationship between “projected root area” and root mass: root area [ $\text{cm}^2$ ]=2.23 × root mass [g]+135.16  $\text{cm}^2$  ( $R^2=0.807$ ). The positive intercept reflects the fact that the ratio between diameter and cross sectional area is larger for fine roots than for coarse roots.

### Statistical analysis

For statistical analyses we used R 2.11.1 (R Development Core Team, Vienna, AT). The data were analysed after log-transformation (mass values) or square-root-transformation (vertical root distribution) by ANOVA using a linear mixed-effect model accounting for the split-plot design of the experiment with two soils in each chamber. The statistical unit oak provenance was nested in species to account for similarity within a given species. Selected differences between treatments, soil and depths were pair-wise tested using contrasts based on  $t$ -tests and considered significant at  $P<0.05$  (Crawley 2009).



**Fig. 1** Examples of 2D rootstock pictures used to calculate the projected root area in four soil layers of each 0.25 m, in either acidic or calcareous (calc.) soil (example shown: *Q. robur* Tägerwilen)

**Results**

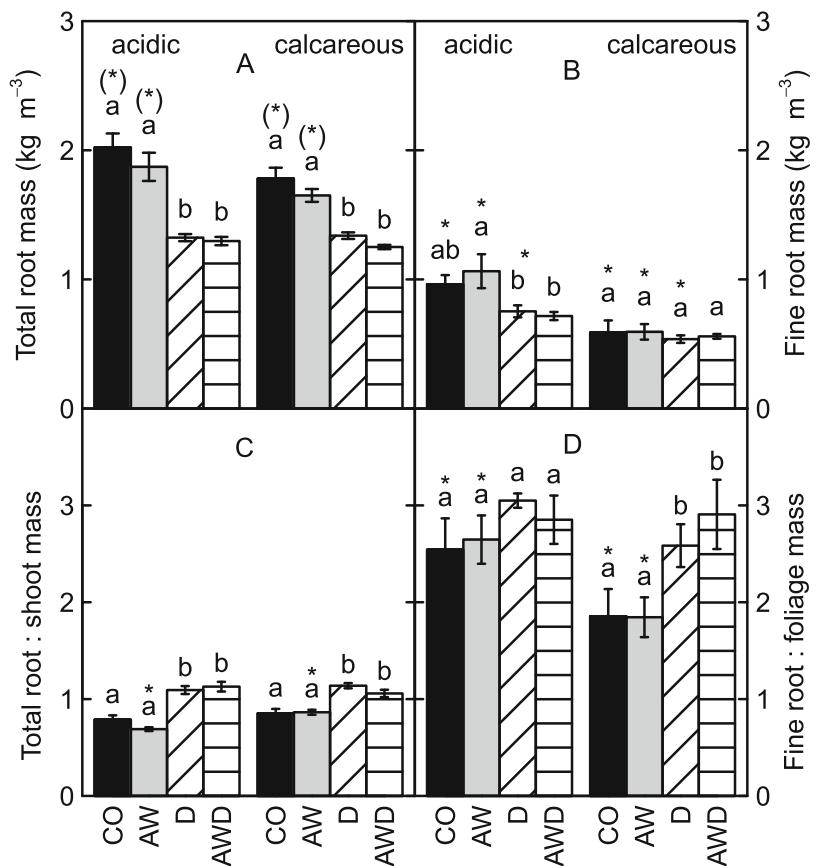
**Total and fine root mass**

Total and topsoil fine root mass were both higher in the acidic than in the calcareous soil in the treatments without droughts, while there was no difference in total root mass between the two soil types in the drought treatments (Fig. 2a/b, Table 2). The drought treatment reduced the total root mass by about one-third in the acidic and by one-fourth in the calcareous soil, irrespective of air warming. Fine root mass, in contrast to total root mass, was reduced by the drought treatment only in the acidic soil. However, this reduction was slightly lower compared to total root mass decrease. Air warming had no effect, neither on total nor fine root mass. As expected, the root:shoot (stem, twigs and foliage) mass ratio was increased on both soils by the drought treatment (Fig. 2c). The ratio was slightly higher on calcareous than on acidic soils in absence of drought stress, but did not differ between

the soils in the drought treatment. The fine root:foliage mass ratio was increased by the drought treatment only in the saplings growing on the calcareous, but not in those on the acidic soil (Fig. 2d). In contrast to the total root:shoot mass ratio, the fine root:foliage mass ratio was higher on the acidic than on the calcareous soil in the treatments with no droughts (Fig. 2d).

