

Soil water, temperature regime and root growth of young oak stands grown in lysimeters subjected to drought stress and air warming

Thomas M. Kuster^{1,2*}, Peter Bleuler¹, Matthias Arend¹, Madeleine S. Günthardt-Goerg¹
and Rainer Schulin²

Zusammenfassung

In einem dreijährigen Lysimeterexperiment untersuchen wir, wie Jungbäume von *Quercus robur*, *Q. petraea* und *Q. pubescens* auf zwei verschiedenen Bodentypen, einem sandig-lehmigen kalkhaltigen und einem lehmig-sandigen sauren, auf erhöhte Lufttemperaturen und/oder längere Trockenperioden reagieren. Wie erwartet sanken die Bodenwasserpotentiale in den Behandlungen mit Trockenperioden auf viel tiefere Werte ab als in den Kontrollen. Dadurch war auf diesen Böden das Wachstum wie auch die Evapotranspiration deutlich niedriger. Dies führte aufgrund von fehlender Transpirationskühlung zu signifikant höheren Lufttemperaturen. Die Behandlung Lufterwärmung hatte weder auf das Wachstum noch auf den Wasserverbrauch einen Effekt. Trockengestresste Eichen investierten relativ gesehen mehr in das Wurzel- und weniger in das Sprosswachstum als Eichen mit genügender Wasserversorgung. In keiner der Behandlungen starben Bäume. Dies zeigt an, dass Eichen mit der Reduktion ihres Wachstums in der Lage sind, längere Trockenperioden ohne größeren Schaden zu überdauern. Eichen auf dem sauren Boden transpirierten mehr Wasser und produzierten signifikant längere Triebe als auf dem kalkhaltigen Boden. Dieses Ergebnis deutet darauf hin, dass auf dem kalkhaltigen Boden ein zusätzlicher Faktor, möglicherweise Mangan, limitierend war.

Schlagwörter: Klimawandel, Boden-Pflanzen-Interaktionen, Bodenwasserhaushalt, Evapotranspiration, Mangan

Summary

In a 3-year lysimeter experiment we investigated how young trees of *Quercus robur*, *Q. petraea* and *Q. pubescens*, growing either on acidic loamy sand or calcareous sandy loam, may respond to higher temperatures and/or more extended drought periods. As intended, the water potential in soils during drought periods was clearly lower than in the control treatment. Decreased evapotranspiration from the drought-stressed stands led to significantly higher air temperatures due to the reduced transpirational chilling effect. The air-warming treatment had only little effect on soil water availability and evapotranspiration. The effects on water consumption by the trees were paralleled by the effects on tree growth. Drought significantly reduced shoot growth, whereas growth did not respond to air-warming. Drought-treated oaks invested relatively more energy in developing roots and less into shoots than trees not subjected to drought. There was no mortality from any of the treatments demonstrating that by reducing their growth rates young oaks can resist drought stress quite well. Oaks growing on irrigated acidic soil consumed more water and produced longer shoots than on the calcareous soil, suggesting that growth was limited by an additional factor: preliminary leaf mineral analyses indicate a potential manganese deficiency in these soils.

Keywords: climate change, soil-plant interactions, soil water regime, evapotranspiration, manganese

Introduction

IPCC scenarios predict a global mean annual temperature increase of approximately 2–6 °C during the 21st century, as well as a change in precipitation patterns (IPCC 2007). In Central Europe, including Switzerland, the mean temperature has increased approximately by 1.5 °C since 1970: this is about 1.5 times more than in the rest of the northern hemisphere (IPCC 2007). Until 2050 the mean temperature in Switzerland is expected to increase by another 1.8 °C in winter and 2.7 °C in summer. The amount of precipitation in 2050 is predicted to be about 8% higher in winter and 17% lower in summer than at present (FREI et al. 2004). Moreover, the number of days without any precipitation

will increase, while extreme rainfall events will be more common (IPCC 2007). Consequently, dry and hot spells like that experienced in summer 2003 will be quite frequent in Central Europe in future (SCHÄR et al. 2004).

