Climate response of above- and belowground productivity and allocation in European beech

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List of abbreviations

AWSC	Available water storage capacity of the soil
C	Carbon
C_a	Area-based carbon concentration
C_m	Mass-based carbon concentration
CEC	Cation exchange capacity
DBH	Diameter at breast height
LAI	Leaf area index
MAP	Mean annual precipitation
MAT	Mean annual temperature
N	Nitrogen
N_a	Area-based nitrogen concentration
N_m	Mass-based nitrogen concentration
NPP	Net primary production
NPP_a	Aboveground net primary production
P	Precipitation
R:S	Root per shoot biomass ratio
Rad	Solar radiation
RAI	Root area index
REW	Relative extractable water
RSVI	Relative stem volume increment
$RSVI_a$	Relative annual stem volume increment
RTD	Root tissue density
SLA	Specific leaf area
SRA	Specific root area
SRL	Specific root length
SVI_a	Annual stem volume increment
T	Temperature
VWC	Volumetric water content
WSC	Water storage capacity
WUE	Water use efficiency
$\Sigma fSUT$	Fraction of fine-grained soil particles $< 200\ \mu m$
ΣUT	Fraction of fine-grained soil particles $< 63\ \mu m$

Chapter 1

General Introduction

Background

Global and regional climate change

Human activity over the past 250 years has increased the amount of greenhouse gases in the atmosphere. Since 1750, atmospheric concentrations of CO_2 have risen from < 280 ppm to 393 ppm in 2012 (Le Quéré and others 2013). Also the concentrations of several other greenhouse gases, such as methane (CH_4) and nitrous oxide (N_2O) are increasing as a result of (agro-) industrial activities (IPCC 2013). Elevated concentrations of atmospheric greenhouse gases have changed Earth's climate, raising the globally averaged combined land and ocean surface temperature by 0.85 ° C between 1880 and 2012 (IPCC 2013). Current models suggest an increase in global temperature by 3.2 – 5.4°C above the mean temperature (1850 – 1900) by the end of the 21st century (IPCC 2013). These changes will very likely cause large impacts on the global hydrological cycle (Huntington 2006; Gerten and others 2007). However, alterations of temperature and, even more, of precipitation will be largely subject to regional and seasonal variations (Klein Tank and others 2002; Brunetti and others 2012). Most climate change scenarios for Central Europe predict a rise in mean annual temperature by 2.5 – 3.5 °C until the end of the 21st century as well as increasing frequency and raised intensity of summer heat waves (Rowell and Jones 2006; Fischer and Schär 2009). Projections of climate change on regional scale for Northern Germany are similar to those referring to Central Europe (Jacob and others 2008; Moseley and others 2012). Concurring shifts of temperature and precipitation will likely result in a substantial aggravation of the climatic water balance during the vegetation period in Germany and many parts of central and southern Europe (Kundzewicz and others 2006; Fischer and others 2012).

Responses of plants, populations and species to climate change

These, on evolutionary time scale, abrupt changes in growing conditions pose a major threat to present plant populations (Walther and others 2002; Parmesan 2006). The capacity of plants to cope with such radical changes basically rest upon three reaction types with differences regarding the spatial and temporal scale: phenotypic plasticity (acclimation), genotypic evolution (adaptation) and changes in distribution (migration) (Anderson and others 2012).

As acclimative responses to environmental changes, plants may alter their physiological, phenological, growth and allocation behaviour by variations of gen expression and

metabolism within species-specific limits. Adaptation alters the potential of plants to acclimate to environmental variations via micro-evolutionary processes on population level, and is therefore regarded as a key factor for a successful adaption of plants to climate change (Bradshaw and others 2006). However, adaptation processes involve genetic changes and therefore typically require several generations to be put into effect. Comparisons of the historical and current distributions of many species suggested their relationships with climate to be largely constant (Bradshaw 1991; Huntley 1991). Therefore, among response processes of plants to current global climate change, only a minor importance is assumed for adaptation (Jump and Peñuelas 2005).

With changes in environmental conditions formerly limiting the species´ distribution range, migration is expected as the most immediate reaction of plants at population level (Thuiller and others 2008). A directional shift of species´ ranges toward higher latitudes and altitudes in response to global warming has been found in paleoecological studies (Prentice and Jolly 2001; Parmesan 2006) as well as in numerous observations of current species´ range shift (Parmesan and Yohe 2003; Peñuelas and Boada 2003; Hickling and others 2006; Chen and others 2011). For the Holocene warming period, several authors estimate the post-glacial migration of *Fagus* and other temperate tree species to have occurred at rates of 60-170 m y^{-1} (McLachlan and others 2005; Bialozyt and others 2012; Feurdean and others 2013). In contrast, simulated future migration rates for such tree species are much slower (Meier and others 2012), likely due to a greater influence of competition and habitat fragmentation during the present warming phase.

As the current increase in concentrations of atmospheric CO_2 is several orders of magnitude greater than in any previous period of rapid change in atmospheric CO_2 during the last 500 million years (Peñuelas and others 2013), present global change may likely exceed the capacities of many plant species – at the individual, population and community level – to assimilate them (Leemans and Eickhout 2004). Beyond global warming, plants are additionally threatened by further impacts like N eutrophication, habitat fragmentation and species invasion. Compared to other biological resources, forest ecosystems and silviculture are especially vulnerable to rapid environmental changes because of extensive life spans and long cultivation periods of temperate forest trees (Spellmann and others 2007).

Plant responses to shifting growing conditions

Global climate change is likely to simultaneously alter many aspects of local growing conditions, regarding climate (e.g. precipitation, temperature, solar radiation) and atmospheric input of elements to forests and other ecosystems. These alterations will directly affect the availability of resources for plants, such as water, light and nutrients (Lindner and others 2010). Besides abiotic conditions, the capture of requisite resources is further influenced by the ability of plants to react to changing conditions with above- and belowground allocation and active incorporation processes.

It is widely assumed that elevated CO_2 concentrations will enhance photosynthesis and reduce stomatal conductance, which in theory enables plants to conserve water and to enhance their water use efficiency (WUE) (Schäfer and others 2002; Battipaglia and others 2013). This CO_2-induced increase in primary productivity and WUE is commonly known as the "fertilization effect" of CO_2 (Farquhar 1997; Hättenschwiler and others 1997). Yet, multiple studies demonstrated that enhanced CO_2 concentrations will not necessarily lead to an increased drought resistance of temperate forests, because stomatal control of many tree species is widely unresponsive to elevated CO_2 (Medlyn and others 2001). In addition, the water conserving effects arising from decreased stomatal conductance can at least partially be compensated by opposing effects like increased leaf area (Peñuelas and others 2011; Donohue and Roderick 2013). Besides effects on the water economy, increases in biomass production are often limited by other environmental factors (De Vries and Posch 2011). Accordingly, results from a free air CO_2 enrichment (FACE) experiment suggested a reduction in water consumption of less than 10% and no significant increase in wood increment in a mature mixed deciduous forest under artificially enhanced CO_2 concentrations (Asshoff and others 2006; Leuzinger and Körner 2007).

Although heat and drought tend to occur simultaneously in nature, both factors are known to provoke stress in plants in very distinct ways (Rennenberg and others 2006). The response of a plant to warmer growing conditions thus primarily depends on whether or not its habitat is limited by water (Lindner and others 2010). With increasing temperature, photorespiration increases faster than photosynthesis (Sage and Kubien 2007), thereby causing negative impacts on the C economy of plants. Under sufficient water supply, plants may respond to moderate warming with an adaption of their optimal temperature for CO_2 assimilation (Gunderson and others 2010). Such acclimation was often observed to result in increased photosynthetic activity and biomass production, if not limited by other resources like nutrients (Peñuelas and others 2013). In contrast, extreme heat is thought to heavily, albeit reversibly

impair photochemistry in photosynthesis or to cause damage to the thylakoid membrane (Schrader and others 2004). Therefore, morphological adaptations which improve both the uptake of nutrients and the thermal balance of leaves are crucial for maintaining the vitality of plants under warming (Michelsen and others 1996; Jónsdóttir and others 2005). In addition to effects on photosynthesis, numerous studies have demonstrated alterations in the timing of developmental events in plants such as leaf unfolding, flowering, plant growth and fruiting as a result of warming climatic conditions (e.g. Menzel and Fabian 1999; Fitter and Fitter 2002; Cleland and others 2007; Wolkovich and others 2012).

Among several climatic factors affecting terrestrial net primary production, increasing deficit in the climatic water balance is estimated the most important (Zhao and Running 2010). Major threats induced by temporal hydrologic imbalances and resulting decreases in the plants´ water potential are inherent dangers of xylem cavitation and embolism as well as the impairment of many biochemical, metabolic and transport processes (Rennenberg and others 2006). Such implications of drought may directly and indirectly cause negative impacts on the C balance of plants and thereby induce a decline in productivity, increases in vulnerability to secondary stresses (e.g. insect infestations, pathogens or frost damage) and may finally lead to the death of plants (Allen and others 2010).

Plants have developed several physiological and morphological mechanisms to improve their water balance, i.e., to reduce water losses to the atmosphere, to enhance water uptake from the soils, or to reduce damages caused by enhanced water tension (Bartels and Sunkar 2005; Maseda and Fernández 2006). As an immediate response to water deficits, plants typically increase their leaf diffusive resistances, which directly down-regulates transpiration but also photosynthesis. Persistent drought stress may also result in complex metabolic impairment involving a decline in rubisco activity that additionally limits C assimilation (Flexas and others 2004). In order to maintain a favourable leaf water status, many plants are able to adjust their leaf osmotic potential by accumulating ions and organic solutes when exposed to drought stress (Chen and Jiang 2010). Besides such physiological short-term reactions, also alterations of morphological structures may contribute to the plants' acclimation to increasing drought. Plants can achieve long-term plastic adjustment to water shortage by increasing their allocation of carbon to the root system (thereby increasing their root:shoot ratio; Xu and others 2007; Shao and others 2008; Dreesen and others 2012), by lowering water losses via reduction of the transpiring leaf surface (Ogaya and Penuelas 2006), and by developing a highly conductive xylem while keeping the cavitation vulnerability of the xylem low (Sperry and others 2002).

European beech forests in a changing climate

European beech (*Fagus sylvatica* L.) is by far the most abundant tree species of Central Europe's natural forest vegetation and one of the economically most important trees (Ellenberg and Leuschner 2010). Owing to an ample physiological tolerance, the distribution range of *F. sylvatica* covers large parts of Central and Western Europe (Figure 1.1) covering sites on a broad range of climatic and edaphic growing conditions, from poor, highly acidic to neutral soils and from high to low precipitation regimes (Leuschner and others 2006). Among other traits, especially a high degree of light interception of mature trees in company with a high shade tolerance of seedlings and saplings make this late-successional tree species an effective competitor to other tree species. As a result of human activities, the abundance of beech was reduced to c. 7 % of its potential areal cover (BMU 2011). While currently beech covers 17.3% of the German forest area, forestry explicitly aims to increase of the proportion of beech in German forests (BMVEL 2004; NLF 2006).
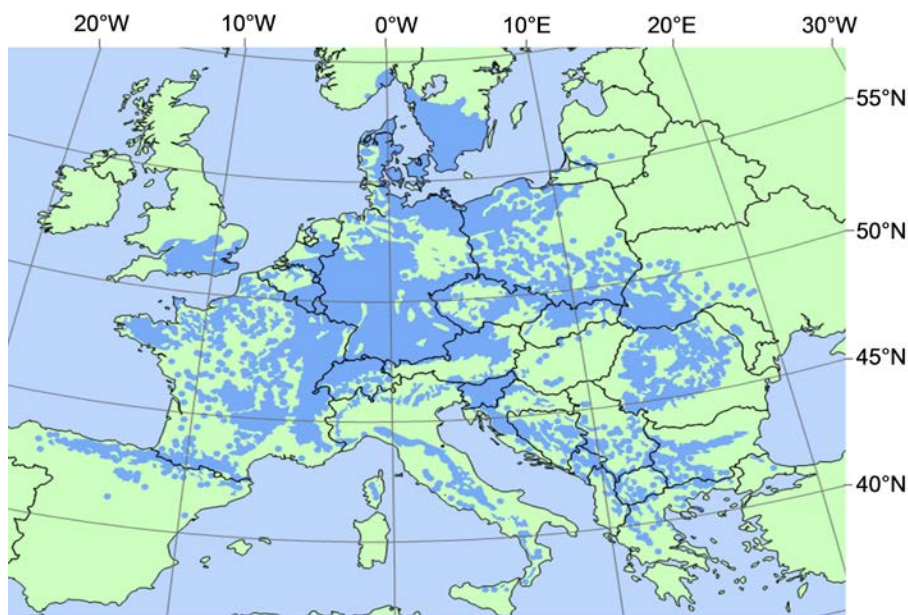

Figure 1.1. Distribution map of *Fagus sylvatica* (Euforgen 2009, www.euforgen.org, modified).

Whether the plasticity of *F. sylvatica* with respect to local growing conditions enables this species to cope with future climate conditions in its current distribution range is controversially discussed (e.g. Leuschner and others 2001; Schraml and Rennenberg 2002; Rennenberg and others 2004; Ammer and others 2005; Bréda and others 2006; Czajkowski and others 2006; Geßler and others 2007; Kölling and others 2007). Compared to other temperate forest trees such as *Quercus*, *Tilia*, *Carpinus*, *Fraxinus*, or *Pinus* species, European beech is considered as relatively drought-susceptible (Roloff and Grundmann 2008; Köcher

and others 2009; Zapater and others 2012). In response to soil water deficits, beech exhibits a drought sensitive stomatal down-regulation of leaf conductance, photosynthesis and sap flow, entailing reductions of canopy carbon (C) gain and stem increment (Dreyer 1997; Leuschner and others 2001; Leuzinger and others 2005; Granier and others 2007). This behaviour is also reflected in results of several dendro-ecological studies which relate summer water availability with current year ring width (Dittmar and others 2003; Lebourgeois and others 2005). However, increased levels of tree mortality in succession to severe drought events are assumed to be related with xylem dysfunction as a consequence of drought-induced cavitation, rather than with C limitation (Bréda and others 2006). Investigations in mature beech trees did not find evidence for leaf osmotic adjustment with soil water deficits (Backes and Leuschner 2000; Leuschner and others 2001) whereas ecotype-specific increases of proline are reported to occur in leaves of young trees (Schraml and Rennenberg 2002). An increase in transpiring leaf surface on sites that are more prone to summer-drought is assumed to be explained by positive influences of enhanced temperature and nitrogen availabilities during the period of leaf development (Meier and Leuschner 2008b). Yet, summer drought was often reported to result in advanced or even premature leaf shedding, maybe induced by embolism, thereby shortening the period of C assimilation under drier climates (Dreyer 1997; Ciais and others 2005; Bréda and others 2006). Numerous studies attribute growth limitation at the southern and south eastern distribution limits of beech to precipitation shortfalls and climatic continentality (Gutiérrez 1988; Biondi 1993; Dittmar and others 2003; Lebourgeois and others 2005), and identify drought stress as the main driver of beech dieback in its southern range edge (Jump and others 2006; Piovesan and others 2008). There are indications that the growth-sensitivity to drought in mature beech trees is somehow reduced when permanently exposed to artificially enhanced CO_2 concentrations (Leuzinger and others 2005; Asshoff and others 2006; Leuzinger and Körner 2007).

Besides precipitation input, also soil texture and plant rooting depth are crucial factors in determining the plant available soil water. Therefore, the vitality of beech is most vulnerable to climate change in regions where soil moisture is already limited by geographical or pedological aspects (e.g. shallow or sandy soils resulting in low water storage capacity) under present site conditions (Rennenberg and others 2004; Overbeck and others 2011). Despite enhancing effects of higher temperatures on mineralisation rates of organic matter, also pedospheric nutrient uptake was shown to be strongly inhibited by reduced transpiration upon enhanced levels of temperature, soil drought and CO_2 concentrations (Rennenberg and others 2009; Schleppi and others 2012).

Environmental influences on productivity and allocation

Productivity of trees equally depends on the acquisition of limited aboveground and belowground resources. Besides site-specific limitations of resources, also mechanisms of competition between plants additionally impair the uptake of requisites, such as water, nutrients and carbon; the latter one primarily indirectly by limitations of light availability. According to *optimal partitioning theory* (OPT), plants should allocate resources to the growth of that organ which acquires the most limiting resource (Thornley 1972; Bloom and others 1985). This theory implies that there is no species-specific equilibrium between single components of growth. Instead, resource allocation patterns within trees are highly dynamic and partitioning is adaptive to changes in growing conditions (Gleeson and Tilman 1992) and tree age (Genet and others 2010). As a variable fraction of photosynthetic C gain in the tree is used for wood production, forestal efforts since long aimed at increasing the proportion of wood by means of stand structural management and genetic selection.

OPT suggests that under limiting conditions of soil resources, root biomass should be produced at higher rates to build more absorptive surface. Studies on the belowground biomass production of temperate tree species in reaction to experimental or natural variations of water availability, however, yield an unclear picture as they report both positive (Joslin and Wolfe 1998; Leuschner and others 2001; Konôpka and others 2005) and negative (Leuschner and Hertel 2003; Leuschner and others 2004; Meier and Leuschner 2008a) shifts in the root:shoot ratio and fine root biomass with enhanced drought. This dissent may be caused by additional influences on fine root biomass by increasing fine root mortality, functional shifts (resource uptake vs. resource storage) or altered patterns of interactions with root symbionts (Eissenstat and others 2000; Mccarthy and Enquist 2007; Kobe and others 2010). It was shown that drought does not only reduce the C assimilation but also limits the C transfer from the tree canopy to the roots (Ruehr and others 2009).

Also the pattern of reproduction in beech is strongly subject to climatic growing conditions. At irregular time intervals, many beech trees of a population synchronously produce large seed crops, called *masting* (Hilton and Packham 2003). In mast years of beech, a large portion of current assimilates and other resources are consumed by the production of reproductive material. Unlike utilization sinks (i.e. vegetative growth, storage, defence), reproductive sinks do not enhance the plants´ ability to gain or to maintain access to resources and therefore, resource investment into reproduction is not thought to be controlled according to optimal partitioning (Doust 1989). However, the temporal concentration of seed production on mast years is also considered a mechanism suitable to increase resource efficiency (Kelly

1994). It is still a matter of debate, which particular climate events synchronize masting but in a majority of studies, either elevated temperature or drought was identified as the proximate factor controlling floral induction in beech (Piovesan and Adams 2001). Although it is considered certain that internal dynamics of carbon or nitrogen (N) must be involved in that regulation (Miyazaki 2013), a causal relationship between assumed climatic triggers and resources could not fully be explained so far. For reasons that are not yet understood, masting in beech occurs at increasing frequency since the last three decades (Övergaard and others 2007). Fructification in beech is inevitably linked to a switch in resource allocation (Drobyshev and others 2010). Therefore, the advanced frequency and intensity of fruit production is likely to substantially alter forest productivity and forest biogeochemical cycles and thus may be another factor constraining vegetative growth and vitality of beech forests in future.

General study aims

In this comparative investigation on above- and belowground productivity of beech forest stands across a precipitation gradient in Northern Germany (540 – 820 mm y^{-1}), species-specific mechanisms of morphological adaptation to alterations of long-term climatic growing conditions in beech (*Fagus sylvatica* L.) should be revealed. Because drought intensity is partly dependent on the water retention and water conduction properties of the soil, additional emphasis is given to the influence of soil texture on the evolvement of soil water deficits in the Pleistocene lowlands of north-western Germany during summer. Results of this study are expected to allow conclusions on future climate responses of *Fagus sylvatica* ranging toward the natural drought-induced limit of this species´ current distribution in Central Germany (Kölling and others 2007; Leuschner 2009).

This dissertation is subdivided into three studies focusing on different aspects of productivity and resource allocation in mature beech forests.

Major study aims were to

i)   disentangle partial influences of precipitation and other climatic parameters on the aboveground productivity and growth partitioning in adult beech trees,

ii)   identify weather variables proximately controlling the reproduction behaviour of *Fagus sylvatica* and to assess trade-offs between vegetative and reproductive growth.

iii)   investigate adaptive responses of belowground allocational and morphological plasticity to shifts in hydrological regimes,

This study was conducted within the research co-operation KLIFF (Klimafolgenforschung in Niedersachsen - Climate impact and adaptation research in Lower Saxony) which aims to increase the knowledge base on consequences of climate change at regional and local scales, in order to develop sustainable adaptation strategies for the management of natural resources in Lower-Saxony, Germany.

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Chapter 2

Materials and methods

Two-factorial plot design: climatic and edaphic drought

The growth sensitivity of mature beech trees to long-term reductions in water availability was studied using a two-factorial plot design. Both factors refer to major determinants of water availability, i.e., precipitation input and soil water storage. For this purpose, 12 mature beech stands with comparable stand structure were selected in the Pleistocene lowlands of north-western Germany. For minimising additional influences by soil chemical variation, all stands grew on comparable geological substrate (Saale glacial meltwater sand or moraine deposits covered by periglacial drift-sand).

Study sites

The study plots are located in six forest districts along a 130 km-long NW-SE transect in the East of the state Lower Saxony and the western part of Saxony-Anhalt; from west to east: Sellhorn (Se), Oerrel (Oe), Unterlüß (Un), Göhrde (Go), Klötze (Kl), Calvörde (Ca, site acronyms in brackets; see Figure 3.1). This transect spans the regions of Lüneburg Heath, Wendland and Altmark and represents a climatic transition from an oceanic to a sub-continental climate with a continuous decrease in mean annual precipitation (MAP; 816 to 543 mm y^{-1}) and a slight increase in mean annual temperature (MAT; 8.4 to 9.1 °C) from west to east (Figure 2.1). Also long-term climate conditions during the vegetation period (April-October) show a clear precipitation-decline from west to east (470-330 mm) and a minor temperature increase (12.7-13.6 °C). The 12 plots were located at elevations of 72 - 125 m a.s.l. in level or only slightly sloping terrain. All stands occurred on highly acidic and nutrient-poor sandy or sandy to loamy soils originating from fluvio-glacial sands or moraine deposits of the penultimate Saale Ice Age (Drenthe and Warthe stadials) covered by periglacial drift sand. The mineral soils (dystric or umbric Arenosols or Podzols) are covered by 4-9 cm-thick organic layers.

In order to include the influence of soil water storage capacity (AWSC) on the water availability of trees in our investigation, pairs of study plots with different soil texture (sandy vs. loamy-sandy) were selected at almost each study site. The initial plot design was slightly modified: at the Oerrel site, no loamy plot was available; at the driest site in Calvörde, one loamy-sandy and two sandy plots were established. Hence, seven out of the 12 study stands grew on more coarse-grained meltwater sands and sandy moraine deposits with low silt and clay content (denoted by the plot-suffix '*S*'), five plots were chosen on loam-richer sandy deposits with higher contents of silt and clay (plot-suffix '*L*'; Figure 2.2). Thus, the plot design consisted of a matrix of 12 beech stands differing in the exposure to climatic and edaphic drought.
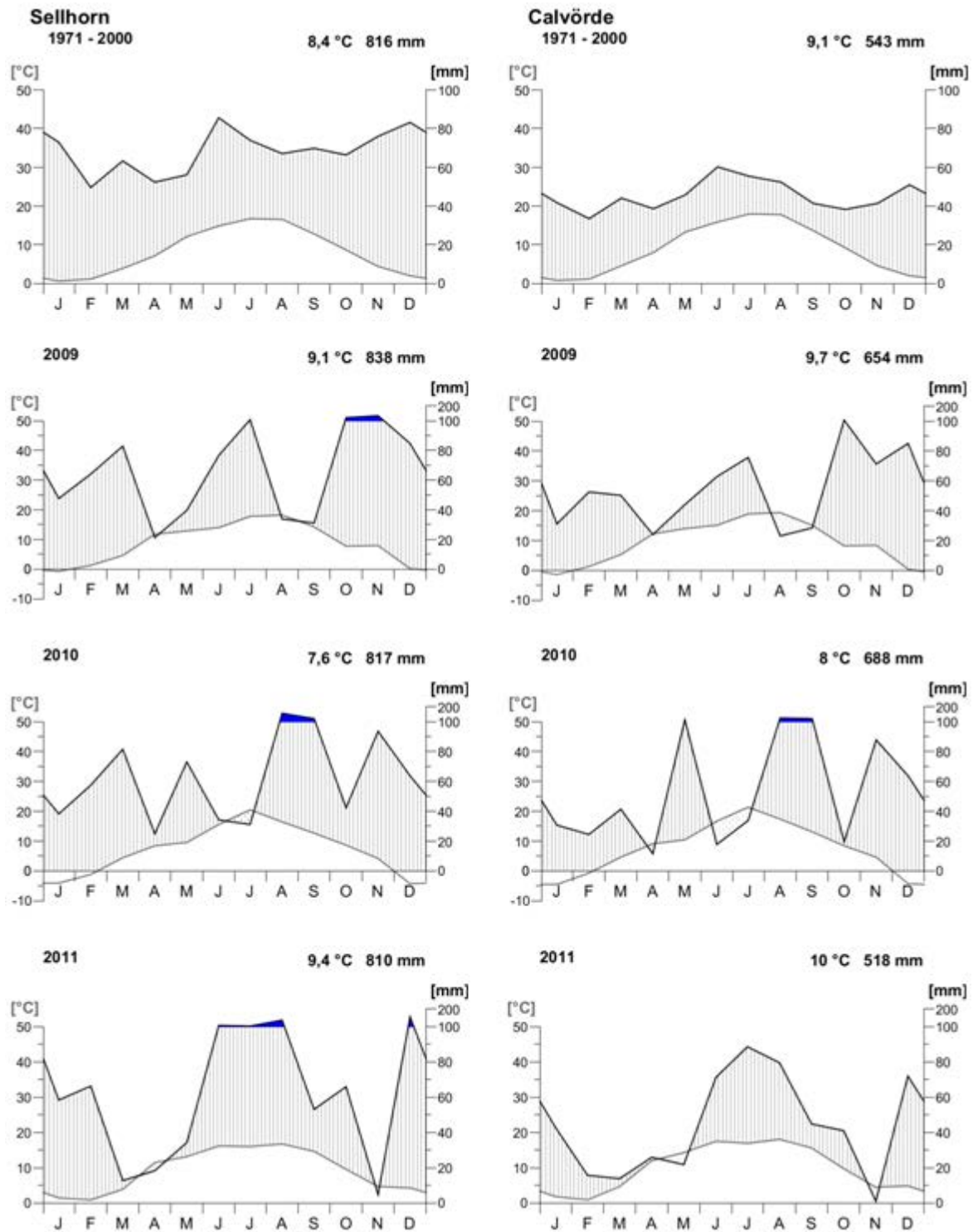
Figure 2.1. Climate diagrams for the two sites located at the moist (Sellhorn) and dry end (Calvörde) of the investigated precipitation gradient in Northern Germany. Values are shown for the long-term averages (1971-2000) and the three study years 2009 (late-summer drought), 2010 (early-summer drought), and 2011 (late-spring drought) in which aboveground net primary production was recorded. Data obtained from the 1km x 1km grid data set from Deutscher Wetterdienst.

The stands were selected for the structural criteria of (i) dominance of beech, (ii) mature age (85-140 years), and (iii) closed canopy (> 95 % canopy closure). All 12 plots were either monospecific beech stands (n = 6) or stands dominated by *F. sylvatica* with some admixture of Sessile oak (*Quercus petraea* Matt. Liebl; n = 5) or Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; n = 1). The cumulative basal area of the stands ranged from 25 to 45 m^2 ha^{-1} with no significant relationship to the shift of long-term climatic conditions. Beech held 81 to 100 % of the stand basal area and 95 to 100 % of the canopy projection area in all stands, except for the Oerrel plot (61 and 84 %, respectively). The mean height of beech trees varied from 24 to 34 m between the stands and tends to decline towards the drier sites. A second tree or shrub layer and a herbaceous layer was lacking in all study plots. With the exception of the study site in Oerrel which was established by planting, all stands originated from natural regeneration. Detailed physiographic and stand structural characteristics of the 12 forest stands are summarized in Table 3.1.

Soil hydrological and chemical analyses

For a high potential rooting depth on sandy soils, investigations of soil properties were executed to a soil depth of 120 cm. Analyses of soil chemical properties, particle size distribution and water retention properties were conducted for each single soil horizon separately. To determine particle size distribution, dried soil samples were pre-treated with 30% H_2O_2 and 4% Na-dithionite-citrate. Particle size classes were separated by sieving (particle size: 2000-20 µm) and sedimentation (particle size < 20 µm). Soil texture averages over the entire 120 cm soil depth were weighted by horizon thickness. The storage capacity for plant-available water (AWSC) of the soils was derived from laboratory desorption curves (3 pF-curves per horizon) at matrix potentials between -300 hPa and -1.5 MPa and subsequently summed up to a profile depth of 1.2 m. Volumetric soil water content (VWC) was continuously measured at 6-h intervals in every plot from July 2009 onwards (plot #12: since March) using time domain reflectrometry probes (TDR, CS616, Campbell Scientific Inc., Logan, UT, USA) installed at 20, 60 and 120 cm soil depth.

Mineral soil samples for chemical analysis were not only taken from the central soil pit but also from four marginal locations on the plot, in order to cover the spatial variability of soil properties. Soil material was sieved and exchangeable cations were extracted using 1 *M* NH$_4$Cl-solution. Cation concentrations were measured by Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES; Optima 5300 DV, PerkinElmer, Wellesley, USA). Effective cation exchange capacity (CEC) was calculated by summing up all exchangeable

cations. The sum of base cations (Na^+, K^+, Ca^{2+} and Mg^{2+}) in relation to CEC is expressed as base saturation (%). The depth and chemical properties of the organic layer (leptomoder or mormoder, see Green et al. 1993) were analyzed in 18 and 6 randomly collected samples per plot, respectively.

Granulometric analysis of the upper 120 cm of the mineral soils showed that sandy soils contained on average 29.1 % ($\pm$ 5.6 %) of fine grained particles < 200 µm, i.e., the fractions of fine sand, silt and clay (ΣfSUT). In contrast, the loam-richer soils showed significantly ($p <$ 0.01, Mann-Whitney U-test) higher fractions of soil particles from these small size classes (mean = 53.1 $\pm$ 3.2 %, Figure 2.2). This difference in soil texture between the two plots of a pair was very distinct on the drier sites of the transect (Go, Kl, Ca), while it was not that pronounced at the two moistest sites (Se, Un). The variability of water storage capacity is known to principally depend on particle size composition of the soils. Accordingly, figures of AWSC (cumulated for 120 cm soil depth) are closely correlated to the proportion of fine-grained soil particles (ΣfSUT) and ranged from 46 to 111 mm for the sandy soils (mean = 81.8 $\pm$ 8.9 mm), and from 78 to 140 mm on the loam-richer soils (mean = 105.4 $\pm$ 11.5 mm). However, an intermediate AWSC value of 107 mm $*120$ cm^{-1} which was derived from pF-curves in plot #7 (Go-S) appears unreliable as it contrasts strongly with the very coarse-grained soil texture over the entire investigated soil depth (Figure 2.2).
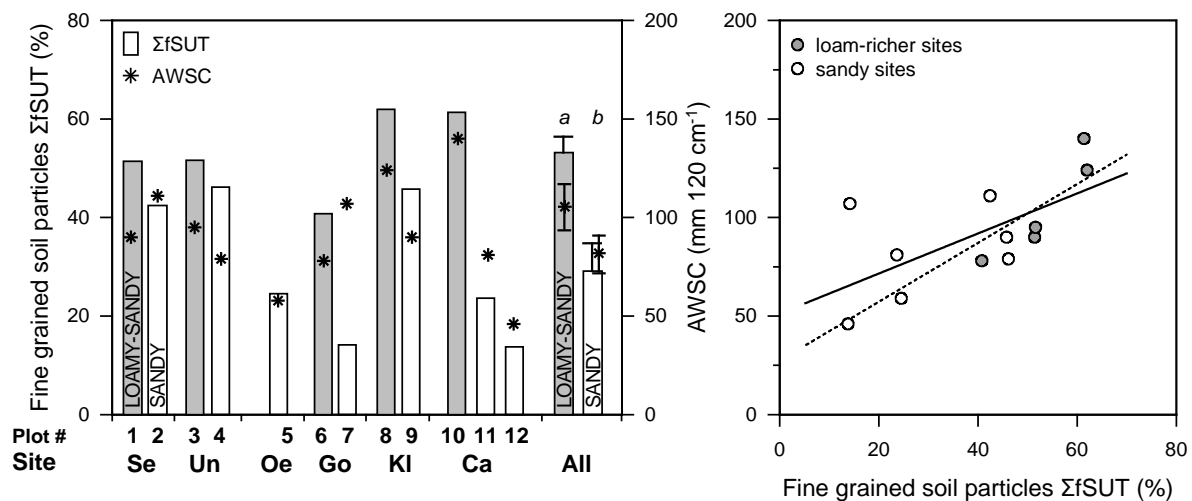

Figure 2.2. Soil physical properties of the 12 study plots. Left part: Fraction of fine grained soil particles (ΣfSUT; particle size < 200µm; indicated by bars) and available water storage capacity (AWSC; indicated by asteriscs) to a soil depth of 120 cm mineral soil. Filled bars = loam-richer soils (N = 5), open bars = sandy soils (N = 7). Small latin letters indicate significant difference in particle size distribution between the two substrate classes (Mann-Whitney U-test, $p <$ 0.01). Right part: Water storage capacity related to the fraction of fine grained soil particles for all study plots (solid line): R^2 = 0.43, p = 0.01; excluding plot #7 (dotted line, see text): R^2 = 0.73; $p <$ 0.001.