The stem and root biomasses were higher in *Quercus robur* than in *Q. petraea* and *Q. pubescens* in all combinations of soil and climate treatments (Fig. 3, Table 2), but the drought-induced growth reduction was stronger in *Q. robur* than in the other two species. Among the four provenances within each species, root and stem masses increased with the aridity of the original provenances sites (Fig. 3), using the climatic average balance between precipitation and potential evapotranspiration as aridity indicator (Table 1). Generally, the growth of *Q. robur* depended less on the aridity of the provenance site than that of *Q. petraea* and *Q. pubescens*.

**Fig. 2** a) Effects of drought and air warming on total root dry mass ( $\text{kg m}^{-3}$ ) after three growing seasons in acidic (left) and calcareous soil ( $\pm$  SE,  $n=8$ ), pooled over all species and provenances, b) fine root dry mass in the topsoil (upper 0.22 m,  $\text{kg m}^{-3}$ ,  $n=4$ ), c) total root:shoot (stem + twigs + foliage) mass ratio ( $n=8$ ), d) fine root:foliage mass ratio ( $n=4$ ). CO: control, AW: air warming, D: drought, AWD: air warming & drought. Results of statistical analysis are given in Table 2. Different letters indicate significant differences ( $P<0.05$ ) between respective treatments in the same soil type. An asterisk indicates a significant difference (\*:  $P<0.05$ , (\*):  $P<0.10$ ) between acidic and calcareous soils for the respective treatment



**Table 2** Main effects and selected interactions of drought (D, continuous vs. discontinuous irrigation), air warming (AW, ambient vs. elevated air temperature), soil type (acidic vs. calcareous), type of species and type of provenance (Prov, nested within species) after three growing seasons on total root mass ( $n=8$ ), stem mass ( $n=8$ ), on the total root:shoot (stem + twigs +

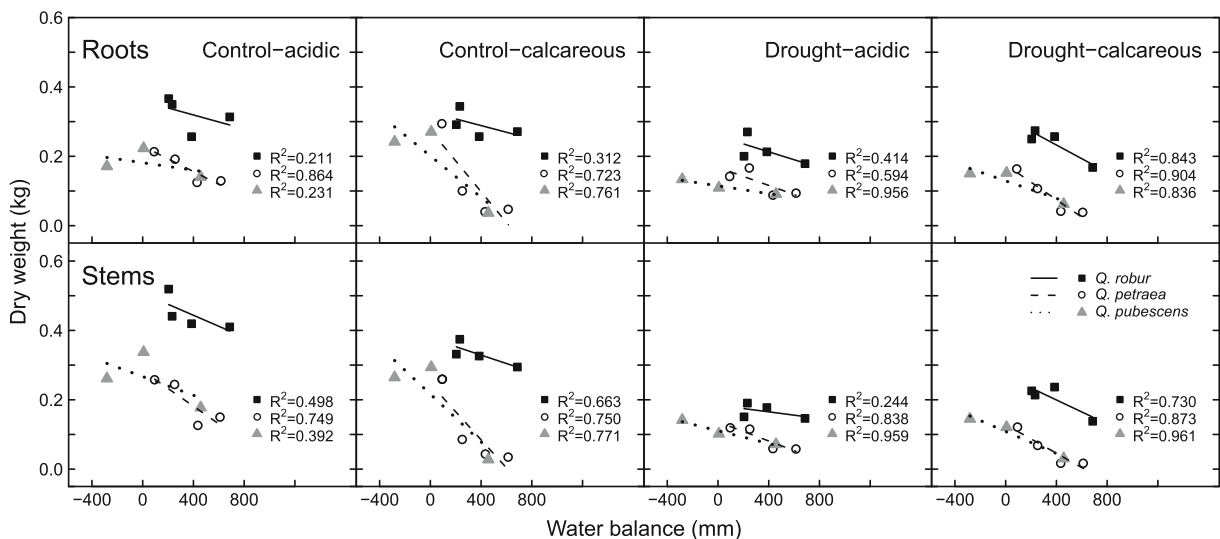
foliage) mass ratio ( $n=8$ ), on fine root mass in the upper 0.22 m ( $n=4$ ), on the fine root mass:foliage mass ratio ( $n=4$ ) and the projected root area ( $n=8$ ). Bold numbers represent significant main and interaction effects ( $P<0.05$ ). Other interactions were not significant

