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Effects of drought on leaf carbon source and growth of European beech are modulated by soil type

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Drought potentially affects carbon balance and growth of trees, but little is known to what extent soil plays a role in the trade-off between carbon gain and growth investment. In the present study, we analyzed leaf non-structural carbohydrates (NSC) as an indicator of the balance of photosynthetic carbon gain and carbon use, as well as growth of European beech (*Fagus sylvatica* L.) saplings, which were grown on two different soil types (calcareous and acidic) in model ecosystems and subjected to a severe summer drought. Our results showed that drought led in general to increased total NSC concentrations and to decreased growth rate, and drought reduced shoot and stem growth of plants in acidic soil rather than in calcareous soil. This result indicated that soil type modulated the carbon trade-off between net leaf carbon gain and carbon investment to growth. In drought-stressed trees, leaf starch concentration and growth correlated negatively whereas soluble sugar:starch ratio and growth correlated positively, which may contribute to a better understanding of growth regulation under drought conditions. Our results emphasize the role of soil in determining the trade-off between the balance of carbon gain and carbon use on the leaf level and growth under stress (e.g. drought).

Drought is expected to become an increasingly important stressor in many ecosystems¹, not only determining forest species growth and productivity^{2,3}, but also persistence and distribution patterns of species^{4,5}. The early life stages of trees are most sensitive and vulnerable to soil water deficit^{6,7}. Progressive drought may influence patterns of tree seedling and sapling establishment and have lasting effects on the composition, dynamics and carbon balance of forests^{8,9}. Meanwhile, progressive drought may affect reforestation projects, where thousands of newly planted saplings die within the first few years of planting¹⁰. Furthermore, extreme drought may lead to forest dieback, potentially converting forests from a net carbon sink into a large carbon source¹¹. Thus, understanding how trees in early stage respond to drought is crucial for predicting the fate of forest ecosystems under future climate conditions^{12,13}.

The plant non-structural carbohydrates (NSC consisting of soluble sugars and starch) formed in leaves during photosynthesis are on the one hand serving as central crossroad in the leaf metabolism¹⁴ and are used to supply heterotrophic plant organs with carbon and energy via the phloem on the other hand. Starch accumulates in the chloroplasts in plant leaves either being under internal control to suit the environmental conditions¹⁵ or being induced due to either high carbon assimilation or low carbon export¹⁶. Drought, imposed as reduced soil water availability and/or atmospheric drought, constrains plant physiology and productivity through the reduction of leaf gas exchange associated with reduced carbon gain, and growth activity associated with carbon investment, which affects the carbon balance in leaves^{17,18}. Thus levels of leaf NSC reflect the balance between carbon gain and carbon utilization with respect to the entire plant source and sink activity. Moreover, leaf or tissue NSC might also act as short-term buffer during insufficient source activities due to environmental stress¹⁹. Generally, growth (i.e. cambial activity) is most sensitive to drought, followed by photosynthesis and respiration (see review by McDowell²⁰). Up to now, most studies have found either no reduction or even an increase in NSC levels of trees under moderate drought^{21–24} and it has been speculated that the higher drought sensitivity of the sink activity

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Source of variation	df	Soluble sugars		Starch		Total NSC		TN		TP	
		F	P	F	P	F	P	F	P	F	P
Within-subject											
Period	1	13.475	0.001	3.145	0.082	4.156	0.046	17.396	<0.001	42.404	<0.001
Period × Treatment	1	23.416	<0.001	26.858	<0.001	0.574	0.452	0.642	0.426	1.200	0.278
Period × Soil	1	12.731	0.001	61.298	<0.001	71.628	<0.001	1.993	0.164	11.770	0.001
Period × Treatment × Soil	1	10.249	0.002	0.054	0.818	7.129	0.010	0.765	0.385	0.503	0.481
Between-subject											
Treatment	1	17.057	<0.001	0.303	0.584	8.575	0.005	1.201	0.278	0.855	0.359
Soil	1	2.248	0.139	37.912	<0.001	30.614	<0.001	41.464	<0.001	21.458	<0.001
Treatment × Soil	1	1.923	0.171	2.526	0.118	0.001	0.997	4.280	0.043	0.294	0.590

Table 1. Summary of three-way repeated measure ANOVA for the effects of treatment and soil type on leaf NSCs (soluble sugars, starch and NSC), nutrients (nitrogen and phosphorus) in European beech saplings.

compared to photosynthesis might be responsible for such transient increase. However, whether this pattern might also be related to source (leaf) carbon storage affecting carbon sink activity (growth) is not clear^{22,25,26}.

Apart from the large number of studies on plant eco-physiological responses to drought, little is known about the effects of soil nutrient status on growth of trees under drought. Among the nutrients needed by plants, nitrogen and phosphorus play vital roles in physiological functioning, and are among the most important limiting nutrients in terrestrial ecosystems^{27–29}. Leaf nitrogen and phosphorus concentrations, which are determined by uptake and loss, can reflect the relationship between plant and soil nutrient status³⁰. The variations in leaf nitrogen/phosphorus ratio are species-specific, and depend on nutrient conditions to which plants are exposed³¹. Nutrient imbalances in plants may also lead to reduced soil nutrient availability to plant growth^{32,33}. However, the effects of nutrient status on the plant's response to drought are less well-known. Up to now, only a few reports suggest that the medium-term drought reduces root nutrient uptake activity³⁴ and nutrient availability in soils^{35,36}, and thus may lead to reduction of nitrogen and phosphorus concentrations in stand biomass³⁶. Low nutrient availability may reduce plant water use efficiency and capacity to adapt to drought³⁷.

Differences in the physiology of the nutrient uptake system may contribute to species-specific variations in drought tolerance³⁸, and soil properties which determine nutrient availability and soil water relations may also play a role in plants' drought tolerance. For instance, calcareous soils often have a much lower water-holding capacity than acidic soils³⁹. As a consequence, trees growing on calcareous soil have to cope with more intense drought conditions compared to trees growing on acidic soil but plants on the former soil often show a higher drought tolerance than those growing on acidic soils^{40,41}. Thiel *et al.*⁴² found that the growth performances of *Fagus sylvatica* L. under drought differed between soil types (sand and loam), where a higher growth reduction was found in the sandy substrate. However, whether the soil type modifies the carbon source-sink relationship and thus plant growth is still unknown.

European beech (*Fagus sylvatica* L.) is an ecologically dominant tree species in Central Europe occupying a wide range of mesic soils with contrasting pH and carbonate content⁴³. It is commonly considered as a drought-sensitive species^{44,45}, especially during early stages of establishment⁴⁶, but it has also been reported that seedlings recover quickly from severe drought episodes and provenances may differ in their drought and post-drought response^{47–51}. To date, the influence of soil type has been rarely considered as an additional factor in drought experiments, although it can interact with other environmental constraints^{52,53}. The present study was undertaken in the framework of the interdisciplinary experiment "BuKlim: beech in a changing climate"⁵³ investigating drought and post-drought responses of European beech provenances on different soil types. By analyzing levels of NSCs, nitrogen, and phosphorus in relation to growth, we aimed at testing: (1) how severe drought influences the relationship between leaf carbon assimilation and NSC export associated with tree growth (i.e. leaf NSC balance), and (2) whether soil types affect this relationship.