Average soil acidity of the 120-cm profiles of mineral soil ranged from pH (KCl) 3.6 to 4.4 (3.5 to 4.1, for the upper 30 cm of mineral soil) and showed a slight increase (i.e., pH-values decreased) towards drier sites ($R^2 = 0.25$, $p < 0.05$). This increase was paralleled by decreasing CEC ($R^2 = 0.25$, $p < 0.05$) and decreasing base saturation ($R^2 = 0.31$, $p < 0.05$) in the upper soil layers (30 cm) with declining MAP. Dry matter analyses of the organic layer showed significantly increasing concentrations of C_{total} ($R^2 = 0.25$, $p < 0.05$), N_{total} ($R^2 = 0.35$, $p < 0.05$) and P_{total} ($R^2 = 0.67$, $p < 0.001$) with increasing MAP, whereas the thickness of the organic layer as well as the C_{org}/N_{org} ratio were largely unaffected by the climatic shift along the climate transect.

Climate during the study period

Monthly data of precipitation, temperature (mean, min, max) and sunshine duration for all study plots were obtained from the 1km x1 km grid data set of the German Meteorological Service (Deutscher Wetterdienst, Offenbach, Germany). To increase data reliability, climatic data regionalized to the 12 study plots were calculated by averaging the data of the nine nearest grid fields for each location.

Annual precipitation (or precipitation totals for the vegetation period) during our four-year study period showed a continuous decrease from west to east in accordance with the long-term pattern of rainfall distribution (Figure 2.1). However, considerable inter-annual variation appeared regarding the seasonality of low water availability; low precipitation was recorded in late-summer 2009 (and 2012, not shown), in early summer 2010 and in spring 2011.This seasonal pattern of rainfall distribution is also reflected in the course of volumetric water content (VWC, Figure 2.3).

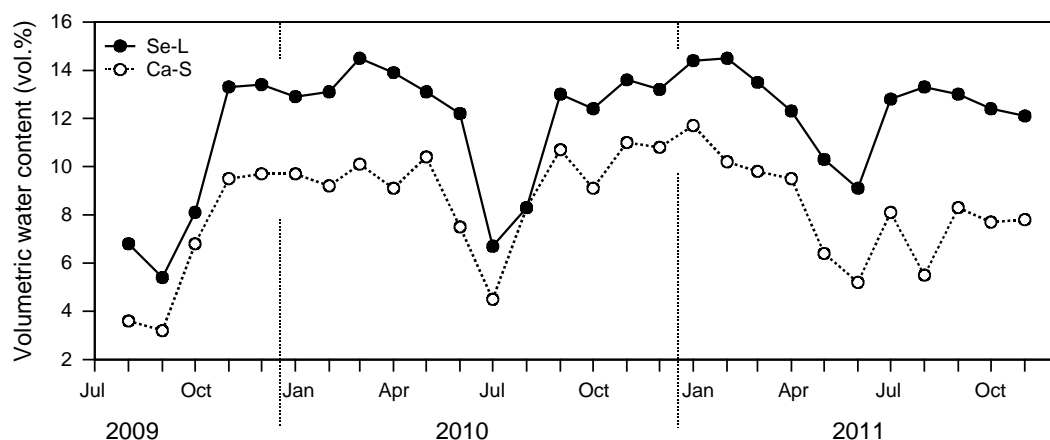**Figure 2.3.** Seasonal course of monthly mean volumetric soil water content (VWC) at 20 cm soil depth at the two sites located at the moist (Sellhorn; loam-richer site #1) and dry end (Calvörde; sandy site #11) of the investigated precipitation gradient. Values are shown for the three study years (2009-2011) in which aboveground net primary production was recorded. The continuous TDR measurements started in July 2009.

Determination of biomass production and allocation patterns

The biomass inventory and productivity measurements were conducted in plots of 30 m × 30 m size (0.09 ha) that were selected in stand sections with representative structure with respect to stem density, canopy closure and tree height. Eleven of the 12 study plots were fenced (40 m × 40 m) and equipped with measuring instruments in early 2009; plot #12 was established in winter 2009/2010. On these plots, all components of aboveground NPP (NPP$_a$; stem wood, leaf mass, flower and fruit production) and fine root production were measured in varying duration of investigations. Total aboveground net primary production (NPP$_a$) was calculated as the total of all components of aboveground biomass production, i.e. the production of wood (timber plus brushwood), bark, leaf mass and fruit mass. Annual above- and belowground biomass production (NPP) in 2010 was approximated by summing the totals of NPP$_a$ and fine root production.

Standing wood biomass and wood mass increment

In April 2009, the trees´ diameter at breast height (DBH) was measured at 1.3 m height with permanently installed dendrometer tapes (UMS, Munich, Germany). DBH increment of the years 2009-2011 was recorded at monthly intervals for all trees of a plot with a DBH > 15 cm and for half of the trees with a DBH of 7-15 cm until April 2012. The stem increment of the remaining trees was recorded at annual intervals. On the two plots with less than 24 beech trees with DBH > 15 cm within the 0.09 ha (plot #1 & 6), stem increment was recorded on an extended plot size of 40 m × 40 m (0.16 ha) in order to include a sufficient number of large beech trees. In winter 2009/2010, the height of all trees within the plots was determined using a terrestrial laser scanner (Imager 5006, Zoller and Fröhlich, Wangen, Germany).

The DBH and height of the trees were used to calculate (i) standing timber volume (wood components with diameters > 7 cm), (ii) wood biomass of timber and brushwood (wood components with diameters < 7 cm), and (iii) bark biomass, applying empirical allometric equations after Bergel (1973), Wutzler and others (2008) and Krauß and Heinsdorf (1996), respectively (details in Chapter 3). By relating the annual stem volume increment (SVI$_a$) of a tree to the initial stem volume at the beginning of each growth period, the relative annual stem volume increment (RSVI$_a$) was obtained. Annual wood mass production was calculated by adding up the annual augmentation of stem wood and brushwood. For calculating standing timber volume and wood dry mass on plot-level, the data of all trees in the plots were summed up and normalized to 1 ha or 1 m^2. In the six plots with presence of other tree species, biomass and production figures on plot-level were corrected by excluding the canopy projection area occupied by these species (0.8-16%; details in Chapter 3).

Leaf and fruit production, C and N allocation between leaves and fruits

The annual production of leaf and fruit biomass was recorded for the years 2009-2012 by litter trapping on each plot. Leaf area of 500 randomly chosen leaves per plot was determined with WinFolia software (Régent Instruments, Quebec, Canada). The following foliar traits were determined: plot means of specific leaf area (SLA), leaf size and individual leaf weight, leaf area index (LAI) and the number of leaves per ground area. The number of beech fruits (nuts) was counted. Samples of upper sun canopy leaves were collected in the late summer on all study plots in 2009 and 2010, and on one plot per study site along the transect in 2011, for the determination of foliar C and N contents with an elemental analyser. The C and N concentrations in fruit mass were analysed in the nuts collected in winter 2009 in the litter traps (details in Chapter 4).

Biomass, morphology and production of fine roots

Standing fine root biomass, fine root morphology and fine root production were investigated on all 12 plots in the organic layer and at two fixed depth levels (0-10 and 10-30 cm) of the mineral soil. Based on results from an earlier investigation on vertical distribution of fine roots in mature beech forests on sandy soils (Leuschner and others 2004), these three horizons are assumed to contain > 75 % of the total stand fine root biomass. Root inventories were carried out in June and September 2009 by soil coring (3.5 cm in diameter) at 20 randomly selected locations per study plot, and the amount of living (biomass) and dead roots (necromass) were determined separately. In order to improve estimations on the fraction of smaller root necromass particles (< 10 mm in length), every third root sample of the two campaigns was analysed in detail applying a method introduced by van Praag and others (1988) and modified by Hertel (1999). From all living rootlets of a soil sample, mean root diameter, specific root surface area (SRA, in $cm^2 \ g^{-1}$), specific root length (SRL, in $m \ g^{-1}$), and root tissue density (in $g \ cm^{-3}$) were determined using a scanner and a visual analysis system (WinRhizo, Régent Instruments Inc., Quebec, Canada). The fine root area index (RAI, m^2 cumulative root surface area per m^2 ground area) of each single horizon was calculated by multiplying the SRA by mean fine root biomass values. Stand total of RAI were generated by summing up the data of the three horizons per soil profile. Fine root tips of each one representative live fine root branch per soil sample were counted and related to the respective dry weight for the determination of specific root tip abundance ($n \ mg^{-1}$). The fine root production in the stands was determined by applying the ingrowth core technique. Each 12 ingrowth cores per study plot were installed at random locations in early summer 2009, and

were re-sampled after 22 months in March 2011. According to continuous examination of single cores, fine root re-colonisation started after a 12-month lag period subsequent to the installation, thus resulting in a 9-month period of root ingrowth. Annual fine root production (in g m^{-2} y^{-1}) was assessed by normalizing the observed fine root growth to 1 year and to 1 m^2 ground area (details in Chapter 3).

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Chapter 3

Climate responses of aboveground productivity and allocation in *Fagus sylvatica*: a transect study in mature forests

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Abstract

According to recent climate change scenarios, temperate forests will be increasingly exposed to droughts in the 21st century which are thought to affect productivity. While decreasing timber yield with reduced precipitation has frequently been reported from temperate forests, the dependence of forest net primary production (NPP) on precipitation is little understood. In a three-year transect study (2009-2011) carried out in 12 mature beech forests (*Fagus sylvatica*) along a precipitation gradient (820 to 540 mm yr^{-1}) in Northern Germany, we measured all aboveground NPP components (NPP$_a$; stem wood, leaf mass, flower and fruit production) and analyzed relationships with monthly weather data. Since we measured NPP$_a$ under a broad range of precipitation levels, drought lengths and mast fruiting intensities, the climatic controls of aboveground productivity and carbon allocation could be analysed in detail. Despite a significant decrease in annual (and growing season) precipitation sums along the transect, NPP$_a$ remained largely invariant in each of the years, but varied remarkably between the years (means of 981, 702, 955 g DM m^{-2} yr^{-1}, respectively). Variation in NPP$_a$ was most closely related to current year's early-summer weather conditions (June-July), while the patterns of biomass allocation to wood, leaf and fruit production responded to the previous summer's weather.

Wood production cannot predict NPP$_a$ in beech due to alternative allocation priorities of vegetative and reproductive growth. Our results show that apparent drought-induced reductions in beech timber yield often are the result of allocation shifts toward fruit production triggered by warm and dry weather in the previous summer.

Introduction

In most temperate regions, forest productivity is controlled by the availability of water and energy (radiation input, temperature and growing season length; Mitscherlich 1975; Becker and others 1995; Dreyer 1997; Bréda and others 2006). With global climatic change, water availability is expected to become increasingly important as a key controlling factor for tree growth especially considering that the frequency and severity of summer droughts are expected to increase (IPCC 2007 and references therein). Forests are more drought-vulnerable under a future warmer and drier climate than other vegetation types such as agricultural crops, simply due to the long lifespan of trees. Given that a typical rotation period in forestry ranges between 80 and 120 years, foresters are facing difficult decisions choosing suitable tree species for the restocking of managed stands at sites where drought intensity is predicted to increase. Whether the native tree species can withstand the expected increase in drought and heat stress intensity is not well studied and a matter of recent debate (Leuschner and others 2001; Rennenberg and others 2004; Ammer and others 2005; Bolte 2005; Geßler and others 2007; Leuschner 2009).

European beech (*Fagus sylvatica* L.) is by far the most abundant tree species found in Central Europe's natural forest vegetation and is also one of the most economically important trees (Ellenberg and Leuschner 2010). Simple extrapolation from the species' climate envelope into a warmer future climate indicates that *Fagus* may be more vulnerable than co-occurring *Quercus, Tilia, Carpinus, Fraxinus or Pinus* species, but less vulnerable than *Picea abies* (L.) Karst. or *Acer pseudoplatanus* L. (Kölling 2007; Roloff and Grundmann 2008; Köcher and others 2009). Dendrochronological evidence shows that beech diameter growth is closely tied to the precipitation and soil moisture regimes in most investigated forest regions of Central and Southern Europe (Biondi 1993; Piovesan and others 2003; Lebourgeois and others 2005). At the southern limit of the species' distribution range in Spain, drought stress has been identified as the main driver of beech dieback (Jump and others 2006). The exceptional drought in summer 2003 resulted in pre-senescent leaf shedding in August and a substantial reduction in canopy carbon gain in many beech stands across Central Europe (Gruber 2004; Ciais and others 2005; Leuzinger and others 2005; Bréda and others 2006). Thus, extended periods of summer drought and heat stress may represent a realistic threat to the vitality and productivity of *Fagus* in large parts of its Central European distribution range, but the thresholds of the species' response to a reduction in summer rainfall are little understood so far.

Water shortage may reduce net primary production through stomatal and/or biochemical limitation of photosynthesis and reductions in tree leaf area (Dreyer 1997), and it may lead to

shifts in within-plant carbon allocation patterns, notably increases in root:shoot ratio and reduced allocation to stem growth (Waring and Schlesinger 1985; Wilson 1988; Oliver and Larson 1996; Litton and others 2007). Not much is known about climate-induced allocation shifts in mature trees (e.g. Meier and Leuschner 2008b); however, this information is urgently needed for a mechanistic understanding of the adaptive response of forest trees to climate change-induced increases in drought intensity.

Studies along precipitation transects provide valuable insights into the drought response of mature trees under the condition that the forest stands are sufficiently comparable with respect to stand age, structure and soil conditions (Leuschner and others 2006; Meier and Leuschner 2008a,b; Scharnweber and others 2011). Unlike throughfall displacement experiments which focus on the mechanisms of the immediate tree drought response, transect studies in mature stands investigate the steady-state response to natural rainfall variation as they cover long-term acclimation and adaptation processes of the trees to reduced precipitation. A combination of both approaches might be the most promising strategy for achieving a better understanding of trees' response to a warmer and drier climate.

With a transect study in 12 mature beech stands along a precipitation gradient (543 - 817 mm yr^{-1}) in northwest Germany, we investigated the climate response of aboveground productivity (NPP$_a$) and carbon allocation patterns in *F. sylvatica* by measuring all components of aboveground productivity (stem wood growth, leaf mass production, flower and fruit production) over a three-year period with similar annual precipitation amounts but contrasting season rainfall distribution. The plot design consisted of six forest regions along the precipitation gradient where in each region a pair of plots was established of which one plot was set up on a sandy soil and the second plot on a sandy-loamy soil in close vicinity to another to cover the variation in soil water storage capacity. For this region, recent climate change scenarios predict a rise in mean annual temperature of c. 2.5°C until the end of the century, a decrease in summer precipitation by c. 10 percent and an increase in the frequency and duration of summer heat waves (Moseley and others 2012). If these scenarios become reality, the beech forests of Northern Germany, and those of many other Central European regions, would be exposed to longer and more severe droughts and a higher evaporative demand in summer.

Within this study we aim to (i) evaluate the dependence of total aboveground productivity (NPP$_a$) on precipitation in beech, (ii) identify differences in the growth response of single components of aboveground productivity (stem growth, leaf and fruit production) to climatic variations, and (iii) disentangle the influences of environmental factors on beech tree growth from those induced by carbon allocation to different aboveground sinks.

Materials und methods

Study sites, climate and soil

The study was conducted in 12 mature beech stands in the Pleistocene lowlands of north-western Germany in the years 2009 to 2011. The plot design consisted of six sites located along a precipitation gradient and each two neighbouring plots per site with different soil texture (sandy vs. loamy-sandy) to cover the edaphic variability in the Pleistocene landscape of the study region. The study sites are located in a 130 km-long NW-SE transect in the East of the state Lower Saxony and the western part of Saxony-Anhalt representing a climatic gradient from an oceanic to a sub-continental climate with a continuous precipitation decrease (817 to 543 mm yr^{-1}, see Figure 3.1) and a slight temperature increase (8.5 to 9.1 °C, Table 3.1) from west to east. The twelve stands were selected in six forest districts (from west to east: Sellhorn (2), Oerrel (1), Unterlüß (2), Göhrde (2), Klötze (2), Calvörde (3, number of plots per site in brackets) at elevations of 72 - 125 m a.s.l.. At the Oerrel site, only one plot (sandy) was available; three plots (two sandy, one sandy-loamy) were established in Calvörde. Eleven of the 12 study sites were fenced and equipped with measuring instruments in early 2009; plot #12 (Calvörde-III) was established in winter 2009/2010.
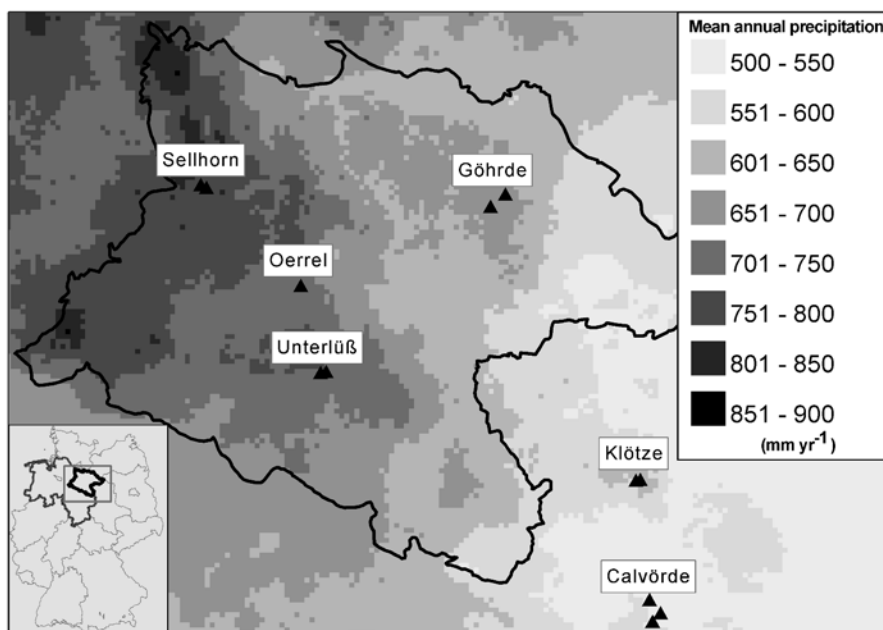
Figure 3.1. Map of the study area in the Pleistocene lowlands of northern Germany with the six study sites along the precipitation gradient from Northwest to Southeast (triangles: location of plots). The black line encircles the area of the Lüneburg Heath. Number of study plots per site=2 (except for Oerrel n=1 and Calvörde n=2 in 2009 and n=3 in 2010-2011). Precipitation data from Deutscher Wetterdienst Offenbach; layout by C. Döring.

All stands occurred on highly acidic and nutrient-poor sandy soils originating from fluvio-glacial sands or moraine deposits of the penultimate Saale Ice Age covered by periglacial drift sand (dystric or umbric Arenosols or Podzols). The mineral soils are covered by thick (4-9 cm) organic layers on the forest floor. Important physiographic and stand structural characteristics of the 12 stands are summarized in Table 3.1. All 12 plots were located in forests consisting either of monospecific beech stands (n = 6) or beech with some admixture of Sessile oak (*Quercus petraea* Matt. Liebl; n = 5) or Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; n = 1). The stands were mature with a mean tree height of 24 to 34 m of the beech trees. All stands originated from natural regeneration with the exception of study site #5 (Oerrel). In the six stands with contribution of oak and Douglas fir (1-8 trees per plot), these species held 3-19 % of the stand's cumulative basal area (an exception was stand #5 with 39 %). The structure of the stands varied within defined limits (closed canopy with 95-100 % canopy closure, trees of mature age: 85-140 years, cumulative basal area 25-45 m^2 ha^{-1}, a second tree or shrub layer and a herbaceous layer were absent in all stands). The biomass inventory and productivity measurements were conducted in plots of 30 m × 30 m size that were selected in stand sections with representative structure with respect to stem density and tree height.

Despite considerable structural variation among the stands, neither basal area nor timber volume were significantly related to mean annual precipitation (standing timber volume: R^2 = 0.08, p = 0.18; stand basal area: R^2 = 0.23, p = 0.06 [basal area tended to increase with decreasing precipitation]; mean basal area per tree: R^2 = 0.01, p = 0.44).

Climatic data and soil hydrological and chemical analyses

Climatic data (precipitation, temperature, sunshine duration) of the study sites were obtained from the 1km x1 km grid data set of the German Meteorological Service (Deutscher Wetterdienst, Offenbach, Germany). Sunshine duration data were converted to solar radiation with the Ångström equation according to Allen and others (1998). Climatic data regionalized to the 12 study plots were generated by averaging the data of the nine nearest grid fields for each location. Volumetric soil water content (VWC) was continuously measured in each study site since July 2009 using time domain reflectrometry probes (TDR, CS616, Campbell Scientific Inc., Logan, UT) installed at a soil depth of 20 cm.

For investigating the impact of weather on forest aboveground productivity, we used climate data from different time periods of the year with an assumed influence on certain development or growth processes of the trees: temperature and radiation means of the growth

period including the preceding late-spring period (April-October) of either the actual or the preceding year ($T_{4\text{-}10}$, $Rad_{4\text{-}10}$), (2) the growth-relevant amount of precipitation was assumed to be the precipitation in the period January-October, thus including the refilling of soil water storage in late winter and early spring ($P_{1\text{-}10}$). (3) Further, the temperature and precipitation in the peak stem growth period (June and July; $P_{6\text{-}7}$, $T_{6\text{-}7}$, $Rad_{6\text{-}7}$) was also considered.

A detailed examination of the mineral soil properties was executed to a depth of 1.2 m in the centre of each plot. For each single soil horizon, analyses of soil chemical properties, particle size distribution and water retention properties were conducted. For characterising soil texture, the percentage of particles < 200 µm diameter (fine sand, silt, clay; ΣfSUT) and of particles < 63µm (silt and clay; ΣUT) was measured. Water retention curves (pF-curves) were established in the laboratory by desorption of intact soil cores placed on suction plates. The capacity of the soil profile for plant-available water (AWSC) was calculated for the investigated soil horizons from the volumetric water content at matrix potentials of -300 hPa and -1.5 MPa and by summing up to a profile depth of 1.2 m. For covering the small-scale variability in soil properties, additional mineral soil material for chemical analysis was collected with a Pürckhauer soil corer at locations close to the four corners of the plot. The depth and chemical properties of the organic layer on the forest floor were analyzed in 18 and 6 randomly collected samples per plot, respectively.

Measurement of tree height, DBH and stem radial growth

The height of all trees within the 30 m x 30 m plots (0.09 ha) was determined in winter 2009/2010 with a precision of 10 cm using a terrestrial laser scanner (Imager 5006, Zoller and Fröhlich, Wangen, Germany). The diameter at breast height (DBH) was measured at 1.3 m height with permanently installed dendrometer tapes (type D1, UMS, Munich, Germany) with a precision of 0.1 mm. Stem wood increment was recorded every 4 weeks between April 2009 and April 2012 for all trees of a plot with a DBH > 15 cm and for at least half of the trees with 7 cm < DBH< 15 cm. On plots that contained less than 24 trees with DBH > 15 cm within the 0.09 ha (N = 2), stem diameter increment was measured on an extended plot of 0.16 ha size (40 m × 40 m) to include a sufficient number of beech trees with larger diameters.

Calculation of stem wood volume, standing wood biomass and wood increment

For calculating the volume of stems and branches ≥ 7 cm in diameter (standing volume of timber), we used the allometric equation:

$$V = \pi * (d/2)^2 * h * f \tag{1}$$

where V is the volume of timber (m^3), d the diameter at breast height (cm), h tree height (m) and f an empirically derived form factor for beech trees (Bergel 1973):

with

$$f = 0.4039 + 0.0017335 * h + (1.1267/h) - (118.188/d^3) + 4.2 * 10^{-6} * d^2 \tag{2}$$

The annual stem volume increment of a tree (SVI_a) was approximated as the increment in volume from April to November of the respective year (calculated from the repeated dendrometer tape readings). This procedure was justified because we observed no stem diameter change in the winter period from November to April. As tree height was measured only once in the study period, the wood volume increase was calculated from the diameter increase whereas height growth was ignored when using equation (1). Comparison with alternative approaches of stem volume increase calculation based on height increment modelling of mature beech trees (Nagel 1999) revealed that this neglect introduced an error of less than 1%. The relative annual stem volume increment of the trees ($RSVI_a$, in percent), was obtained by relating the SVI_a increase to the stem volume at the beginning of a growth period (V_{April}):

$$RSVI_a = ((V_{November}) - (V_{April})) / (V_{April}) * 100\% \tag{3}$$

The biomass of wood components with diameters >7 cm (stem wood or timber) and <7 cm (brushwood, i.e. small-diameter branches and twigs) was estimated from an empirical equation given by Wutzler and others (2008):

$$m_{t,b} = c_0 * d^{c1} * h^{c2} \tag{4}$$

which is based on the harvest of 170 (276) beech trees at 4 (6) sites in Central Europe (brushwood data in brackets) and gives stem wood or brushwood mass (m_t and m_b) in kg per tree. The coefficients have the following values: c_0 = 0.00775 (0.466), c_1 = 2.11 (1.85), c_2 = 1.21 (-0.349) (brushwood in brackets).

The annual production of bark was estimated after Krauß and Heinsdorf (1996):

$$\ln m_{bark} = -5.55435 + 1.1303 * \ln d - 1.4828 * \ln h \tag{5}$$

with m_{bark} given in kg per tree.

For calculating plot-level data of standing wood volume and wood dry mass, the data of all trees in the 0.09 ha-plots were summed up and normalized to 1 ha or 1 m^2. In the six plots with presence of oak or Douglas fir, we measured the canopy projection area (8-point canopy silhouettes) occupied by these species using a canopy projection mirror (self-constructed in the Department of Remote Sensing, University of Göttingen) and used the proportion of the

stand area filled by these species to correct the beech biomass and production figures by extrapolating to a hypothetical monospecific beech stand.

Measurement of leaf and fruit production

The annual production of leaf and fruit biomass was recorded with ten litter traps (aperture 0.28 m^2) located systematically on each plot. Beechnut consumption by deer or rodents was excluded by fencing the plots and placing the traps inaccessible for rodents. The collected litter material was separated into leaves, flowers and fruits and sorted by tree species, oven-dried at 70°C for 48 h, and weighed. In each plot, 500 randomly chosen beech leaves were collected from the litter traps, scanned and the leaf size determined with WinFolia software (Régent Instruments, Quebec, Canada) to calculate the stand leaf area index (LAI). On study plots with presence of other tree species, we calculated the leaf mass and leaf area index for the stands by including the admixed species. For quantifying the fruit production on the stand level, we applied the same correction as for wood biomass by extrapolating to a hypothetical monospecific beech stand. Aboveground net primary production (NPP$_a$) was calculated by summing up all components of aboveground production, i.e. the production of wood (timber plus brushwood), bark, leaf mass and fruit mass.

Statistical analysis

Relationships between climatic and soil parameters and aboveground productivity components for each single year (2009, 2010 or 2011) were analyzed by Pearson correlation analysis. Prior to analysis, we z-transformed all explanatory and response variables in the data set from the 12 sites and three years for achieving comparability among variables. In order to analyze the repeated observations, we then fitted a linear mixed model (LMM) using the environmental variables as fixed and 'study site' and 'year of observation' as crossed random factors. The *P*-values for the environmental variables were obtained from a likelihood ratio test (LRT) conducted against a model with just the random effects. To account for inter-correlation between explanatory variables, we performed (semi-)partial correlation analyses to achieve a stepwise elimination of co-varying factors.

All analyses were conducted using R statistical software (R Development Core Team 2011) with additional functions provided by the R packages *lme4* (Bates and Maechler 2010) and *ppcor* (Kim 2012). All data were tested for normal distribution (Shapiro-Wilk test). Significance was determined at P<0.05 throughout. Linear regressions were calculated with the program Xact 8.03 (SciLab, Hamburg, Germany) and regression lines are displayed at a significance level of P <0.05.

Table 3.1. Summary of climatic, edaphic, and stand structural properties of the 12 beech stands in north-western Germany. Mean annual precipitation (MAP) and temperature (MAT) refer to the period 1971-2000 (regionalised by C. Döring from the national weather stations network data base provided by DWD, Deutscher Wetterdienst). Mean tree height figures refer to all beech trees constituting the upper canopy layer. Mean diameter in breast height considers all beech trees > 7 cm stem diameter; stem density and cumulative basal area refer to all trees > 7 cm stem diameter in a plot and may include a few individuals of other species in certain plots (see Methods section). Soil chemical properties refer to the upper 30 cm of the mineral soil (N: total nitrogen; Al: NH_4Cl-exchangeable aluminium; P: total phosphorus; data provided by M. Jansen and C. Döring, unpublished). Fine-grained soil particles include fine sand, silt and clay (particles size < 200 µm) expressed in % of total soil mass (0 – 120 cm soil profile). The water storage capacity is calculated for the upper 120 cm of the mineral soil.

Plot no.	1	2	3	4	5	6	7	8	9	10	11	12
Site code	Se	Se	Un	Un	Oe	Go	Go	Kl	Kl	Ca	Ca	Ca
Coordinates	53°10' N	53°10' N	52°50' N	52°50' N	52°59' N	53°07' N	53°09' N	52°37' N	52°37' N	52°24' N	52°23' N	52°22' N
	09°57' E	09°57' E	10°19' E	10°19' E	10°14' E	10°49' E	10°52' E	11°14' E	11°15' E	11°16' E	11°17' E	11°16' E
Elevation (m a.s.l.)	127	130	120	117	90	85	85	102	85	72	75	105
MAP (mm) / MAT (°C)	816 / 8.4	816 / 8.4	766 / 8.4	766 / 8.4	741 / 8.6	675 / 8.6	665 / 8.7	615 / 8.7	614 / 8.7	543 / 9.0	544 / 9.1	559 / 9.0
Annual precipitation 2009 (mm) / temperature (°C)	838 / 9.1	838 / 9.1	815 / 9.2	815 / 9.2	758 / 9.3	702 / 9.3	686 / 9.4	737 / 9.4	726 / 9.5	654 / 9.7	649 / 9.7	658 / 9.6
Annual precipitation 2010 (mm) / temperature (°C)	817 / 7.6	817 / 7.6	833 / 7.6	833 / 7.6	766 / 7.7	744 / 7.7	726 / 7.8	746 / 7.8	744 / 7.8	672 / 8.0	684 / 8.1	708 / 8.0
Annual precipitation 2011 (mm) / temperature (°C)	810 / 9.4	810 / 9.4	710 / 9.6	710 / 9.6	710 / 9.6	677 / 9.6	666 / 9.7	573 / 9.7	573 / 9.8	509 / 10.0	515 / 10.1	530 / 10.0
Stand age (yr)	127	127	115	115	95	142	133	c.125	c.125	131	97	87
Mean tree height (m)	31.4	28.0	28.4	25.3	27.2	30.2	24.6	33.8	30.2	28.3	23.8	25.5
Stem density (no. ha^{-1})	156	367	411	611	500	122	289	267	478	300	711	578
Mean diameter in breast height (cm)	46.7	29.6	26.1	18.6	21.7	51.0	30.7	43.3	29.0	36.6	23.4	24.9
Stand basal area (m^2 ha^{-1})	31.0	30.7	28.5	24.3	32.3	26.6	24.4	44.9	40.8	33.3	33.2	32.6
Proportion of beech (% of basal area)	100	95	100	81	61	100	94	100	81	97	100	100
Timber volume (m^3 ha^{-1})	490	395	378	227	287	407	289	758	516	454	374	402
Thickness of organic layer (cm)	7.5	9.1	6.5	7.3	6.9	9.0	8.8	4.1	6.4	7.5	6.6	8.0
pH value (H_2O) of mineral soil	4.2	4.2	4.4	4.3	4.0	4.3	4.3	4.4	4.3	4.2	4.3	4.1
C/N ratio of mineral soil (g g^{-1})	15.6	24.2	25.8	24.1	17.8	22.9	25.5	11.9	15.7	15.9	13.2	19.0
N concentration of mineral soil (g kg^{-1})	0.28	0.46	0.40	0.47	0.78	0.41	0.51	0.46	0.49	0.34	0.42	0.33
P concentration of mineral soil (mg kg^{-1})	63	79	71	106	238	59	97	121	97	126	111	133
Al concentration of mineral soil (g kg^{-1})	0.53	0.52	0.58	0.31	0.42	0.46	0.79	0.48	0.54	0.38	0.57	0.38
Cation exchange capacity (µmol$_c$ g^{-1})	16.1	27.5	18.4	24.2	22.7	20.2	26.5	21.3	17.3	18.6	14.7	14.2
Base saturation of mineral soil (%)	24.3	9.7	14.8	8.3	13.0	6.7	2.8	14.4	9.7	7.4	5.0	6.9
Fraction of fine-grained (< 200 µm) soil particles (%)	51	42	52	46	25	41	14	62	46	61	24	14
Water storage capacity mineral soil (mm 120 cm^{-1})	90	111	95	79	59	78	107	124	90	140	81	46

Results

Weather conditions during the study period

The long-term annual precipitation means (1971-2000; January – December, P_{yr}) and the means of the growing season plus the early spring moisture recharge period (January – October, P_{1-10}) showed a continuous decrease from west to east along the studied transect (P_{yr}: 817 to 543 mm, Table 3.1; P_{1-10}: 657 to 451 mm, Figure 3.2a). In all three study years, the rainfall distribution patterns followed this long-term gradient with 2010 being wetter than 2009 and 2011 (P_{1-10}: 620 to 495, 660 to 526 and 652 to 443 mm in 2009, 2010 and 2011, respectively). The steeper precipitation decrease from west to east in 2011 (absolute P_{1-10} difference: 209 mm) was closer to the long-term rainfall distribution patterns than the gradients in 2009 and 2010 (P_{1-10} differences: 125 and 134 mm). Extended rainless periods occurred in August and September 2009 (late summer), in June and July 2010 (early summer) and from March to May 2011 (spring). Accordingly, the water content (VWC) of the mineral soil reached seasonal minima in these three dry periods at all study sites (Figure 3. 3a, b).
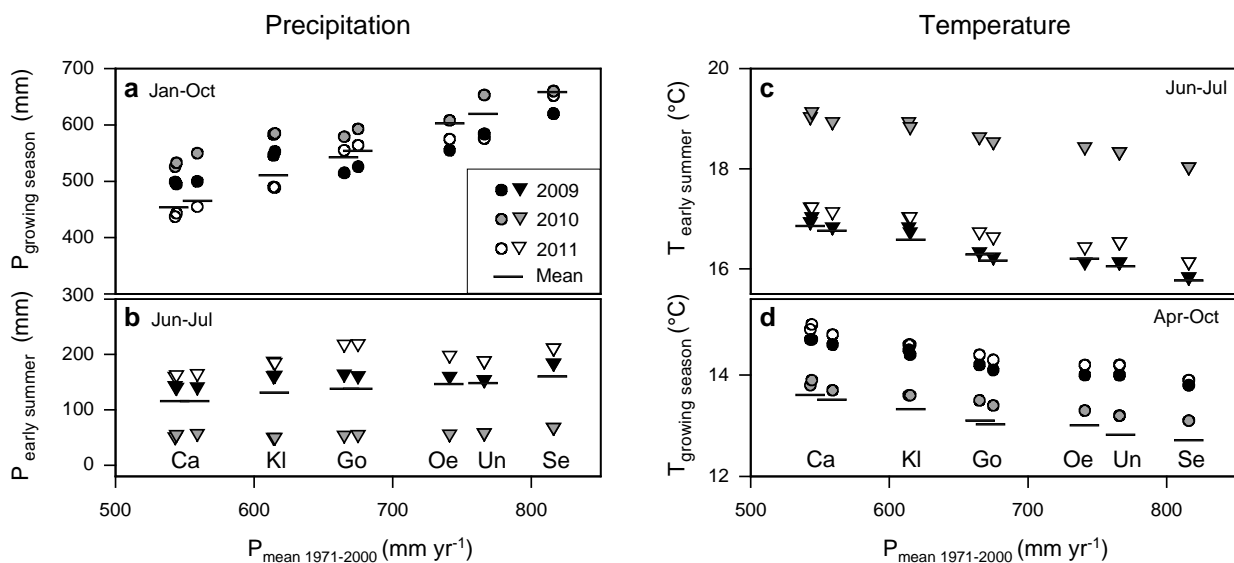

Figure 3.2. Precipitation and temperature in the period 2009-2011 at the six study sites along the transect. Precipitation data are totals for growing season plus the early spring moisture recharge period (January-October; a) and early summer (June-July; b). Temperature means refer to early summer (c) and growing season (April-October; d). Horizontal bars give the long-term precipitation and temperature means (1971-2000; data from Deutscher Wetterdienst Offenbach). The study sites are arranged from east to west according to their position along the precipitation gradient. Ca – Calvörde, Kl – Klötze, Go – Göhrde, Oe – Oerrel, Un – Unterlüß, Se – Sellhorn.