	D	AW	Soil	Species	Prov	D × Soil	D × Prov	Soil × Prov	D × Soil × Prov
Total root mass	< <b>0.001</b>	0.727	< <b>0.001</b>	<b>0.028</b>	< <b>0.001</b>	<b>0.025</b>	<b>0.003</b>	< <b>0.001</b>	<b>0.033</b>
Stem mass	< <b>0.001</b>	0.691	< <b>0.001</b>	0.052	< <b>0.001</b>	<b>0.015</b>	0.204	< <b>0.001</b>	0.228
Total root:shoot mass ratio	< <b>0.001</b>	0.694	< <b>0.001</b>	0.359	< <b>0.001</b>	<b>0.042</b>	0.125	< <b>0.001</b>	0.262
Fine root mass	<b>0.002</b>	0.696	< <b>0.001</b>	-	-	0.050	-	-	-
Fine root:foliage mass	<b>0.004</b>	0.769	<b>0.015</b>	-	-	0.114	-	-	-
Total projected root area	< <b>0.001</b>	0.665	0.451	<b>0.003</b>	< <b>0.001</b>	0.162	<b>0.003</b>	< <b>0.001</b>	0.094
0.00 – 0.25 m	< <b>0.001</b>	0.659	< <b>0.001</b>	<b>0.003</b>	< <b>0.001</b>	<b>0.001</b>	<b>0.035</b>	< <b>0.001</b>	<b>0.009</b>
0.25 – 0.50 m	<b>0.001</b>	0.817	0.328	<b>0.006</b>	< <b>0.001</b>	0.375	<b>0.009</b>	< <b>0.001</b>	0.348
0.50 – 0.75 m	0.457	0.256	< <b>0.001</b>	<b>0.007</b>	< <b>0.001</b>	0.190	<b>0.003</b>	< <b>0.001</b>	0.116

The main and interaction effects on the projected root area in the lowest soil layer (0.75–1.00 m) could not be calculated as the model assumptions could not be fulfilled despite square-root-transformations

Differences in growth between the provenances were reduced when water became a limiting factor in the drought treatments. This indicates a higher drought responsiveness of the provenances from the more arid

sites than of those from the more humid sites. This observed trend was systematic and consistent in all three species and for both soils. Comparing the two soils, growth on the calcareous soil depended more on



**Fig. 3** Relationship of water balances (mm) at the original provenance site (Table 1) to root and stem dry weights of the investigated oak provenances in the treatments without (control, air warming) and with droughts (drought, air warming & drought) on acidic and calcareous soil ( $n=16$ ). Data of corresponding treatments with and without air-warming are pooled as the air-warming treatment had no significant effect

on the presented data (Table 2). Over all treatments, species, provenances and both soils, the negative slope of the correlation lines was highly significant for root ( $R^2=0.772$ ,  $P<0.001$ ) and for stem growth ( $R^2=0.823$ ,  $P<0.001$ ). The Italian provenance *Quercus pubescens* Arezzo was excluded from this analysis due to missing water balance data

the aridity of the provenance site than growth on the acidic soil. The mean growing season temperature at the original provenance site showed no influence on tree growth, neither above nor below ground (not shown).

Effect of drought and soil properties on vertical root mass distribution

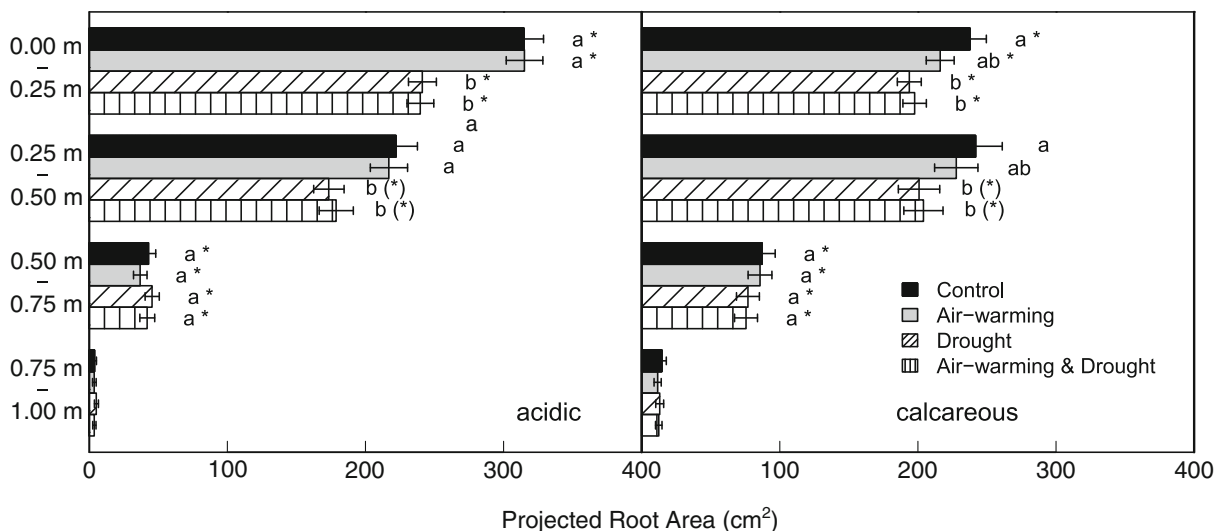
The effect of drought-induced root mass reduction decreased with soil depth (Fig. 4, Table 2). As a result, the centre of mass in the vertical root distribution shifted to lower depths. These downward shifts were found in all three species (Fig. 5). In contrast to drought, air warming had no effect on the vertical root mass distributions (Fig. 4, Table 2). Figure 4 also shows an influence of the soil on the depth distributions of root mass. In the acidic soil, root mass density was highest in the top 0.25 m, averaging 53 % of the total root mass over all treatments and species/provenances, whereas only 38 % of the root mass was located at 0.25 – 0.50 m and only 8 % at 0.50 – 0.75 m depth. Below 0.75 m, there were almost no roots in the acidic soil (< 1 %). In comparison to the acidic soil, the root mass distribution was shifted to