How will global warming, higher air temperatures and drought periods, affect trees in Central Europe? For example, *Picea abies* and *Fagus sylvatica*, widespread and important trees in forestry, are known to be vulnerable to high temperatures and soil water deficits (FRIEDRICHS et al. 2009). Therefore, looking ahead, forest management has to think about a shift to other, more heat and drought tolerant tree species. Oaks are known to be tolerant to drought stress as well as heat waves because of their taproots, xeromorphic leaf structure and effective stomatal control

¹ Swiss Federal Research Institute WSL, Zürcherstraße 111, CH-8903 BIRMENS DORF

² Institute of Terrestrial Ecosystems ITES, ETH Zürich, Universitätsstraße 16, CH-8092 ZÜRICH

* Ansprechpartner: Thomas M. Kuster, thomas.kuster@wsl.ch

of transpirational water loss (ABRAMS 1990, KUBISKE and ABRAMS 1993) and have been reported to grow and to be competitive in regions with low precipitation rates and comparatively high temperatures (CHIATANTE et al. 2006, WOHLGEMUTH 2006). Higher air temperatures could favour the growth rates of plants by extending vegetation periods, increasing nutrient turnover rates and accelerating metabolism processes (SAXE et al. 2001, SCHEFFER et al. 2002, MORIN et al. 2010). Drought is expected to decrease aboveground growth rates (OGAYA and PENUELAS 2007), whereas root growth is often increased relative to shoot growth, in particular in deeper soil layers where water in general remains available for longer periods than at the surface, while reduced shoot growth reduces transpirational water losses (JACOBS et al. 2009).

The aim of this study was to investigate how the most widespread oaks in central European temperate forests, *Q. petraea*, *Q. pubescens* and *Q. robur*, will react to increasing air temperatures and/or drought periods and if they can be considered for silviculture in future. Using lysimeters in open top chambers (OTC), we exposed mixed young oak stands on two different soil types to elevated air temperatures and artificial drought periods and studied the response of tree growth, soil water regime and microclimate to these treatments.

Material and Methods

Study Site and Experimental design

The study was part of the multidisciplinary experiment "Quercu" conducted in the model ecosystem facility of

the Swiss Federal Research Institute WSL, Birmensdorf, Switzerland (47°21'54" N, 8°27'54" E, 450 m a.s.l.). The facility consists of 16 open top chambers (OTC). The hexagonal OTC's were 3 m in height and had a useful surface area of 6 m². Each OTC was subdivided into two 1.5 m deep concrete lysimeter compartments which were filled with a 0.5 m drainage layer of pure quartz gravel to allow free percolation. On top of this drainage layer, the lysimeters compartments were filled with either an unlayered calcareous (sandy loam, Fluvisol, pH 7.3) or two-layered acidic forest soil (loamy sand, haplic Alisol; subsoil: 0.85 m, pH 4.2; topsoil, 0.15 m, pH 4.0), in 2005. After one year of soil settlement, 24 two-year old saplings of *Quercus petraea*, *Q. pubescens* and *Q. robur* from four different proveniences each were planted in a random distribution in spring 2006 in each of the compartments and were grown with sufficient water supply and at ambient air temperature during one vegetation period.

From 2007 to 2009 four different treatments with four replicates each were applied: air-warming, drought, their combination and a control. The treatments were arranged in a Latin square. The side walls of the OTCs with the air-warming treatment were kept more closed than those of the control treatment. As a result, the green-house effect of the chambers increased the air temperature during daytime by about 1-2° C more in the air-warming treatment than in the control treatment during periods of growth (Figure 3). Control and air-warming treated OTCs were watered with 10 mm deionised water, enriched with nutrients, every 2-3 days, whereas there was no irrigation in the drought-