The mean air temperature in the growing season (April-October, T_{4-10}) increases in its long-term mean by 0.9 K along the transect from west to east and did so in all three study years (Figure 3.2d). All three growing seasons were warmer than the long-term average (plus

1.0-1.2 and 1.2-1.4 °C in 2009 and 2011, respectively, while 2010 was not that warm: +0.2-0.4 °C deviation).

When considering the weather conditions in the peak growth period in June and July, the summer 2010 was the driest and warmest of the three observation years despite the high precipitation amount (P_{1-10}) in this year (Figure 3.2b, c). The early-summer temperature (T_{6-7}) in 2010 exceeded the long-term mean by more than 2 °C at all six sites and the early-summer precipitation was less than the average. In contrast, the early-summer weather in 2009 and 2011 reflected the long-term mean with respect to precipitation, temperature and radiation at all sites.
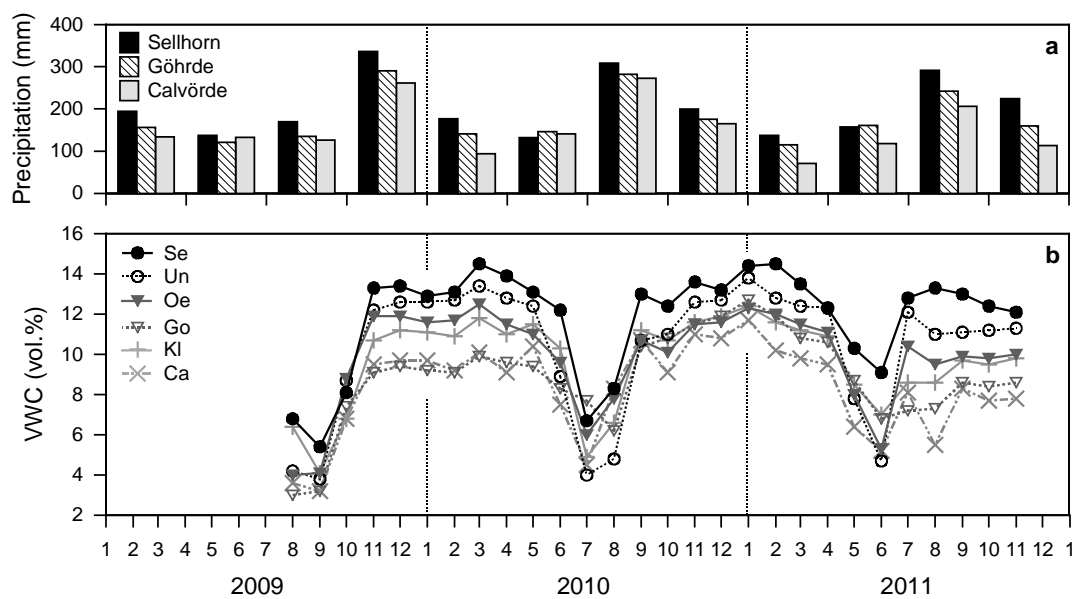

Figure 3.3. Three-monthly precipitation totals (a) and seasonal course of monthly mean volumetric soil water content at 20 cm soil depth (b) at three or six sites along the transect in the years 2009 to 2011 (moist sites: Sellhorn and Unterlüß, intermediate sites: Oerrel and Göhrde, dry sites: Klötze and Calvörde). *Se*: site no. 1 (Sellhorn); *Un*: site no. 3 (Unterlüß); *Oe*: site no. 5 (Oerrel); *Go*: site no. 6 (Göhrde); *Kl*: site no. 8 (Klötze); *Ca*: site no. 11 (Calvörde). The continuous TDR measurements started in July 2009. Precipitation data by Deutscher Wetterdienst, Offenbach, Germany.

Aboveground biomass production

With two mast years in the study period, aboveground biomass production (NPP$_a$, the sum of wood, leaf and fruit production) ranged among the 12 plots and three study years from 634 to 1305 g DM m^{-2} yr^{-1} with a considerable inter-annual variation (means of 982, 702 and 955 g m^{-2} yr^{-1} in 2009, 2010 and 2011, respectively; Table 3.2). While wood mass production (stem wood, brushwood <7 cm diameter, and bark) varied more than two fold between the years (means of 452, 359 and 212 g m^{-2} yr^{-1} across all plots in 2009, 2010 and 2011, respectively), the production of leaf biomass was less variable in this period (range: 231 to

364 g m^{-2} yr^{-1}) with annual means of 306, 326 and 264 g m^{-2} yr^{-1} in 2009, 2010 and 2011, respectively. In 2009 and 2011, we observed mast events in nearly all study plots with a higher fruit mass production measured in 2011 (367 to 603 g m^{-2}) than in 2009 (96 to 422 g m^{-2}). In 2009, we found a steep increase in fruit mass production from the moist to the dry end of the transect while such a gradient was absent in 2011 (Figure 3.4d). In both mast years, the Oerrel plot (#5) showed very low fruit mass production (24 and 136 g m^{-2}). In 2010, fruit production was low across the whole transect with values between 3.6 g m^{-2} (plot #4) and 42.9 g m^{-2} (plot #11).

Table 3.2. NPP$_a$ and production of wood, leaf and fruit mass in the 12 (11) beech stands along the transect in 2009, 2010 and 2011 (means and range; 2009: n=11). NPP$_a$ includes wood (timber and brushwood), bark, leaf, flower and fruit mass production. RSVI$_a$= relative stem volume increment per year. LAI = leaf area index.

Year	NPP$_a$ (g m^{-2} yr^{-1})	Wood mass production (g m^{-2} yr^{-1})	Leaf mass production (g m^{-2} yr^{-1})	Flower & fruit mass production (g m^{-2} yr^{-1})	LAI (m^2 m^{-2})	RSVI$_a$ (% yr^{-1})
2009	981.3 (831-1305)	452.3 (250-755)	305.5 (237-364)	223.5 (24-422)	7.8 (5.9-9.4)	1.7 (0.8-2.8)
2010	701.8 (634-846)	359.0 (293-491)	326.3 (294-363)	16.4 (4-43)	7.1 (6.3-7.7)	1.3 (0.7-1.8)
2011	954.8 (772-1158)	212.9 (129-361)	264.4 (231-306)	477.4 (137-603)	6.2 (5.6-7.2)	0.8 (0.3-1.7)
2009-11	876.4	338.2	298.6	239.6	7.0	1.2

Aboveground production and its dependence on precipitation

A surprising result is that none of the productivity components (production of wood, leaf, and flower and fruit mass) showed a consistent dependence on precipitation (P_{1-10}). All three components remained more or less invariant across the precipitation gradient in 2010 and 2011 and correlated significantly with precipitation only in one of the three years (2009) in the sample of 11 plots (Figure 3.4d – f). In 2009, wood production decreased considerably with a reduction in precipitation (means of 596 g m^{-2} on the study site Unterlüß (plots #3 and 4), and of 255 g m^{-2} on the Calvörde plots #10 and 11); leaf mass production decreased in parallel but with a less steep slope (means of 349 and 264 g m^{-2} on the same plots). In the same year, we recorded a more than four fold increase in the production of fruits and flowers with decreasing precipitation along the transect (from <100 to >400 g m^{-2} yr^{-1}; Figure 3.4d) almost compensating for the decrease in wood and leaf biomass production (all trends significant at P <0.01, Figure 3.4d). Remarkably, total aboveground productivity (NPP$_a$) showed a considerable inter-annual variation but did not respond to the precipitation gradient (P_{1-10}) in any of the three years (Figure 3.4a-c). Also in the analysis of the entire three-year data set, NPP$_a$ was not affected by P_{1-10} but instead increased significantly with rising early-

summer precipitation of the current year (P_{6-7}), while wood and leaf mass production increased with higher precipitation in the preceding year's summer ($P_{(Y-1),6-7}$; Table 3.3).
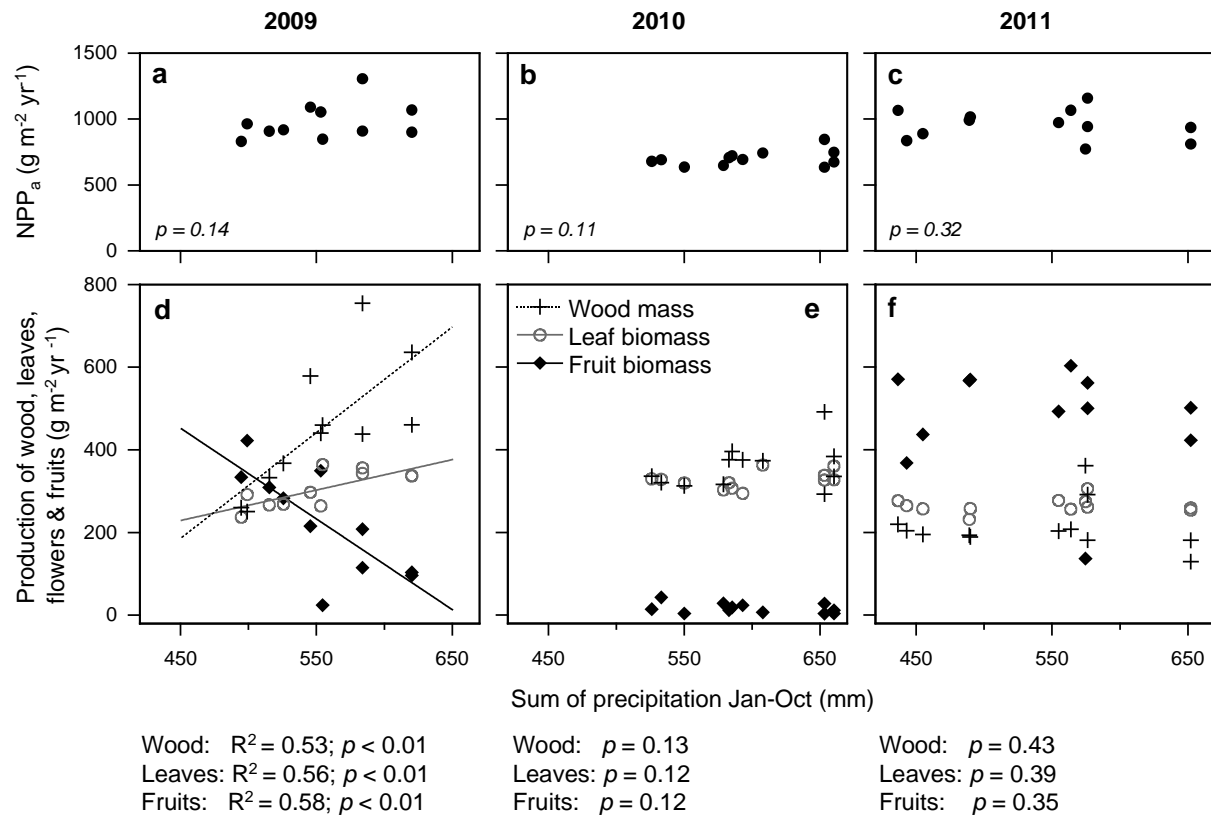

Figure 3.4. Aboveground biomass production in the years 2009 to 2011 in relation to growing season precipitation P_{1-10}. NPP$_a$ (A-C) and production of wood, leaf, and flower and fruit biomass (D-F). Wood production 2009: y = -965.7 + 2.56x, R^2 = 0.53, p < 0.01; leaf biomass production 2009: y = -102.1 + 0.74x, R^2 = 0.56, p < 0.01; flower and fruit production 2009: y = 1438.9 - 2.19x, R^2 = 0.58, p < 0.01. The production of wood mass includes brushwood (<7 cm). NPP$_a$ is the total of wood, leaf and fruit mass production.

Effects of temperature, radiation and soil factors on productivity

Apart from the effect of growing season precipitation, we tested another 20 climatic and edaphic factors for their influence on NPP$_a$ and wood, leaf and fruit mass production. Similar to precipitation, the average temperature and the cumulative solar radiation of the entire current growing season (T_{4-10}, Rad_{4-10}) seemed to have no (or little) impact NPP$_a$ or single components. Again, early-summer conditions (June and July) turned out to be important for aboveground biomass production, as NPP$_a$ was negatively related to temperature (T_{6-7}) and radiation (Rad_{6-7}, marginally significant) of that time span (Table 3.3). Across all three years, we also found negative effects of the preceding year's summer radiation on NPP$_a$.

In contrast to NPP$_a$, the allocation to single components (wood, leaf and fruit biomass) seemed to be subject to weather conditions of the preceding year (*Y-1*). Early-summer conditions of the year prior to each observation year (*Y-1,6-7*) seemed to control the growth of

single components of aboveground productivity. The growth of wood and leaf biomass showed a strong negative correlation with radiation ($Rad_{(Y-1),6-7}$) and – in case of leaf production also temperature ($T_{(Y-1),6-7}$) – of the preceding summer (Table 3.3). Fruit mass production significantly responded to the same conditions, but in opposite direction – negatively to precipitation and positively to temperature and radiation of the preceding early summer while current year conditions had no influence.

The effects of soil physical and chemical factors on NPP_a and wood, leaf and fruit mass production were remarkably small. Soil moisture (VWC) influenced none of the productivity components neither across the 2-year period 2010-2011 (measurements in 2009 incomplete; Table 3.3) nor in individual years (Table 3.A1). A higher storage capacity for plant-available water (AWSC) was positively related to fruit production but not to the other production components, while NPP_a increased with a higher content of fine grained soil particles. The only soil chemical factor with a significant effect on productivity was $pH(H_2O)$ which had a positive influence on NPP_a and also fruit mass production, while neither C/N ratio, base saturation nor exchangeable aluminium concentration in the soil had significant effects (except for a negative effect of soil N_{tot} content on fruit production and a positive one on wood production in 2011, Tables 3.3 and A 3.1).

Biotic controls of aboveground productivity

Stem density, mean DBH and the standing stock of wood biomass had no consistent influence on NPP_a or any of the three productivity components. Fruit mass production increased with stand age in 2011 and in the entire data set, and NPP_a increased with age in 2011 (Tables 3.A1, 3.3). Apart from the influence of environmental conditions, the productivity components were related to each other. With nearly equal annual leaf mass production, variation in NPP_a predominantly resulted from shifts in the production of wood and fruit biomass (Table 3.3). A significant positive correlation between LAI and NPP_a was visible only in 2010, when the radiation sums of the growth period were lowest (Table 3.A1). Wood mass production was positively related to current season leaf mass or LAI for the entire study period (Table 3.3) and for the single study years (to leaf mass in 2009 and 2011; to LAI in 2010 and 2011; Table 3.A1). Moreover, the production of both wood mass and leaf mass was highly negatively affected by the amount of simultaneously produced fruit mass (Table 3.3, Figure 3.5a, b): in the two mast years, wood production showed a significant negative response to fruit mass production (P< 0.05, Figure 3.5b) indicating a strong control of wood production by C allocation priorities.

Table 3.3. Results of regression analyses between NPP_a, the production of wood, leaf and fruit mass production and relative stem volume increment ($RSVI_a$) (dependent variables) and more than 30 climatic, edaphic, stand-structural and production-related parameters (entire data set for 2009-2011). Given are the standardized regression coefficient estimates and the significance level (asteriscs) from linear mixed models (crossed random factors 'site' and 'year') after z-transformation of the data. P = precipitation, T = temperature, Rad = solar radiation, VWC = volumetric water content at 20 cm mineral soil depth, AWSC = soil water storage capacity, $\sum$fSUT = percentage of soil particles < 200µm. The numbers give the time period considered (months), Y-1 = preceding year. Significance levels: *P<0.05; ** P <0.01; *** P <0.001. P values were derived from a likelihood ratio test (conducted against the random effects only; see Methods section). Significant correlations are in bold. [1] VWC values only for 2010 and 2011. [2] Soil physical properties refer to the upper 120 cm of the mineral soil. [3] Soil chemical properties refer to the upper 30 cm of the mineral soil.

	Dependent variables				
	NPP_a	Wood mass	Leaf mass	Fruit mass	$RSVI_a$
Climatic parameters					
P 1-10	- 0.02	0.21	0.27	- 0.14	0.07
P 6-7	**0.67***	0.18	- 0.02	0.01	- 0.04
P(Y-1) 1-10	0.21	**0.52****	**0.67*****	**- 0.32****	**0.67*****
P(Y-1) 6-7	0.16	**0.91*****	**1.14*****	**- 0.83*****	**0.92*****
T 4-10	0.09	- 0.39	**- 0.64****	**0.34***	- 0.54
T 6-7	**- 0.79****	- 0.48	- 0.76	0.46	- 0.79
T(Y-1) 4-10	- 0.24	- 0.33	**- 0.48***	0.22	- 0.56
T(Y-1) 6-7	0.14	- 0.53	**- 0.75*****	**0.68****	**- 0.80***
Rad 4-10	0.40	0.02	- 0.13	0.29	0.25
Rad 6-7	- 0.51	0.15	**0.59***	- 0.13	0.31
Rad(Y-1) 4-10	**- 0.90****	- 1.72	- 3.33	**- 0.76***	- 2.20
Rad(Y-1) 6-7	0.02	**- 1.43***	**- 0.74*****	**0.90*****	**- 2.19****
VWC 4-10 [1]	- 0.02	0.03	0.05	- 0.03	0.05
VWC 6-7 [1]	- 0.09	- 0.03	- 0.01	- 0.04	- 0.13
Production-related parameters					
Wood mass production	**0.42****	-	**0.53*****	**- 0.42*****	**0.79*****
Leaf mass production	0.27	**0.50****	-	**- 0.33****	**0.58*****
Fruit mass production	**0.47***	**- 0.86*****	**- 0.79*****	-	**- 0.85*****
Soil parameters					
AWSC [2]	0.25	0.01	- 0.08	**0.20***	- 0.30
$\sum$ fSUT [2]	**0.27***	0.1	0.03	0.14	- 0.20
C/N ratio [3]	0.18	0.18	0.21	- 0.02	**0.48****
N [3]	- 0.09	0.15	0.19	**- 0.19***	**0.39***
Base sat. [3]	0.06	0.19	0.21	- 0.11	- 0.04
CEC [3]	0.03	0.08	0.14	- 0.05	0.31
pH H_2O [3]	**0.35***	0.15	- 0.17	**0.20***	- 0.30
pH KCl [3]	0.13	0.02	0.04	0.07	0.21
Al [3]	0.09	0.04	- 0.15	0.07	- 0.04
P [3]	- 0.01	- 0.10	0.06	0.05	0.18
Stand structural parameters					
Stand age	0.19	- 0.04	- 0.17	**0.20***	- 0.22
Stem density	- 0.12	- 0.01	0.12	- 0.11	0.26
DBH	0.05	- 0.10	- 0.28	0.15	**- 0.46***
LAI	0.16	**0.44****	**0.82*****	**- 0.25***	**0.75*****
Standing wood biomass	0.14	0.01	- 0.28	0.15	**- 0.53****

Relative stem volume increment ($RSVI_a$) showed similar responses to environmental and biotic variables as wood mass increment. Leaf mass and stand leaf area (LAI) were significantly negatively related to fruit mass production (Table 3.3); leaf mass production was not only affected by fruit production in the two mast years but also in the non-mast year 2010 (Figures 4.3, 4.5a, Table 3.A1). The negative relationship between fruit mass and LAI was generally weaker and gained significance only in 2009 and the entire three-year data set.

Wood and leaf mass production appear to be affected differently by enhanced fruiting as is suggested when the productivity components are expressed as fractions of NPP_a (Figure 3.5c). While stand leaf mass fraction responded to a small increase in fruit production (0 - c. 20 % of NPP_a) with a steep decline from c. 50 % to about 30 % of NPP_a , the wood fraction was not visibly reduced by low fruit proportion rates. In contrast, a further increase in the fruit production fraction to 20-60 % of NPP_a occurred mainly at the expense of wood production, whereas the proportion of leaf mass production did not decrease further.
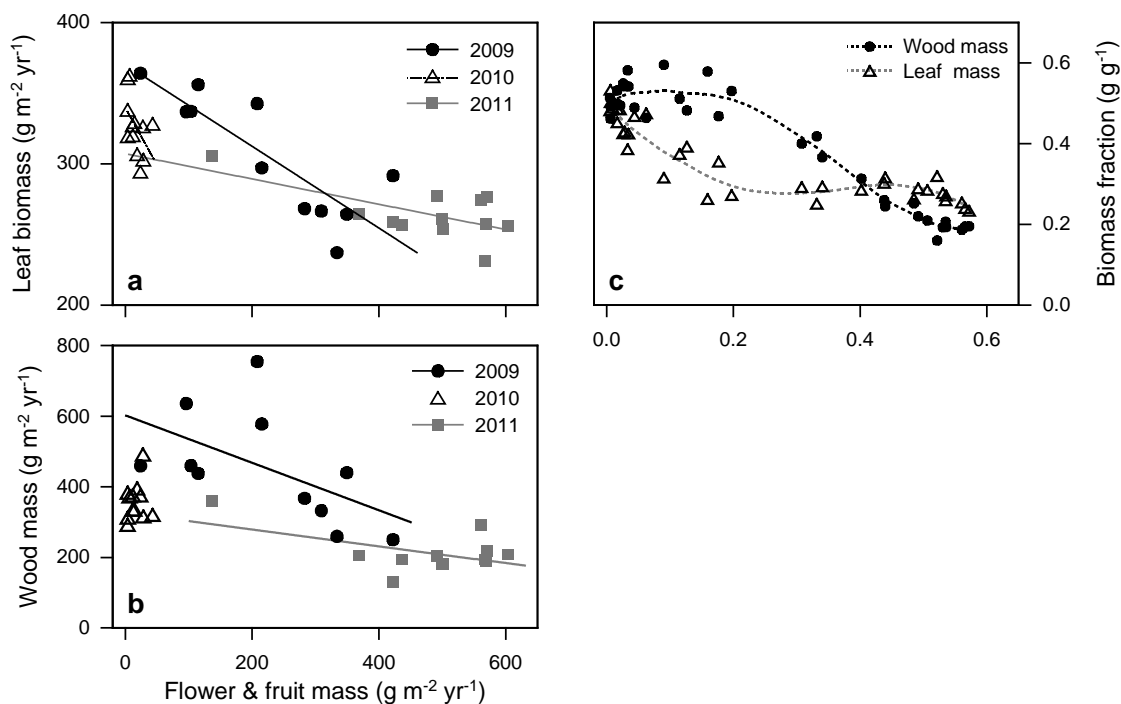

Figure 3.5. Relationship of (A) leaf biomass and (B) wood biomass production to fruit mass production in the 12 (2009: N=11) stands in the years 2009-2011. Leaf mass production as a function of fruit mass production in 2009: y = 370.2 - 0.29x, R^2= 0.71, *p*<0.001; for 2010: y = 339.6 - 0.81x, R^2=0.25, *p*=0.05; for 2011: y = 307.1 - 0.09x, R^2= 0.41, *p*<0.05. Wood mass production as a function of fruit mass production in 2009: y = 602.5 - 0.67x, R^2= 0.30, *p*<0.05; for 2011: y = 326.9 - 0.24x, R^2= 0.27, *p*<0.05. Wood mass production contains brush wood (<7 cm). (c) Leaf and wood mass production as fractions of NPP_a as dependent on fractional fruit mass production in the study period 2009-2011.

Since NPP_a and annual wood biomass production were influenced in mast years by the synchronous production of leaf mass and fruit mass, we conducted a partial correlation analysis for examining the influence of growing season precipitation (P_{1-10}) on productivity in more detail. We assumed that the alternative investment of carbohydrates in fruit, leaf or wood mass production could have masked a possible precipitation effect on NPP_a and wood mass production. By controlling for variation in fruit mass production or LAI, we found that growing season precipitation indeed did not affect NPP_a or wood production (Table 3.4). A significant correlation between P_{1-10} and wood production in 2009 disappeared when the influences of LAI and fruit mass production were removed. The negligible effect of growing season precipitation is also visible in another result of the partial correlation analysis: the effects of LAI (positive) and fruit mass production (negative) on wood production (and also $RVSI_a$, results not shown) were only marginally altered when we controlled for the influence of P_{1-10} in the analysis. However, the partial correlation analysis revealed the expected positive influence of LAI on NPP_a that was only weakly visible in the ordinary correlation analyses. Similarly, for 2010 and 2011, the positive influence of LAI on wood mass production was verified. This analysis also confirmed the negative relation between fruit and wood mass production in the two mast years when we removed the influences of LAI and precipitation. The positive effect of LAI and the negative influence of fruit mass production on wood production apparently were of similar size but opposing direction in the year 2011, while P_{1-10} remained insignificant as explanatory as well as co-varying variable.

The analysis of factors influencing total aboveground productivity (NPP_a) led to three surprising results: (i) the aboveground productivity of the 12 beech stands was not dependent on current year's precipitation (P_{1-10}) as is visible in Figure 3.4a-c. Instead, current early-summer precipitation (P_{6-7}) apparently is favouring productivity while high temperatures (and radiation) in these months are limiting aboveground growth. (ii) The influence of LAI on NPP_a was low with a significant positive effect only in the year (2010) with lowest radiation sums from April to October. (iii) Neither soil chemistry nor stand age or stem density impacted on NPP_a (except for a positive age effect in 2011).

Rather, aboveground productivity in a given year appeared to be largely dependent on carbon allocation patterns that may switch between a priority of wood mass or fruit mass production. This is indicated by high correlation coefficients between wood mass production and NPP_a in 2009 and 2010 ($R = 0.80$ and 0.95, $P < 0.01$ and 0.001), but between fruit mass production and NPP_a in 2011 ($R = 0.84$, $P < 0.001$; Table 3.A1). Allocation patterns explain a large part of the variation in the productivity components and seem to respond to the preceding year's early-summer weather conditions, where high temperatures and radiation are

promoting the production of fruit mass at the expense of leaf and especially wood biomass in the subsequent growing season.

Table 3.4. Pearson correlation coefficient (R) for relationships between aboveground biomass production and variables of environmental and phenological conditions: growing season precipitation (P_{1-10}), concurrently developed fruit mass (FM) and LAI. Partial correlation analyses were performed for the three growing season 2009, 2010 and 2011 while holding constant the influences of the remaining third (and fourth) variables. Significant correlations in bold. Significance levels: *P<0.05; **P<0.01; ***P<0.001. In case of P_{1-10} as explanatory variable, semi-partial correlation was applied.

Explanatory	Partial variable	NPP$_a$			Wood mass production		
		2009	2010	2011	2009	2010	2011
P_{1-10}	-	0.35	0.38	- 0.15	**0.73**	0.36	- 0.05
P_{1-10}	LAI	0.26	0.14	- 0.17	0.56	0.16	- 0.07
P_{1-10}	FM	0.38	0.46	- 0.09	0.37	0.43	- 0.13
P_{1-10}	LAI+FM	0.4	0.31	- 0.14	0.37	0.28	- 0.17
Fruit mass	-	0.04	0.2	**0.84***	**- 0.55***	0.17	**- 0.52***
Fruit mass	LAI	0.22	0.51	**0.92***	- 0.37	0.41	**- 0.60***
Fruit mass	P_{1-10}	0.5	0.39	**0.83***	0.01	0.35	- 0.53
Fruit mass	LAI+ P_{1-10}	0.59	**0.58***	**0.92***	**- 0.61***	0.48	**- 0.62***
LAI	-	0.18	**0.60***	0.41	0.46	**0.51***	**0.52***
LAI	FM	0.28	**0.71**	**0.75***	0.13	**0.60***	**0.61***
LAI	P_{1-10}	0.01	0.52	0.41	0.15	0.42	**0.52***
LAI	FM+ P_{1-10}	0.36	**0.65***	**0.75**	0.18	**0.53***	**0.62***

Discussion

The rainfall-productivity relationship in Fagus sylvatica

Against the backdrop of climate change, many studies on the drought stress tolerance of temperate forest trees have been published in recent years. Particular attention has been paid to the impacts caused by the exceptionally severe summer drought of 2003 in Europe, as it may represent an increasingly probable future climate event. However, the main sources of information on climate-growth relationships have been analyses of either tree ring increment (Dittmar and others 2003; Di Filippo and others 2007) or whole-ecosystem carbon balance based on CO_2 flux measurements (Ciais and others 2005; Granier and others 2007). To our knowledge, the current study is the first attempt to analyse the drought response of aboveground productivity and carbon allocation of a target tree in (almost) monospecific mature forest stands across a precipitation gradient on similar geological substrates. Meier and Leuschner (2008a,b) studied the leaf area and root mass of *Fagus sylvatica* stands along a precipitation gradient on moderately fertile sandstone in Central Germany, but they did not address net primary production. Other precipitation gradient studies in temperate forests included a tree species turnover (for example, in the Pacific Northwest region of the USA; Gholz 1982), which makes it difficult to draw conclusions on species responses to a precipitation decrease. Detailed analyses of aboveground net primary production (NPP_a) in Central European monospecific beech forests at maturity gave productivity figures in the range of $890 - 1240$ g DM m^{-2} yr^{-1} (mean: 1050 g m^{-2} yr^{-1} with one outlier at 1730 g m^{-2} yr^{-1}; Ellenberg and Leuschner 2010), but the existing data are too limited to examine precipitation effects on NPP_a. The NPP_a figures from the 12 stands of our study agree well with these reference data (640 to 1310 g m^{-2} yr^{-1}, mean: 880 g m^{-2} yr^{-1}).

An unexpected result of our study in the 12 beech stands is that NPP_a did not significantly decrease along the precipitation gradient, despite ~30 % (270 mm yr^{-1}) less mean annual precipitation at the dry end of the transect and the driest site (Calvörde) being located close to the natural drought-induced range limit of *Fagus sylvatica* in Central Germany (Kölling 2007; Leuschner 2009). In 2009, NPP_a differed by not more than 10 % between the moist (838 mm yr^{-1}) and dry ends (649 mm yr^{-1}) of the transect. In 2010 and 2011, NPP_a showed no declining tendency in response to decreasing precipitation (P_{1-10} and P_{yr}), which is in sharp contrast to the steep precipitation gradient in 2011 (810 to 510 mm yr^{-1}). The insignificant rainfall effect on NPP_a also persisted when aboveground productivity was related to precipitation figures of the preceding year (or of the 30-year mean) instead of the recent year's precipitation.