lower depths in the calcareous soil. On average, 41 % of the roots were located in the top 0.25 m, 42 % at 0.25 – 0.50 m, 16 % at 0.50 – 0.75 m and 2 % below 0.75 m.

Compared to the *Q. robur* provenances, the vertical root distribution patterns of *Q. petraea* and *Q. pubescens* were much more diverse among provenances, especially in the calcareous soil (Fig. 5). In the acidic soil, the provenance Arezzo differed most from the other *Q. pubescens* provenances, with distinctly smaller projected root areas in the upper 0.5 m depth than the other provenances. In the calcareous soil, the *Q. petraea* and *Q. pubescens* provenances originating from the drier sites showed a similar downward shift in vertical root mass distribution as the *Q. robur* provenances, whereas those from the more humid sites did not.

Discussion

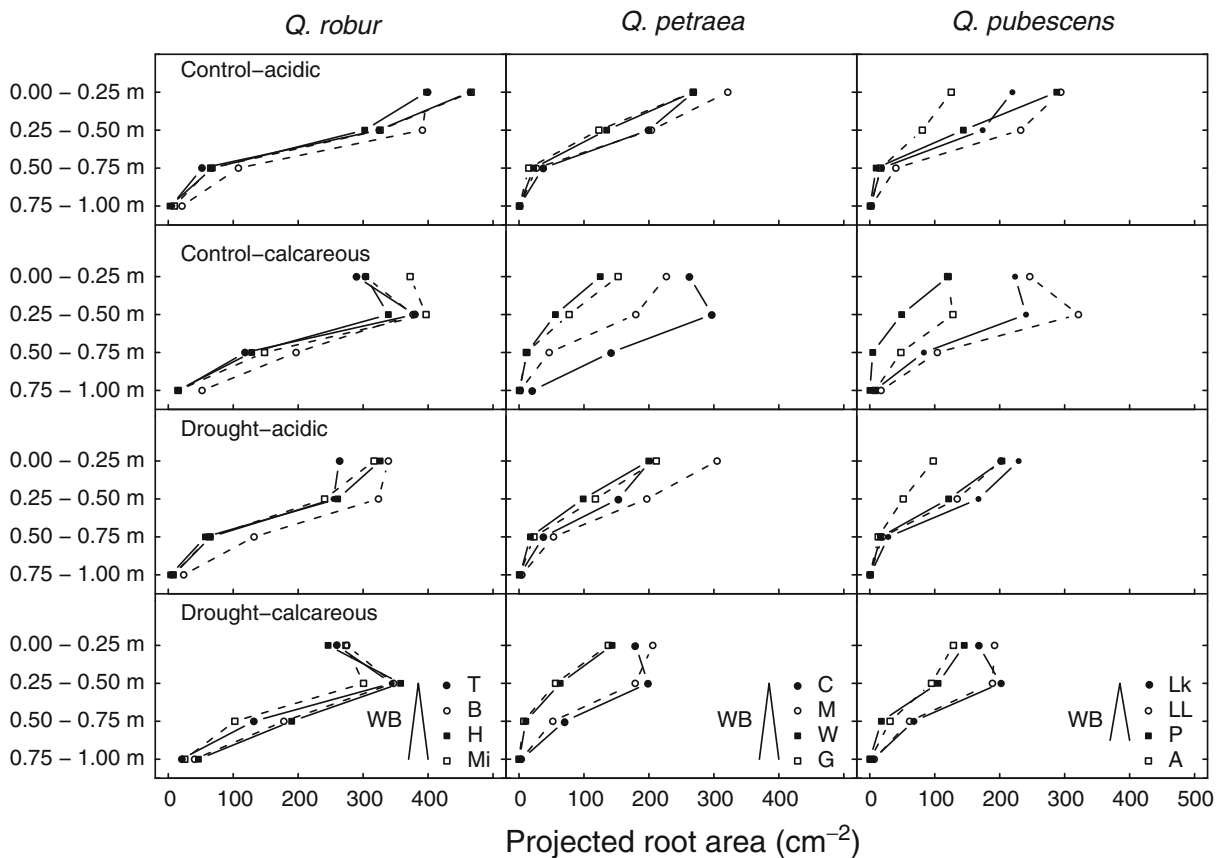
The correlations between biomass production and climatic water balances of the provenance sites of origin included in this study indicate substantial genetic adaptation of these provenances to local soil humidity