Results

Non-structural carbohydrates (NSCs). Highly significant effects were found for treatment and the interaction between treatment and sampling period on leaf soluble sugar concentration (% DW) ($p < 0.01$, Table 1). Drought increased leaf soluble sugar concentration on acidic soil by +25.2% relative to the control ($p < 0.05$), but no increase was observed on calcareous soil (Fig. 1A). After re-watering (50d), soluble sugar concentration fully recovered to the control level on both soil types.

Leaf starch concentration (% DW) was significantly affected by soil type and the interactions between soil type and sampling period and between treatment and sampling period ($p < 0.001$, Table 1). Drought decreased the starch concentration by 26% in plants on acidic soil ($p < 0.05$), but no significant decrease was observed on calcareous soil (Fig. 1B). After re-watering, leaf starch concentration on acidic soil has slightly increased in previously drought-exposed re-watered plants (3.00% DW) compared to controls (2.62% DW) ($p > 0.05$), but on the calcareous soil, this increase was much more pronounced, rising from 2.22% DW to 3.20% DW ($p < 0.05$).

There was a significant effect of treatment, soil type and interaction between soil type and sampling period on total NSC concentrations (% DW) ($p = 0.01$, Table 1). The pattern of total NSC concentrations affected by the treatments was similar to the one of soluble sugar on both soils (Fig. 1C). Drought increased NSC on acidic soil ($p < 0.05$), but not so on calcareous soil. For the latter, total NSC concentrations in the control (September) and

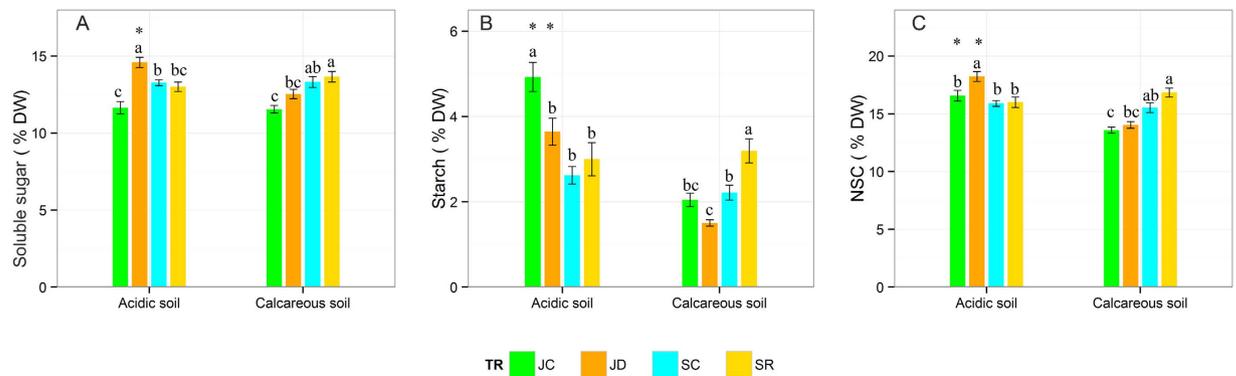


Figure 1. Mean values (\pm SE) of concentrations (% DW) for soluble sugars (A), starch (B) and total NSC (C) from *Fagus sylvatica* L. leaves grown on acidic and calcareous soils and exposed to drought and re-watering treatments. Asterisks indicate significant differences between acidic and calcareous soils for a certain treatment. Different lowercase letters indicate significant differences between treatments within one soil type ($p < 0.05$). (JC: control in July; JD: drought in July; SC: control in September; SR: drought (re-watering) in September).

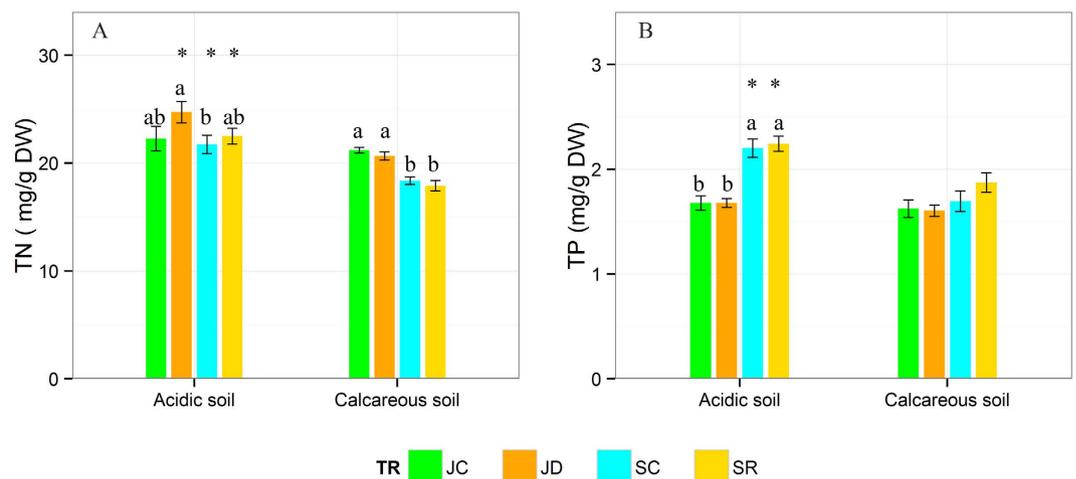


Figure 2. Mean values (\pm SE) of concentrations (mg/g DW) for nitrogen (A), phosphorous (B) from *Fagus sylvatica* L. leaves grown on acidic and calcareous soils and exposed to drought and re-watering treatments. Asterisks indicate significant differences between acidic or calcareous soil for a certain treatment. Lowercase letters indicate significant differences between treatments within one soil type ($p < 0.05$). (JC: control in July; JD: drought in July; SC: control in September; SR: drought (re-watering) in September).

re-watering treatment was higher than the total NSC concentrations in the drought treatment before re-watering ($p < 0.05$). In summary, concentrations of soluble sugars, starch, and NSC on acidic soil were higher than on calcareous soil in both, the control or drought treatment in July ($p < 0.05$). After re-watering, no soil-related differences were observed (Fig. 1C).

Leaf nutrients. Leaf nitrogen and phosphorus concentrations significantly differed between the two soil types ($p < 0.001$, Table 1). Furthermore, the interaction between soil type and treatment significantly affected leaf nitrogen concentration ($p < 0.05$), while the interaction between soil type and sampling period significantly affected leaf phosphorus concentration ($p = 0.001$). Both, drought and re-watering had no effects on the leaf nitrogen and phosphorus concentrations over the two soil types compared to the corresponding control (Fig. 2A,B). Leaf nitrogen concentration on acidic soil was higher than on calcareous soil across two sampling periods, while only during the latter period (September) this was the case for leaf phosphorus concentration ($p < 0.05$) (Fig. 2A,B).