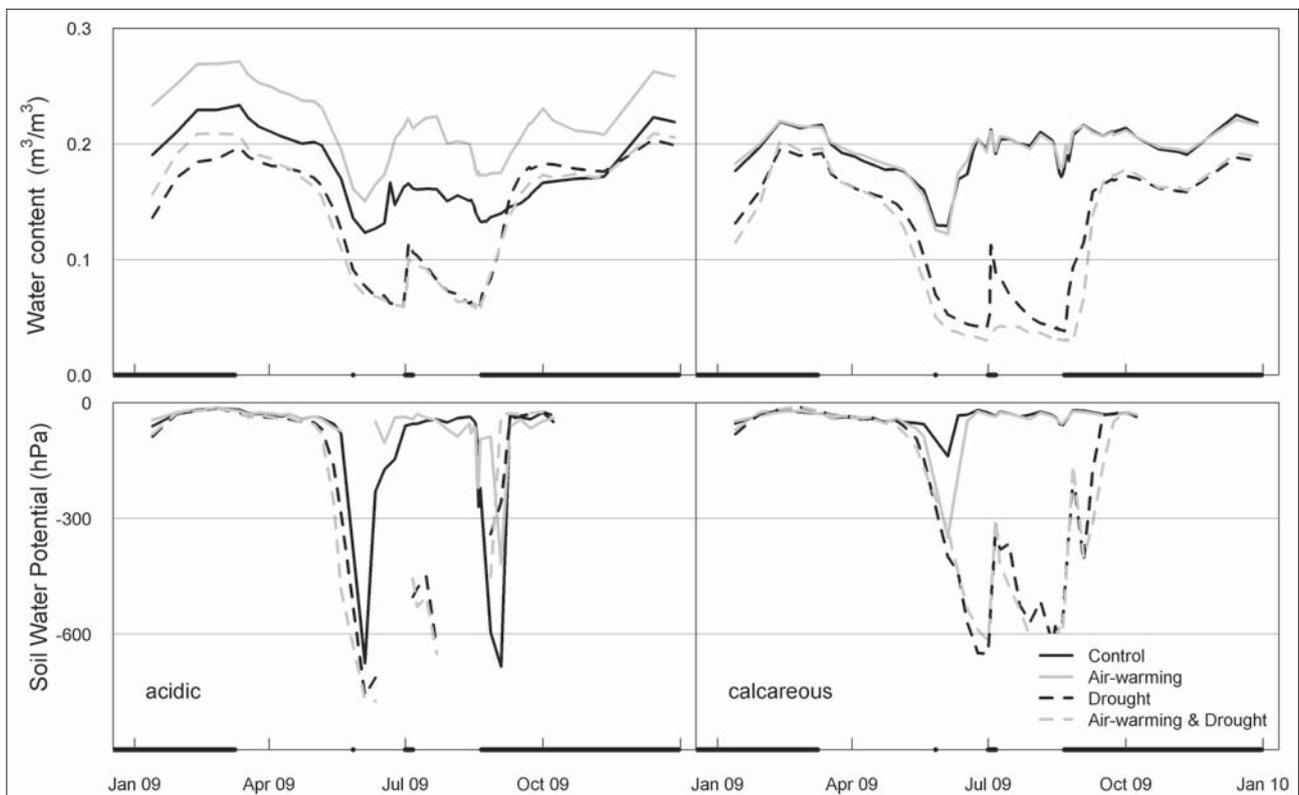


Figure 1: Mean weekly water content (n=4) and water potential in 2009 (n=8) in acidic (left) and calcareous (right) soil. Bold lines on the x-axis refer to periods when drought treated chambers were irrigated.