However, for the entire three-year study period, we found a positive influence of current-year early-summer precipitation (P_{6-7}) on NPP$_a$ (Table 3.3) which is in line with findings of many other authors (Piovesan and others 2003; Lebourgeois and others 2005; García-Suárez and others 2009; Friedrichs and others 2009; Weber and others 2013), who all regard precipitation or soil moisture availability during early summer as the key climatic factor controlling beech growth. From stand-level eddy covariance measurements, Granier et al. (2007) concluded that Central and Western European beech forests reduce their canopy gross photosynthetic rate, when the extractable water in the soil profile is exhausted by more than 60 %, irrespective of seasonal dynamics.

Apart from a likely growth-limiting effect of low soil water contents during the peak growth period (June-July), the low NPP$_a$ values measured in 2010 (mean of 702 g m^{-2} yr^{-1} across al stands, compared to 981 and 955 g m^{-2} yr^{-1} in 2009 and 2011, respectively) could have been caused either by the recovery of the trees´ carbon reserves from the exhaustive mast year 2009, or by reduced carbon assimilation due to lower incident radiation in 2010. Reduced stem growth after masting events appears conceivable, as the refilling of carbohydrate reserves represents a C sink that strongly competes for assimilates (Lacointe 2000; Vanninen and Mäkelä 2000; Barbaroux and Bréda 2002; Silpi and others 2007) and photosynthate allocation to storage pools is considered as the main reason for observed mismatches between meteorologically quantified C assimilation und biometrically measured growth (Hoch and others 2003; Gough and others 2009; Mund and others 2010). However, in an investigation on masting and diameter growth in Southern Sweden over five decades, Drobyshev and others (2010) found negative effects of masting on stem growth to be restricted to the respective current mast year. Correspondingly, in our study, such a 'carryover effect' from 2009 is an unlikely cause of the relatively low 2010 NPP$_a$ figure, as the productivity patterns across the transect did not mirror the very pronounced fructification increase toward the drier sites observed in the preceding year 2009. Since the radiation total from April to October was lower in 2010 and bud break occurred approx. 2-3 weeks later than in 2009 and 2011 at all sites, one would assume a relatively low canopy carbon gain in the season of 2010. However, our analysis did not show a positive relation between current season radiation totals (Rad_{4-10} and Rad_{6-7}) and NPP$_a$ in this year. We assume that the most likely explanation of the 2010 depressions in NPP$_a$ and wood production throughout the transect was the coincidence of reduced canopy C gain and enhanced belowground sink strength due to the drought in June-July 2010. This explanation would match with the results of Hertel and others (2013) that show significant increases in fine root biomass and fine root

productivity in response to decreasing precipitation in the same beech stands we examined in this study (see below). Finally, in accordance with results obtained by Bourioaud and others (2005), one may argue that our calculations might have underestimated wood mass production (and thus NPP_a) especially in 2010, since the stem increment at breast-height may be more sensitive to drought events in June and July than it is at higher stem positions.

In accordance with studies on climatic drivers of radial growth in beech trees at low altitude sites, we also find a negative effect of current early-summer temperature (T_{6-7}) on NPP_a, which likely is a consequence of the negative relation between precipitation and temperature (Dittmar and Elling 1999; Dittmar and others 2003; Mölder and others 2011; Scharnweber and others 2011). Our results suggest that P_{6-7} is the main climatic driver of current-year NPP_a in these beech forests. We explain the insignificance of the precipitation effect on NPP_a in the 12 stands in all three study years primarily with the small variation in P_{6-7} along the transect in these years (compare Figure 3.2c).

Climate effects on carbon allocation

Similar to NPP_a, the components of aboveground productivity (woody tissues, leaves, flowers and fruits) did not show consistent relationships with either the current season´s or the current year early-summer´s precipitation. Only in 2009, we observed a significant decline in wood production and leaf biomass along the rainfall gradient with productivity decreases by c. 50 and 20 %, respectively, from the wet end to the dry end of the transect. As this decrease coincided with an almost equivalent increase in fruit production, the likely explanation is a shift in carbon allocation along the precipitation gradient. In the two succeeding years, however, stem wood and leaf production did not respond to the current season´s climate conditions. When the entire study period is analyzed, the early-summer conditions of the year prior to the observation year appeared as the main factors controlling the productivity of the three aboveground biomass components (see Table 3.3).

In contrast to aboveground productivity, the production of beech fine root biomass seems to be more closely related to the regional precipitation regimes. In a study on fine root dynamics in the 12 beech stands, Hertel and others (2013) detected increases in fine root biomass (in 2009) and in fine root productivity (in 2010) with decreasing annual precipitation along the transect. Fine root production ranged between 139 and 479 (mean: 263) g DM m^{-2} yr^{-1} in 2010, which is comparable to a mean tree fine root production rate of 306 g m^{-2} yr^{-1} reported by Finér and others (2011) in a literature analysis for boreal and temperate forests.

According to these figures, the belowground productivity fraction rises from 21 % of NPP_{total} in the five moister stands (P>700 mm yr^{-1}) to 31 % in the seven drier stands (P <700 mm yr^{-1}) pointing to an allocation shift from aboveground to belowground carbon investment in response to reduced water availability in beech trees.

Facing the finite availabilities of nutrients, water and energy, the investment of resources into one process will result in a decrease of resources allocated to another process, linking different life-history traits through constraining relationships (Obeso 2002). Dry matter analyses during mast years showed that developing beech nuts may incorporate large amounts of nutrients and photoassimilates (Burschel 1966; Paar 2004; Schmidt 2006; Jochheim 2007), which according to the 'costs of reproduction hypothesis' will limit vegetative growth, i.e., the production of leaf and wood biomass (Reekie and Bazzaz 1987a,b). In accordance with observations on the crown condition during mast years (Innes 1994; Eichhorn and Paar 2000; Schmidt 2006; Seidling 2007), we found a strong negative relationship between the amounts of stand leaf biomass and annual fruit mass produced in the two mast years; this relation existed even in the non-mast year 2010. Further, in both mast years, wood mass production (and relative volume increment) declined in response to increasing fruit production supporting earlier studies that demonstrated a measurable negative effect of masting on wood production and shoot elongation in beech (Holmsgaard 1955; Dittmar and others 2003; Drobyshev and others 2010; Han and others 2011).

Without doubt, the decrease in vegetative growth associated with rising reproductive effort can partly be explained by a high sink strength of developing fruits for recently assimilated carbon, which has previously been found in beech and in a number of other tree species (Kozlowski and Pallardy 1997; Hoch and Keel 2006). Beyond these single components´ growth limitations due to alteration of sink priorities, the direct costs of reproduction may further be amplified by consequences arising from extensive fruiting, often referred to as indirect costs of reproduction (Bazzaz and others 1987). Such indirect costs are generated in masting trees because the inflorescences of beech displace leaf-bearing shoots, thereby reducing the number of leaf buds (Innes 1994; Gruber 1998; Seidling 2007). In addition to a resource allocation shift from wood to fruit production, wood increment may also be affected by reduced canopy C gain due to a smaller leaf area in mast years (Bartelink 1997).

In order to separate such direct and indirect effects on wood production and NPP_a resulting either from fructification or reduced precipitation, we conducted a partial correlation analysis which revealed that fruit production and a reduction in LAI both had negative effects

of roughly similar size on wood production. Despite this growth-depressing effect, NPP_a increased with fruit production in each single year (significant in 2010 and 2011), and the NPP_a figures of the two mast years were higher than that of the non-mast year 2010. Contrasting growth responses of woody tissues and foliage to masting events may reflect the particular constraining relationships in the context of seasonal growth dynamics of diffuse-porous trees. Beech trees which allocated up to c. 20% of NPP_a to fruit production showed a marked response by proportionally reducing leaf production, which is an expression of strong competition for carbohydrate reserves between flowers and leaves in spring (Kozlowski 1992; Dyckmann and others 2000; Hoch 2005). This corresponds with the observation of Barbaroux and Bréda (2002) and Barbaroux and others (2003) that the formation of beech early-wood is largely dependent on the current season's carbon assimilation rate. Only when fruit production exceeded 20% of NPP_a, we found a substantial decline of the fraction of wood production in beech. In contrast, the leaf fraction was barely affected by a further rise in the proportion of fruit biomass production beyond 20% of NPP_a (on sink strength alternations of single tissues see Cannell and Dewar 1994).

It is known since long that specific climatic conditions are triggering the masting of beech. High fruit production occurs mainly in years following warm and dry summers as it was found by e.g. Matthews (1955); Piovesan and Adams (2001); Övergaard and others (2007) and also in our study. We found the amount of fruit production to be tightly correlated with the radiation and temperature (positively) and the precipitation amount (negatively) of the previous year´s June and July, while wood and leaf production showed a significant response in opposite direction. This finding matches with recent reports about a negative relationship between stem increment and the preceding summer's temperature and are in line with an increasing sensitivity of radial growth in *F. sylvatica* to drought events of the previous growing season (Lebourgeois and others 2005; Eichhorn and others 2008; Friedrichs and others 2009; Weber and others 2013). In agreement with Di Filippo and others (2007) and Drobyshev (2010) we suggest that such growth reductions are not primarily a response to stressful weather conditions that impair carbon assimilation or growth processes directly, but rather are caused by allocational shifts resulting from climate-triggered fructification events. Our results confirm the view that increases in the frequency and intensity of masting events in beech, as they were observed in the past decades (Hilton and Packham 1997; Paar and others 2000; Övergaard 2007), are resulting in significant reductions of stem wood production in this species (Dittmar and others 2003; Drobyshev and others 2010).

Conclusions

From the results of this transect study, we draw the following conclusions: First, annual or growing season precipitation totals, which often are used for characterizing the local growing conditions of forest stands, apparently are only subordinate determinants of aboveground productivity in the beech forests of North-west Germany. Instead, at these lowland sites, NPP_a and stem wood production were found to be primarily controlled by the precipitation and soil moisture content in the peak growing period (June and July). Second, in the absence of a correlation between total and wood production across our 3-yr study period, wood production (or radial increment) cannot be regarded as a reliable predictor of NPP_a in beech. Reasons are the varying proportion of wood production to total aboveground productivity and the obvious competition between wood and fruit mass production for carbohydrates resources. Third, the reduction in stem wood production in mast years is to a large extent attributable to shifts in aboveground carbon allocation which can explain most of the observed temporal and spatial variation in the productivity of the three aboveground biomass components; these shifts are triggered by the weather conditions in June and July of the preceding year. High temperatures and radiation sums induce the formation of flower buds with the consequence that substantial resources are shifted to reproduction in the subsequent year at the expense of leaf and especially wood mass production. This allocation shift can explain the frequently observed sensitivity of beech growth to a preceding warm or dry summer (as, for example, subsequent to the exceptional heat in summer 2003).

In the context of climate change and the assumed future reduction in summer rainfall in parts of Central Europe, we predict that the likely increase in the frequency of summer heat waves will play a critical role (Schär et al. 2004) because it should trigger masting events in beech. Our results suggest that the resulting shift in carbon allocation towards regeneration (and probably also to root production) will impair timber yield more than any direct negative effect of drought or heat on carbon gain and/or hydraulic functioning, as long as species-specific tolerance thresholds are not crossed. Future research on safety margins in the hydraulic system and about the response of carbon assimilation and plant respiration to drought periods in adult stands are needed to better understand the sub-letal response to reduced precipitation. Finally, a decisive role will be played by the frequency of extremely dry summers (as those in 1976 and 2003) which have been found to significantly increase the mortality of adult beech trees in many Central and Western Europe forests (Bréda and others 2006). These extreme events may destabilize beech forests if soil moisture levels fall below critical thresholds for extended periods in early summer.

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Appendix

Table A. 3.1. Pearson correlation coefficients (*R*) for relationships between aboveground production parameters and variables of climatic, edaphic, stand structural and production-related parameters in the 12 beech stands in the years 2009, 2010 and 2011. Given are the standardised regression coefficient estimates and the significance level (asterisks) from linear mixed models (crossed random factors 'site' and 'year') after z-transformation of the data. P = precipitation, T = temperature, Rad = solar radiation, VWC = volumetric water content at 20 cm mineral soil depth, AWSC = soil water storage capacity, ∑fSUT = percentage of soil particles < 200µm. The numbers give the time period considered (months), Y-1 = preceding year. Significance levels: *$P<0.05$; ** $P<0.01$; *** $P<0.001$. P values were derived from a likelihood ratio test. Significant correlations are in bold.

	Dependent variables											
	NPP$_a$			Wood mass production			Leaf mass production			Fruit mass production		
	2009	**2010**	**2011**	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**	**2009**	**2010**	**2011**
Climatic parameters												
P 1-10	0.35	0.38	- 0.15	**0.73****	0.36	- 0.05	**0.75****	0.37	0.09	**- 0.77****	- 0.37	- 0.12
P 6-7	0.10	0.10	- 0.02	0.45	- 0.01	- 0.08	0.38	0.48	- 0.05	**- 0.57***	- 0.32	0.03
P(Y-1) 1-10	0.22	0.39	- 0.01	**0.65***	0.35	- 0.04	**0.78****	0.46	0.11	**- 0.81****	- 0.43	- 0.01
P(Y-1) 6-7	0.14	0.18	- 0.38	**0.58***	0.19	- 0.26	**0.75****	0.19	0.04	**- 0.82*****	- 0.31	- 0.45
T 4-10	- 0.17	- 0.33	0.07	**- 0.59***	- 0.31	0.01	**- 0.76****	- 0.37	- 0.09	**0.80****	0.39	0.07
T 6-7	- 0.11	- 0.28	0.17	**- 0.54***	- 0.24	- 0.02	**- 0.73****	- 0.37	- 0.12	**0.79****	0.35	0.18
T(Y-1) 4-10	- 0.18	- 0.32	0.05	**- 0.61***	- 0.29	- 0.01	**- 0.78****	- 0.35	- 0.12	**0.82*****	0.35	0.07
T(Y-1) 6-7	- 0.12	- 0.29	0.11	**- 0.55***	- 0.26	0.04	**- 0.75****	- 0.36	- 0.13	**0.80****	0.32	0.10
Rad 4-10	- 0.20	- 0.39	0.13	**- 0.60***	- 0.44	- 0.15	**- 0.88*****	- 0.17	- 0.21	**0.82*****	0.3	0.22
Rad 6-7	- 0.14	- 0.33	0.15	**- 0.59***	- 0.34	- 0.18	**- 0.89*****	- 0.31	- 0.23	**0.88*****	0.42	0.25
Rad(Y-1) 4-10	- 0.32	- 0.43	- 0.24	**- 0.70****	- 0.28	- 0.14	**- 0.94*****	**- 0.80*****	0.18	**0.82*****	0.47	- 0.17
Rad(Y-1) 6-7	- 0.15	- 0.42	0.02	**- 0.61***	- 0.34	0.01	**- 0.88*****	**- 0.56***	0.12	**0.89*****	0.42	**0.53***
VWC 4-10 [1]		0.23	- 0.15		0.26	- 0.08		- 0.07	0.19		0.08	- 0.13
VWC 6-7 [1]		0.09	- 0.24		0.18	- 0.18		- 0.14	0.09		- 0.11	- 0.14
Production-related parameters												
NPP$_a$	-	-	-									
Wood mass	**0.80****	**0.95*****	0.02	-	-	-						
Leaf mass	0.21	0.28	0.31	**0.60***	0.03	**0.56***	-	-	-			
Fruit mass	0.04	0.20	**0.84*****	**- 0.55***	0.17	**- 0.52***	**- 0.84*****	**- 0.50***	**- 0.64***	-	-	-
Soil parameters												
AWSC [2]	0.40	0.26	0.48	- 0.03	0.27	- 0.23	- 0.22	- 0.03	- 0.10	**0.55***	0.09	**0.54***
∑ fSUT [2]	0.47	0.31	0.49	0.23	0.39	- 0.21	0.16	- 0.03	- 0.12	0.18	- 0.14	**0.55***
C/N ratio [3]	0.28	0.16	0.38	0.40	0.18	0.15	0.38	0.05	0.50	- 0.30	- 0.10	0.20
N [3]	- 0.21	0.22	- 0.30	0.08	0.11	**0.71****	0.28	0.43	0.08	- 0.43	- 0.12	**- 0.61***
Base sat. [3]	0.23	0.36	- 0.20	0.45	0.37	- 0.06	0.51	0.22	- 0.05	- 0.47	- 0.27	- 0.14
CEC [3]	- 0.01	0.06	0.08	0.15	0.02	0.12	0.28	0.26	- 0.03	- 0.30	- 0.24	0.02
pH H$_2$O [3]	**0.64***	0.32	**0.65***	0.34	0.45	- 0.17	- 0.28	**- 0.52***	0.08	0.38	0.44	**0.65***
pH KCl [3]	0.19	0.01	0.29	0.19	- 0.01	- 0.32	0.02	- 0.18	0.41	- 0.03	0.36	0.35
Al [3]	0.14	0.19	0.11	0.07	0.19	- 0.06	- 0.42	- 0.32	0.28	0.21	**0.62***	0.09
P [3]	0.01	- 0.36	0.14	- 0.10	- 0.37	- 0.15	0.15	0.06	- 0.01	0.08	- 0.21	0.19
Stand structure												
Stand age	0.20	0.01	**0.55***	- 0.04	0.16	- 0.39	- 0.26	- 0.43	- 0.11	0.35	0.09	**0.69****
Stem density	- 0.11	- 0.08	- 0.33	0.01	- 0.26	0.23	0.10	0.42	0.13	- 0.17	0.01	- 0.42
DBH	- 0.03	- 0.05	0.24	- 0.20	0.14	- 0.40	- 0.36	**- 0.57***	- 0.38	0.34	0.13	0.45
LAI	0.18	**0.60***	0.41	0.46	0.51	**0.52***	**0.92*****	**0.88****	**0.90*****	**- 0.68***	- 0.33	0.03
Standing wood biomass	0.31	0.16	0.19	0.05	0.30	- 0.32	- 0.39	- 0.37	**- 0.57***	0.41	0.05	0.40

[1] VWC values only for 2010 and 2011. [2] Soil physical properties refer to the upper 120 cm of the mineral soil.
[3] Soil chemical properties refer to the upper 30 cm of the mineral soil.

Chapter 4

Climatic drivers of mast fruiting in European beech and resulting C and N allocation shifts

Hilmar Müller-Haubold · Dietrich Hertel · Christoph Leuschner

Abstract

European beech shows mast fruiting at intervals of 2-20 years with recent increase in frequency. It is not precisely known which climatic or endogenous factors are the proximate causes of masting. We recorded fruit mass production in 11 beech stands across a climate gradient over four years, analysed the influence of climatic, edaphic and stand structural parameters on fructification, and quantified carbon (C) and nitrogen (N) allocation to leaf and fruit mass production. The solar radiation total in June and July of the year preceding a mast year (JJ_{-1}) was the parameter most closely related to fruit mass production, whereas no influence was found for drought. Radiation induced flowering and subsequent fruit production in beech apparently through a threshold response when the long-term mean of June-July radiation was exceeded by more than 5 %. Full masting was associated with a significantly smaller leaf size and stand leaf area in the mast year and it significantly lowered foliar N content in the mast and post-mast year. We conclude that radiation totals and the N status of the foliage jointly govern the temporal pattern of masting in beech, presumably by controlling the photosynthetic activity in early summer. Anthropogenic increases in N deposition and atmospheric [CO_2] thus have the potential to increase masting frequency which can substantially alter forest productivity and forest biogeochemical cycles.

Key words: climatic cues, drought, Fagus sylvatica, fruit mass production, leaf area reduction, leaf nitrogen depletion, masting, reproductive ecology, resource dynamics, solar radiation

Introduction

Many temperate tree species exhibit a remarkable switching of carbon and nutrient allocation patterns between vegetative growth and reproduction. At irregular time intervals, large amounts of seeds are produced, a phenomenon known as mast fruiting or masting (Janzen 1976; Kelly 1994). In European beech (*Fagus sylvatica* L.), the most important tree species of Central Europe's natural forest vegetation, the quantity of fruit production differs by orders of magnitude between mast and non-mast years, and even among different mast years, fruit production varies widely (Hilton and Packham 1997). In central and northern Europe, mast years of beech were reported to have occurred at intervals of 2-20 years during the last three centuries with a mean interval length of 4-7 years (Hilton and Packham 2003; Övergaard and others 2007; Paar and others 2011, and references therein).

The diversity of hypotheses about the ultimate reasons of masting, which attribute this reproductive behaviour to evolutionary advantages related to predator satiation or increased pollination efficiency (Janzen 1971; Nilsson and Wästljung 1987; Kelly and Sork 2002), comes along with difficulties in identifying those factors that immediately trigger fructification events, i.e. represent the 'proximate causes of masting'. There is general agreement that masting in beech occurs subsequently to warm and dry summers (Büsgen and Münch 1929; Matthews 1963; Burschel 1966; Gruber 2003a; Hilton and Packham 2003) with a high level of synchronisation over large areas (Wachter 1964; Perrins 1966). This hints to a powerful and species-specific climatic trigger of fructification (Kelly and Sork 2002). However, positive anomalies of temperature, irradiance and soil drought are highly inter-related, which makes it difficult to distinguish between influential and only co-varying factors. Besides summer weather conditions immediately preceding a mast year, it was proposed that masting in beech could additionally be promoted by cool and wet summer weather two years prior to a masting event (Piovesan and Adams 2001; Drobyshev and others 2010), by the absence of spring frost during the current mast year (Lindquist 1931; Gruber 2003b), and by higher soil nitrogen availability (Borchers and others 1964; Le Tacon and Oswald 1977). It remains unclear whether the development of floral primordia in beech is an immediate reaction to a single exogenous factor such as elevated temperature (Lindquist 1931; Holmsgaard and Olsen 1960; Drobyshev and others 2010), high solar radiation (Matthews 1955; Schmidt 2006) or soil desiccation (Wachter 1964; Piovesan and Adams 2001). Or, it could be a response to a combination of ambient factors which indirectly control masting through the alteration of endogenous state factors such as plant-internal carbohydrate or nitrogen levels or budgets (Han and others 2008; Miyazaki 2013).

It has frequently been shown that a carbon allocation shift toward reproduction in the course of mast years results in reduced vegetative growth in terms of wood production (Schweingruber 1996; Koenig and Knops 1998; Selås and others 2002; Mund and others 2010) and leaf mass production (Innes 1994; Eichhorn and Paar 2000; Seidling 2007). Since leaf area is the key variable controlling the fluxes of gases and energy in the canopy, this implies that masting-induced variation in LAI and leaf morphology must affect the cycling of carbon and other elements in the forest (Jarvis and Leverenz 1983).

The linkage between mast fruiting and leaf area and its consequences for forest productivity have not been studied satisfactorily. Global warming is predicted to alter most or all climatic parameters being discussed as possible triggers of mast fruiting in beech. Therefore, a mechanistic understanding of the drivers of masting and its consequences for productivity and ecosystem carbon cycling is of great interest not only for tree physiologists but also for forestry.

We addressed this topic by measuring the production of fruit and leaf mass in eleven mature beech stands across a precipitation gradient (543 - 816 mm y^{-1}) in two full mast years and two non-mast years and analysed the influence of various climatic, edaphic and stand structural parameters on fruit mass production. The stands were of similar structure and all grew on sandy soil of relatively low fertility. Half of the stands stocked on soil with higher water storage capacity which allowed distinguishing between effects of climatic drought and edaphic drought on masting behaviour.

Study aims were (i) to identify climatic variables which act as triggers for mast fruiting in beech, (ii) to assess the importance of edaphic and stand structural factors in their possible role as contributing factors influencing masting intensity, (iii) to analyse the effects of fruit production on leaf mass production, and (iv) to estimate the degree of resource shifting between fruit and leaf production for carbon and nitrogen in mast years. By studying a matrix of beech stands along climatic and edaphic gradients, we tested the hypotheses that (1), beech masting is not a response to adverse weather conditions such as drought or heat stress as suggested in the environmental prediction hypothesis (e.g. Piovesan and Adams 2005), and (2) the resource consumption associated with masting results in significant reductions of the assimilating leaf area in the same year. To our knowledge, a direct proof of hypothesis (2) at the stand level does not yet exist.

This study is part of a more comprehensive investigation about climate change impacts on the productivity of European beech in northern Germany (KLIFF program) which also includes the study of other productivity components (stem wood and fine root production).

Materials und methods

Study area and sites

The study was conducted in the four years 2009 to 2012 in eleven beech forests (*Fagus sylvatica*) in the Pleistocene lowlands of north-west Germany. The stands are located at five study sites in the states of Lower Saxony and Saxony-Anhalt along a 130-km-long NW-SE transect (Figure 4.1). This transect represents the transition from an oceanic to a sub-continental climate with a continuous gradient in precipitation (816 to 543 mm y^{-1}) and temperature (8.4 to 9.1 °C, Table 4.1) from west to east. At all sites, two study plots differing in soil texture (sandy and sandy-loamy) were established to account for the edaphic heterogeneity in the Pleistocene landscape. The study sites are located in the forest districts Sellhorn (Se), Unterlüß (Un), Göhrde (Go) and Klötze (Kl) (two study plots each), whereas at the driest site Calvörde (Ca), three plots were established (two sandy, one sandy-loamy). All forests are situated at low elevations (72 - 130 m a.s.l.) on nutrient-poor, highly acidic sandy soils with variable silt content (dystric or umbric Arenosols or Podzols) which are covered by thick (4-9 cm) organic layers. The collection of fruit and leaf litter and other fine litter components took place from 2009 to 2012 on plots of 30 m x 30 m size in stands characterized by (i) dominance of beech, (ii) mature age (85-140 years), and (iii) closed canopy without larger gaps (> ~10 m in diameter). The years 2009 and 2011 were full mast years in beech, 2010 and 2012 were years with very low fruit production (non-masting years). All plots are situated in either monospecific beech stands (n = 6) or in beech-dominated stands with some admixture of Sessile oak (*Quercus petraea* Matt. Liebl; n = 4) or Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; n = 1). In all stands, beech trees represented >80% of the stands' cumulative basal area (24-45 m^2 ha^{-1}) and >95% of the canopy cover. The eleven stands originated from natural regeneration. The beech trees reached a height of 24 to 34 m; a second tree or shrub layer was lacking in all study plots. The study sites were fenced and equipped with litter traps in early 2009 (plot #12 in winter 2009/2010). Litter production records from one additional forest stand (plot #5: Oerrel, Table 4.1 and Figure 4.1) were not used in this study since beech reached a lower canopy cover here.

Table 4.1. Summary of environmental conditions and stand structural properties of the 12 beech stands in north-western Germany. Mean annual precipitation (MAP) and temperature (MAT) refer to the period 1971-2000. Mean diameter in breast height covers all beech trees > 7 cm stem diameter; stem density and cumulative basal area refer to all trees > 7 cm stem diameter in a plot and may include a few individuals of other species in certain plots (see Methods section). Soil chemical properties refer to the upper 30 cm of the mineral soil (N: total nitrogen; Al: NH_4Cl-exchangeable aluminium; P: total phosphorus; data provided by M. Jansen and C. Döring, unpublished). Fine-grained soil particles include fine sand, silt and clay (fSUT: particle size < 200 µm) or silt and clay only (UT: particle size < <63 µm) expressed in % of total soil mass (0 – 120 cm soil profile). The water storage capacity (AWSC) is calculated for the upper 120 cm of the mineral soil. Climate data provided by DWD, Deutscher Wetterdienst and regionalised by C. Döring. Data from plot #5 (Oerrel) was not considered in this study (s. Methods).

| Plot no.	1	2	3	4	5	6	7	8	9	10	11	12
Site code	Se	Se	Un	Un	Oe	Go	Go	Kl	Kl	Ca	Ca	Ca
Coordinates	53°10' N 09°57' E	53°10' N 09°57' E	52°50' N 10°19' E	52°50' N 10°19' E	52°59' N 10°14' E	53°07' N 10°49' E	53°09' N 10°52' E	52°37' N 11°14' E	52°37' N 11°15' E	52°24' N 11°16' E	52°23' N 11°17' E	52°22' N 11°16' E
Elevation (m a.s.l.)	127	130	120	117	90	85	85	102	85	72	75	105
MAP (mm) / MAT (°C)	816 / 8.4	816 / 8.4	766 / 8.4	766 / 8.4	741 / 8.6	675 / 8.6	665 / 8.7	615 / 8.7	614 / 8.7	543 / 9.0	544 / 9.1	559 / 9.0
Annual prec. (mm) / Temp. (°C) 2009	838 / 9.1	838 / 9.1	815 / 9.2	815 / 9.2	758 / 9.3	702 / 9.3	686 / 9.4	737 / 9.4	726 / 9.5	654 / 9.7	649 / 9.7	658 / 9.6
Annual prec. (mm) / Temp. (°C) 2010	817 / 7.6	817 / 7.6	833 / 7.6	833 / 7.6	766 / 7.7	744 / 7.7	726 / 7.8	746 / 7.8	744 / 7.8	672 / 8.0	684 / 8.1	708 / 8.0
Annual prec. (mm) / Temp. (°C) 2011	810 / 9.4	810 / 9.4	710 / 9.6	710 / 9.6	710 / 9.6	677 / 9.6	666 / 9.7	573 / 9.7	573 / 9.8	509 / 10.0	515 / 10.1	530 / 10.0
Annual prec. (mm) / Temp. (°C) 2012	772 / 8.8	772 / 8.8	749 / 9.0	749 / 9.0	705 / 9.0	648 / 9.0	638 / 9.1	634 / 9.2	629 / 9.2	549 / 9.5	550 / 9.5	568 / 9.4
Stand age (yr)	127	127	115	115	95	142	133	c.125	c.125	131	97	87
Stem density (no. ha^{-1})	156	367	411	611	500	122	289	267	478	300	711	578
Mean diameter in breast height (cm)	46.7	29.6	26.1	18.6	21.7	51.0	30.7	43.3	29.0	36.6	23.4	24.9
Stand basal area (m^2 ha^{-1})	31.0	30.7	28.5	24.3	32.3	26.6	24.4	44.9	40.8	33.3	33.2	32.6
Proportion of beech (% of basal area)	100	95	100	81	61	100	94	100	81	97	100	100
C/N ratio of mineral soil (g g^{-1})	15.6	24.2	25.8	24.1	17.8	22.9	25.5	11.9	15.7	15.9	13.2	19.0
N concentration of mineral soil (g kg^{-1})	0.28	0.46	0.40	0.47	0.78	0.41	0.51	0.46	0.49	0.34	0.42	0.33
P concentration of mineral soil (mg kg^{-1})	63	79	71	106	238	59	97	121	97	126	111	133
Al concentration of mineral soil (g kg^{-1})	0.53	0.52	0.58	0.31	0.42	0.46	0.79	0.48	0.54	0.38	0.57	0.38
Cation exchange capacity (µmol$_c$ g^{-1})	16.1	27.5	18.4	24.2	22.7	20.2	26.5	21.3	17.3	18.6	14.7	14.2
Base saturation of mineral soil (%)	24.3	9.7	14.8	8.3	8.3	6.7	2.8	14.4	9.7	7.4	5.0	6.9
Fine grained soil particles $\sum$ fSUT ($\sum$ UT) (%)	51 (12)	42 (17)	52 (21)	46 (15)	46 (8)	41 (18)	14 (5)	62 (32)	46 (16)	61 (54)	24 (10)	14 (5)
AWSC mineral soil (mm 120 cm^{-1})	90	111	95	79	79	78	107	124	90	140	81	46
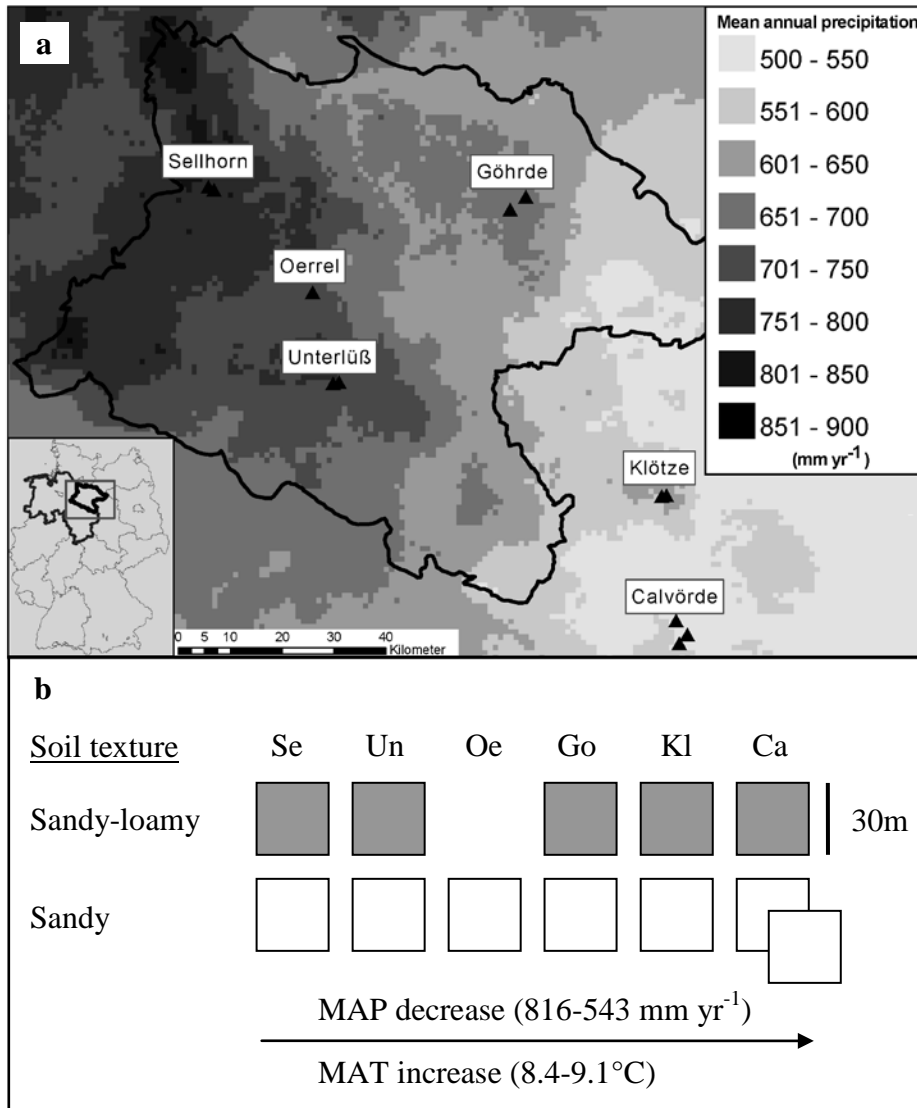
Figure 4.1. Study plot design: **a)** Map of the study area in northern Germany with the six study sites along the precipitation gradient from Northwest to Southeast (triangles: location of plots). The black line encircles the area of the Lüneburg Heath. Layout by C. Döring. **b)** Scheme of the plot design: two study plots per site (except Oerrel: n=1; Calvörde: n=2 in 2009 and n=3 in 2010-2012) located on contrasting soil texture in the six forest districts (Se = Sellhorn, Un = Unterlüß, Oe = Oerrel, Go = Göhrde, Kl = Klötze, Ca = Calvörde). Mean annual precipitation (MAP) and temperature (MAT) data (1971-2000) from Deutscher Wetterdienst, Offenbach.