Growth. The two factors, treatment (control vs. drought) and soil (acidic vs. calcareous), had distinct effects on SLA, annual shoot, and stem increment but no interactive effects on them (Table 2). Shoot increment and SLA were significantly affected by soil ($p < 0.05$), while stem increment by treatment ($p < 0.001$). Overall, saplings grown on calcareous soil had higher annual shoot increment than on acidic soil ($p < 0.05$), with 68.00 ± 3.80 cm in control and 61.13 ± 4.35 cm in the drought treatment compared to 47.80 ± 4.13 cm in control and 40.73 ± 3.08 cm in the drought treatment on acidic soil (Fig. 3A). The drought treatment reduced the stem increment by 33.55% on acidic soil ($p < 0.05$), with 4.92 ± 0.42 mm for control and 3.27 ± 0.33 mm for drought, and by 28.6% on

Source of variation	df	Shoot increment (H)		Stem increment (D)		SLA	
		F	P	F	P	F	P
Treatment	1	3.24	0.093	19.91	<0.001	0.02	0.833
Soil	1	27.52	<0.001	2.13	0.152	5.64	0.028
Treatment × Soil	1	0.00	0.980	0.02	0.882	1.27	0.274

Table 2. Summary of two-way ANOVA for the effects of treatment and soil type on shoot- (cm yr^{-1}), stem-growth (mm yr^{-1}) and SLA (cm^2/g) of *Fagus sylvatica* L. saplings.

calcareous soil ($p < 0.05$), with 5.39 ± 0.30 mm for control and 3.85 ± 0.35 mm for drought (Fig. 3B). Opposite to shoot increment, the saplings had higher SLA on acidic soil than on calcareous soil. For example, SLA was 171.67 ± 5.55 cm^2/g on acidic soil and 155.74 ± 3.68 cm^2/g on calcareous soil for plants in the control treatment (Fig. 3C).

Correlation between resources and growth. According to Konôpka *et al.*⁵⁴ and Michelot *et al.*⁵⁵, height and diameter increments of European beech almost ceased in July. We therefore investigated the correlation between resources (including leaf soluble sugar, starch, NSC, ratio of soluble sugar to starch, nitrogen and phosphorus concentrations) in July and the annual growth status (shoot and stem increment). Over all treatments and soil types, shoot increment was negatively correlated with starch ($r = -0.497$, $p < 0.01$) and total NSC ($r = -0.524$, $p < 0.01$), as well as nitrogen concentration ($r = -0.277$, $p < 0.05$) (Table 3). A significantly positive correlation, however, was found between shoot increment and the ratio of leaf soluble sugar to starch ($r = 0.468$, $p < 0.01$). Stem increment was negatively correlated only with leaf soluble sugar concentrations when all data were pooled ($r = -0.270$, $p < 0.05$). However, this trend was altered between different treatments, with a positive correlation occurring in the controls ($r = 0.370$, $p < 0.05$) and a negative correlation in the drought treatments ($r = -0.256$, $p > 0.05$).

Discussion

Drought effects. Drought resulted in increased leaf total NSC concentrations, but the magnitude differed between the two soil types (Table 1 and Fig. 1C). There are inconsistent results in respect to plant NSC responses to water deficit, such as accumulation/maintenance^{21–24,56} or depletions^{57–59}. Recently, it has been proposed that plant NSC accumulation or depletion under water deficit depends on species-specific strategies^{2,60}. In the present study, we aimed at testing how the leaf NSC accumulation representing the net effect of C gain vs. C use and export under drought may be related to growth (Fig. 1 and Table 3). As a result of the greater sensitivity of growth (turgor-driven cell expansion) compared to the sensitivity of photosynthesis to water deficit, moderate water stress is often associated with an increase in NSC and a ‘surplus’ of photosynthates which the plant is unable to use for the more drought-sensitive, turgor-driven cell growth⁶¹. Only recently, Hagedorn *et al.*⁶² provided this hypothesis as they observed an increase in NSC in roots and with a time lag also for leaves during drought onset. These authors, however, assumed that down-regulation of photosynthesis would counteract the accumulation of starch in leaves over the longer term. In the present study, this assumption could be confirmed, as there was rather a decrease in starch content on both soil types indicating reduced short-term storage. In contrast, there was a significant increase in sugar concentration on the acidic soil. Under water deficit, soluble sugar could aid in desiccation tolerance through osmotic adjustment and stabilization of membranes and proteins⁵⁷. For beech, Ruehr *et al.*⁶³ observed reduced export of recent assimilates out of the leaf into the phloem under drought supporting the hypothesis of osmotic adjustment. After stress relief, soluble sugar and total NSC concentration of previously drought-treated saplings recovered to the level of controls, which is in accordance with similar studies for *F. sylvatica* L. or other species^{64–66}. Gallé & Feller⁵⁰ found that net photosynthesis rate of *F. sylvatica* L. completely recovered within 4 weeks, meanwhile stomatal conductance remained permanently lower, leading to an increased ‘intrinsic water use efficiency’. We have now published a paper on photosynthesis in the same experiment showing full recovery within 2 to 3 weeks and “overshooting” photosynthesis after full recovery⁵¹.

Soil drought may increase soil solute concentrations, which might promote nutrient uptake since uptake is positively correlated to external solute concentrations. However, soil water availability could be most important due to the role of water as carrier in nutrient uptake and transport. A reduction of water availability may reduce nutrient diffusivity and mass flow⁶⁷ and, in addition, a reduction of the root uptake capacity for nutrients has been observed³⁸. In our study, the two observed nutrient elements (nitrogen and phosphorus) were only slightly or not at all affected by drought (Fig. 2). Our results are consistent with some studies^{68–71}, but not with others^{44,72,73}. For instance, by analyzing mineral nutrition of *F. sylvatica* L. seedlings from eleven provenances, Peuke & Rennenberg⁷⁴ found that drought led to a reduction in leaf phosphorus concentration, but had no significant effects on leaf nitrogen. Based on a meta-analysis, He & Dijkstra⁷⁵ suggested that, negative effects on plant nitrogen and phosphorus are alleviated with extended duration of drought and with drought-re-watering cycles. Over time, plants may adjust their growth, morphology, and physiochemical characteristics to acclimatize to water deficit. For example, by enhancing root growth and extension (increasing the root:shoot ratio) to absorb more water and nutrients from deeper soil layers^{76,77}. Our results imply that nitrogen and phosphorus availability may not be limited for sapling growth in the present study, while a slight increase in leaf nitrogen content on acidic soil may reflect more soil nitrogen availability than on calcareous soil (Fig. 2).