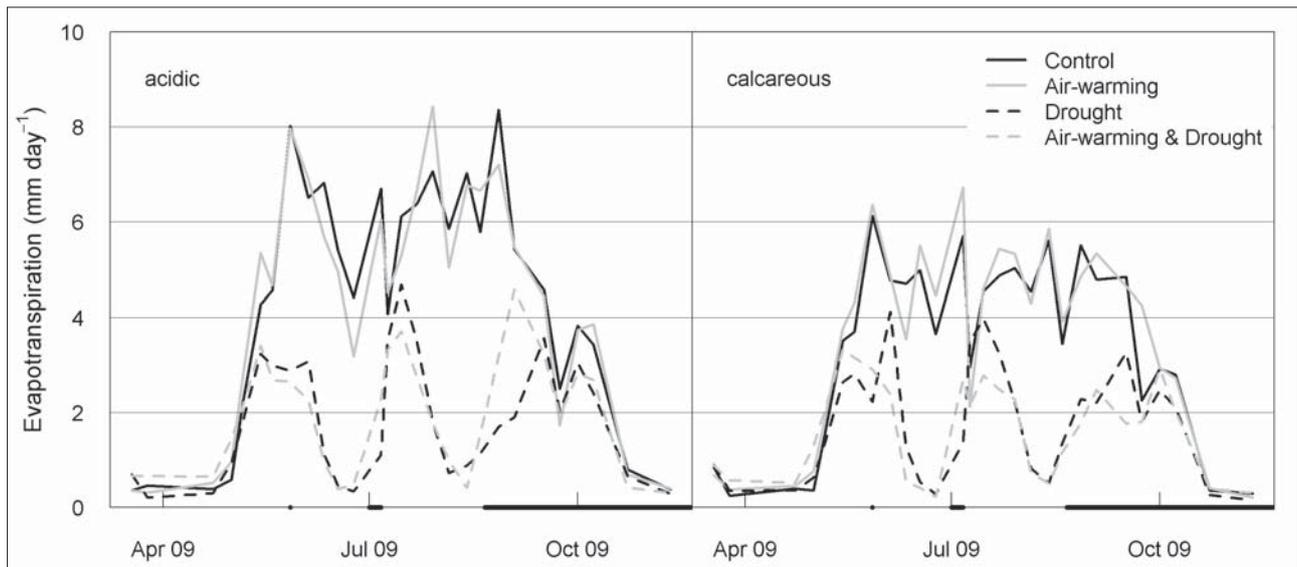


Figure 2: Mean daily evapotranspiration (mm) in 2009 on acidic (left) and calcareous (right) soil, $n=4$. Bold lines on the x-axis refer to periods when drought treated chambers were irrigated.

treated OTCs for several weeks in a row (-43% to -60% irrigation during the vegetation periods (April to October) compared to the long term mean, *Figure 1*). Drought periods were interrupted by intensive irrigation, simulating heavy rainfall. In the non-growing period, the roofs of the OTCs stayed permanently open to expose all treatments to natural precipitation.

Measurements of Soil Water and Temperature Regime

Soil water regime was monitored by manual weekly measurements of soil water content (SWC) using time domain reflectory (TDR 100; Campbell Scientific Inc., USA) in each soil type at a depth of 50-75 cm and manual weekly measurements of soil water potential (SWP) with tensiometers (self-made, measuring device: DPM-80/2; Keller, CH) at a depth of 56-68 cm with two repetitions in each soil type. Leakage water was collected in containers below the lysimeters and the volume was measured every week. Evapotranspiration (ET) was calculated by solving the equation $ET=I+P-DR\pm\Delta W$, where I stands for irrigation, P for precipitation, DR for drainage and ΔW for the change in SWC. Air temperature at a height of 120 cm was automatically measured every hour with shaded EL-USB-2 data loggers (Lascar Electronics Ltd., UK) in each OTC.

Biomass and Growth Measurements

Shoot growth of all trees was measured during each vegetation period from 2007 to 2009. In spring 2010, roots were harvested and maximal root length was determined. A 2D picture from each rootstock was taken from the front. Images were edited with ImageJ 1.44h (U.S. National Institutes of Health, USA) and the projected root area in five layers, each 20 cm deep, was determined with IDL 7.1 (ITT Visual Information Solutions, USA).

Statistical Analysis

All statistical analyses were done with R 2.11.1 (R: A language and environment for statistical computing, R Development Core Team, AT). Treatment and interaction effects were analysed with a three-way full factorial design (irrigation, air-warming and soil) by analysis of variance with a level of significance of $p < 0.05$ (MANOVA, linear mixed-effect models). The split-plot design of this experiment was considered in all statistical analyses, if needed. Measurements were transformed before analysis to guarantee models assumptions. Significant differences between single factors were tested with Tukey HSD.

Results and Discussion

Water Household, Evapotranspiration and Temperature Regime 2009

As intended, drought treatment significantly lowered soil water potential (SWP) as well as soil water content (SWC) in both soils in 2009 (*Figure 1*). After rewetting in July and August 2009, SWP and SWC in drought treated soils slightly increased, however, levels still stayed below those of regularly watered soils. Surprisingly, under humid conditions, air-warming increased SWC in the acidic soil type, whereas air-warming had neither an effect in drought treated, both acidic and calcareous, nor in humid, calcareous soil. During periods of a plant's high demand for water (June & August 2009), SWC and SWP in the control treatment were significantly lower in the acidic as compared to the calcareous soil indicating a higher water consumption of oaks growing on acidic soil.