**Fig. 4** Effects of drought and air warming on root mass distribution (projected root area, cm<sup>2</sup>) in four different soil layers, each 0.25 m deep, in either acidic (left) or calcareous soil (right), means of all species and provenances, ± SE, n= 8). Different letters indicate significant differences (P<0.05) between respective treatments in the same soil type and

layer. An asterisk indicates a significant difference (\*: P< 0.05, (\*): P<0.10) between acidic and calcareous soils for the respective treatment and soil layer. The pair-wise comparisons in the lowest soil layer (0.75 – 1.00 m) could not be calculated as the model assumptions could not be fulfilled despite square-root-transformations





**Fig. 5** Vertical root mass distributions (projected root area,  $\text{cm}^2$ ) of the provenances of the three oak species, as affected, by soil type and drought treatment. Data of corresponding treatments with and without air warming are pooled, as the air-warming treatment had no significant effect on root growth ( $n=16$  for each

provenance/soil/drought treatment combination). The provenances are sorted in ascending order by water balances at their sites of origin as presented in Table 1. The abbreviations used for the provenances are the same as given in Table 1. Statistical analysis can be found in Table 2

conditions. As expected the provenances originating from drier sites produced under drought conditions more biomass than those from more humid sites. However, provenances from drier sites, with also substantially more biomass under well-watered conditions, showed a higher drought-induced biomass reduction than provenances from more humid sites. Therefore, these results were only in partial agreement with the first hypothesis. While we have no explanation at present, this observed trend was systematic and consistent in all three species and for both soils. The similarity of the correlations for both soils suggests that there was little influence of nutrient availability in the soil on the variation in growth among the provenances, while differences on the species level were larger. An improved drought tolerance of the southern oak provenances used in this experiment was also

found by Arend et al. (2011), who monitored shoot height and diameters over three growing seasons on acidic soil. It is also consistent with the results of Jensen and Hansen (2010) for *Quercus robur* and of Bruschi (2010) for *Q. petraea*. There was no correlation between air temperature at the provenances origins and mass data in the present experiment, as reported for example in *Q. petraea* by Vitasse et al. (2009). The variation in temperature among the sites was probably too low.

Apart from provenance, also soil water availability had a strong influence on root and shoot growth. As in other oak studies, drought-induced reductions were stronger in shoot than in root mass, leading to an increased root:shoot mass ratio (Thomas and Gausling 2000; Broadmeadow and Jackson 2000; Joslin et al. 2000; Gieger and

Thomas 2002; Fotelli et al. 2000; Thomas 2000a). This well-known shift in growth allocation from above to below ground can be interpreted as an acclimatisation to enhance water uptake capacity in relation to transpirational water loss. It is in line with this interpretation that fine root mass was relatively less reduced by drought than total root mass, as fine roots are the most important root fraction for water and nutrient uptake. In agreement with our findings, Fotelli et al. (2000) reported that *Q. pubescens* roots <2 mm were proportionally less reduced by drought than roots >5 mm. Moreover, Thomas (2000a) found that drought had no effect on the fine root mass of *Q. pubescens* seedlings and even a positive influence on fine root mass in *Q. petraea*. In line with these findings, Vogt et al. (1996) derived a weak but significant relationship from a review of literature data according to which fine root mass of trees tends to increase with decreasing precipitation.