Soil effects. Soil properties (e.g. pH, texture, nutrient availability) could affect plant growth^{53,78} and its response to water deficit^{3,42,79}. For instance, Kuster *et al.*³ reported that oaks produced more biomass on the acidic

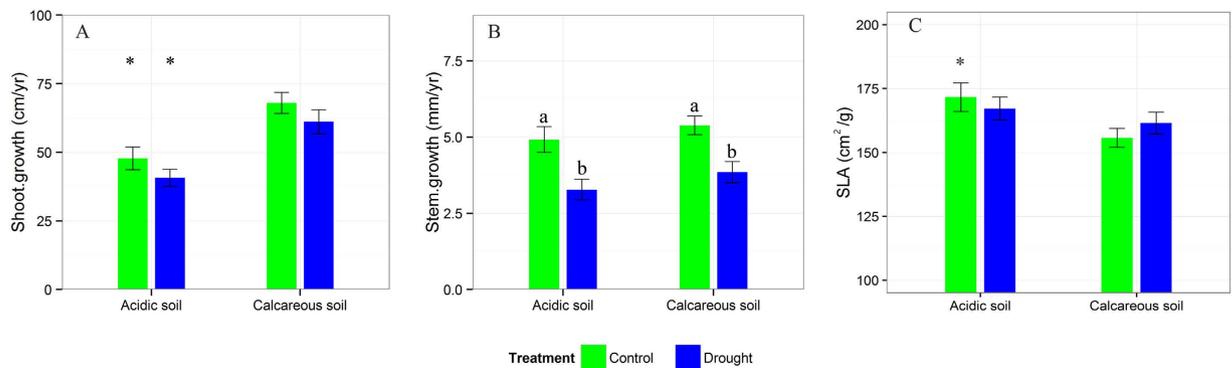


Figure 3. Mean values (\pm SE) for shoot growth (cm/yr) (A), stem diameter growth (mm/yr) (B) and SLA (cm^2/g) (C) from *Fagus sylvatica* L. saplings grown on acidic and calcareous soils and exposed to drought and re-watering treatments. Asterisks indicate significant differences between acidic and calcareous soil for a certain treatment. Different lowercase letters denote significant differences between treatments within a soil type ($p < 0.05$).

	Total		Control (n = 30)						Drought (n = 30)					
			Sub-total		Acidic soil		Calcareous soil		Sub-total		Acidic soil		Calcareous soil	
	H	D	H	D	H	D	H	D	H	D	H	D	H	D
Soluble sugars	0.243	-0.270*	-0.008	0.370*	-0.003	0.447	0.056	0.242	-0.293	-0.256	-0.037	-0.210	0.295	-0.097
Starch	-0.497**	0.061	-0.588**	-0.150	-0.225	-0.165	-0.413	0.408	-0.587**	-0.371*	-0.376	-0.406	-0.249	-0.338
NSC	-0.524**	0.240	-0.508**	0.093	-0.170	0.259	-0.193	0.472	-0.505**	-0.364*	-0.307	-0.462	0.245	-0.186
TN	-0.277*	0.229	-0.404*	-0.319	-0.462	-0.300	-0.305	-0.474	-0.120	-0.055	0.354	0.092	0.510	0.127
TP	0.099	0.003	-0.129	-0.062	-0.187	-0.408	-0.009	0.356	-0.070	0.061	0.385	0.063	-0.123	0.145
Soluble sugars:Starch	0.468**	0.017	0.619**	0.148	0.292	0.422	0.401	-0.235	0.621**	0.338	0.298	0.338	0.332	0.238
SLA	-0.109	-0.151	-0.084	-0.218	0.530*	-0.172	-0.345	-0.155	-0.135	-0.097	0.371	-0.071	-0.356	-0.051

Table 3. Correlation analysis between growth parameters (H: shoot increment (cm); D: stem increment (mm)), carbon (soluble sugars, starch and total NSC) and nutrients (nitrogen and phosphorus), SLA (cm^2/g) measured in July (before re-watering) for *Fagus sylvatica* L. saplings grown on different soils (acidic vs. calcareous) under different treatments (control vs. drought). Numbers in bold indicate statistical significance at the 5% level, where * $p < 0.05$; ** $p < 0.01$.

than on the calcareous soil in the absence of drought, while under water deficit, the relative growth reduction on the acidic soil was higher than on the calcareous soil. Also Thiel *et al.*⁴² found that drought negatively impacted growth of European beech, while the sandy substrate caused more growth reduction than the loamy substrate. However, our growth data showed that European beech saplings favored and were better adapted to the calcareous soil with a higher shoot increment, which is consistent with former studies for the same species^{78,80}. In the present study, drought decreased the growth of plants on both soils to a comparable extent (Fig. 3). However, leaf soluble sugar and total NSC concentrations on acidic soil were higher than on calcareous soil under the control and drought treatment. This contrasting pattern between growth and leaf NSC on the two soil types implied that soil types associated with soil chemical and physical properties modify or even determine the availability of carbohydrates to plant growth. On the other hand, soil types may reduce the sink activity, which in turn may result in less NSC investment to growth and thus lead to decreasing growth rate but increasing NSC concentration. An increased leaf NSC concentration can in turn down-regulate photosynthesis⁸¹, and thus decreases the growth rate.

The present study revealed a negative correlation between shoot growth and leaf starch concentration, as well as a positive correlation between shoot growth and leaf soluble sugar:starch ratio in drought-stressed saplings. Similar results have been reported by Woodhams and Kozłowski⁸² more than a half-century ago. Leaf soluble sugars produced by photosynthesis export from the source leaves into the phloem, and are used directly for plant growth⁸³. Hence, leaf sugars are a short-term pool and starch is a temporary storage induced due to either high carbon assimilation or low carbon export. On the other hand, drought may restrict the sink activity, and thus constrain the NSC export from leaves and NSC use, leading to decreased growth accompanied with leaf starch accumulation⁸⁴. Up to now, there are only a few studies with herbaceous species showing that starch (or the ratio of soluble sugars to starch) is a major integrator in the regulation of plant growth^{85–87}. Fast growing species for example, operate in a less conservative manner, diverting a slightly larger proportion of the newly assimilated carbon into soluble sugar export for growth and retaining less of starch to act as a short-term reserve or buffer against changes in environmental conditions⁸⁶. Our results show the same for a woody, late successional plant species.

Conclusions

The present study revealed that drought reduced shoot and stem growth of beech grown in acidic soil rather than in calcareous soil, indicating that soils with different physical and chemical properties can influence plants' drought tolerance. We, therefore, suggest that soil type should be considered as an additional modifying parameter when examining the influences of stress (e.g. drought) on plants. Drought led, in general, to increased total NSC concentrations but decreased growth rate, which may imply a priority of carbon storage over growth for drought-stressed plants. The negative correlation between starch concentration and growth, as well as a positive correlation between soluble sugar:starch ratio and growth as revealed by this study, may contribute to a better understanding of growth regulation under drought conditions. We speculate that growth of drought-stressed trees depends upon a soluble sugar-starch relation rather than a higher level of the total NSC, which is needed to be further verified for other woody species.