Measurement of leaf and fruit production, leaf area and leaf morphology

The annual production of non-woody litter (leaves and fruits) was recorded with ten litter traps (aperture: 0.28 m^2) on each plot. The collectors were placed in a systematic pattern within a grid with 8 m mesh width, inaccessible for deer or rodents. From the fresh leaf material of every plot (10 collectors), 500 beech leaves were randomly selected and scanned and the leaf size determined with WinFolia software (Régent Instruments, Quebec, Canada). The collected litter material was sorted by tree species, oven-dried at 70°C for 48 h and

weighed; the number of beech fruits (nuts) was counted. The following foliar traits were determined: plot means of specific leaf area (SLA), leaf size and individual leaf mass. From total leaf mass and mean SLA, leaf area index (LAI) and the number of leaves per ground area were calculated. For the five plots with admixture of other tree species, a canopy projection mirror (self-constructed in the Department of Remote Sensing, University of Göttingen) was used for quantifying the canopy projection area (8-point canopy silhouettes) of these species. Figures of leaf biomass production and LAI were then corrected using the proportion of the stand area occupied by non-beech trees (0.5-5 %).

Carbon and nutrient content of leaves and fruits

The concentrations of carbon (C) and nitrogen (N) in green leaves were analysed in the years 2009-2011, but not in 2012. Samples of upper sun canopy leaves were collected by crossbow shots (in 2009) or tree climbing (in 2010 and 2011) at the beginning of September in the three years. On each plot, 4-5 dominant or co-dominant trees were chosen and leaves from 5-8 branches per tree used for the analyses. In the two masting years 2009 and 2011, leaves for chemical analysis were collected from non-fruit bearing branchlets. Chemical analyses were carried out in 2009 and 2010 on all study plots (N = 10 and 11, respectively). In 2011, leaf sampling took place on only six plots (# 2, 4, 7, 9, 11, and 12), i.e. one plot per study site, along the climatic gradient (except for two plots at the driest site Calvörde). The C and N concentrations in fruit mass were analysed in the nuts collected in autumn 2009 in the litter traps. We separated the reproductive material into nuts and cupulae and analysed composite samples from the litter collectors of each plot for these two fractions. Prior to analysis, the organic material was oven-dried at 70°C to constant weight, milled and dried again before determining the C and N concentrations with an elemental analyser (NA 2500, CE-Instruments, Rodano, Milan, Italy).

By multiplying the concentrations of C and N with the collected leaf litter mass in a plot, we estimated the stand totals of C and N contained in stand leaf biomass. The C and N content per unit leaf area (C_a, N_a) or per individual leaf (C_{leaf}, N_{leaf}) were calculated by dividing the stand totals of C and N in leaf biomass by stand leaf area or by the total number of leaves per ground area, respectively. The annual C and N demand for fruit production ($C_{Fruitmass}$, $N_{Fruitmass}$) was calculated by multiplying fruit mass with the respective C and N concentrations. Mass-based C and N concentrations in nuts (C_{mNut}, N_{mNut}) and cupulae (C_{mCup}, N_{mCup}) showed a very low variability across the gradient in 2009, irrespective of climate conditions and fruit production quantities. Therefore, we used the mean concentration

values of 2009 (C: 49.93 ± 0.39 % and 49.35 ± 0.57 % for C_{mNut} and C_{mCup}, respectively; N: 2.78 ± 0.10 % and 0.46 ± 0.03 % for N_{mNut} and N_{mCup}, respectively) for estimating the C and N amount accumulated in the fruit biomass of 2011.

Climate data

We used monthly data of precipitation, mean and maximum air temperature and sunshine duration from the 1km x1km grid data set of the German Meteorological Service (Deutscher Wetterdienst, Offenbach, Germany) and averaged the data of 3 x 3 km grids encompassing the study plots. Maximum temperature (Temp $_{max}$) was calculated as the monthly mean of daily maxima. Monthly totals of solar radiation (direct plus diffuse irradiance) was calculated by applying the Ångström equation (Allen and others 1998) to sunshine duration data.

Soil hydrological and chemical analyses

Soil physical and chemical properties were analysed in soil pits dug to 1.2 m depth in the centre of every plot by sampling all morphologically distinct soil horizons (Table 1). Water retention curves (pF-curves) were established in the laboratory by desorption of intact soil cores placed on suction plates. The storage capacity for plant-available water (AWSC) was calculated for each soil horizon (three pF-curves per horizon) at matrix potentials between -300 hPa and -1.5 MPa and subsequently summed up over the total profile depth of 1.2 m. In addition, particle size classes were separated by sieving (particle size: 2000-20 µm) and sedimentation (particle size < 20 µm) in order to determine the percentage of particles < 200 µm diameter (fine sand, silt, clay; ΣfSUT) and of particles < 63µm (silt and clay; ΣUT). Soil texture averages over the entire 120 cm soil depth were weighted by horizon thickness.

Volumetric soil water content (VWC) was measured at 6-h intervals in every plot from July 2009 onwards (plot #12: since March 2010) using time domain reflectrometry probes (TDR, CS616, Campbell Scientific Inc., Logan, UT, USA) installed at 20 cm soil depth. From these records, we calculated the relative extractable water (REW) according to Granier and others (1999) as a fraction of the maximum extractable water content using equation (1):

$$REW = (W - W_m) / (W_F - W_m) \qquad (1)$$

with W = available soil water, W_m = the minimum water content recorded in the period 2009-2012 on a given plot, W_F = soil water content at field capacity (i.e. saturating water content after completion of free drainage).

Unlike the soil physical parameters, the soil chemical characterisation focussed on the upper 30 cm of the mineral soil only. For additional chemical analyses, mineral soil material was collected in the central soil pit and at four marginal locations on the plot using a soil corer. The pH of the sieved mineral soil was measured in 1 M KCl-solution. Exchangeable cations were extracted from sieved soil with 1 M NH$_4$ Cl-solution and then measured by Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES; Optima 5300 DV, PerkinElmer, Wellesley, USA). Effective cation exchange capacity (CEC) was calculated as the sum of exchangeable cations. Base saturation (%) is the proportion of the sum of base cations (Na$^+$, K$^+$, Ca^{2+} and Mg^{2+}) in CEC.

Data analysis

We standardized all explanatory and response variables in the data set from the eleven study plots and four years to ensure comparability among variables. The regression coefficients of the standardized data ('Beta weights') express the relative degree of variation of the response variable with variation of the independent variable by one standard deviation. These regression coefficients allow comparing the relative influence of the independent variables on the dependent variables.

The climate dependence of fruit production was analysed using monthly weather data from the two years preceding a mast event (mast year-2, and mast year-1) and the mast year itself. For reducing the influence of inter-annual differences in the phenology of *Fagus* (e.g. differences in the timing of bud burst), we used moving averages of two months in width, e.g., 'early spring' (March/April), 'mid spring' (April/May), 'late spring' (May/June), 'early summer' (June/July), and so forth. Thus, a total climate data set of 128 weather variables (the four climate parameters precipitation, mean and maximum temperature, and solar radiation x 32 time windows) was used for analysing the climate - fruit production relationship. Not only monthly mean temperature was considered but maximum temperature as well, because we assumed that fructification might respond to extreme rather than average thermal conditions. Weather parameters with a likely effect on masting were identified with a two-step procedure: First, simple linear regressions between annual fruit mass production and selected weather parameters were calculated individually for the two mast years 2009 and 2011 and jointly for these two years pooled. Second, the entire four-year observation period was analysed for climate effects on masting with linear mixed-effects models (LMM) using the weather variables as fixed and 'study site' and 'year of observation' as crossed random factors. Likelihood ratio tests (LRT), conducted against a reference model, in which the observed

variable was left out, were used to test for significant effects. Another 19 edaphic, stand structural and productivity-related parameters were also tested for their influence on fruit production. By assuming that mast fruiting is triggered by climatic variation, the most likely climatic driver as identified in the previous analyses was included as a covarying factor in these analyses.

For analysing assumed effects of mast fruiting on leaf mass and other leaf properties, we regressed stand leaf biomass, LAI, the number of leaves per ground area and leaf morphological traits (mean leaf size and mass, SLA) on the fruit mass production of the current and the preceding year. Beta weights were calculated by LMM analyses for the total observation period (2009-2012) and for the pooled two mast years (2009, 2011) in order to contrast responses in masting and non-masting years. For assessing the importance of resource competition between leaf and fruit production in mast years, we analysed the relationship between foliar C and N concentrations and the total C and N pools in fruit mass.

All statistical analyses were conducted with R software (R Development Core Team 2012) with additional functions provided by the R package *lme4* (Bates and Maecheler 2010). Probability of fit to normal distribution was tested by a Shapiro-Wilk test (P ≤ 0.05). Visualization of linear regressions was conducted using the program Xact 8.03 (SciLab, Hamburg, Germany); regression lines are shown at a significance level of *P* <0.05.

Results

Weather conditions in 2009-2012

Annual precipitation decreased and mean annual temperature increased from west to east along the transect in all four study years, consistent with the long term climatic gradient. In 2011, the decrease in annual precipitation from west to east was steepest (810 to 509 mm y^{-1}); it was associated with particularly low precipitation at the dry end of the transect (Table 4.1). The trends of decreasing precipitation and increasing temperature and solar radiation existed also during the vegetation period (April-October) in the four years (Figure 4.2). Highest annual mean temperatures were recorded in 2011 and lowest in 2010 with a positive or negative temperature deviation from the long-term average of 1 K at all five sites. The mean temperature of the vegetation period was higher than the long term mean in all study years (+1.0-1.2 and +1.2-1.4 K in 2009 and 2011, +0.2-0.4 and +0.3-0.5 K in 2010 and 2012, respectively).

The weather conditions in early summer (June-July) were not anomalous in the four summers except for the very warm and dry summer 2010, when rainfall reached only 47-65 mm along the transect (mean 1971-2000: 116-159 mm) and temperature and solar radiation exceeded the long term averages by +2.1-2.3 K and + ~20 %, respectively.

Leaf and fruit mass production

We recorded two full masting events (2009, 2011) in the four studied years which both were preceded and followed by years with low fruit production at all sites. In 2009, fruit mass production ranged from 105 g m^{-2} yr^{-1} on the two plots at the moistest site Sellhorn to 422 g m^{-2} yr^{-1} on the loamy-sandy plot at the driest site Calvörde (335 g m^{-2} yr^{-1} on the corresponding sandy plot). It increased significantly with decreasing mean annual precipitation, as did the fraction of fruit biomass in total annual litter production (Figure 4.3). In 2011, heavy masting occurred throughout the transect with no dependence on precipitation means (368-603 g m^{-2} yr^{-1}, Table 2). The fruit production patterns across the transect were not related to each other in the two mast years. Seed production was very low in 2010 and 2012 (means of 18 and 15 g m^{-2} yr^{-1}).

Leaf mass production averaged at 290 g m^{-2} y^{-1} in the eleven stands during the four years. In contrast to fruit mass, the inter-annual variation in leaf mass production was relatively low (223-360 g m^{-2} y^{-1}; Table 4.2). LAI varied between 5.3 and 8.8 in the eleven stands during the four years (overall mean: 6.9). The inter-annual variation in total non-woody litter production (leaf and fruit mass) was very high (from 281 g m^{-2} y^{-1} in 2010 [plot# 9] to 862 g m^{-2} y^{-1} in the mast year 2011 [plot #3]; Table 4.2), despite a negative correlation between leaf and fruit mass production in mast years. Data on the main parameters of leaf and fruit production considered in this study are summarised in Table A.4.1 in the Appendix.
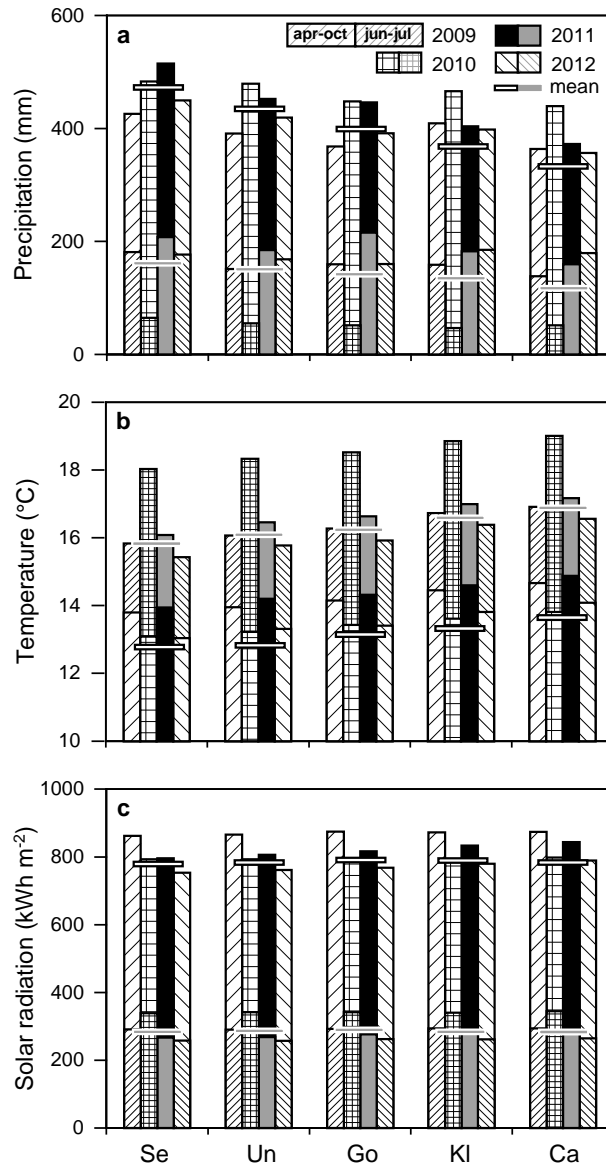
Figure 4.2. Precipitation (a), temperature (b) and solar radiation (c) in 2009-2012 at the five study sites. Values shown refer to two periods: ´growing season´ (April-October: P_{4-10}, T_{4-10}, Rad_{4-10}) and ´early summer´ (June-July: P_{6-7}, T_{6-7}, Rad_{6-7}). Horizontal bars indicate long-term means (blank bars: weather conditions $_{4-10}$; grey bars: weather conditions $_{6-7}$). The study sites are arranged according to their position along the precipitation gradient. Se – Sellhorn, Un – Unterlüß, Go – Göhrde, Kl – Klötze, Ca – Calvörde. Climate data from Deutscher Wetterdienst, Offenbach.
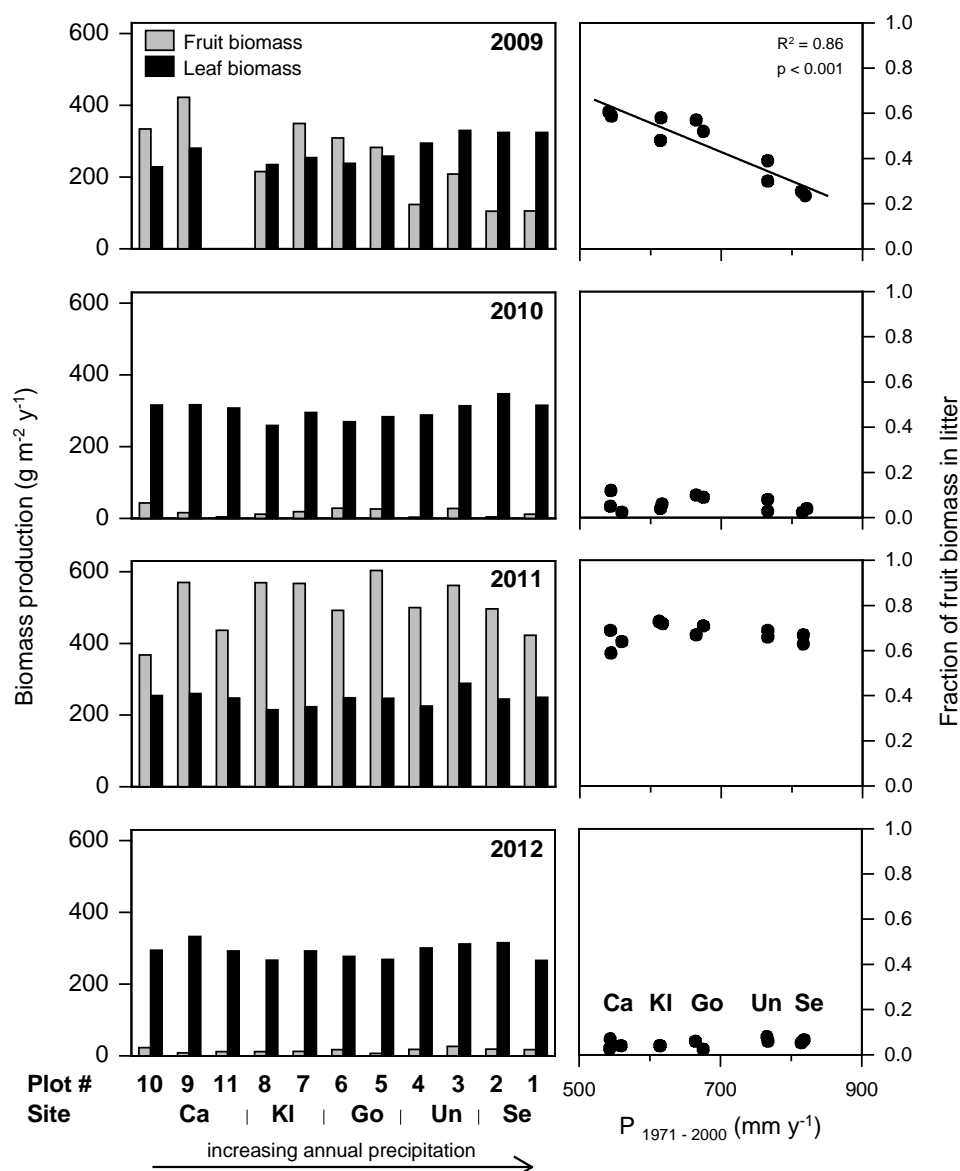
Figure 4.3. Annual production of leaf mass (black bars) and fruit mass (grey bars) in the 11 (2009: 10) study plots during 2009-2012. The study plots are arranged according to their position along the precipitation gradient. Black circles indicate fruit mass expressed as fraction of total annual litter production (leaves, fruits) along the precipitation gradient. Fruit and leaf litter data from 10 litter traps per site.

Table 4.2. Production of leaf and fruit mass in the 11 (2009: 10) beech stands along the transect in 2009-2012 (means and range). LAI: leaf area index.

Year	Leaf mass production (g m^{-2} yr^{-1})		LAI (m^2 m^{-2})		Fruit mass production (g m^{-2} yr^{-1})		Total litter production (g m^{-2} yr^{-1})	
2009	287.4	(237-342)	7.4	(5.9-8.8)	245.5	(105-422)	532.9	(430-714)
2010	312.7	(269-360)	6.9	(5.9-7.7)	17.7	(4-43)	330.4	(281-371)
2011	255.0	(223-300)	6.0	(5.3-7.1)	507.9	(368-603)	762.9	(632-862)
2012	303.9	(276-345)	7.5	(6.2-8.7)	15.3	(7-26)	319.2	(285-354)
2009-12	289.8		6.9		195.5		485.3	

Climatic drivers of mast fruiting

The analysis of the whole data set (4-y study period) with mixed-effects models showed a close positive relation of fruit mass to the radiation totals and maximum temperatures in June-August of the preceding year (year-1), but a negative one to precipitation in June-August, while the influence of the current summer and that of year-2 was small (Table 4.3: last three columns). Similar results were obtained with linear regression analyses considering only the two mast years (2009 and 2011; Table 4.3: first three columns). Accordingly, radiation in June-August of year-1 was the most influential factor (R = 0.86-0.93, P <0.001), but maximum temperature in this period was also very important (R = 0.81-0.82, P < 0.001). Moreover, the radiation total and maximum temperature from July-September of year-2 also exerted a strong positive effect on masting, but the radiation influence was weaker than in the year-1 (see also Beta weights in Table 4.3). As in the mixed model analyses, current-year weather conditions appeared of minor importance for masting intensity: a positive influence was detected for the maximum temperature of current year May-June but not for radiation or precipitation. Linear regression analyses on weather-fruiting relationships for the mast year 2009 yielded very similar results as in the analysis of the pooled data (Table A.4.2 in the Appendix). In contrast, the variability of fruit production during the very heavy masting year 2011 was not related to any of the three climatic factors, nor measures of soil water availability (R = 0.12 and 0.33 for soil water content VWC and relative extractable water REW in June/July of year-1, respectively; P > 0.05). Of all 128 tested climate parameters, the June-July solar radiation of year-1 (JJ$_{-1}$) showed the closest relationship with annual fruit mass and the strongest relative influence exerted by any climate parameter in that period (Beta = 0.88 in the mixed effects models, P < 0.0001; Table 4.3: last column).

Fruit mass production increased linearly with the June-July solar radiation total in year-1 when a threshold of ~300 kWh m^{-2} was passed (Figure 4.4 a) or when the long-term radiation mean in mid-summer (285-291 kWh m^{-2}) was exceeded by more than 5 percent (or 10-15 kWh m^{-2}) (Figure 4.4b). The mast year 2009 exceeded the long-term radiation mean in June/July by 8-13 %, that of 2011 by 17-21 %. A similar analysis for maximum and mean temperature in JJ$_{-1}$ also indicated threshold values (~ +1.5 and +1.0 K; Figures 4.4 c-f) but the correlation with fruit mass production was less tight and the relative effect on fruit mass was lower than for radiation. For summer precipitation, no clear lower threshold value appeared (Figures 4.4 g and h).
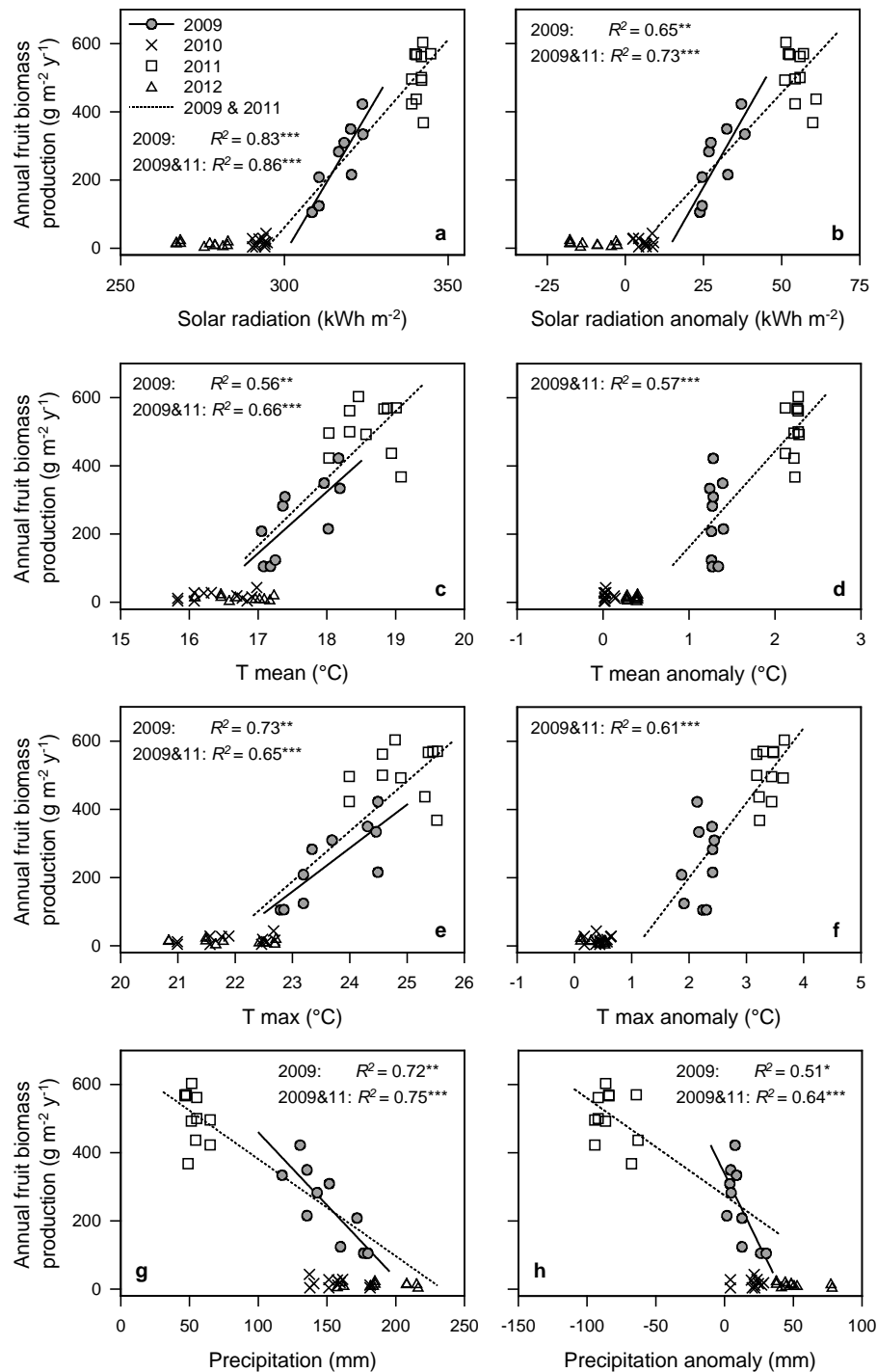
Figure 4.4. Relationship between annual fruit mass production and weather conditions in early summer one year prior to the masting (June & July of Year -1). (a) Total solar radiation; Fruit production 2009: y = -2442.9 + 16.24x, R^2 = 0.83, P < 0.001; for mast years (2009 & 2011): y = -1621.3 + 11.01x, R^2 = 0.86, P < 0.001. (b) Solar radiation, plot-specific deviation from the long-term mean (1971-2000); Fruit production 2009: y = -222.7 + 16.06x, R^2 = 0.65, P < 0.01; 2009 & 2011: y = -39.4 + 9.89x, R^2 = 0.73, P < 0.001. (c) Mean temperature; Fruit production 2009: y = -2926.4 + 180.6x, R^2 = 0.56, P < 0.01; 2009 & 2011: y = -3183.9 + 197.04x, R^2 = 0.66, P < 0.001. (d) Mean temperature deviation from the long-term mean; Fruit production 2009 & 2011: y = -118.4 + 280.66x, R^2 = 0.57, P < 0.001. e) Maximum temperature; Fruit production 2009: y = -2774.0 + 127.5x, R^2 = 0.72, P < 0.01; 2009 & 2011: y = -3185.1 + 146.72x, R^2 = 0.65, P < 0.001. (f) Maximum temperature deviation from the long term mean; Fruit production 2009 & 2011: y = -239.2 + 219.54x, R^2 = 0.61, P < 0.001. (g) Sum of precipitation; Fruit production 2009: y = 887.2 - 4.28x, R^2 = 0.73, P < 0.01; 2009 & 2011: y = 666.2 – 2.85x, R^2 = 0.75, P < 0.001. (h) Rainfall deviation from the long-term mean; Fruit production 2009: y = 338.5 – 8.26x, R^2 = 0.51, P < 0.05; 2009 & 2011: y = 274.8 – 2.85x, R^2 = 0.64, P < 0.001.

Table 4.3. Results of regression analyses between annual fruit mass production and two-monthly means of climatic conditions in the mast year and the two years prior to masting. The pooled data of the two masting years (2009 & 2011) were analysed with Pearson correlations. For the total observation period (2009-2012), standardized regression coefficients were estimated from linear mixed models (crossed random factors 'site' and 'year') after z-transformation of the data. *P* values 2009-2012 were derived from a likelihood ratio test (conducted against the random effects only; see Methods section). Significance levels: *$P<0.05$; ** $P<0.01$; *** $P<0.001$ (in bold). Prec = precipitation, T max = maximum temperature, Rad = solar radiation.

2-month period	Mast years 2009 & 2011			Total period 2009 – 2012		
	Pearson´s R			Beta weight		
Mast year -2	Prec	T max	Rad	Prec	T max	Rad
Mar-Apr	0.00	- 0.22	- 0.31	- 0.15	0.54**	0.48*
Apr-May	- 0.38	0.35	0.65**	0.03	**0.61***	0.54**
May-Jun	- 0.61**	- 0.23	0.45*	- 0.10	0.32**	1.41**
Jun-Jul	- 0.41	- 0.03	0.44*	- 0.31*	0.21*	0.64
Jul-Aug	**- 0.85***	**0.84***	**0.86***	- 0.15	0.19*	0.47**
Aug-Sep	- 0.43	**0.86***	**0.86***	- 0.54*	0.35**	**0.84***
Sep-Oct	- 0.04	0.42	0.44*	- 0.20**	0.16*	0.17
Oct-Nov	0.55*	0.66**	- 0.61**	- 0.22*	0.04	- 0.07
Mast year -1						
Mar-Apr	- 0.42	**0.81***	**0.82***	- 0.28*	0.21	0.22
Apr-May	0.59**	- 0.54*	- 0.42	0.32*	- 0.97**	- 0.68**
May-Jun	0.40	- 0.36	**- 0.71***	0.01	0.21	0.05
Jun-Jul	**- 0.87***	**0.81***	**0.93***	**- 0.54***	**0.59***	**0.88***
Jul-Aug	- 0.31	**0.82***	**0.86***	**- 0.25***	0.23*	**0.39***
Aug-Sep	0.39	- 0.21	- 0.39	- 0.09	0.19	- 0.27
Sep-Oct	0.68**	- 0.51*	0.14	- 0.22*	0.19	- 0.31
Oct-Nov	- 0.39	- 0.31	0.26	- 0.37**	0.11	- 0.06
Mast year						
Mar-Apr	- 0.60**	0.27	0.58**	- 0.19*	0.18	0.26
Apr-May	- 0.28	0.19	- 0.35	0.01	0.36*	0.15
May-Jun	0.16	**0.81***	0.31	0.02	0.22*	- 0.16
Jun-Jul	0.22	0.64**	- 0.55*	- 0.14	0.25*	- 0.02
Jul-Aug	0.32	- 0.31	- 0.39	- 0.18	0.21*	0.45
Aug-Sep	- 0.57**	- 0.46*	- 0.56	- 0.28	0.19	0.32

Non-climatic factors with possible influence on fructification

In the mast year 2009, linear models describing fruit mass production were not improved when parameters related to soil moisture, soil chemistry or stand structure were included in addition to the climatic variable radiation in JJ_{-1} (Table 4.4). However, in 2011 with very high fruit production, the model fit was better when the proportion of fine-grained soil particles ($\Sigma fSUT$ and ΣUT: 2011), water storage capacity (AWSC: 2009/2011), soil N content, stand age (all positive effects) or stem density (negative effect) were included; this was also valid for the combined data set of 2009 and 2011.

Table 4.4. The influence of soil physical and chemical and stand structural parameters on fruit mass production during the mast years 2009 and 2011 in the 11 stands as explored with different types of models. Given are beta weights from linear models (for the single mast years 2009 or 2011) or from linear mixed models (pooled data of both mast years 2009&2011; crossed random factors 'site' and 'year'). The first row presents a model that uses only solar radiation of the summer-1 (Rad_{6-7} (Y-1)) as explaining variable. The following rows present models in which (Rad_{6-7} (Y-1) was combined with other possibly explaining variables (listed under 'Stand conditions') to model fruit mass production. The columns present the beta weights for the explaining variables used in the respective model ('Stand') with inclusion of the parameter radiation as co-variable ('Rad.') for the two mast years and the pooled data (2009&2011). P values (asterisks) were derived from a likelihood ratio test conducted against models using the second explaining variable only (in single-year analyses) or against models using the second explaining variable and random effects only (pooled data; see Methods section). AWSC = soil water storage capacity; $\sum$fSUT/ $\sum$UT = percentage of soil particles < 200µm / < 63µm; VWC/ RWC = volumetric/ relative water content at 20 cm mineral soil depth, expressed as the means of early summer (June-July) of the previous year. Significance levels: [+] P<0.1; *P<0.05; ** P <0.01; *** P <0.001. Significant correlations are in bold.