Root growth reduction in response to drought was most pronounced in the top 0.25 m of both soils, resulting, in accordance with our second hypothesis, in shifts of the centre of root mass towards lower depths, where water was still more available (Kuster et al. 2012a). The fact that root distributions were also shifted to lower depths in the calcareous soil relative to those in the acidic soil, irrespective of the treatment, indicates that water and nutrient availability differed also between the two soils. In fact, in the acidic soil nutrients such as N, Ca, K and Mn were much more concentrated in the upper 0.15 m and less concentrated at lower depths (Kuster et al. 2012a, b), leading to a high root density in the acidic topsoil. In contrast in the calcareous soil, nutrients were more evenly distributed over depth, including P and Mn, which were found to be growth limiting in the calcareous soil. We may speculate that in the calcareous soil oak roots were acclimatised to maximise P and Mn mobilisation and uptake. According to our tensiometer measurements, water availability was generally sufficiently high for uninhibited root uptake in both soils at all depths in the control treatment, and thus do not explain the observed differences in root distribution between the two soils, although there was a slight gradient to lower availability with depth in the acidic soil and the opposite trend of slightly increasing soil moisture with depth in the calcareous soil (Kuster et al. 2012a).

In contrast to the third hypothesis, the air-warming treatment had no influence on the growth and vertical allocation of roots. With a maximum increase in topsoil temperature of 1 °C during the growing season, the treatment was probably too mild to cause detectable changes in root growth, in particular as temperatures reached up to 20 °C in summer. Thus, they came already close to the optimum soil temperature for root growth in oaks, which was reported to be about 25 °C (Lyr and Garbe 1995; Lyr 1996). Close to the temperature optimum, measurable responses in tree root growth to temperature changes are expected only if there is no other limiting factor (Pregitzer et al. 2000). Teskey and Hinckley (1981) found in a study on *Quercus alba* that soil temperature was the most important factor for root growth up to 17 °C, whereas above 17 °C soil water potential became more important. Also in a recent review, Way and Oren (2010) revealed no strong warming effect on tree root growth.

Comparing species responses to drought stress, *Q. robur* appears to be more sensitive as the absolute reduction in biomass was higher than in *Q. petraea* and *Q. pubescens*. Moreover, lower root:shoot mass ratios in *Q. robur* indicate a minor drought tolerance than in *Q. petraea*. Other studies on our model ecosystems came to results that are in line with our findings. The drought treatment reduced net photosynthesis more strongly in *Q. robur* than in the other two species (Arend et al. 2012), and also caused more foliage injury in *Q. robur* (Günthardt-Goerg et al. 2012). However, regarding the relative abundance of the ectomycorrhizal fungus *Cenococcum geophilum*, drought generally decreased its abundance on the root system of *Q. petraea* and *Q. pubescens*, whereas colonisation of *Q. robur* roots was not influenced by drought (Herzog et al. 2012). Air warming tended to increase the abundance of *C. geophilum* on all oak species, also under water limiting conditions.

Apart from heat and drought tolerance, also traits such as frost resistance have to be considered when evaluating oak provenances for future central European forestry. With increased abundance of extreme conditions varying between cold/wet and hot/dry periods in a changing climate (IPCC 2007), tolerance to late frosts requires particular attention in the selection of oak species and provenances. When provenances from sites with milder climates will be selected, they may be less frost resistant than provenances from colder areas of central Europe (Jensen and Deans 2004).

However in the present study, temperature at the selected provenance sites was not correlated to growth response.

## Conclusions

Oak saplings are able to acclimatise to water limiting conditions by increasing their root:shoot mass ratio and by shifting the root mass downwards to layers where water is often longer available. We expect that mature oak trees are even more drought tolerant as they are able to grow roots in deeper soil layers (Hanson et al. 2001; Leuzinger et al. 2005). Therefore, we conclude that central European oak species are highly suitable for a future climate, in particular on sites that become too dry for beech or spruce (van Hees 1997; Thomas 2000a; Leuschner et al. 2001). Thereby, special attention has to be dedicated to the origin of seed material. Given that the provenances from drier sites, with overall better growth, showed more biomass loss at water limiting conditions than provenances from more humid sites, it remains questionable whether provenances from drier sites are better suited for a future climate.

**Acknowledgements** Our particular acknowledgement is for the valuable advice and expertise of Matthias Dobbertin (†). We will keep him in our memories, both as an excellent scientist and as an irreplaceable friend. Furthermore, we thank Peter Bleuler, Martin Keller, Patrick Schleppei, Terry Menard, the internship students, the research unit Forest Soils and Biogeochemistry, the research group Phytopathology and the garden team of WSL for their help in performing the experiment. We also acknowledge Corina Del Fabbro, the Seminar for Statistics of ETHZ and the Central Laboratory of WSL for their support in sample and data analysis.