Materials and Methods

Experimental design and treatments. The present study was conducted in the model ecosystem facility of the Swiss Federal Research Institute WSL (47°21'54"N, 8°27'5"E, 545 m a.s.l.), Birmensdorf, Switzerland. The facility consists of 16 ortho-hexagonal open top chambers (OTCs) of 3.5 m in height and 1.0 m in side length, each equipped with an automated irrigation system and a sliding roof closing automatically at the onset of rainfall. The experiment was designed as a split-plot experiment with whole-plot treatments control (8 OTCs) and drought/re-watering (8 OTCs)⁵³. Drought development was followed by measurements of soil moisture in each lysimeter at 10 cm soil depth (5TM, Decagon, USA). Each OTC is split into two lysimeters with a plantable area of 3 m² each. In each OTC, one of the two lysimeters was randomly selected to be filled with 100-cm-deep acidic (haplic Alisol) forest soil, and the other one with calcareous forest soil (sub-plot factor). The acidic and calcareous soils had a pH of 4.0 and 6.9, respectively, with different chemical composition but comparable soil texture (Table S1; see also Kuster *et al.*³; Arend *et al.*⁵¹). The most differing mineral elements were calcium with a 10 times higher availability in calcareous soil and manganese with a 13 times higher availability in acidic soil, respectively. In spring 2011, 24 saplings with ~20 cm in height from 12 *Fagus sylvatica* L. provenances (2 saplings each) were transplanted in each lysimeter (sub-sub-plot factor)⁵³.

From November to April, the sliding roofs of the chambers were kept open to allow natural precipitation. By closing the sliding roofs from May to October, natural precipitation was excluded. The chambers were irrigated every second or third day with 50 l m⁻² deionized water, enriched with nutrients to simulate the average composition of ambient rainfall (see also Kuster *et al.*³). During hot summer periods, the irrigation intensity and frequency was increased to counterbalance higher rates of evapotranspiration and hold the soil moisture at 10 cm soil depth above 20%. With this target value, soil moisture in deeper soil layers was above field capacity as indicated by a constant outflow of drainage water at the bottom of the lysimeters. In 2014, when the saplings had reached a height of up to 2 m, a severe, long-lasting summer drought was imposed in the 8 OTCs with drought treatment, by reducing irrigation from 22 May to 2 August, and the 8 controls were irrigated as described above. After the first saplings reached predawn water potentials below -2.0 MPa, the 8 drought OTCs were intensely re-watered for 1 day with 200 l m⁻² and afterwards regularly irrigated as described above.

Leaf sampling. To reduce the work and costs of chemical analysis, the present study used only 3 provenances originating from xeric, semi-xeric and mesic forest sites (Table S2). During 10:00am-03:00 pm, leaf material was collected from randomly chosen lysimeters under control (n = 5) or drought treatment (n = 5) (Table S2) on both soil types (n = 60), one day before re-watering (July 31st) and 50 days after re-watering (September 19th). In each lysimeter, a single sapling of the xeric, semi-xeric and mesic provenance was selected. For each individual, 5-8 healthy and fully developed leaves (depending on the leaf size) were harvested, and immediately frozen in liquid nitrogen, and stored at -80 °C. After being scanned for leaf area (Image J v1.48) to determine specific leaf area (SLA, cm²/g DW), all samples were dried to a constant weight at 65 °C for 72 h. Finally, all samples were ground with a mixer mill MM400 (Retsch, Germany) for further analysis.

Total soluble sugar and starch concentration. The powdered material (~50 mg) was put into a 10 ml centrifuge tube, where 5 ml of 80% ethanol was added. The mixture was incubated at 80 °C in a water bath shaker for 30 min, and then centrifuged at 10,000 rpm for 5 min. The pellets were extracted two more times with 80% ethanol. Supernatants were retained, combined and stored at -20 °C for soluble sugar determinations. The ethanol-insoluble pellet was used for starch extraction. Glucose was used as a standard. Soluble sugars were determined using the anthrone method⁸⁸. The starch concentration was measured spectrophotometrically at 620 nm using anthrone reagent, and was calculated by multiplying glucose concentrations by the conversion factor of 0.9⁸⁹. Concentration of soluble sugars and starch was expressed on a dry matter basis (% DW). Concentration of non-structural carbohydrates (NSC) was obtained by summing up the total soluble sugar and starch concentrations.

Leaf nitrogen and phosphorus concentration. For determination of leaf nitrogen (N) and phosphorus (P) concentrations (mg/g DW), finely ground material (~50 mg) was firstly digested with H₂SO₄ and H₂O₂ for further analysis. Leaf nitrogen concentration was then measured using the Kjeldahl method (Kjeltec 2200, FOSS, Sweden), while leaf phosphorus concentration was determined with the molybdenum blue spectrophotometric procedure (6505 UV spectrophotometer, UK)⁹⁰.

Growth measurement. Annual shoot growth was determined on current-year leader shoots at the end of the growing season. Seasonal stem diameter increment was calculated from measurements of the stem diameter (10 cm above ground) at the start and end of the growing season.

Statistical analysis. All statistical analyses were conducted by using R statistical software (RStudio version 0.98.953, <http://www.rstudio.com/>). Shapiro-Wilk and Bartlett's tests were firstly used to test for normality and homogeneity of variances respectively, and all variables met the assumption for further variance analysis. Pre-analysis revealed no significant differences between provenances for all responsive variables (except for phosphorus). Therefore, we pooled the three provenances into one species. The linear mixed-effects models (R package-nlme) were used to determine the effects of three fixed factors, i.e. sampling period (July vs. September), treatment (control vs. drought-rewatering) and soil type (acidic vs. calcareous soil) on each response variable, provenance and growth chamber were considered as random factors. The response variables included leaf non-structural carbohydrate concentrations (soluble sugars, starch, total NSC), nutrient concentration (nitrogen, phosphorus) and growth increment (annual shoot and stem increment) on both soils. Significant differences in each response variable between the treatments within each soil type, as well as differences across soil types were compared by lsmeans (least squares means estimates, R package-lsmeans) and adjusted by the Tukey adjustment to identify pairwise differences ($p < 0.05$).