Type of regression model		2009		2011		2009 & 2011	
Stand conditions	**+ Radiation**	**Stand**	**Rad.**	**Stand**	**Rad.**	**Stand**	**Rad.**
-	Rad_{6-7} (Y-1)	**-**	**1.93*****	**-**	1.25	**-**	**1.62*****
Soil moisture-related parameters							
AWSC [1]	+ Rad_{6-7} (Y-1)	0.15	**1.76*****	0.13	0.69	**0.14***	**1.36*****
$\sum$ fSUT [1]	+ Rad_{6-7} (Y-1)	0.05	**1.96*****	**0.18[+]**	1.04	0.13	**1.71*****
$\sum$ UT [1]	+ Rad_{6-7} (Y-1)	0.12	**1.74****	**0.20[+]**	0.29	**0.15***	**1.29*****
VWC 6-7 (Y-1) [2]	+ Rad_{6-7} (Y-1)	-	-	0.15	1.55	-	-
RWC 6-7 (Y-1) [2]	+ Rad_{6-7} (Y-1)	-	-	0.14	1.67	-	-
Soil chemical parameters							
C/N ratio [3]	+ Rad_{6-7} (Y-1)	0.08	2.14**	0.07	1.19	0.05	**1.76*****
N [3]	+ Rad_{6-7} (Y-1)	0.07	**2.01*****	**0.18[+]**	1.93	**0.14[+]**	**1.89*****
Base saturation [3]	+ Rad_{6-7} (Y-1)	0.00	1.94**	0.04	1.60	0.01	**1.67*****
CEC [3]	+ Rad_{6-7} (Y-1)	0.05	2.01**	0.10	1.35	0.07	**1.75*****
Al [3]	+ Rad_{6-7} (Y-1)	0.01	1.92**	- 0.04	1.19	0	**1.61*****
P [3]	+ Rad_{6-7} (Y-1)	- 0.02	**1.93*****	- 0.04	1.44	- 0.03	**1.63*****
Stand structural parameters							
Stem density	+ Rad_{6-7} (Y-1)	- 0.12	**2.03*****	**- 0.17[+]**	1.49	**- 0.15***	**1.84*****
DBH	+ Rad_{6-7} (Y-1)	0.08	**1.92*****	0.13	1.42	**0.11[+]**	**1.64*****
Stand age	+ Rad_{6-7} (Y-1)	0.09	**1.96*****	**0.20***	0.97	**0.16***	**1.72*****
Biomass production of preceding year [2]							
Wood biomass	+ Rad_{6-7} (Y-1)	-	-	**0.20[+]**	1.58	-	-
Leaf biomass	+ Rad_{6-7} (Y-1)	-	-	- 0.10	0.89	-	-
Fruit biomass	+ Rad_{6-7} (Y-1)	-	-	- 0.11	1.96	-	-
Fine roots	+ Rad_{6-7} (Y-1)	-	-	**- 0.25***	1.16	-	-
$\sum$ NPP	+ Rad_{6-7} (Y-1)	-	-	- 0.08	1.56	-	-

[1] Soil physical properties refer to the upper 120 cm of the mineral soil. [2] VWC/ RWC values and biomass production figures of the preceding year only for 2011. [3] Soil chemical properties refer to the upper 30 cm of the mineral soil.

In contrast, soil water content (VWC, REW) in the early summer of year-1 (or of other periods) as a co-variable did not improve model accuracy in 2011 (no data available for the mast year 2009). In 2011, fruit mass production correlated positively with wood increment and negatively with fine root production in the year-1 (Hertel and others 2013; no data available for the mast year 2009). Fruit production was not dependent on the production of other components (leaves, fruits) or NPP in the preceding year. Low beta weights indicate that the edaphic and stand structural parameters were only of minor importance in the explanation of fruit mass production relative to the climatic factor.

Masting effects on leaf production and leaf morphology

Annual leaf mass production and LAI were significantly reduced in masting years (Table 4.5; visible in the mast years 2009 and 2011 and also in the 4-y data set). Mean leaf size and leaf mass decreased upon a mast while SLA increased. Consequently, leaf mass loss was larger than leaf size reduction with rising fruit production. The numbers of leaves and fruits were negatively correlated to each other in masting years. However, this effect did not explain the full observed variation in leaf numbers across the entire 4-y data set (see also Table A.4.3 in the Appendix). The impact of masting on crown conditions was largely restricted to the current mast year. Neither leaf production (biomass or number of leaves per ground area) nor the size or mass of individual leaves varied significantly with fruit mass of the preceding (mast) year. However, a positive relation existed between the amount of fruit produced and SLA and LAI in the year following a masting event, reflecting the release from resource shortage during the 2009 mast.

Table 4.5. Relationships between annual fruit mass production (independent variable) and several leaf mass and leaf morphology traits (dependent variables) for the mast years and the respective year before masting (previous year) in the 11 stands. Standardized regression coefficients from linear mixed models (crossed random factors 'site' and 'year') are given for the total study period (2009-2012) and for the pooled mast years only (2009&2011). P values were derived from a likelihood ratio test (conducted against the random effects only; see Methods section). Significance levels: *$P<0.05$; ** $P <0.01$; *** $P <0.001$. Significant correlations are in bold.

		Leaf biomass	LAI	SLA	Leaf size	Leaf weight	Number of leaves [1]
Mast year							
All	2009-2012	- **0.68***	- **0.71**	0.15	- **0.47***	- **0.43***	- 0.29 (- 0.47)
Mast	2009&2011	- **0.97***	- **1.17***	**0.39**	- 0.14	- **0.49***	- **0.90** (- **0.91**)
Previous year							
All	2010-2012	0.07	**0.61**	**0.20***	- 0.44	- 0.47	- 0.05 (- 0.04)
Mast	2010&2012	- 0.18	0.29	**0.33***	- 0.70	- 0.55	0.25 (0.43)

[1] The number of leaves per stand area was further correlated with the number of fruits per stand area (Beta coefficients in brackets).

Masting effects on the nutrient status of the foliage

The N and C concentrations in beech nuts (N_{mNut}, C_{mNut}) and cupulae (N_{mCup}, C_{mCup}) were very constant across the eleven stands and were influenced neither by climate nor masting (data for 2009: N_{mNut} = 2.78 ± 0.10 %; N_{mCup} = 0.46 ± 0.03 %; C_{mNut} = 49.93 ± 0.39 %; C_{mCup} = 49.35 ± 0.57 %; no data for 2011). In contrast, leaf N and C concentrations (N_m, C_m) significantly decreased in the mast years 2009 and 2011 with increasing N and C demand for fruit production (R = ⁻0.66 and ⁻0.65, P <0.01; Table 4.6). Similarly, N content per leaf area (N_a) and per individual leaf (N_{leaf}) decreased with increasing fruit production in the masting years (R = ⁻0.51 and ⁻0.39, P <0.05 and <0.1). The amounts of C and N directed to the production of stand leaf biomass ($C_{Leafmass}$, $N_{Leafmass}$) strongly decreased with increasing fruit production in both mast years (R = -0.77 and -0.79, P < 0.01; Table 4.6) as a consequence of both decreased leaf mass production (Table 4.5) and lowered foliar concentrations of C and N. The plant-internal resource shift from leaf to fruit mass production was stronger for N than for C (~0.50 g N withdrawn from leaf production per g N invested in fruit mass vs. ~0.25 g C per g C; Figures 4.5a, b).

Effects on the leaf nutrient status due to resource consumption by mast seeding were not limited to the current mast year: Also in the non-mast year 2010, N concentrations (N_m, N_a and N_{leaf}) as well as C_m significantly decreased with enhanced resource dedication to fruit production in 2009 (Table 4.6). Astonishingly, a significant depletion of N in leaf biomass ($N_{Leafmass}$) occurred in response to N allocation to reproductive material of the preceding year (by -0.28 g $N_{Leafmass}$ per g $N_{Fruitmass}$ in 2009/2010), notwithstanding higher levels of total leaf biomass produced in 2010 (Figure 4.5c). In contrast, total leaf carbon (or C_a) in 2010 were not affected by the preceding masting, as a decrease in C_m was almost compensated by higher leaf biomass.

We found no effect of foliar N content and N in total leaf biomass in the non-masting year 2010 on the amount of N directed to fruit production in the mast year 2011 (Table 4.6). In contrast, the relation between foliar C content and C in total leaf biomass in 2010, and the amount of carbon allocated to fruit production in 2011 was negative.

Table 4.6. *Upper part of table*: Relationships between the C and N demand of annual fruit mass production ($C_{Fruitmass}$, $N_{Fruitmass}$; independent variables) and the C and N content in the leaves produced in the two mast years 2009 and 2011 in the 11 stands (dependent variables: parameters C_m, N_m – per leaf mass; C_a, N_a – per leaf area; C_{leaf}, N_{leaf} – per individual leaf; $C_{Leafmass}$, $N_{Leafmass}$ – total C or N in stand leaf mass). The results of the analysis of pooled data (2009 + 2011) are also given. *Lower part of table*: Variation of the C and N content in leaves and stand leaf mass produced in the non-mast year 2010 in the 11 stands in relation to the amount of fruit mass produced either in the preceding (2009) or the following mast year (2011). Relationships are characterised by Pearson´s correlation coefficient R. For $C_{Leafmass}$ and $N_{Leafmass}$, also regression coefficients b are given (in brackets). Leaf samples were collected in early September from the upper canopy in all three years. The number of forest stands sampled along the transect varied among the years (2009: N=10, 2010: 11, 2011: 6; see Methods section). $C_{Fruitmass}$ and $N_{Fruitmass}$ for 2011 were calculated based on the all-site average of the C and N concentration in nuts ($C_{m\,Nut}$, $N_{m\,Nut}$) and cupulae ($C_{m\,Cup}$, $N_{m\,Cup}$) determined in 2009.
Significance levels: $^+P<0.1$; $*P<0.05$; $** P <0.01$; $*** P <0.001$. Significant correlations are in bold.

Relations within mast years	n	**Carbon**					**Nitrogen**				
		C_m	C_a	C_{leaf}	$C_{Leafmass}$ (*b*)		N_m	N_a	N_{leaf}	$N_{Leafmass}$ (*b*)	
Mast year 2009	10	**-0.81****	**-0.47$^+$**	-0.23	**-0.68***	**(-0.27)**	**-0.43$^+$**	**-0.45$^+$**	-0.26	**-0.63***	**(-0.49)**
Mast year 2011	6	0.36	-0.22	-0.56	**-0.72***	**(-0.14)**	0.28	0.09	-0.33	-0.25	(-0.12)
2009 & 2011	16	**-0.66****	0.09	0.08	**-0.77*****	**(-0.21)**	**-0.65****	**-0.51***	**-0.39$^+$**	**-0.79*****	**(-0.48)**
Relations across years - Non-mast year 2010 related to:											
Fruit mass 2009	10	**-0.82****	-0.41	**-0.51$^+$**	-0.35	(-0.08)	**-0.56***	**-0.71****	**-0.59***	**-0.50$^+$**	**(-0.28)**
Fruit mass 2011	11	-0.28	**-0.74****	**-0.57***	-0.39	(-0.13)	0.12	-0.33	-0.21	-0.13	(-0.16)
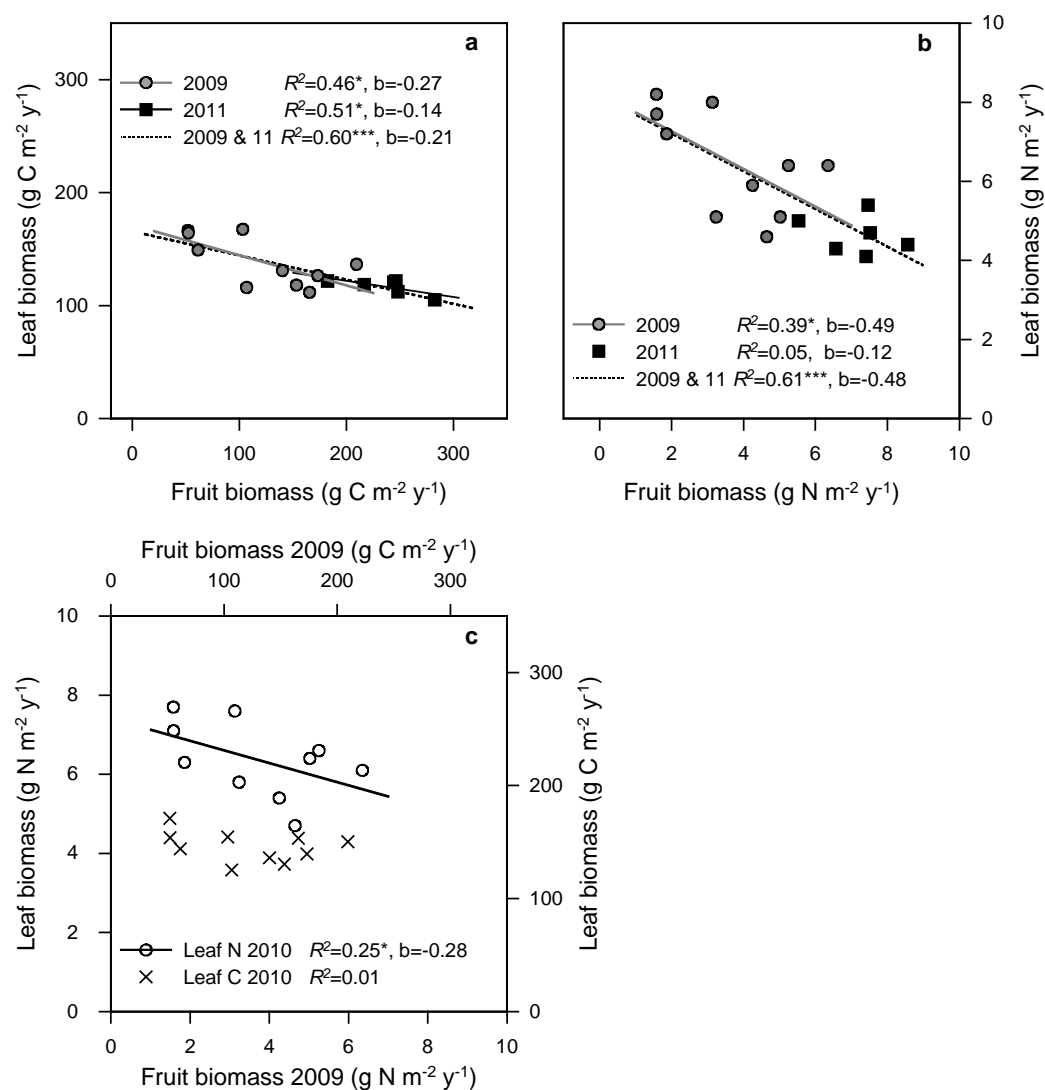
Figure 4.5. Amount of C (a) and N (b) in the stand leaf litter in relation to the C and N amount in the corresponding fruit mass produced in the mast years 2009 or 2011 across the 11 stands. (c) C or N in the leaf biomass of the non-mast year 2010 in relation to C and N in fruit mass in the preceding masting in 2009 across the 11 stands.

Discussion

Climatic triggers of masting in beech

A synchronization of masting in beech has long been attributed to variation in weather conditions (Övergaard and others 2007) but, as anomalies of temperature, radiation and drought strongly coincide, there is still disagreement on which climate parameters may act as a cue for the initiation of flowering and fructification. The results of this analysis reveal a tight control of beech fructification by levels of solar radiation in June and July one year prior to the mast year (JJ_{-1}). June and July are assumed to include the period of floral induction in beech (Holmsgaard 1962; Hilton and Packham 1997; Piovesan and Adams 2001) and the importance of radiation intensity for floral induction and flower bud differentiation has already been shown for a broad range of flowering plants (Nanda 1962; Havelange and Bernier 1983; Owens 1995; Miyazaki, Osawa and Waguchi 2009). Switching reproduction behaviour in response to continuous variation in climatic inevitably requires a tipping reaction beyond a certain threshold value (Schauber and others 2002; Kon and others 2005). Our results show that the fruit biomass production of beech in the north-west German lowlands steeply increased when the solar radiation totals in JJ_{-1} exceeded a threshold value of ~300 kWh m^{-2} in these two months. This threshold is only slightly (~5 %) above the long-term means at our study sites (285-291 kWh m^{-2}).

Besides a positive relation to JJ_{-1} global radiation, fruit mass production was also positively correlated with temperature and negatively with precipitation in that period. Nonetheless, in comparison to temperature or precipitation parameters, the correlation between solar radiation and fruit production was closer and exhibited a significantly larger effect size. While Kelly et al. (2013) showed for a large number of mast-fruiting species and plant families from New Zealand that annual fruit production is better predicted by temperature differences between mast year -1 and mast year -2 than by absolute temperatures, such a trigger could not be confirmed for beech in this study (see Figure A.4.1 in the Appendix). Our results also do not provide support for an assumed positive effect of cool and moist summer weather in mast year-2 on fructification intensity (Piovesan and Adams 2001; Drobyshev and others 2010).

The result of the correlation analysis that fructification is cued by excess of radiation and not high temperatures in the preceding summer is supported by two other independent observations in our region. First, fruit mass production in 2008 was very low according to forest monitoring data in the state of Lower Saxony, despite the JJ_{-1} temperature in 2007

exceeding the long term mean by up to 1.2K (1.3K for maximum temperature), presumably because solar radiation was 10-20 kWh m^{-2} below the long term mean (Figure A.4.2 in the Appendix). Second, very low beech fruit production was recorded in all study years in a stand in which beech were partly shaded by taller oak trees (stand #5, which was not included in our analysis), while all other climatic and edaphic conditions were comparable.

The strong dependence of fruiting on radiation regimes was visible in the spatial variation of seed production in the mast year 2009 and also in the inter-annual fruit mass variation in the pooled data set. However, in the heavy mast year 2011, when our record of fruit mass production was higher than any figure reported for beech nut crop size in the literature, fruit mass variation across our stands was remarkably independent from any climate factor. We explain the absence of a significant climate-fructification relationship in 2011 with very high radiation input to all eleven beech stands in the preceding summer: As incident radiation in June/July of 2010 greatly exceeded (by ~15 %) the assumed threshold of 300 kWh m^{-2} at all study sites, and thus probably triggered the full physiological response, the influence of other site factors which affect the vitality and productivity of beech stands, probably gained in importance in that year.

Stand structure influenced fruit production only to a relatively small extent. Our data point at increasing fruit production with increasing stand age, which can be interpreted with Genet, Bréda and Dufrêne (2010) as the outcome of an age-related shift in the C allocation patterns in mature beech trees. In our study, the intensity of fruit production was negatively related to stem density as it was also reported for *C. japonica* (Taira and others 2000). In correspondence, stand thinning is known to increase fruit production in temperate forests (Owens 1995; Kiyono and others 2003; Perry and others 2004), possibly reflecting release from competition for light or soil resources.

Does soil drought trigger masting in beech?

Our study did not produce supporting evidence for a positive soil drought effect on the intensity of fruit production. Instead, we found a positive effect of soil water storage capacity and the abundance of fine soil particles on fruit production. We thus assume a positive, and not a negative effect of soil moisture on both flowering and seed development, which is in line with results from a rainfall exclusion experiment with *Quercus ilex* (Pérez-Ramos and others 2010). Hence, we suppose that the observed negative relationship between fruit mass production and precipitation in the preceding summer in our data is caused by a negative interrelation between rainfall and sunshine and thus does not reflect a drought effect. This

interpretation matches the conclusion of Drobyshev and others (2010) that soil water depletion seems not to be a triggering factor for beech masting in Sweden (but see Piovesan and Adams 2001).

C and N allocation shifts from leaf production to fruit production

Many studies on C allocation in woody plants have demonstrated that vegetative growth, especially the increment of stem and branch wood, is suppressed by the high sink strength of reproductive structures (e.g. Koenig and Knops 1998, 2000; Kelly and Sork 2002; Drobyshev and others 2010). However, leaf production is also reduced upon masting. Our data support observations of increased defoliation rates or crown transparency reported for masting beech trees (Innes 1994; Eichhorn and Paar 2000; Seidling 2007), as total leaf mass, stand leaf area index, and the size and mass of single leaves all were significantly reduced in mast years in our study. For the two mast years, we also found a decreasing number of leaves per ground area in response to rising dry fruit mass (or number of seeds), which according to Gruber (1998) can be explained by the fact that beech flower buds develop from transformed leaf bud primordia. Decreasing leaf size or leaf bud weight in response to fruit production was also observed in other species such as *Fagus crenata* (Hiura and others 1996; Han and others 2008), *Styrax obassia* (Miyazaki and others 2002) and *Betula papyrifera* (Chapin and Moilanen 1991). Due to significant SLA increases, leaf area in the study stands was less reduced upon mast fruiting than leaf dry mass, which helped to partly maintain the assimilating surface in masting trees (Miyazaki and others 2002, Han and others 2011).

Besides decreasing leaf dry mass, we found significantly reduced concentrations of both C and N in response to increasing allocation of these nutrients to fruit production in mast years. This demonstrates a competitive superiority of developing fruits to attract photoassimilates and nutrients, even from neighbouring non-fruiting shoots (Kozlowski and Pallardy 1997; Hoch and Keel 2006; Miyazaki and others 2007).

In comparison to C, total N in leaf mass was depleted roughly twice as strongly by rising resource allocation toward fruit growth in current mast years, and foliar C/N ratio consequently increased ($R = 0.58$, $P < 0.01$ in the pooled data set of 2009 & 2011, not shown). The depleted foliar N pool in 2010 is a consequence of fruit production in the preceding mast year, which suggests that it takes more than one year for a beech tree to restock the N pool available for leaf formation in succession to a heavy masting event. Shortage of N in leaves, buds and branches as a consequence of masting has been observed in several other tree species as well (McDowell and others 2000; Miyazaki and others 2002; Han and others 2008, 2011).

Interactions between weather and resource dynamics as drivers of beech masting

From the finding that intensive mast years are usually followed by one or more years with low fruit production in beech and other temperate tree species, it has often been concluded that internal resource dynamics must also be involved in the proximate control of masting (Sork and others 1993; Hilton and Packham 1997; Kon and others 2005). Accordingly, fruiting is considered to reflect resource availability in a linear (*resource matching*, Kelly 1994) or nonlinear threshold-driven manner (*resource budget*, Isagi and others 1997) or, alternatively, fixed resource levels are assumed to act as a necessary precondition of a masting response in reaction to weather cues (e.g. Smaill and others 2011). Apart from these alterantive concepts about the possible interaction between weather and resource availability, it is also a matter of current debate, whether C or N (or possibly P) is the key element in such a regulation (e.g. Hoch and others 2013, Ichie and others 2013, Miyazaki 2013).

Strong enhancement of fructification by above-average solar radiation in JJ_{-1} as found in this study may suggest that flowering of beech is initiated when the photosynthetic carbon gain of the early summer exceeds a critical threshold value. Increased carbon gain in this period might also help to meet the additional C expenses needed for developing flower primordia, as we measured a 2.2-fold higher dry weight of flower buds than of leaf buds (data not shown); this matches observations from *Fagus crenata* (Han and others 2008). A positive correlation between the number of male flowers and non-structural carbohydrate (NSC) levels was found in the conifer *Cryptomeria japonica* (Miyazaki and others 2009). Ohto and others (2001) showed for *Arabidopsis* that the regulation of genes controlling the floral transition is dependent on carbohydrate concentrations.

However, our results on resource shifts between leaf and fruit mass indicate that, among various costs of reproduction, N rather than C must be considered the 'hard currency' in the process of fruit production in beech. Similar to this study, the availability of nitrogen (or site fertility) was identified as a predisposing or promoting factor of fruit production in other studies on *Fagus* (Borchers and others 1964; Paar and others 2004; Övergaard and others 2007) and *Nothofagus* species (Davis and others 2004; Smaill and others 2011), especially at N-limited sites. But, given the high spatial variability in soil N availability across large continuous masting areas, it is not likely that definite thresholds of plant-internal N reserves proximately cue (or also predispose for) a masting response. The impact of N on

masting is more likely an indirect effect through promotion of higher photosynthetic rates and possibly by supporting larger leaf areas which in turn increases carbon gain.

The results of this study suggest that the masting pattern of beech is controlled by both climatic triggers and plant-internal resource levels. While enhanced levels of photosynthetic carbon gain in early summer probably cue the initiation of flower buds by exceedance of certain NSC threshold values, a subsequent induction of flowering likely is inhibited in a current mast year due to resource allocation toward fruit growth by three mechanisms. This are (i) a reduction in leaf area and (ii) lowered foliar N content, which both negatively affect canopy carbon gain (Jarvis and Leverenz 1983; Evans 1989), and (iii) a large export of current photoassimilates toward developing fruits (Hoch and Keel 2006). All three mechanisms should reduce NSC availability and hence dampen the susceptibility of beech trees to a subsequent floral induction through elevated radiation as the synchronising cue.

Masting in a changing climate

The increased frequency of masting in beech as recorded over the last three decades in central and northern Europe indicates that the physiological thresholds of the fructification response are exceeded at increasingly shorter intervals, presumably caused by fertilizing effects of increased atmospheric $[CO_2]$ and N deposition (Hilton and Packham 1997; Övergaard and others 2007; Han and others 2011). Reduced intervals of exclusively vegetative growth between masting events have the potential to alter the cycling of C and nutrients in beech forest ecosystems. Detailed study of aboveground net primary production (ANPP) at our study sites in 2009-2011 revealed that fruit biomass production accounted for up to 57% of ANPP in the heavy mast year 2011 (Müller-Haubold and others 2013). These findings suggest that, besides increasing summer drought stress, also the frequency of mast fruiting can be a factor which might reduce wood production and height growth of beech in future, if masting frequency remains at the current high level or even increases further.

Conclusion

While evidence in support of the environmental prediction hypothesis and for the role of drought stress as masting cue was weak (hypothesis 1), our results indicate that fruit production of beech closely follows the radiation total received in June and July preceding a mast year. Since no other biochemical process is so closely linked to radiation as photosynthesis, we assume that floral induction in beech is triggered by higher rates of carbon assimilation in early summer. The massive C and N allocation shift associated with fruit production reduces the assimilation capacity of the canopy in the mast year and in the following year (hypothesis 2), which likely lowers carbohydrate availability needed for a subsequent floral induction. Allowing for the importance of N for photosynthesis, its pronounced depletion upon masting in our data suggests a key role for the plant-internal N level as the potential driver for the temporal pattern of masting events in beech.

Acknowledgements

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Appendices
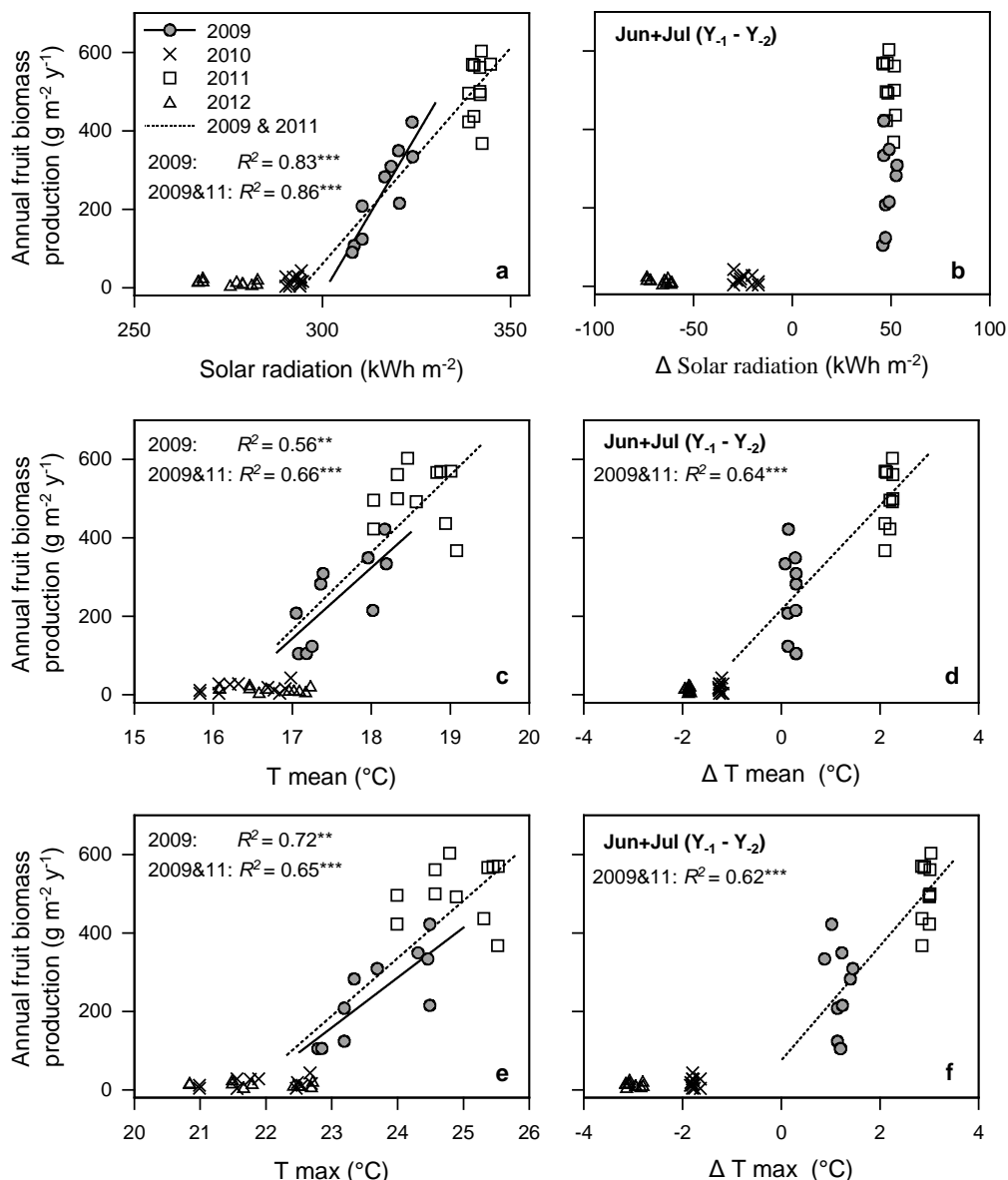
Figure A. 4.1. Relationship between annual fruit biomass production and weather conditions in early summer one year prior to the masting (JJ$_{-1}$) across the 11 stands in four years (2009-2012). Seed production was better predicted by absolute solar radiation or (maximum) temperature (a, c, e) than by climatic differentials (Δ; b, d, f) between the two previous years (radiation/temperature in JJ$_{-1}$ minus radiation/temperature in JJ$_{-2}$). (a) Total solar radiation; Fruit production 2009: y = -2442.9 + 16.24x, R^2 = 0.83, P < 0.001; for both mast years (2009 & 2011): y = -1621.3 + 11.01x, R^2 = 0.86, P < 0.001. (b) Δ solar radiation (JJ$_{-1}$ - JJ$_{-2}$). (c) Mean temperature; Fruit production 2009: y = -2926.4 + 180.6x, R^2 = 0.56, P < 0.01; 2009 & 2011: y = -3183.9 + 197.04x, R^2 = 0.66, P < 0.001. (d) Δ mean temperature; Fruit production 2009 & 2011: y = 216.6 + 133.1x, R^2 = 0.64, P < 0.001. E) Maximum temperature; Fruit production 2009: y = -2774.0 + 127.5x, R^2 = 0.72, P < 0.01; 2009 & 2011: y = -3185.1 + 146.72x, R^2 = 0.65, P < 0.001. (f) Δ maximum temperature; Fruit production 2009 & 2011: y = 74.9 + 146.5x, R^2 = 0.62, P < 0.001.
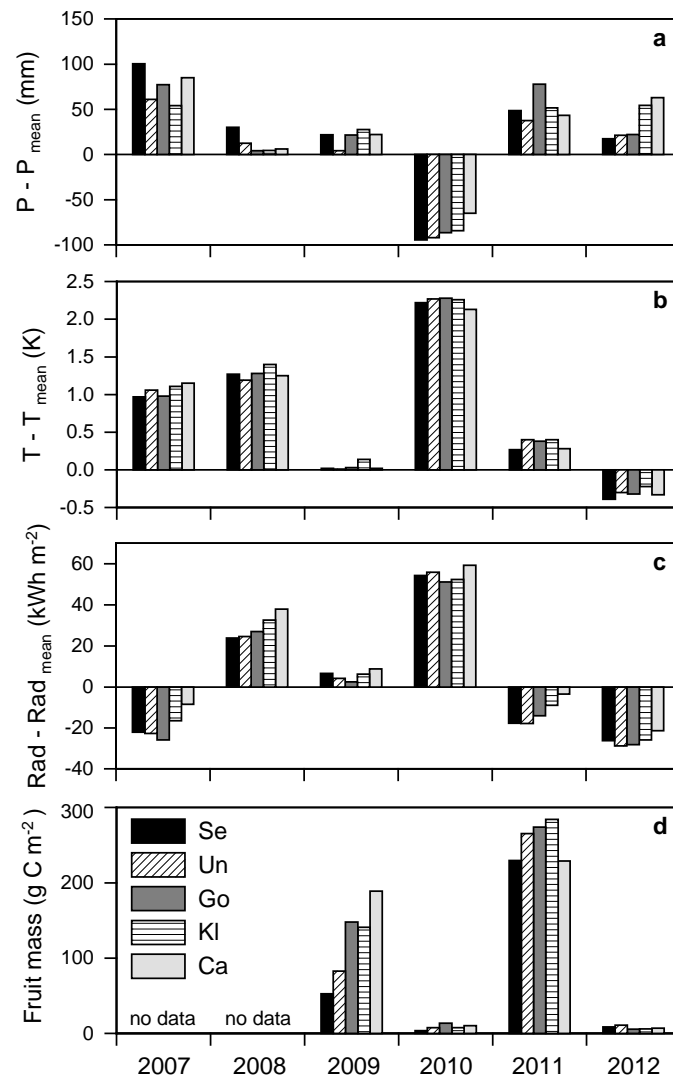
Figure A. 4.2. Weather anomalies of early summer in the six years 2007-2012 (relative to the 1971-2000 mean) and fructification in the years 2009-2012. Data of precipitation (a), temperature (b) and solar radiation (c) refer to June-July. Weather data and fruit production data (d) are averaged over all study plots of a site (climate data from Deutscher Wetterdienst, Offenbach).