For funding we are gratefully indebted to the Velux foundation (project number: 489).

## References

- Arend M, Kuster T, Günthardt-Goerg MS, Dobbertin M (2011) Provenance-specific growth responses to drought and air warming in three European oak species (*Quercus robur*, *Q. petraea* and *Q. pubescens*). *Tree Physiol* 31(3):287–297. doi:10.1093/treephys/tpr004
- Arend M, Brem A, Kuster TM, Günthardt-Goerg MS (2012) Seasonal photosynthetic responses of three European oak species (*Quercus robur*, *Q. petraea* and *Q. pubescens*) to severe drought and elevated daytime temperature. *Plant Biol*. doi:10.1111/j.1438-8677.2012.00625.x
- Broadmeadow MSJ, Jackson SB (2000) Growth responses of *Quercus petraea*, *Fraxinus excelsior* and *Pinus sylvestris* to elevated carbon dioxide, ozone and water supply. *New Phytol* 146(3):437–451
- Bruschi P (2010) Geographical variation in morphology of *Quercus petraea* (Matt.) Liebl. as related to drought stress. *Plant Biosyst* 144(2):298–307. doi:10.1080/11263501003672462
- Callaway RM (1990) Effects of soil-water distribution on the lateral root development of 3 species of California oaks. *Am J Bot* 77(11):1469–1475
- CH2011 (2011) Swiss climate change scenarios CH2011. C2SM, MeteoSwiss, ETH, NCCR Climate, and OcCC, Zurich
- Crawley MJ (2009) *The R book*. Wiley, Chichester
- Ellenberg H, Leuschner C, Dierschke H (2010) *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht*. Utb, vol 8104, 6th edn. Ulmer, Stuttgart
- Fotelli MN, Radoglou KM, Constantinidou HIA (2000) Water stress responses of seedlings of four Mediterranean oak species. *Tree Physiol* 20(16):1065–1075
- Friedrichs DA, Trouet V, Büntgen U, Frank DC, Esper J, Neuwirth B, Löffler J (2009) Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees-Struct Funct* 23(4):729–739. doi:10.1007/s00468-009-0315-2
- Galle A, Haldimann P, Feller U (2007) Photosynthetic performance and water relations in young pubescent oak (*Quercus pubescens*) trees during drought stress and recovery. *New Phytol* 174(4):799–810. doi:10.1111/j.1469-8137.2007.02047.x
- Gieger T, Thomas FM (2002) Effects of defoliation and drought stress on biomass partitioning and water relations of *Quercus robur* and *Quercus petraea*. *Basic Appl Ecol* 3(2):171–181
- Göransson H, Wallander H, Ingerslev M, Rosengren U (2006) Estimating the relative nutrient uptake from different soil depths in *Quercus robur*, *Fagus sylvatica* and *Picea abies*. *Plant Soil* 286(1–2):87–97. doi:10.1007/s11104-006-9028-0
- Günthardt-Goerg MS, Kuster TM, Arend M, Vollenweider P (2012) Foliage response of young central European oaks to air warming, drought and soil type. *Plant Biol*. doi:10.1111/j.1438-8677.2012.00665.x
- Hanson PJ, Todd DE, Amthor JS (2001) A six-year study of sapling and large-tree growth and mortality responses to natural and induced variability in precipitation and throughfall. *Tree Physiol* 21(6):345–358
- Herzog C, Peter M, Pritsch K, Günthardt-Goerg MS, Egli S (2012) Drought and air warming affects abundance and exoenzyme profiles of *Cenococcum geophilum* associated with *Quercus robur*, *Q. petraea*, and *Q. pubescens*. *Plant Biol*. doi:10.1111/j.1438-8677.2012.00614.x
- IPCC (2007) *Climate change 2007: synthesis report*. Cambridge University Press, Cambridge
- Jensen JS, Deans JD (2004) Late autumn frost resistance of twelve north European provenances of *Quercus* species. *Scand J For Res* 19(5):390–399. doi:10.1080/02827580410019391
- Jensen JS, Hansen JK (2010) Genetic variation in responses to different soil water treatments in *Quercus robur* L. *Scand J For Res* 25(5):400–411
- Joslin JD, Wolfe MH, Hanson PJ (2000) Effects of altered water regimes on forest root systems. *New Phytol* 147(1):117–129