Drought treatment significantly reduced evapotranspiration on both acidic and calcareous soil (*Figure 2*). After rewetting, evapotranspiration from drought treated plots increased and no differences between drought and regularly watered OTCs remained, indicating that the oaks recovered, comple-

Table 1: Mean shoot length growth 2007-2009 (cm) and mean maximal root length 2009 (cm), \pm 1SE, n=8. Different letters refer to significant differences within a row, * refers to significant differences between acidic (a) and calcareous (c) soils within a treatment.

	Soil	Control	Air-Warming	Drought	Air-Warming & Drought
Shoot length (cm)	a	179.6 \pm 8.6 ^a	217.4 \pm 1.7 ^a	107.8 \pm 3.8 ^b	111.5 \pm 7.5 ^b
	c	135.5 \pm 5.3 ^a	153.9 \pm 3.4 ^a	95.9 \pm 4.4 ^b	102.3 \pm 4.2 ^b
Max. root length (cm)	a	88.4 \pm 2.3 ^a	81.3 \pm 2.2 ^a	87.9 \pm 2.6 ^a	85.6 \pm 1.3 ^a
	c	91.4 \pm 3.4 ^a	88.8 \pm 1.3 ^a	92.1 \pm 1.6 ^a	91.9 \pm 1.3 ^a

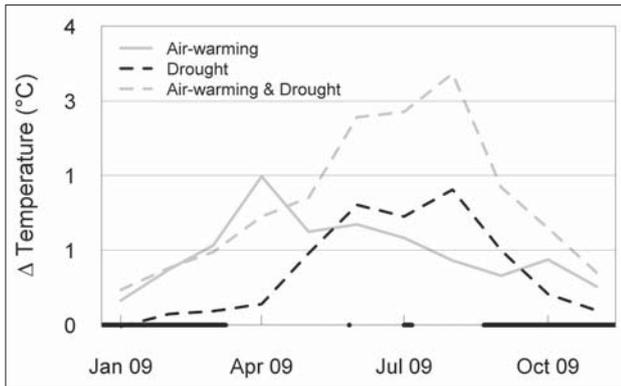


Figure 3: Mean monthly temperature ($^{\circ}$ C) in relation to the control treatment, n=4. Bold lines on the x-axis refer to periods when drought treated chambers were irrigated.

tely. Air-warming had no effect on evapotranspiration, neither on acidic, nor calcareous soil. Under humid conditions, evapotranspiration from acidic soil was significantly higher than from calcareous. In contrast, no differences between the two soil types remained during drought conditions. This finding is in line with the lower SWC and SWP in acidic soil as well as with the higher above ground biomass of oaks on well watered acidic soil (Table 1).

The air-warming treatment significantly increased the mean monthly daytime (8 a.m. to 6 p.m., UTC+1) air temperatures in the OTCs by about 1-2 $^{\circ}$ C in relation to the control (Figure 3). Further, drought treatment also increased the air temperature significantly as a consequence of a reduced transpirational chilling effect (Figure 2). Rewetting in July 2009 slightly reduced the monthly temperature difference between control and drought treated soils, however, this effect was not significant. The combination of air-warming and drought led to even higher temperatures as these two single effects have been added together.

Growth parameters 2009

Drought treatment significantly decreased shoot growth from 2007 to 2009 (Table 1). In contrast, there was no significant response to air-warming under both drought and humid soil conditions. There was no mortality in all treatments indicating that oaks can get through starve out drought periods quite well by reducing their growth; a conclusion which gains more weight when taking into account that our drought treatment (-43% precipitation during the vegetation period 2009) was much more severe than the model predicts (-23% precipitation during summer in 2070 (FREI et al. 2004)). On regularly watered

soils, shoot growth was significantly higher on the acidic than on the calcareous soil. Under drought conditions, no significant differences between the two soils in the above ground growth remained: this finding is in line with the fact that oaks, growing under natural conditions, prefer acidic soil (LANDOLT and BÄUMLER 2010). The manganese availability in the soil, which increases with decreasing soil pH (SCHEFFER et al. 2002), could be a possible explanation for our finding. Indeed, the first foliage analyses (2007) show that manganese availability in calcareous soil (control calcareous soil: 60 \pm 4 ppm; control acidic soil: 2023 \pm 84 ppm) is close to the deficiency level (35 to 100 ppm, BERGMANN 1993).