References

- IPCC. Summary for Policymakers. In Climate Change 2013: The Physical Science Basis. *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge Univ. Press, Cambridge, UK, 2013) (2013).
- Mitchell, P. J., O'Grady, A. P., Tissue, D. T., Worledge, D. & Pinkard, E. A. Co-ordination of growth, gas exchange and hydraulics define the carbon safety margin in tree species with contrasting drought strategies. *Tree Physiology* **34**, 443–458, doi: 10.1093/treephys/tpu014 (2014).
- Kuster, T., Arend, M., Bleuler, P., Günthardt-Goerg, M. S. & Schulin, R. 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 Biology* **15**, 138–147, doi: 10.1111/j.1438-8677.2011.00552.x (2013).
- Kursar, T. A. *et al.* Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. *Functional Ecology* **23**, 93–102, doi: 10.1111/j.1365-2435.2008.01483.x (2009).
- Choat, B. *et al.* Global convergence in the vulnerability of forests to drought. *Nature* **491**, 752–755, doi: 10.1038/nature11688 (2012).
- Alexou, M. Development-specific responses to drought stress in Aleppo pine (*Pinus halepensis* Mill.) seedlings. *Tree Physiology* **33**, 1030–1042, doi: 10.1093/treephys/tpt084 (2013).
- Cavender-Bares, J. & Bazzaz, F. A. Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia* **124**, 8–18, doi: 10.1007/PL00008865 (2000).
- Smith, M. D. The ecological role of climate extremes: current understanding and future prospects. *Journal of Ecology* **99**, 651–655, doi: 10.1111/j.1365-2745.2011.01833.x (2011).
- Doughty, C. E. *et al.* Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature* **519**, 78–82, doi: 10.1038/nature14213 (2015).
- Harper, R. J., Smettem, K. R. J., Carter, J. O. & McGrath, J. F. Drought deaths in *Eucalyptus globulus* (Labill.) plantations in relation to soils, geomorphology and climate. *Plant and Soil* **324**, 199–207, doi: 10.1007/s11104-009-9944-x (2009).
- Ciais, P. *et al.* Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* **437**, 529–533, doi: 10.1038/nature03972 (2005).
- Engelbrecht, B. J., Kursar, T. & Tyree, M. Drought effects on seedling survival in a tropical moist forest. *Trees* **19**, 312–321, doi: 10.1007/s00468-004-0393-0 (2005).
- Anderegg, W. R. L. Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. *New Phytologist* **205**, 1008–1014, doi: 10.1111/nph.12907 (2015).
- Buchanan, B. B., Gruissem, W. & Jones, R. L. *Biochemistry and molecular biology of plants* (John Wiley & Sons, 2015).
- Zeeman, Samuel C., Smith, Steven M. & Smith, Alison M. The diurnal metabolism of leaf starch. *Biochemical Journal* **401**, 13–28, doi: 10.1042/bj20061393 (2007).
- Beck, E. & Ziegler, P. Biosynthesis and Degradation of Starch in Higher Plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **40**, 95–117, doi: 10.1146/annurev.pp.40.060189.000523 (1989).
- Körner, C. Carbon limitation in trees. *Journal of Ecology* **91**, 4–17, doi: 10.1046/j.1365-2745.2003.00742.x (2003).
- Allen, C. D., Breshears, D. D. & McDowell, N. G. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**, 1–55, doi: 10.1890/ES15-00203.1 (2015).
- Blessing, C. H., Werner, R. A., Siegwolf, R. & Buchmann, N. Allocation dynamics of recently fixed carbon in beech saplings in response to increased temperatures and drought. *Tree Physiology* **35**, 585–598, doi: 10.1093/treephys/tpv024 (2015).
- McDowell, N. G. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant physiology* **155**, 1051–1059, doi: 10.1104/pp.110.170704 (2011).
- O'Brien, M. J., Leuzinger, S., Philipson, C. D., Tay, J. & Hector, A. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change* **4**, 710–714, doi: 10.1038/nclimate2281 (2014).
- Sala, A., Woodruff, D. R. & Meinzer, F. C. Carbon dynamics in trees: feast or famine? *Tree Physiology* **32**, 764–775, doi: 10.1093/treephys/tpv143 (2012).
- Anderegg, W. R. L. *et al.* The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proceedings of the National Academy of Sciences* **109**, 233–237, doi: 10.1073/pnas.1107891109 (2012).
- O'Brien, M. J., Burslem, D. F. R. P., Caduff, A., Tay, J. & Hector, A. Contrasting nonstructural carbohydrate dynamics of tropical tree seedlings under water deficit and variability. *New Phytologist* **205**, 1083–1094, doi: 10.1111/nph.13134 (2015).
- Wiley, E. & Helliker, B. A re-evaluation of carbon storage in trees lends greater support for carbon limitation to growth. *New Phytologist* **195**, 285–289, doi: 10.1111/j.1469-8137.2012.04180.x (2012).
- Palacio, S., Hoch, G., Sala, A., Körner, C. & Millard, P. Does carbon storage limit tree growth? *New Phytologist* **201**, 1096–1100, doi: 10.1111/nph.12602 (2014).
- Chapin, F. S. The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.* **11**, 233–260, doi: 10.1146/annurev.es.11.110180.001313 (1980).
- Reich, P. B., Grigal, D. F., Aber, J. D. & Gower, S. T. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology* **78**, 335–347, doi: 10.1890/0012-9658 (1997).
- Gessler, A., Schaub, M. & McDowell, N. G. The role of nutrients in drought-induced tree mortality and recovery. *New Phytologist*, doi: 10.1111/nph.14340 (2016).
- Townsend, A. R., Cleveland, C. C., Asner, G. P. & Bustamante, M. M. Controls over foliar N:P ratios in tropical rain forests. *Ecology* **88**, 107–118, doi: 10.1890/0012-9658 (2007).
- Güsewell, S. N. P ratios in terrestrial plants: variation and functional significance. *New Phytologist* **164**, 243–266, doi: 10.1111/j.1469-8137.2004.01192.x (2004).
- Koerselman, W. & Meuleman, A. F. M. The Vegetation N:P Ratio: a New Tool to Detect the Nature of Nutrient Limitation. *Journal of Applied Ecology* **33**, 1441–1450, doi: 10.2307/2404783 (1996).