- Kozłowski TT, Pallardy SG, Kramer PJ (1991) The physiological ecology of woody plants. *Physiological ecology*. Academic, San Diego
- Kubiske ME, Abrams MD (1993) Stomatal and nonstomatal limitations of photosynthesis in 19 temperate tree species on contrasting sites during wet and dry years. *Plant Cell Environ* 16(9):1123–1129
- Kuster TM, Arend M, Bleuler P, Günthardt-Goerg MS, Schulin R (2012a) Water regime and growth of young oak stands subjected to air-warming and drought on two different forest soils in a model ecosystem experiment. *Plant Biol*. doi:10.1111/j.1438-8677.2011.00552.x
- Kuster TM, Schleppe P, Hu B, Schulin R, Günthardt-Goerg MS (2012b) Nitrogen dynamics in oak model ecosystems subjected to air warming and drought on two different soils. *Plant Biol*. doi:10.1111/j.1438-8677.2012.00686.x
- Landolt E, Bäumler B (2010) *Flora indicativa - ecological indicator values and biological attributes of the flora of Switzerland and the Alps*, 2nd edn. Haupt, Bern
- Leuschner C, Backes K, Hertel D, Schipka F, Schmitt U, Terborg O, Runge M (2001) Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. *For Ecol Manag* 149 (1–3):33–46
- Leuzinger S, Zotz G, Asshoff R, Körner C (2005) Responses of deciduous forest trees to severe drought in Central Europe. *Tree Physiol* 25(6):641–650
- Lyr H (1996) Effect of the root temperature on growth parameters of various European tree species. *Ann Sci For* 53(2–3):317–323. doi:10.1051/forest:19960214
- Lyr H, Garbe V (1995) Influence of root temperature on growth of *Pinus sylvestris*, *Fagus sylvatica*, *Tilia cordata* and *Quercus robur*. *Trees-Struct Funct* 9(4):220–223
- Pregitzer KS, King JA, Burton AJ, Brown SE (2000) Responses of tree fine roots to temperature. *New Phytol* 147(1):105–115
- Primault B (1981) Extension de la validité de la formule suisse de calcul de l'évapotranspiration. *Arbeitsberichte der Schweizerischen Meteorologischen Zentralanstalt*, vol no 103. Schweizerische Meteorologische Zentralanstalt, Zürich
- Schär C, Vidale PL, Luthi D, Frei C, Haberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heatwaves. *Nature* 427 (6972):332–336
- Scharnweber T, Manthey M, Criegee C, Bauwe A, Schroder C, Wilmking M (2011) Drought matters - declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. *For Ecol Manag* 262 (6):947–961. doi:10.1016/j.foreco.2011.05.026
- Teskey RO, Hinckley TM (1981) Influence of temperature and water potential on root growth of white oak. *Physiol Plant* 52(3):363–369
- Thomas FM (2000a) Growth and water relations of four deciduous tree species (*Fagus sylvatica* L., *Quercus petraea* Matt. Liebl., *Q. pubescens* Willd., *Sorbus aria* L. Cr.) occurring at Central-European tree-line sites on shallow calcareous soils: physiological reactions of seedlings to severe drought. *Flora* 195(2):104–115
- Thomas FM (2000b) Vertical rooting patterns of mature *Quercus* trees growing on different soil types in northern Germany. *Plant Ecol* 147(1):95–103. doi:10.1023/a:1009841921261
- Thomas FM, Gausling T (2000) Morphological and physiological responses of oak seedlings (*Quercus petraea* and *Q. robur*) to moderate drought. *Ann For Sci* 57(4):325–333
- van Hees AFM (1997) Growth and morphology of pedunculate oak (*Quercus robur* L) and beech (*Fagus sylvatica* L) seedlings in relation to shading and drought. *Ann Sci For* 54(1):9–18
- Vitasse Y, Delzon S, Bresson CC, Michalet R, Kremer A (2009) Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Can J For Res-Rev Can Rech For* 39 (7):1259–1269. doi:10.1139/x09-054
- Vogt KA, Vogt DJ, Palmiotto PA, Boon P, OHara J, Asbjornsen H (1996) Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant Soil* 187(2):159–219
- Way DA, Oren R (2010) Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiol* 30(6):669–688. doi:10.1093/treephys/tpq015
- Wohlgemuth TR (2006) *Wald und Klimawandel*. Forum für Wissen 2006. Eidgenössische Forschungsanstalt für Wald Schnee und Landschaft WSL, Birmensdorf