Table A. 4.1. Production of leaf and fruit mass in the 11 (2009: 10) beech stands along the transect in 2009-2012 (means and standard deviation). LAI: leaf area index; SLA: specific leaf area; C_m, N_m: mass-based; C_a, N_a: area-based; C_{leaf}, N_{leaf}: per individual leaf; $C_{Leafmass}$, $N_{Leafmass}$: total C or N in stand leaf mass; *n.m.*: not measured. [1] Foliar C and N content was analysed from 2009-2011 (2011 only on sites # 2, 4, 6, 8, 10 and 11). [2] Fruit C and N content (nuts and cupulae) was analysed only in 2009. [3] Total C and N in fruit biomass were calculated based on the all-site-means for nuts and cupulae in 2009.

	2009	2010	2011	2012	Overall mean
Number of study plots	10	11	11	11	
Leaf production and morphology					
Leaf biomass production (g m^{-2} yr^{-1})	287.4 ± 41.2	312.7 ± 26.1	255.0 ± 21.0	303.9 ± 22.5	289.8 ± 35.5
LAI (m^2 m^{-2})	7.4 ± 1.0	6.9 ± 0.5	6.0 ± 0.5	7.5 ± 0.8	6.9 ± 0.8
SLA (m^2 kg^{-1})	25.7 ± 1.7	22.2 ± 1.3	23.8 ± 0.8	24.6 ± 1.9	24.0 ± 1.9
Leaf size (cm^2)	17.4 ± 1.4	19.6 ± 1.1	17.3 ± 2.1	22.0 ± 1.9	19.1 ± 2.5
Leaf mass (mg)	68.2 ± 5.1	90.6 ± 7.1	75.4 ± 9.3	90.8 ± 10.1	81.8 ± 12.6
Number of leaves (m^{-2})	4052 ± 606	3541 ± 302	3553 ± 545	3430 ± 430	3681 ± 565
C and N allocation to leaves [1]					
C_m (mg g^{-1})	472 ± 11	491 ± 8	463 ± 14	*n.m.*	478 ± 12
C_a (g m^{-2})	18.9 ± 1.4	21.1 ± 1.3	19.9 ± 0.7	*n.m.*	20.0 ± 1.6
C_{leaf} (mg)	32.7 ± 2.4	41.3 ± 3.1	35.0 ± 4.5	*n.m.*	36.7 ± 5.1
$C_{leaf\ biomass}$ (g m^{-2} yr^{-1})	138.8 ± 21.7	145.9 ± 12.8	116.7 ± 6.7	*n.m.*	136.8 ± 19.1
N_m (mg g^{-1})	22 ± 2	20 ± 2	18 ± 2	*n.m.*	21 ± 2
N_a (g m^{-2})	0.87 ± 0.10	0.91 ± 0.08	0.79 ± 0.08	*n.m.*	0.87 ± 0.10
N_{leaf} (mg)	1.54 ± 0.20	1.80 ± 0.22	1.37 ± 0.23	*n.m.*	1.60 ± 0.26
$N_{leaf\ biomass}$ (g m^{-2} yr^{-1})	6.44 ± 1.30	6.33 ± 0.90	4.62 ± 0.47	*n.m.*	5.88 ± 1.22
C and N allocation to fruit biomass production [2] [3]					
Fruit mass production (g m^{-2} yr^{-1})					
$C_{m\ Nut}$ (mg g^{-1})	499.3 ± 3.9	*n.m.*	*n.m.*	*n.m.*	–
$C_{m\ Cupulae}$ (mg g^{-1})	493.5 ± 5.7	*n.m.*	*n.m.*	*n.m.*	–
$C_{nut\ biomass}$ (g m^{-2} yr^{-1})	55.2 ± 25.0	4.0 ± 2.8	114.1 ± 16.7	3.4 ± 1.3	43.9 ± 48.7
$C_{cupulae\ biomass}$ (g m^{-2} yr^{-1})	66.6 ± 30.2	4.8 ± 3.4	137.9 ± 20.2	4.2 ± 1.6	53.1 ± 0.5
$C_{fruit\ biomass}$ (g m^{-2} yr^{-1})	121.8 ± 55.3	8.8 ± 6.3	252.0 ± 37.0	7.6 ± 3.0	97.0 ± 107.5
$N_{m\ Nut}$ (mg g^{-1})	27.9 ± 0.7	*n.m.*	*n.m.*	*n.m.*	–
$N_{m\ Cupulae}$ (mg g^{-1})	4.6 ± 0.3	*n.m.*	*n.m.*	*n.m.*	–
$N_{nut\ biomass}$ (g m^{-2} yr^{-1})	3.07 ± 1.39	0.22 ± 0.16	6.35 ± 0.93	0.19 ± 0.07	2.45 ± 2.71
$N_{cupulae\ biomass}$ (g m^{-2} yr^{-1})	0.62 ± 0.28	0.04 ± 0.03	1.29 ± 0.19	0.04 ± 0.02	0.49 ± 0.55
$N_{fruit\ biomass}$ (g m^{-2} yr^{-1})	3.69 ± 1.68	0.27 ± 0.19	7.64 ± 1.12	0.23 ± 0.09	2.94 ± 3.26

Table A. 4.2. Results of regression analyses between annual fruit mass production and two-monthly means of climatic conditions in the mast year and year-1 and year-2 before the masting events. The pooled data of the mast years 2009 and 2011 was analyzed with Pearson correlations (correlation coefficient R). The total observation period (2009-2012) was analyzed using standardized regression coefficient estimates from linear mixed models (crossed random factors 'site' and 'year') after z-transformation of the data. P values 2009-2012 were derived from a likelihood ratio test (conducted against the random effects only; see Methods section).
Significance levels: *$P<0.05$; ** $P<0.01$; *** $P<0.001$ (in bold).

Time relative to a masting		Precipitation				Maximum temperature				Radiation			
		Pearson´s R			LMM	Pearson´s R			LMM	Pearson´s R			LMM
Year	Months	2009	2011	2009&11	2009-2012	2009	2011	2009&11	2009-2012	2009	2011	2009&11	2009-2012
Mast year -2	Mar-Apr	- 0.57	- 0.22	0.00	- 0.15	0.40	0.18	- 0.22	0.54**	0.42	0.43	- 0.31	0.48*
	Apr-May	0.22	0.15	- 0.38	0.03	0.71*	0.15	0.35	**0.61***	0.44	0.24	0.65**	0.54**
	May-Jun	- 0.22	0.29	- 0.61**	- 0.10	0.41	0.07	- 0.23	0.32**	0.62	- 0.14	0.45*	1.41**
	Jun-Jul	- 0.34	0.56	- 0.41	- 0.31*	0.39	0.08	- 0.03	0.21*	0.38	- 0.06	0.44*	0.64
	Jul-Aug	- 0.86**	0.08	**- 0.85***	- 0.15	0.82**	0.07	**0.84***	0.19*	0.81**	- 0.05	**0.86***	0.47**
	Aug-Sep	- 0.29	- 0.15	- 0.43	- 0.54*	0.84**	0.58	**0.86***	0.35**	0.42	0.51	**0.86***	**0.84***
	Sep-Oct	- 0.43	0.10	- 0.04	- 0.2**	0.43	- 0.03	0.42	0.16*	0.75*	0.17	0.44*	0.17
	Oct-Nov	- 0.57	0.12	0.55*	- 0.22*	0.36	- 0.16	0.66**	0.04	0.44	- 0.11	- 0.61**	- 0.07
Mast year -1	Mar-Apr	- 0.39	- 0.04	- 0.42	- 0.28*	0.85**	- 0.07	**0.81***	0.21	0.64	- 0.17	**0.82***	0.22
	Apr-May	0.29	0.22	0.59**	0.32*	0.43	0.09	- 0.54*	- 0.97**	- 0.45	- 0.08	- 0.42	- 0.68**
	May-Jun	- 0.24	0.30	0.40	0.01	0.41	0.06	- 0.36	0.21	0.37	- 0.35	**- 0.71***	0.05
	Jun-Jul	- 0.85**	- 0.47	**- 0.87***	**- 0.54***	0.85**	0.13	**0.81***	**0.59***	0.91***	- 0.44	**0.93***	**0.88***
	Jul-Aug	- 0.42	- 0.06	- 0.31	**- 0.25***	0.41	0.03	**0.82***	0.23*	0.88***	- 0.41	**0.86***	**0.39***
	Aug-Sep	- 0.61	0.21	0.39	- 0.09	0.62	- 0.01	- 0.21	0.19	0.33	- 0.24	- 0.39	- 0.27
	Sep-Oct	- 0.44	- 0.11	0.68**	- 0.22*	0.41	- 0.55	- 0.51*	0.19	- 0.38	- 0.13	0.14	- 0.31
	Oct-Nov	- 0.74*	- 0.21	- 0.39	- 0.37**	0.56	- 0.13	- 0.31	0.11	0.69*	- 0.31	0.26	- 0.06
Mast year	Mar-Apr	- 0.41	0.01	- 0.60**	- 0.19*	0.42	- 0.01	0.27	0.18	0.08	- 0.61	0.58**	0.26
	Apr-May	0.17	- 0.35	- 0.28	0.01	0.82**	- 0.00	0.19	0.36*	- 0.15	- 0.06	- 0.35	0.15
	May-Jun	- 0.16	0.55	0.16	0.02	0.73*	0.45	**0.81***	0.22*	- 0.51	- 0.07	0.31	- 0.16
	Jun-Jul	- 0.34	0.21	0.22	- 0.14	0.42	0.06	0.64**	0.25*	0.40	- 0.07	- 0.55*	- 0.02
	Jul-Aug	- 0.66*	- 0.13	0.32	- 0.18	0.59	- 0.04	- 0.31	0.21*	0.43	- 0.19	- 0.39	0.45
	Aug-Sep	- 0.36	- 0.20	- 0.57**	- 0.28	0.85**	- 0.06	- 0.46*	0.19	0.73*	- 0.07	- 0.56**	0.32

Table A. 4.3. Results of correlation analyses between several traits of leaf production and annual fruit mass production during both the same and the previous year in 11 beech stands. Values shown are the Pearson correlation coefficients *R* for each single study year (2009, 2010, 2011, and 2012) and for the total study period (2009-2012). Significance levels: *P<0.05; ** P <0.01; *** P <0.001. Significant correlations are in bold. [1] Number of leaves was also correlated with the number of fruits (in brackets). [2] Foliar nitrogen content was analyzed only from 2009-2011 (2011 only on sites # 2, 4, 6, 8, 10 and 11).

	Leaf biomass	LAI	SLA	Leaf size	Leaf weight	Number of leaves [1]	
Current year							
2009	**- 0.64***	**- 0.58***	**0.60***	0.17	**- 0.54***	**- 0.59***	(- **0.57***)
2010	- 0.12	- 0.08	0.05	- 0.43	- 0.43	0.20	(0.20)
2011	- 0.10	0.08	**0.57***	- 0.44	**- 0.56***	0.39	(0.09)
2012	0.22	- 0.14	- 0.41	0.22	0.45	- 0.26	(- 0.26)
2009-2012	**- 0.69*****	**- 0.53*****	0.18	**- 0.61*****	**- 0.60*****	0.08	(0.05)
Previous year							
2010	- 0.20	- 0.03	0.22	- 0.13	- 0.38	0.03	(0.03)
2011	0.43	0.20	- 0.51	- 0.13	0.26	0.26	(0.26)
2012	0.09	0.27	0.31	- 0.46	- 0.50	0.50	(**0.57***)
2010-2012	**0.53****	**0.68*****	0.27	**0.66*****	**0.49****	- 0.05	(- 0.04)

Chapter 5

Fine root biomass and dynamics in beech forests across
a precipitation gradient –
is optimal resource partitioning theory applicable to
water-limited mature trees?

Dietrich Hertel · Tanja Strecker · Hilmar Müller-Haubold · Christoph Leuschner

Summary

1. Optimal resource partitioning theory predicts that plants should increase the ratio between water absorbing and transpiring surfaces under short water supply. An increase in fine root mass and surface area relative to leaf area has frequently been found in herbaceous plants but supporting evidence from mature trees is scarce and several results are contradictory.

2. In 12 mature *Fagus sylvatica* forests across a precipitation gradient ($820 - 540$ mm yr^{-1}), we tested several predictions of the theory by analysing the dependence of standing fine root biomass, fine root production and fine root morphology on mean annual precipitation (MAP), the precipitation of the study year, and stand structural and edaphic variables. The water storage capacity of the soil (WSC) was included as a covariable by comparing pairs of stands on sandy (lower WSC) and loam-richer soils (higher WSC).

3. Fine root biomass, total fine root surface area, fine root production, and the fine root/leaf biomass production ratio markedly increased with reduced MAP and precipitation in the study year, while WSC was only a secondary factor and stand structure had no effect.

4. The precipitation effect on fine root biomass and production was more pronounced in stands on sandy soil with lower WSC, which had, at equal precipitation, a higher fine root biomass and productivity than stands on loam-richer soil.

5. The high degree of allocational plasticity in mature *F. sylvatica* trees contrasts with a low morphological plasticity of the fine roots. On the more extreme sandy soils, a significant decrease in mean fine root diameter and increase in specific root area with decreasing precipitation was found; a similar effect was absent on the loam-richer soils.

6. *Synthesis*. In support of optimal partitioning theory, mature *Fagus sylvatica* trees showed a remarkable allocational plasticity as a long-term response to significant precipitation reduction with a large increase in the size and productivity of the fine root system, while only minor adaptive modifications occurred in root morphology. More severe summer droughts in a future warmer climate may substantially alter the above-/below-ground C partitioning of this tree species with major implications for the forest C cycle.

Key-words: carbon allocation, Fagus sylvatica, fine root production, fine root turnover, plant–climate interactions, precipitation reduction, root area index, root morphology, root : shoot ratio, sandy soils, soil water storage capacity

Introduction

Tree fine roots (roots <2 mm in diameter) are minor in terms of total forest biomass but play a prominent role in the functioning of forest ecosystems (e.g. Nadelhoffer & Reich 1992; Vogt *et al.* 1996; Jackson *et al.* 1997; Matamala *et al.* 2003; Silver *et al.* 2005). Due to their relatively short lifespan and rapid turnover, fine roots represent a major sink for the trees' annual carbohydrate gain (Fogel & Hunt 1983; Ruess *et al.* 1996; Gill & Jackson 2000) and play a central role in soil C dynamics (Fogel 1985; Nadelhoffer & Raich 1992; Vogt *et al.* 1996; Gill & Jackson 2000; Hendricks *et al.* 2006). It has been estimated that fine root growth may account for about a third of the global annual net primary production (Jackson *et al.* 1997), which emphasises the important role of fine root dynamics in the global C cycle. Moreover, even in this small diameter category, root dynamics may differ among different fine root branch orders (Withington *et al.* 2006; Guo *et al.* 2008; Espeleta *et al.* 2009; Sun *et al.* 2011) due to their different physiological activity.

Many factors are affecting root growth and root system size (e.g. Schenk 2005). In addition to temperature, nutrient availability, soil acidity and some other biotic and abiotic factors, water availability has been found to be a key factor influencing the fine root biomass and fine root turnover of trees (Pregitzer *et al.* 1993; Eissenstat *et al.* 2000; Lauenroth & Gill 2003; Leuschner & Hertel 2003). It has frequently been documented that trees growing in more xeric habitats have elevated root:shoot (R:S) ratios due to a shift in carbon and nutrient allocation toward the roots, thereby increasing the ratio between water absorbing and transpiring surfaces (e.g. Walter & Stadelmann 1968; Coomes & Grubb 2000). A rise in root:shoot ratio would match with the prediction of optimal partitioning theory for conditions when water is limiting (Bloom *et al.* 1985; Poorter & Nagel 2000; Reich 2002). Such a response has been observed in trees subjected to experimental drought (e.g. deVisser *et al.* 1994; van Hees 1997; Tomlinson & Anderson 1998), but is also evident from comparisons of different tree species across natural gradients of water availability (Santantonio & Hermann 1985; Coomes & Grubb 2000; Hertel *et al.* 2008).

Other results from seedlings experiments or from mature trees are less supportive of optimal partitioning theory. The few studies that do compare the fine root system of mature trees of the same species or similar forest types at different water availabilities give no conclusive support for this theory. While the studies by Kalisz *et al.* (1987), Cuevas (1995), Parker & van Lear (1996), Bakker *et al.* (2006) and Hertel *et al.* (2008) revealed a higher fine root biomass at sites with lower water availability, the results of Santantonio & Herman

(1985), Steele *et al.* (1997), Leuschner *et al.* (2004) and Meier & Leuschner (2008a) showed a lower root biomass in drier than more moist environments. Data compilations surveying existing root studies found either no consistent effect of water availability on the fine root biomass of forest stands (Coomes & Grubb 2000; Finér *et al.* 2007; Finér *et al.* 2011a) or a positive relationship between mean annual precipitation (MAP) and fine root biomass (Leuschner & Hertel 2003; Finér *et al.* 2007) which contradicts optimal partitioning theory. Schenk & Jackson (2002) detected no dependence of the maximum rooting depth of trees on MAP in water-limited environments; accordingly, no general trend seems to exist in trees to explore larger soil volumes under conditions of reduced water availability.

Even less is known about precipitation effects on tree fine root production. Most of the relevant studies have investigated the consequences of a seasonal or experimental increase in soil drought on fine root dynamics (e.g. Teskey & Hinckley 1981; Burton *et al.* 2000; Leuschner *et al.* 2001a; Tierney *et al.* 2003; Mainiero & Kazda 2006; Gaul *et al.* 2008), while only a handful of studies examined trees or stands growing along precipitation gradients or at sites differing in soil water availability (e.g. Santantonio & Herman 1985; López *et al.* 1998; Leuschner *et al.* 2004; West *et al.* 2004; Hertel *et al.* 2008; Meier & Leuschner 2008a). These results are not consistent and match with the results of global reviews of root dynamics in forest ecosystems by Vogt *et al.* (1996) and Finér *et al.* (2011b) who concluded that precipitation is in general only a weak factor influencing tree fine root production. This conclusion might be due to the fact that the majority of existing related root studies refers to experiments with potted tree saplings (e.g. Davidson *et al.* 1992; Fotelli et al. 2004; Meier & Leuschner 2008b; Winkler *et al.* 2010) and not investigations with mature trees. Given that saplings often differ substantially in their physiology and C allocation patterns from adult trees (e.g. Rice & Bazzaz 1989; Coleman *et al.* 1994; McConnaughay & Coleman 1999; Norby & Jackson 2000; Reich 2002), extrapolation of the results to mature trees and forests is problematic.

The potential for water uptake of fine roots is more likely to be related to the surface area of roots rather than to the biomass of roots (Coomes and Grubb 2000). Moreover, fine root morphology and turnover are tightly linked (Eissenstat and Yanai 1997; Eissenstat *et al.* 2000). Hence, changes in fine root morphological properties (such as specific fine root area or length) may also play an important role in the response of the trees' fine root system to differences in soil water availability. Producing fine roots of higher surface area and length, and a larger number of root tips per unit carbon invested may therefore help to optimise the cost-benefit ratio of fine roots of a tree (Eissenstat and Yanai 1997; Eissenstat *et al.* 2000;

Ostonen *et al.* 2007) and may increase the root water uptake capacity (Fitter 1986; Eissenstat 1991; Paula & Pausas 2011). Unfortunately, quantitative information on trends of root morphology along gradients of soil moisture has been rarely gathered so far.

European beech (*Fagus sylvatica* L.) is the most abundant tree species of central Europe's temperate broad-leaved forests and is playing a key role in forestry (Ellenberg & Leuschner 2010). Although this species tolerates a broad range of edaphic conditions (Leuschner *et al.* 2006) and exists under a MAP range from c. 500 to >2000 mm yr^{-1}, it reaches its highest vigour in sub-oceanic to oceanic climates and has been found to respond sensitively to drought (Magnani & Borghetti 1995, Backes & Leuschner 2000, Leuschner *et al.* 2001a, Leuzinger *et al.* 2005, Granier *et al.* 2007, Köcher *et al.* 2009, Rühr *et al.* 2009). For many regions of central Europe, climate change scenarios predict a higher frequency and intensity of drought events and more frequent summer heat waves in the coming decades (Schär *et al.* 2004, Rowell and Jones 2006, IPCC 2007; Allen *et al.* 2010) which may pose an additional threat to *F. sylvatica* (e.g. Rennenberg *et al.* 2006; Scholze *et al.* 2006; Allen *et al.* 2010; Kreutzwieser & Geßler 2010). The majority of studies on the drought susceptibility of *F. sylvatica* are seedling or sapling studies with a focus on physiological and morphological responses of the above-ground organs (Davidson *et al.* 1992; Fotelli *et al.* 2004; Rose *et al.* 2009). Accordingly, beech is more vulnerable to drought-induced xylem embolism than, for example, temperate oak species (Cochard *et al.* 2001). It reduces stem growth upon summer droughts and may respond with pre-senescent leaf shedding in exceptionally dry summers as in 2003, despite a sensitive stomatal regulation (Leuschner *et al.* 2001a; Bréda *et al.* 2006; Köcher *et al.* 2009). Increased drought-induced mortality has been observed in *F. sylvatica* stands not only at the southern range limit (Jump *et al.* 2006) but also locally in temperate central Europe (e.g. Wagenhoff & Wagenhoff 1975; Renaud & Nageleisen 2005 in Bréda *et al.* 2006).

In contrast to the numerous studies on the drought response of leaves, branches and stems, much less is known yet about the drought response of the fine root system of *F. sylvatica*; a more general pattern of the below-ground response of beech and other broad-leaved tree species to water shortage has not yet emerged. Three types of responses are possible, (i) an absolute increase in the water-absorbing root surface area (or fine root biomass), (ii) no increase, but a rising root:shoot ratio due to a reduction in leaf area, or (iii) a decrease in fine root surface area or biomass because carbohydrate availability is limiting root growth and/or root mortality increases. Only (i) and (ii) are conform to optimal partitioning theory. The type of response may depend on the vitality and pre-adaptation of the trees and the growing

conditions (Tognetti *et al.* 1995; Cordell *et al.* 1998; Meier & Leuschner 2008b; Rose *et al.* 2009) and is likely to vary with species (e.g. Stout & Sala 2003; Bréda *et al.* 2006; Rennenberg *et al.* 2006). A better understanding of the root system response of *F. sylvatica* and other tree species to water limitation is urgently needed in order to reach more robust predictions about the future of temperate forests under a drier climate.

This study uses a precipitation gradient approach with 12 mature stands on Pleistocene sandy soils in the northern German lowlands to analyse adaptive responses of the fine root system of *F. sylvatica* to reduced water availability. The main goal of the study was to search for evidence in support of, or against, the validity of optimal partitioning theory in mature stands of a temperate broad-leaved tree species. In the study region with acidic, nutrient-poor soils, *F. sylvatica* develops shallow fine root systems that are additionally exposed to periodic summer drought at the dry end of the transect. We studied not only the precipitation effect along the gradient (MAP range: 820 – 540 mm yr^{-1}) but also considered variation in soil water storage capacity (WSC, range: 140 – 46 mm for 1.2 m of profile depth) because drought intensity is largely dependent on the water retention and water conduction properties of the soil.

Based on existing knowledge and with a focus on mature *F. sylvatica* trees we hypothesised that (i) in contradiction to optimal partitioning theory, reduced precipitation does not lead to a significant carbon allocation shift to the fine root system and a higher fine root biomass at drier sites, but (ii) fine root production and fine root turnover increase with reduced precipitation due to higher mortality and compensatory root growth, (iii) rooting is more shallow at wetter than drier sites, (iv) fine roots respond to reduced precipitation with lower mean diameters and higher specific root area and root length, and (v) reduced soil water storage capacity primarily affects fine root morphology and not standing fine root biomass and turnover.

Material and methods

Study sites, climate and edaphic conditions

In a two-factorial plot design with the factors precipitation and water storage capacity (WSC), 12 study plots of 50 m x 50 m size were established in mature stands of European beech along a precipitation gradient in north-western Germany (52-53° N) and examined for fine root biomass and dynamics in 2009 and 2010. The stands were selected in 6 forest districts (from moist to dry: Sellhorn (acronym 'Se'), Unterlüß ('Un'), Oerrel ('Oe'), Göhrde ('Go'), Klötze ('Kl'), and Calvörde ('Ca') along a 130km-long transect covering beech forests from an oceanic climate in the North-West to forests from a sub-continental climate in the South-east. The first four districts are located in the lowlands of the German state of Lower Saxony, the latter two in the Saxony-Anhalt lowlands. Mean annual precipitation decreases more or less continuously along the transect from c. 820 to 540 mm yr^{-1} (Table 5.1) while mean annual temperature (MAT) slightly increases (8.5 to 9.2 °C). For covering the variation in soil water storage capacity, pairs of plots on sandy and loam-richer soil were selected at every study site (except for the site Oerrel, see below), thus creating a matrix of 12 plots differing in the exposure to climatic and edaphic drought. All selected beech stands grow on acidic, nutrient-poor sandy or sandy to loamy soils derived from glacial deposits of the penultimate Ice Age (Saale Ice Age, Drenthe and Warthe stadials) at elevations of 70-130 m a.s.l.. Seven plots were selected on more coarse-grained meltwater sands and sandy moraine deposits with low silt and clay content and typically a smaller water storage capacity (WSC) (hereafter termed 'sandy' or 'sa'), five plots were chosen on loam-richer sandy deposits (mostly loamy or sandy-loamy moraine deposits) with higher silt and clay content and, in most cases, higher WSC (termed 'loam-richer' or 'lo'). No loam-richer plot was available at the Oerrel site; two sandy plots were chosen at the Calvörde site.

The soil types were dystric or umbric Arenosols or Podzols (WRB classification) with 4-9 cm-thick organic layers. Soil chemical parameters characterising nutrient availability and soil acidity status (total C, N and P concentrations, base saturation at the cation exchangers, pH) were measured at each six (organic layer) or four (mineral soil) randomly chosen sampling locations in all plots; the total carbon and nitrogen concentrations were determined by gaschromatography, the total P concentration with ICP-OES analysis after HNO_3 digestion, the plant-available cation concentrations after NH_4Cl extraction and subsequent element analysis in the percolate by ICP-OES. The loam-richer soils contained on average 27% of fine-grained particles (<63 µm) in the bulk mineral soil, the sandy soils only 11% (Table 5.1). For determining the amount of water retained in the soil at matrix potentials >-1.5 MPa and <-300 hPa (as a conventional definition of 'plant-extractable water' in sandy soils as a

measure of WSC), soil cores were desorbed by suction in the laboratory. Accordingly, the WSC of the sandy plots varied between 46 and 111 mm in the profile to 1.2 m depth (mean: 78.0 ± 7.9 mm), that of the loam-richer plots between 78 and 140 mm (mean: 105.4 ± 11.5 mm; difference between substrate types significant). Volumetric soil water content was continuously recorded with TDR probes (CS616, Campbell Scientific, Cambridge, UK) at 4 soil depths (organic layer to 1.2 m) in all 12 plots.

The study year 2009 received average rainfall in most parts of the transect but was by 1.0-1.2 K warmer than the average. For illustrating the soil hydrological conditions in their regional and seasonal variation across the transect, Figure 5.1 presents the fluctuation of volumetric soil water content in the densely rooted organic Oh horizon for the moistest site (Sellhorn at the western transect end) and the driest site (Calvörde at the eastern end) in the period August 2009 - December 2010 (measurements began in August 2009). Volumetric soil water contents were recorded every 6 hours using one time domain reflectrometry probe (TDR, CS616, Campbell Scientific Inc., Logan, UT) per site.

All 12 stands were either pure beech stands (n = 7) or stands dominated by *F. sylvatica* with admixture of a few (1-8) Sessile oak (*Quercus petraea* Matt. Liebl.) trees. Beech held between 81% and 100% of stand basal area in all stands except for stand Oe-S (61%). The above-ground structure of the stands varied within defined limits (95-100 % canopy closure, no recent impact of forest management, mature tree age). A second tree or shrub layer and a herbaceous layer were absent in all stands. Despite some variation in mean tree height, stem density, stem diameter in breast height and cumulative basal area among the stands (see Table 5.1), stand basal area and above-ground woody biomass were not significantly dependent on the MAP variation along the transect ($P = 0.06$ and 0.18, $R^2 = 0.23$ and 0.08, respectively).
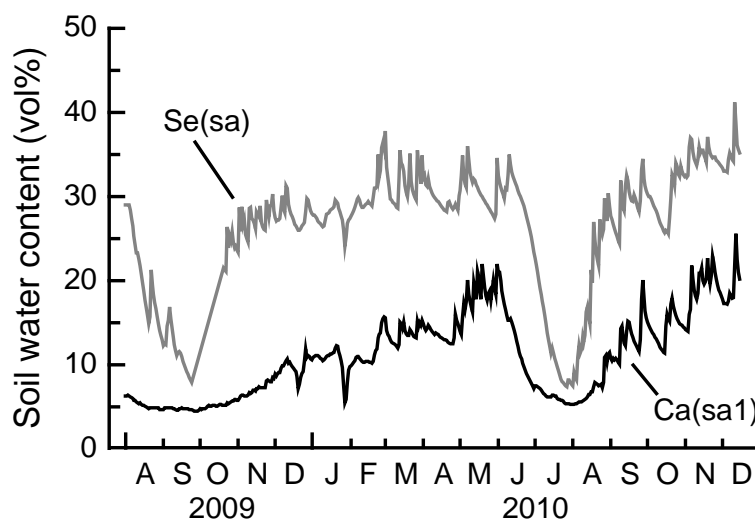
Figure 5.1. Seasonal course of volumetric soil water content in the densely rooted organic Oh layer in the period August 2009 to December 2010 in the moistest beech stand Sellhorn (sandy substrate, plot #2) at the western transect end and the driest stand Calvörde (sandy substrate, plot #11). The measurements began in August 2009.

Table 5.1. Summary of climatic, edaphic, and stand structural properties of the 12 *Fagus sylvatica* stands in north-western Germany. Substrate type: loam-richer soil (lo) and sandy soil (sa). Mean annual precipitation (MAP) and temperature (MAT) refer to the period 1971-2000 (regionalised by C. Döring from the national weather stations network data base provided by DWD, Deutscher Wetterdienst). Data on stand age were obtained from the local forest administration. Leaf area index and annual leaf production are derived from leaf litter collection in each 10 litter traps (aperture 0.28 m^2) per plot. Soil chemical properties refer to the upper 30 cm of the mineral soil (data provided by M. Jansen and C. Döring, unpublished). Fine-grained soil particles include silt and clay (particles size < 63 µm) expressed in % of total soil mass (0 – 120 cm soil profile, data obtained from M. Jansen). The water storage capacity is calculated for the upper 120 cm of the mineral soil.