33. Wright, I. J. *et al.* Assessing the generality of global leaf trait relationships. *New Phytologist* **166**, 485–496, doi: 10.1111/j.1469-8137.2005.01349.x (2005).
34. Gefler, A. *et al.* Climate and forest management influence nitrogen balance of European beech forests: microbial N transformations and inorganic N net uptake capacity of mycorrhizal roots. *European Journal of Forest Research* **124**, 95–111, doi: 10.1007/s10342-005-0055-9 (2005).
35. Sardans, J. & Peñuelas, J. Drought decreases soil enzyme activity in a Mediterranean *Quercus ilex* L. forest. *Soil Biology and Biochemistry* **37**, 455–461, doi: 10.1016/j.soilbio.2004.08.004 (2005).
36. Sardans, J., Peñuelas, J. & Ogaya, R. Experimental drought reduced acid and alkaline phosphatase activity and increased organic extractable P in soil in a *Quercus ilex* Mediterranean forest. *European Journal of Soil Biology* **44**, 509–520, doi: 10.1016/j.ejsobi.2008.09.011 (2008).
37. Sardans, J., Rivas-Ubach, A., Estiarte, M., Ogaya, R. & Peñuelas, J. Field-simulated droughts affect elemental leaf stoichiometry in Mediterranean forests and shrublands. *Acta Oecologica* **50**, 20–31, doi: 10.1016/j.actao.2013.04.002 (2013).
38. Kreuzwieser, J. & Gessler, A. Global climate change and tree nutrition: influence of water availability. *Tree Physiology* **30**, 1221–1234, doi: 10.1093/treephys/tpq055 (2010).
39. Lewis, T. & Subcommittee, T. H. Developing timber harvesting prescriptions to minimize site degradation. Report No. 0771890737, (BC Ministry of Forests, 1991).
40. Contran, N. *et al.* Physiological and biochemical responses of *Quercus pubescens* to air warming and drought on acidic and calcareous soils. *Plant Biology* **15**, 157–168, doi: 10.1111/j.1438-8677.2012.00627.x (2013).
41. Hu, B., Simon, J. & Rennenberg, H. Drought and air warming affect the species-specific levels of stress-related foliar metabolites of three oak species on acidic and calcareous soil. *Tree Physiology* **33**, 489–504, doi: 10.1093/treephys/tpu025 (2013).
42. Thiel, D. *et al.* Different reactions of central and marginal provenances of *Fagus sylvatica* to experimental drought. *European Journal of Forest Research* **133**, 247–260, doi: 10.1007/s10342-013-0750-x (2014).
43. Peters, R. *Beech Forests* (Springer Netherlands, 1997).
44. Geßler, A., Keitel, C., Nahm, M. & Rennenberg, H. Water Shortage Affects the Water and Nitrogen Balance in Central European Beech Forests. *Plant Biology* **6**, 289–298, doi: 10.1055/s-2004-820878 (2004).
45. Gefler, A. *et al.* Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees* **21**, 1–11, doi: 10.1007/s00468-006-0107-x (2007).
46. Lendzion, J. & Leuschner, C. Growth of European beech (*Fagus sylvatica* L.) saplings is limited by elevated atmospheric vapour pressure deficits. *Forest Ecology and Management* **256**, 648–655, doi: 10.1016/j.foreco.2008.05.008 (2008).
47. Aranda, I. *et al.* Variation in photosynthetic performance and hydraulic architecture across European beech (*Fagus sylvatica* L.) populations supports the case for local adaptation to water stress. *Tree Physiology* **35**, 34–46, doi: 10.1093/treephys/tpu101 (2015).
48. Tognetti, R., Johnson, J. & Michelozzi, M. The response of European beech (*Fagus sylvatica* L.) seedlings from two Italian populations to drought and recovery. *Trees* **9**, 348–354, doi: 10.1007/BF00202499 (1995).
49. Zang, U. *et al.* Fate of recently fixed carbon in European beech (*Fagus sylvatica*) saplings during drought and subsequent recovery. *Tree Physiology* **34**, 29–38, doi: 10.1093/treephys/tpu110 (2014).
50. Gallé, A. & Feller, U. Changes of photosynthetic traits in beech saplings (*Fagus sylvatica*) under severe drought stress and during recovery. *Physiologia Plantarum* **131**, 412–421, doi: 10.1111/j.1399-3054.2007.00972.x (2007).
51. Arend, M., Sever, K., Pflug, E., Gessler, A. & Schaub, M. Seasonal photosynthetic response of European beech to severe summer drought: Limitation, recovery and post-drought stimulation. *Agricultural and Forest Meteorology* **220**, 83–89, doi: 10.1016/j.agrformet.2016.01.011 (2016).
52. Körner, C. The Grand Challenges in Functional Plant Ecology. *Frontiers in plant science* **2**, 1–3, doi: 10.3389/fpls.2011.00001 (2011).
53. Arend, M., Gessler, A. & Schaub, M. The influence of the soil on spring and autumn phenology in European beech. *Tree Physiology* **36**, 78–85, doi: 10.1093/treephys/tpv087 (2016).
54. Konôpka, B., Pajtk, J., Bošela, M., Hlásny, T. & Sitková, Z. Inter- and intra-annual dynamics of height increment in young beech and spruce stands in relation to tree size and weather conditions. *Forestry Journal* **60**, 52–60, doi: 10.2478/forj-2014-0005 (2014).
55. Michelot, A., Simard, S., Rathgeber, C., Dufrêne, E. & Damesin, C. Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. *Tree Physiology* **32**, 1033–1045, doi: 10.1093/treephys/tps052 (2012).
56. Duan, H. *et al.* Carbon dynamics of eucalypt seedlings exposed to progressive drought in elevated [CO₂] and elevated temperature. *Tree Physiology* **33**, 779–792, doi: 10.1093/treephys/tpu061 (2013).
57. Adams, H. D. *et al.* Nonstructural leaf carbohydrate dynamics of *Pinus edulis* during drought-induced tree mortality reveal role for carbon metabolism in mortality mechanism. *New Phytologist* **197**, 1142–1151, doi: 10.1111/nph.12102 (2013).
58. Piper, F. Drought induces opposite changes in the concentration of non-structural carbohydrates of two evergreen *Nothofagus* species of differential drought resistance. *Annals of Forest Science* **68**, 415–424, doi: 10.1007/s13595-011-0030-1 (2011).
59. Hartmann, H., Ziegler, W. & Trumbore, S. Lethal drought leads to reduction in nonstructural carbohydrates in Norway spruce tree roots but not in the canopy. *Functional Ecology* **27**, 413–427, doi: 10.1111/1365-2435.12046 (2013).
60. Nardini, A. *et al.* Rooting depth, water relations and non-structural carbohydrate dynamics in three woody angiosperms differentially affected by an extreme summer drought. *Plant Cell Environ* **39**, 618–627, doi: 10.1111/pce.12646 (2016).
61. Woodruff, D. R. *et al.* Linking nonstructural carbohydrate dynamics to gas exchange and leaf hydraulic behavior in *Pinus edulis* and *Juniperus monosperma*. *New Phytologist* **206**, 411–421, doi: 10.1111/nph.13170 (2015).
62. Hagedorn, F. *et al.* Recovery of trees from drought depends on belowground sink control. *Nature Plants* **2**, 16111, doi: 10.1038/nplants.2016.111 (2016).
63. Ruehr, N. K. *et al.* Drought effects on allocation of recent carbon: from beech leaves to soil CO₂ efflux. *New Phytologist* **184**, 950–961, doi: 10.1111/j.1469-8137.2009.03044.x (2009).
64. Gallé, A., Haldimann, P. & Feller, U. Photosynthetic performance and water relations in young pubescent oak (*Quercus pubescens*) trees during drought stress and recovery. *New Phytologist* **174**, 799–810, doi: 10.1111/j.1469-8137.2007.02047.x (2007).
65. Rodriguez-Calcerrada, J., Shahin, O., del Carmen del Rey, M. & Rambal, S. Opposite changes in leaf dark respiration and soluble sugars with drought in two Mediterranean oaks. *Functional Plant Biology* **38**, 1004–1015, doi: 10.1071/FP11135 (2011).
66. Parida, A., Dagaonkar, V., Phalak, M., Umalkar, G. V. & Aurangabadkar, L. Alterations in photosynthetic pigments, protein and osmotic components in cotton genotypes subjected to short-term drought stress followed by recovery. *Plant Biotechnol Rep* **1**, 37–48, doi: 10.1007/s11816-006-0004-1 (2007).
67. Aroca, R. In *From Morphological to Molecular Features* (Springer, 2012).
68. Lu, Y. W. *et al.* Intraspecific variation in drought response of *Populus cathayana* grown under ambient and enhanced UV-B radiation. *Annals of Forest Science* **66**, 613, doi: 10.1051/Forest/2009049 (2009).
69. Hu, B. *et al.* Nitrogen partitioning in oak leaves depends on species, provenance, climate conditions and soil type. *Plant Biology* **15**, 198–209, doi: 10.1111/j.1438-8677.2012.00658.x (2013).
70. Li, M. H. *et al.* Responses of leaf nitrogen and mobile carbohydrates in different *Quercus* species/provenances to moderate climate changes. *Plant Biology* **15**, 177–184, doi: 10.1111/j.1438-8677.2012.00579.x (2013).
71. Rose, L., Leuschner, C., Köckemann, B. & Buschmann, H. Are marginal beech (*Fagus sylvatica* L.) provenances a source for drought tolerant ecotypes? *European Journal of Forest Research* **128**, 335–343, doi: 10.1007/s10342-009-0268-4 (2009).