Oaks, growing in regularly watered acidic soil, had higher projected root areas in the upper 40 cm than drought treated oaks, whereas below 40 cm, no significant difference between the treatments remained (Figure 4). Thus, well watered trees built up more roots in the top soil layers to absorb the regular water input, whereas drought treated trees invested relatively more energy in developing roots in lower soil layers to access deeper lying soil water during drought periods. In calcareous soil, no treatment effects on root distribution were measured except from the top soil layer where drought treated oaks built up fewer roots than in the control treatment. Comparing the two soils in the top soil layer, oaks in the acidic soil had significantly higher projected root areas. At a depth of 20-40 cm no differences between the two soil types remained and below 40 cm, the projected root area was significantly higher in calcareous than in acidic soil.

In contrast to above ground growth, treatments had no significant effect on maximal root length (Table 1), indicating that all trees completely used the rooting depth available (100 cm). The soil type had only an influence on the total root length in the air-warming treated OTC where the roots in calcareous were longer than in acidic soil.

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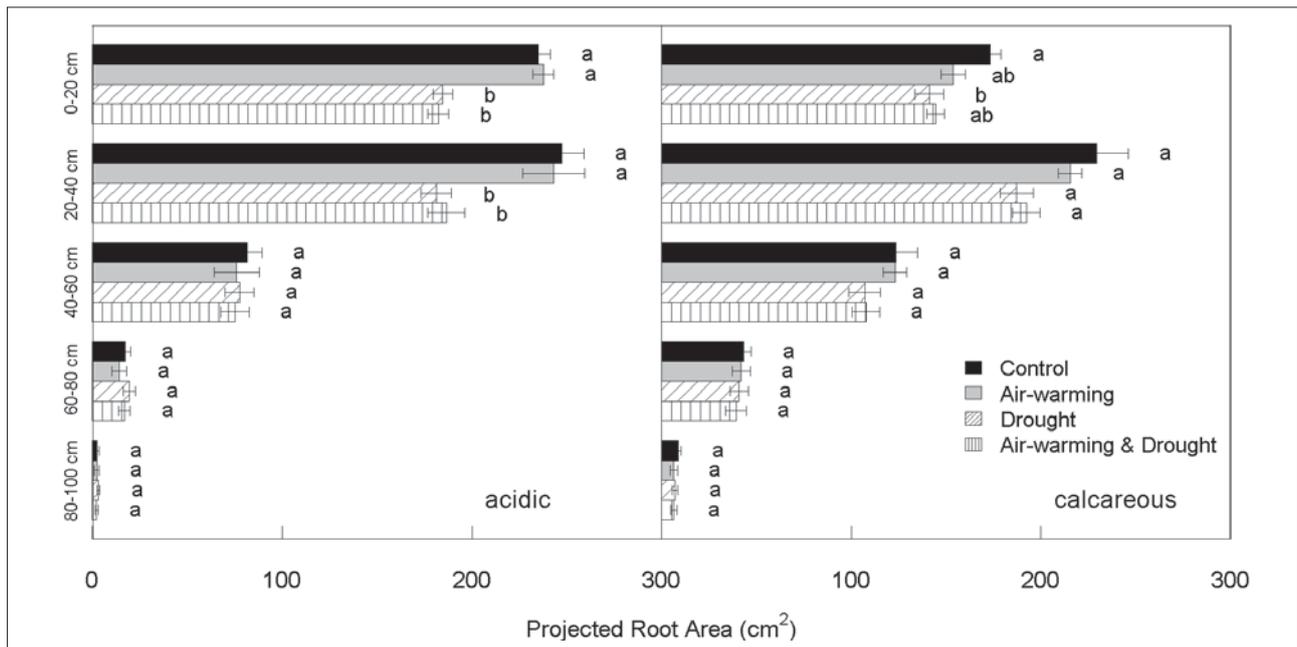


Figure 4: Projected root area (cm^2) in five different soil layers in acidic (left) and calcareous soils (right), $\pm 1\text{SE}$, $n=8$. Different letters refer to significant differences between the treatments within a soil layer.

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