72. Kuster, T., Schleppi, P., Hu, B., Schulin, R. & Günthardt-Goerg, M. S. Nitrogen dynamics in oak model ecosystems subjected to air warming and drought on two different soils. *Plant Biology* **15**, 220–229, doi: 10.1111/j.1438-8677.2012.00686.x (2013).
73. Sánchez-Gómez, D., Robson, T. M., Gascó, A., Gil-Pelegrín, E. & Aranda, I. Differences in the leaf functional traits of six beech (*Fagus sylvatica* L.) populations are reflected in their response to water limitation. *Environmental and Experimental Botany* **87**, 110–119, doi: 10.1016/j.envexpbot.2012.09.011 (2013).
74. Peuke, A. D. & Rennenberg, H. Carbon, nitrogen, phosphorus, and sulphur concentration and partitioning in beech ecotypes (*Fagus sylvatica* L.): phosphorus most affected by drought. *Trees* **18**, 639–648, doi: 10.1007/s00468-004-0335-x (2004).
75. He, M. & Dijkstra, F. A. Drought effect on plant nitrogen and phosphorus: a meta-analysis. *New Phytologist* **204**, 924–931, doi: 10.1111/nph.12952 (2014).
76. Taeger, S., Sparks, T. H. & Menzel, A. Effects of temperature and drought manipulations on seedlings of Scots pine provenances. *Plant Biology* **17**, 361–372, doi: 10.1111/plb.12245 (2015).
77. Kuster, T., Arend, M., Günthardt-Goerg, M. & Schulin, R. Root growth of different oak provenances in two soils under drought stress and air warming conditions. *Plant and Soil* **369**, 61–71, doi: 10.1007/s11104-012-1541-8 (2013).
78. Spinnler, D., Egli, P. & Körner, C. Four-year growth dynamics of beech-spruce model ecosystems under CO₂ enrichment on two different forest soils. *Trees* **16**, 423–436, doi: 10.1007/s00468-002-0179-1 (2002).
79. Günthardt-Goerg, M. S., Kuster, T. M., Arend, M. & Vollenweider, P. Foliage response of young central European oaks to air warming, drought and soil type. *Plant Biology* **15**, 185–197, doi: 10.1111/j.1438-8677.2012.00665.x (2013).
80. Spinnler, D., Egli, P. & Körner, C. Provenance effects and allometry in beech and spruce under elevated CO₂ and nitrogen on two different forest soils. *Basic and Applied Ecology* **4**, 467–478, doi: 10.1078/1439-1791-00175 (2003).
81. Quentin, A. G., Close, D. C., Hennen, L. M. H. P. & Pinkard, E. A. Down-regulation of photosynthesis following girdling, but contrasting effects on fruit set and retention, in two sweet cherry cultivars. *Plant Physiology and Biochemistry* **73**, 359–367, doi: 10.1016/j.plaphy.2013.10.014 (2013).
82. Woodhams, D. H. & Kozłowski, T. T. Effects of Soil Moisture Stress on Carbohydrate Development and Growth in Plants. *American Journal of Botany* **41**, 316–320 (1954).
83. Dietze, M. C. *et al.* Nonstructural Carbon in Woody Plants. *Annual Review of Plant Biology* **65**, 667–687, doi: 10.1146/annurev-arplant-050213-040054 (2014).
84. Lemoine, R. *et al.* Source-to-sink transport of sugar and regulation by environmental factors. *Frontiers in Plant Science* **4**, doi: 10.3389/fpls.2013.00272 (2013).
85. Sulpice, R. *et al.* Starch as a major integrator in the regulation of plant growth. *Proceedings of the National Academy of Sciences* **106**, 10348–10353, doi: 10.1073/pnas.0903478106 (2009).
86. Smith, A. M. & Stitt, M. Coordination of carbon supply and plant growth. *Plant, Cell and Environment* **30**, 1126–1149, doi: 10.1111/j.1365-3040.2007.01708.x (2007).
87. Purdy, S. J., Maddison, A. L., Cunniff, J., Donnison, I. & Clifton-Brown, J. Non-structural carbohydrate profiles and ratios between soluble sugars and starch serve as indicators of productivity for a bioenergy grass. *AoB Plants*, doi: 10.1093/aobpla/plv032 (2015).
88. Seifter, S., Dayton, S., Novic, B. & Muntwyler, E. The Estimation of Glycogen with the Anthrone Reagent. *Archives of Biochemistry* **25**, 191–200 (1950).
89. Osaki, M., Shinano, T. & Tadano, T. Redistribution of carbon and nitrogen compounds from the shoot to the harvesting organs during maturation in field crops. *Soil Science and Plant Nutrition* **37**, 117–128 (1991).
90. Page, A. L. *Methods of soil analysis. Part 2. Chemical and microbiological properties* (American Society of Agronomy, Soil Science Society of America, 1982).

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Author Contributions

M. Arend, M. Li, J. Liu, M. Schaub, A. Gessler and A. Rigling conceived the experiment, J. Liu, M. Li and M. Arend conducted the experiment, J. Liu, W. Yang and Y. Ni analysed the samples, J. Liu, M. Arend, M. Li, M. Schaub, A. Gessler and Z. Jiang wrote the paper. All authors reviewed the manuscript.

Additional Information

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