Plot no.	1	2	3	4	5	6	7	8	9	10	11	12
Site code	Se	Se	Un	Un	Oe	Go	Go	Kl	Kl	Ca	Ca	Ca
Substrate type	lo	sa	lo	sa	sa	lo	sa	lo	sa	lo	sa1	sa2
Coordinates	53°10' N	53°10' N	52°50' N	52°50' N	52°59' N	53°07' N	53°09' N	52°37' N	52°37' N	52°24' N	52°23' N	52°22' N
	09°57' O	09°57' O	10°19' O	10°19' O	10°14' O	10°49' O	10°52' O	11°14' O	11°15' O	11°16' O	11°17' O	11°16' O
Elevation (m a.s.l.)	127	130	120	117	90	85	85	102	85	72	75	105
Mean annual temperature (°C)	8.5	8.5	8.5	8.5	8.7	8.7	8.7	8.8	8.9	9.1	9.2	9.1
Mean annual precipitation (mm)	816	816	766	766	741	675	665	615	614	543	544	559
Annual precipitation 2009	838	838	815	815	758	702	686	737	726	654	649	658
Annual precipitation 2010	817	817	833	833	766	744	726	746	744	672	684	708
Stand age (yr)	127	127	115	115	95	142	133	c.125	c.125	131	97	87
Mean tree height (m)	31.4	28.0	28.4	25.3	27.2	30.2	24.6	33.8	30.2	28.3	23.8	25.5
Stem density (no. ha^{-1})	156	367	411	611	500	122	289	267	478	300	711	578
Mean diameter in breast height (cm)	46.7	29.6	26.1	18.6	21.7	51.0	30.7	43.3	29.0	36.6	23.4	24.9
Stand basal area (m^2 ha^{-1})	31.0	30.7	28.5	24.3	32.3	26.6	24.4	44.9	40.8	33.3	33.2	32.6
Timber volume (m^3 ha^{-1})	490	395	378	227	287	407	289	758	516	454	374	402
Leaf area index (m^2 m^{-2})	6.9	7.5	7.5	7.5	7.6	6.8	6.3	7.7	7.0	7.2	6.9	6.7
Leaf production 2010 (g m^{-2} yr^{-1})	327.2	360.5	326.4	338.1	362.9	294.3	302.8	306.7	320.1	329.4	328.2	319.4
Thickness of organic layer (cm)	7.5	9.1	6.5	7.3	6.9	9.0	8.8	4.1	6.4	7.5	6.6	8.0
pH value (H$_2$O) of mineral topsoil	4.2	4.2	4.4	4.3	4.0	4.3	4.3	4.4	4.3	4.2	4.3	4.1
C/N ratio of mineral topsoil (g g^{-1})	15.6	24.2	25.8	24.1	17.8	22.9	25.5	11.9	15.7	15.9	13.2	19.0
N concentration of mineral topsoil (g kg^{-1})	0.28	0.46	0.40	0.47	0.78	0.41	0.51	0.46	0.49	0.34	0.42	0.33
P concentration of mineral topsoil (mg kg^{-1})	63	79	71	106	238	59	97	121	97	126	111	133
Cation exchange capacity (µmol$_c$ g^{-1})	16.1	27.5	18.4	24.2	22.7	20.2	26.5	21.3	17.3	18.6	14.7	14.2
Base saturation of mineral topsoil (%)	24.3	9.7	14.8	8.3	13.0	6.7	2.8	14.4	9.7	7.4	5.0	6.9
Fraction of fine-grained (< 63 µm) soil particles (%)	11.9	17.2	21.0	14.9	7.8	17.7	4.4	32.0	16.4	53.5	9.6	4.7
Water storage capacity mineral soil (mm 120 cm^{-1})	90	111	95	79	59	78	80	124	90	140	81	46

Fine root inventory

For determining the amount of standing live and dead fine root mass in the soil of the 12 stands, root inventories were carried out in June and September 2009 (early and late growing season) by extracting soil samples with a corer (3.5 cm in diameter) from the organic layer and the upper mineral soil (0-10 and 10-30 cm soil depth) at 20 randomly selected locations per study plot. June represented a wetter early-summer period, September a drier late-summer phase in 2009. The soil samples were transferred to plastic bags and stored at 4 °C in the laboratory. The samples were cleaned from soil residues by soaking in water prior to the root extraction procedure using a sieve with a mesh size of 0.25 mm. Only tree fine roots were considered for analysis. Larger rootlets (> 10 mm in length, < 2 mm in diameter) were extracted by hand with tweezers. Living (biomass) and dead roots (necromass) were distinguished under the stereo-microscope by inspecting colour, root elasticity, and cohesion of the cortex, periderm and stele (e.g. Persson 1978; Hertel & Leuschner 2002). While this fine root fraction represents the majority of living fine root mass (>95%), a large proportion of fine root necromass consists of smaller root fragments not recovered with this method (Bauhus and Bartsch 1996; Leuschner *et al.* 2001b). In order to quantify this fraction of dead fine root mass, a third of the samples were subjected to a very detailed analysis of smaller root necromass particles (< 10 mm in length) applying a method introduced by van Praag *et al.* (1988) and modified by Hertel (1999). After extraction of the larger rootlets, the residue of the sample was evenly spread on a large sheet of filter paper (730 cm^2) with 36 squares marked on it. Six of the squares were randomly selected and analysed under the stereo-microscope for even the smallest dead fine root fragments. The mass of small dead root fragments detected in the sub-samples was extrapolated to the samples, that were not subjected to this detailed analysis, by use of a regression equation that relates the mass of small dead roots to large necromass rootlets (> 10 mm in length); this regression equation was established in the six sub-samples analysed in detail. The fine root biomass and necromass of every sample was dried at 70 °C for 48 h and weighed. We did not separate the fine roots by branch order as done in some recent studies to hold account on the importance of fine root heterogeneity in branch order topology (see e.g. Pregitzer *et al.* 2002; Guo *et al.* 2008) (i) due to the enormously high numbers of rootlets <2 mm in diameter in a single soil sample the were recorded in the 12 forest stands (approximately > 30.000 individual fine rootlets) and (ii) since we aimed at comparatively studying the living and dead fine root mass with the latter fraction lacking the possibility of such a branch order analysis. However, we considered the most dynamic first root branch order (i.e. the root tips) of the living fine roots in a separate

approach (see below). The data of the two inventories were expressed as fine root dry mass per soil volume at a given soil depth (in g m^{-3}) and as fine root mass profile total (in g m^{-2}) by adding the three analysed soil horizons. Earlier investigation of the vertical distribution of fine root mass in *F. sylvatica* stands conducted on similar soil in the direct vicinity of one of the selected forest stands (site 'Unterlüß') to a soil depth of 350 cm revealed that more than 85 % of the fine root biomass profile total was located in the organic layer and the upper 40 cm of the mineral soil (Leuschner *et al.* 2004); this indicates that our inventory has covered >75% of the fine root biomass total in the 12 stands.

Fine root morphology

All living rootlets of a soil sample were analysed for their mean root diameter, specific root surface area (SRA, in cm^2 g^{-1}), specific root length (SRL, in m g^{-1}), and root tissue density (in g cm^{-3}) using a scanner and a WinRhizo (Régent Instruments Inc., Quebec, Canada) visual analysis system. The fine root area index (RAI, m^2 cumulative root surface area per m^2 ground area) was calculated analogous to leaf area index from the SRA and mean fine root biomass values of the three soil horizons that were added to receive the RAI total of the soil profile (organic layer plus upper 30 cm mineral soil). The abundance of fine root tips (i.e. the first branch order of the rootlets) was determined for every soil sample by counting under the stereo-microscope all living tips of each one representative live fine root branch. Tip abundance was expressed on a root dry mass basis (specific root tip abundance, n mg^{-1}). The rootlets were also inspected microscopically for the abundance of clearly visible ectomycorrhizae in order to record the degree of root tip colonization by ectomycorrhizal fungi.

Fine root production

We used the ingrowth core technique for measuring fine root growth in the 12 stands and to obtain an estimate of annual fine root production (Persson 1980; Powell and Day 1991; Majdi 1996). In comparison to other techniques, this approach has been found to give rather conservative figures of fine root production in temperate forests (e.g. Hertel & Leuschner 2002; Hendricks *et al.* 2006; Finér *et al.* 2011b). In May/June 2009, 12 ingrowth cores each were installed in the 12 plots at random locations; they were re-sampled after 22 months in March 2011. For installing the ingrowth cores, a soil corer (diameter 3.5 cm) was dug through the organic layer to a depth of 20 cm in the mineral soil and the soil and root material was

extracted. The bulk soil was cleaned by hand from all macroscopically visible live and dead rootlets and the soil material subsequently replaced into the hole in its natural sequence of horizons, thereby conserving the natural structure of the soil as much as possible. The minimum distance between two ingrowth cores was at least 2 m. The edges of the cores were marked accurately at the soil surface. For minimising soil disturbance and allowing for barrier-free access of growing roots to the cores, no mesh gaze was used to enclose the cores. For recording the start of the re-colonisation process of the cores by invading roots, we continuously harvested single cores in the first months after installation. Accordingly, fine-root growth started in the bulk of the ingrowth cores around June 2010, i.e. after a 12-month lag period following the initial disturbance. We harvested all 144 cores in March 2011 (i.e. 9 months after the assumed start of re-colonisation) to guarantee an extended growth period allowing for a complete re-colonisation of the soil in the cores. We therefore did also not observe a significant portion of pioneer roots in the extracted root samples that would be morphologically and functionally different from the common branched fibrous fine roots in the soil (see Polverigiani *et al.* 2011; Zadworny & Eissenstat 2011). We carefully extracting the soil core, quantified the dry mass of larger (>10 mm length) fine root branches (living and dead) in the core as described above, and expressed the data as fine root growth per soil volume and 9 months. We assumed that the existing live and dead root mass in the core represented the root mass produced in the period and that root fragments broken off the main root branches were negligible. Annual fine root production (in g m^{-2} yr^{-1}) was estimated by extrapolating the fine root growth during the 9-month period to an entire year and relating it to m^2 ground area. An estimate of fine root turnover in the study plots was obtained by relating annual root production to mean standing fine root biomass (Aber *et al.* 1985; Aerts *et al.* 1992; Gill & Jackson 2000).

The annual production of leaf biomass was recorded with each 10 litter traps (aperture 0.28 m^2) per plot. The collected litter material was separated into leaves, flowers and fruits and sorted by tree species, oven-dried at 70°C for 48 h, and weighed. In each plot, 500 randomly chosen beech leaves were collected from the litter traps, scanned and the leaf size determined with WinFolia software (Régent Instruments, Quebec, Canada) to calculate stand leaf area index (LAI).

Statistical analyses

All data sets were tested for Gaussian distribution using a Shapiro & Wilk test. Normally distributed data were tested for significant differences with ANOVA followed by pair-wise

comparison after Scheffé ($P < 0.05$) that included a correction for multiple pair-wise comparisons. In order to test for the effect of the two different geological substrates (sandy vs. loam-richer material), the influence of soil depth and the interaction of both factors on fine root morphological traits, a two-factorial ANOVA procedure was conducted. The calculations were performed with the software package SAS, version 8.01 (SAS Institute, Cary, North Carolina, U.S.A.). In order to analyse the differentiation of the 12 study plots with respect to climatic and soil chemical characteristics, we conducted a Principal Components Analysis. The matrix species factors were: study plot, soil texture type, mean annual temperature, mean annual precipitation, annual precipitation of the study year 2009, annual precipitation of the study year 2010, C/N ratio, cation exchange capacity (CEC) and base saturation of the cation exchangers of the upper mineral soil, mean tree height, mean diameter at breast height (dbh), stem density, stand basal area, leaf area index (LAI), annual leaf production, fine root biomass, fine root necromass, fine root live/dead ratio, root area index (RAI), root area/leaf area index ratio, annual fine root production, fine root/leaf production ratio, fine root turnover rate, average fine root diameter, specific root area (SRA), and specific root length (SRL). The PCA analyses were conducted with the package CANOCO, version 4.5 (Biometris, Wageningen, The Netherlands). We regressed various fine root traits of the sandy and loam-richer plots on MAP and the precipitation of the respective study year using the software package Xact (version 8.03, SciLab, Hamburg, Germany). A multiple linear regression analysis was done using the software package SAS to analyse the influence of various climate (mean annual precipitation 'MAP', annual precipitation 2009 'AP2009', annual precipitation 2010 'AP2010'), soil physical (water storage capacity of the mineral soil and percent fine-grained soil particles) and above-ground structural variables (stand basal area, tree density, timber volume and leaf area index) on the fine root biomass or fine root productivity in the 12 *F. sylvatica* stands.

Results

Environmental and stand structural gradients across the beech plot matrix

The Principal Components Analysis on the similarity of the 12 beech stands in terms of environmental (climate and soil) and stand structural and functional properties revealed a more or less continuous distribution of the 12 study plots along 4 different axes that explained 84% of the total variance of the data set (Table 5.2). Axis 1 with an eigenvalue of 0.35 strongly coincided with the climatic factors MAP, annual precipitation of the study year, and

MAT, reflecting the precipitation decrease by 270 mm yr^{-1} and the temperature increase by 0.7°C along the transect from the wet to the dry end (Table 5.1). Important root traits including fine root biomass, root area index, root area/leaf area index ratio, and fine root production correlated also with the first axis but in opposite direction than precipitation indicating a negative relationship between precipitation and fine root biomass and fine root production. Part of the root traits correlated also with axis 2 (root morphological traits) or with axis 3 (fine root necromass, fine root turnover). Variables characterising stand above-ground structure correlated either with axis 1 (tree height, stand basal area, timber volume) or with axis 2 (stem diameter, stem density). An exception was leaf area index with a positive relation to axis 1. Axis 2 (eigenvalue 0.22) showed a close relation to soil texture (with the stands with sandy soil being located more toward the positive end and the loam-richer stands situated toward the negative end of this axis) and soil chemical properties (most strongly to the C/N ratio of the mineral soil). Axis 3 (eigenvalue 0.19) showed only a weak association with abiotic variables, but coincided with some single above-ground stand structural variables as well as with fine root turnover.

Live and dead fine root mass

The mean fine root biomass (live roots) in the organic layer and the upper 30 cm of the mineral soil ranged from 289 to 704 g m^{-2} in the 12 beech stands (Figure A.5.1 in the Appendix). The 7 stands with a MAP <700 mm yr^{-1} showed a significantly higher mean fine root biomass (573 ± 28 g m^{-2}) than the 5 stands with MAP >700 mm yr^{-1} (354 ± 26 g m^{-2}, Figures 5.2 and A.5.1). Moreover, drier beech stands showed a higher proportion of the standing fine root biomass in the organic layer and the upper 10 cm of the mineral soil than stands with higher precipitation. Stand fine root biomass showed a significant negative relation to MAP; this relation was even stronger when fine root biomass was scaled to the precipitation amount of the study year, showing an increase in fine root biomass by 139 g m^{-2} per 100 mm decrease in annual precipitation (Figure 5.2). This relation also appeared when the stands on sandy or loam-richer soil were analysed separately (Table 5.3). A closer look shows that the increase in fine root biomass occurred mainly in the organic layer and the mineral topsoil (0-10 cm) but not in the deeper mineral soil (significant trends $P < 0.01$ in both upper layers, Figure A.5.1). The multiple regression analysis with climatic, edaphic and stand structural parameters identified the precipitation in the study year as the only significant predictor of fine root biomass (Table 5.4). Neither stem density nor stem diameter or timber volume had a significant influence on fine root biomass.

Table 5.2. Results of a Principal Components Analysis (PCA) on the differentiation of the 12 *Fagus sylvatica* stands with respect to climatic and soil properties, and various above-ground and below-ground tree variables. Given are the loadings of the selected variables along the four explanatory axes. Numbers in brackets below the axes indicate the eigenvalues of the axes. Numbers in bold mark the variables with closest correlation to the respective axis.

Variables	Axis 1 (EV 0.348)	Axis 2 (EV 0.216)	Axis 3 (EV 0.186)	Axis 4 (EV 0.088)
Climate factors				
MAT	**0.904**	0.133	-0.311	-0.178
MAP	**-0.934**	-0.163	0.087	0.055
AP2009	**-0.957**	0.057	-0.017	0.106
AP2010	**-0.933**	-0.072	0.074	0.138
Soil properties				
Texture type	0.227	**-0.624**	-0.408	0.401
C/N	-0.420	**-0.740**	0.423	-0.010
N concentration	-0.132	-0.395	-0.370	**0.496**
P concentration	0.139	-0.116	**-0.668**	0.365
CEC	-0.401	**-0.447**	0.235	**0.484**
Base saturation	**-0.661**	**0.644**	-0.119	-0.072
Stand structural variables				
Tree height	-0.331	**0.799**	0.280	-0.015
Diameter at breast height	-0.026	0.595	**0.623**	-0.299
Stem density	0.270	-0.382	**-0.704**	0.190
Stand basal area	0.263	**0.746**	-0.317	0.210
Timber volume	0.145	**0.909**	0.117	0.085
LAI	**-0.580**	0.244	-0.475	0.183
Annual leaf production	**-0.611**	-0.259	**-0.675**	0.027
Root-related variables				
Fine root biomass	**0.780**	-0.234	0.518	0.078
Fine root necromass	0.276	-0.423	**0.762**	0.369
Fine root live/dead ratio	**0.577**	0.303	**-0.560**	-0.454
RAI	**0.859**	-0.013	0.417	0.275
RAI/LAI	**0.844**	-0.104	0.452	0.231
Annual fine root production	**0.887**	-0.214	-0.263	-0.128
Fine root/leaf production ratio	**0.929**	-0.180	-0.111	-0.112
Fine root turnover	0.273	-0.132	**-0.809**	-0.192
Fine root diameter	-0.372	**-0.524**	0.007	-0.433
SRA	0.179	**0.635**	-0.196	**0.608**
SRL	0.149	**0.715**	-0.142	0.542
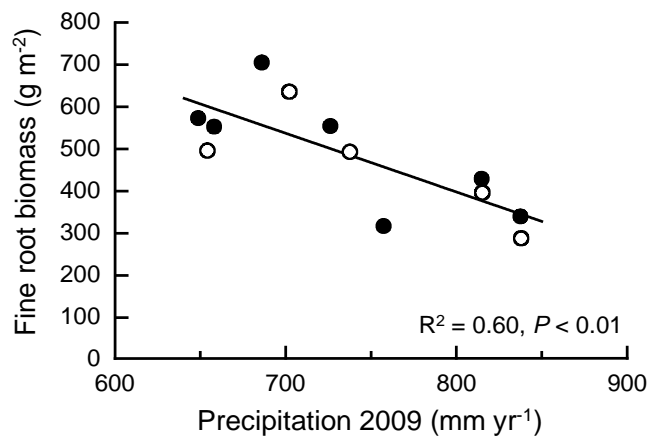
Figure 5.2. Relationship between fine root biomass (organic layer and 0-30 cm of mineral soil) and the annual precipitation of the study year 2009 for the 12 *Fagus sylvatica* stands. Open circles mark the loam-richer plots, filled circles the sandy plots.

The dependence of fine root biomass on soil texture was not visible in the multiple regression but showed up in a significantly higher fine root biomass in the stands on sandy soil as compared to those on loam-richer soil when precipitation was equal (525 ± 52 vs. 463 ± 58 g m^{-2}, $P < 0.01$). The variation in mean fine root necromass (dead fine roots) showed a less clear picture across the 12 stands (Figure A.5.1). Despite a 40% larger mean necromass in the drier stands (<700 mm yr^{-1} MAP) as compared to the moister ones (>700 mm yr^{-1}) (687 ± 99 vs. 490 ± 69 g m^{-2}), fine root necromass showed a significant dependence neither on MAP nor on the precipitation of the study year (Table 5.3). The fine root live/dead ratio showed a slight but exponential increase from the wet to the dry stands (Table 5.3). The ratio was below unity in most of the stands in the wetter part of the transect but exceeded 1.0 in the 3 beech stands at the driest site Calvörde in the South-east (MAP <560 mm yr^{-1}). No systematic difference in the ratio was found between the stands on sandy and loam-richer soil.

Table 5.3. Results of linear or simple non-linear (*) regression analyses on the response of several root-related traits to mean annual precipitation (MAP) and annual precipitation in the study year (2009 or 2010) for the total data set (12 plots) or the sandy (7 plots) or loam-richer *Fagus sylvatica* plots (5 plots). Statistically significant relationships are printed in bold (P <0.05). The direction of the slope of the regression line is given in brackets.

Variable	Source							
	MAP		Annual precipitation in study year		Annual precipitation in study year		Annual precipitation in study year	
	All plots (N = 12)		All plots (N = 12)		Sandy plots (N = 7)		Loam-richer plots (N = 5)	
	R^2	P	R^2	P	R^2	P	R^2	P
Fine root biomass	**0.46** (-)	**<0.01**	**0.60** (-)	**<0.01**	**0.57** (-)	**<0.05**	**0.63** (-)	**<0.05**
Fine root necromass	0.01 (-)	0.36	0.07 (-)	0.21	0.03 (-)	0.36	0.17 (-)	0.25
Fine root live / dead ratio	**0.61* ** (-)	**<0.01**	**0.40* ** (-)	**<0.05**	0.42* (-)	0.06	0.32 (-)	0.16
RAI	**0.57** (-)	**<0.01**	**0.65** (-)	**<0.001**	**0.65** (-)	**<0.05**	**0.63** (-)	**<0.05**
RAI / LAI ratio	**0.49** (-)	**<0.01**	**0.63** (-)	**<0.01**	**0.62** (-)	**<0.05**	**0.70** (-)	**<0.05**
Percentage of RAI in organic layer	0.15 (-)	0.10	**0.36** (-)	**<0.05**	**0.49** (-)	**<0.05**	0.24 (-)	0.20
Annual fine root production	**0.59** (-)	**<0.01**	**0.67** (-)	**<0.001**	**0.83** (-)	**<0.01**	**0.81** (-)	**<0.05**
Fine root / leaf production ratio	**0.64** (-)	**<0.001**	**0.71** (-)	**<0.001**	**0.88** (-)	**<0.01**	**0.71** (-)	**<0.05**
Fine root production per unit LAI	**0.57** (-)	**<0.01**	**0.67** (-)	**<0.001**	**0.88** (-)	**<0.01**	**0.78** (-)	**<0.05**
Fine root turnover	0.05 (-)	0.25	0.13 (-)	0.12	0.15 (-)	0.20	0.33 (-)	0.15
Fine root diameter	0.18 (+)	0.08	0.06 (+)	0.22	**0.48** (+)	**<0.05**	0.08 (-)	0.32
Specific root area	0.03 (-)	0.30	0.00 (-)	0.36	**0.50** (-)	**<0.05**	0.04 (+)	0.32
Specific root length	0.03 (-)	0.29	0.00 (-)	0.48	**0.44** (-)	**<0.05**	0.07 (+)	0.33
Root tissue density	0.03 (+)	0.30	0.02 (+)	0.33	0.08 (+)	0.27	0.00 (+)	0.49
Specific root tip abundance	0.01 (+)	0.39	0.03 (-)	0.32	0.09 (-)	0.26	0.02 (+)	0.41
Mycorrhizal colonization rate	0.03 (+)	0.30	0.01 (-)	0.37	0.02 (+)	0.37	0.10 (-)	0.30

Table 5.4. Results of a multiple linear regression analysis on the influence of various climate (mean annual precipitation 'MAP', annual precipitation 2009 'AP2009', annual precipitation 2010 'AP2010'), soil physical/chemical (water storage capacity of the mineral soil and percent fine-grained soil particles, soil nutrient properties) and above-ground structural variables (stem diameter, stem density, stand basal area, timber volume and leaf area index) on the fine root biomass or fine root productivity in the 12 *Fagus sylvatica* stands. Given are the coefficients of determination (R^2) for each model as well as parameter estimates for the variables with significant influence that were included in the models, and the F and P values for these predictors. Significant predictors were only the two precipitation parameters AP2009 and AP2010, and the percentage contribution of fine particles to soil dry mass at marginal significance ($P = 0.07$).

Variable	Model R^2	Predictor (parameter estimate)		
Fine root biomass	0.60 (*P* < 0.01)	Intercept (1511.6) *F value: 31.9* *P < 0.001*	AP2009 (-1.35) *F value: 14.9* *P < 0.01)*	
Fine root production	0.77 (*P* < 0.01)	Intercept (1333.3) *F value: 46.1* *P < 0.001*	AP2010 (-1.35) *F value: 28.1* *P < 0.001*	ΣUT (-2.98) *F value: 4.1* *P = 0.07*

Fine root morphology and root area index

Fine root morphology was much less influenced by precipitation than fine root biomass, but showed a significant dependence on the soil horizon, i.e. the depth in the soil (Tables 5.2, 5.3 and 5.5). Mean root diameter d in the size class <2 mm (fine roots) varied between 0.35 and 0.58 mm across the 12 stands (Table 5.6) although fine root individuals showed no significant differences in their principal branching architecture (data not shown). Despite this large variation, mean fine root diameter showed no relation to MAP or annual precipitation in the study year when all 12 stands were considered (Tables 5.3 and 5.5). However, when the seven stands on sandy soil are analysed separately, mean root diameter decreased significantly with decreasing precipitation in the study year ($R^2 = 0.48$, Table 5.3) while no such effect existed for the stands on loam-richer soil. Similarly, specific root area (SRA) and specific root length (SRL) in the whole data set were not related to MAP or annual precipitation in the study year but showed a significant increase with decreasing annual precipitation in the study year when only the sandy plots were analysed (Table 5.3). All three traits (d, SRA and SRL) depended on the soil horizon (depth in soil) while the influence of soil texture (sandy vs. loam-richer soil) and of the texture x horizon interaction was not significant (Table 5.5).

Table 5.5. Results of a two-way Analysis of Variance (ANOVA) on the influence of two different soil texture classes (sandy vs. loam-richer soil) and three different soil horizons and the interaction of the two variables on various morphological traits of the live fine roots in the 12 *Fagus sylvatica* stands. Given are the F and *P* values of the three source variables and the coefficient of determination (R^2) of the model.

Variable	Source			
	Substrate	Soil horizon	Substrate x soil horizon	Model R^2
Fine root diameter	0.65 (n.s.)	9.49 ($P < 0.001$)	1.92 (n.s.)	0.042 ($P < 0.001$)
Specific root area	0.04 (n.s.)	28.74 ($P < 0.001$)	0.48 (n.s.)	0.098 ($P < 0.001$)
Specific root length	0.11 (n.s.)	22.91 ($P < 0.001$)	0.48 (n.s.)	0.080 ($P < 0.001$)
Root tissue density	0.78 (n.s.)	26.25 ($P < 0.001$)	0.19 (n.s.)	0.091 ($P < 0.001$)
Specific root tip abundance	1.16 (n.s.)	0.26 (n.s.)	0.16 (n.s.)	0.003 (n.s.)
Mycorrhizal colonizations rate	1.57 (n.s.)	4.74 ($P < 0.01$)	0.95 (n.s.)	0.018 ($P < 0.05$)

Fine root tissue density varied in its mean between 0.49 and 0.78 g cm^{-3} (Table 5.6) with no influence of precipitation or soil texture but a significant influence of soil horizon (Tables 5.3 and 5.5). However, this effect was weak (only 9% of the variation in tissue density explained). We found an unexpected relative invariance of specific root tip abundance (tips

per fine root dry mass) and of the percentage of root tips colonized by ectomycorrhizal fungi across the 12 beech stands. Root tip abundance (means of 17.2 – 36.1 tips mg^{-1}) and percental colonization rate (63.8 – 85.2%) were found to be influenced neither by precipitation nor by soil texture, but mycorrhizal colonization rate decreased significantly with increasing depth in the soil (Table 5.3 and 5.5).

The cumulative surface area of fine roots in the soil (root area index RAI in m^2 root surface area per m^2 ground area) ranged from c. 5 to 13 m^2 m^{-2} in the 12 stands (Figure 5.3A). Sites with >700 mm yr^{-1} MAP had a significantly smaller RAI (5.5 ± 0.2 m^2 m^{-2}) than sites with less than 700 mm yr^{-1} (10.3 ± 0.5 m^2 m^{-2}), and RAI was negatively correlated with precipitation ($R^2 = 0.57$ for MAP and 0.65 for the precipitation in the study year, Table 5.3, Figure 5.3A). The root area index to leaf area index ratio (RAI/LAI) more than doubled along the transect from <0.8 at the wet end to >1.6 at the dry end (Figure A.5.2). The finding of a significant increase from the wet to the dry stands in the proportion of fine root surface area that was located in the organic layer was unexpected (from c. 35 to 50 % of total RAI, Figure 5.3B). The increasing concentration of root surface area in the upper soil profile with decreasing annual precipitation was more pronounced in the sandy than the loam-richer soils ($R^2 = 0.49$ vs. 0.36, respectively, Table 5.3).
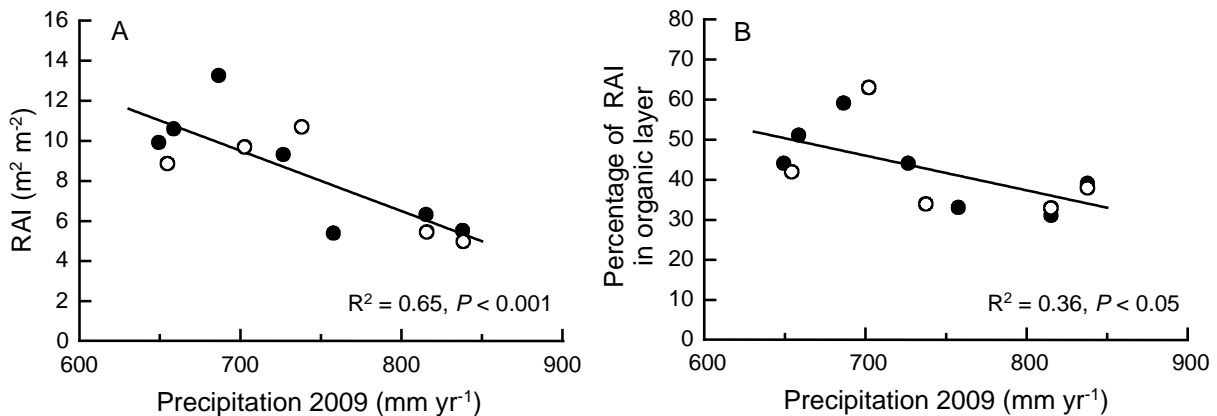
Figure 5.3. (A) Dependence of fine root area index (RAI, organic layer and 0-30 cm of mineral soil) on annual precipitation in the study year 2009 for the 12 *Fagus sylvatica* stands. (B) Fraction of RAI (in % of soil profile total) located in the organic layer as a function of annual precipitation in the study year 2009 for the 12 *Fagus sylvatica* stands. Open circles stand for the loam-richer plots, filled circles for the sandy plots.

Table 5.6. Summary of morphological traits of the live fine roots in the organic layer and two mineral soil horizons in the 12 *Fagus sylvatica* stands. Substrate types: sandy (sa) and loam-richer (lo). Given are means and standard errors for the second inventory in September 2009. Results of statistical analyses on significant differences between plots and between soil horizons are omitted for clarity. For a more general statistical analysis of the data, see Tables 5.3 and 5.5.

Plot no.	1	2	3	4	5	6	7	8	9	10	11	12
Site code	Se	Se	Un	Un	Oe	Go	Go	Kl	Kl	Ca	Ca	Ca
Substrate type	lo	sa	lo	sa	sa	lo	sa	lo	sa	lo	sa1	sa2
Fine root diameter (mm)												
Organic layer	0.37 ± 0.01	0.45 ± 0.03	0.40 ± 0.03	0.38 ± 0.01	0.42 ± 0.01	0.44 ± 0.01	0.38 ± 0.01	0.35 ± 0.01	0.38 ± 0.01	0.39 ± 0.01	0.38 ± 0.02	0.37 ± 0.01
0-10 cm mineral soil	0.40 ± 0.02	0.52 ± 0.05	0.42 ± 0.02	0.38 ± 0.02	0.47 ± 0.03	0.49 ± 0.02	0.41 ± 0.02	0.39 ± 0.01	0.41 ± 0.01	0.41 ± 0.02	0.42 ± 0.02	0.39 ± 0.02
10-30 cm mineral soil	0.41 ± 0.02	0.44 ± 0.02	0.45 ± 0.02	0.44 ± 0.03	0.42 ± 0.02	0.58 ± 0.07	0.39 ± 0.02	0.48 ± 0.04	0.47 ± 0.03	0.38 ± 0.01	0.41 ± 0.02	0.38 ± 0.02
Specific root area (cm^2 g^{-1})												
Organic layer	219 ± 24	193 ± 22	175 ± 11	198 ± 11	201 ± 17	168 ± 12	202 ± 10	259 ± 25	189 ± 13	185 ± 11	210 ± 10	214 ± 16
0-10 cm mineral soil	233 ± 32	159 ± 20	178 ± 16	188 ± 15	198 ± 19	129 ± 15	137 ± 14	156 ± 11	150 ± 9	184 ± 19	159 ± 8	187 ± 10
10-30 cm mineral soil	196 ± 16	147 ± 11	136 ± 13	147 ± 10	162 ± 18	108 ± 8	158 ± 6	135 ± 12	131 ± 10	156 ± 10	151 ± 10	181 ± 16
Specific root length (m g^{-1})												
Organic layer	20.2 ± 3.3	15.7 ± 2.7	15.2 ± 1.4	17.5 ± 1.3	15.6 ± 1.6	12.5 ± 1.0	16.9 ± 0.9	24.7 ± 3.0	16.5 ± 1.7	15.9 ± 1.3	18.3 ± 1.3	19.0 ± 1.7
0-10 cm mineral soil	20.0 ± 3.0	12.1 ± 2.3	14.4 ± 1.7	16.4 ± 1.9	14.9 ± 1.9	9.4 ± 1.4	11.5 ± 1.7	13.2 ± 1.4	12.1 ± 1.0	15.5 ± 1.7	12.5 ± 1.0	16.2 ± 1.5
10-30 cm mineral soil	16.2 ± 1.8	11.5 ± 1.2	10.8 ± 1.6	11.8 ± 1.4	13.0 ± 1.8	7.1 ± 0.8	13.4 ± 1.1	10.7 ± 1.5	10.0 ± 1.2	13.6 ± 1.2	12.8 ± 1.2	16.6 ± 2.0
Root tissue density (g cm^{-3})												
Organic layer	0.55 ± 0.04	0.54 ± 0.04	0.62 ± 0.02	0.56 ± 0.02	0.58 ± 0.11	0.58 ± 0.03	0.53 ± 0.02	0.49 ± 0.04	0.60 ± 0.03	0.59 ± 0.02	0.52 ± 0.02	0.55 ± 0.04
0-10 cm mineral soil	0.51 ± 0.03	0.55 ± 0.02	0.60 ± 0.04	0.59 ± 0.03	0.49 ± 0.03	0.71 ± 0.06	0.78 ± 0.05	0.67 ± 0.03	0.69 ± 0.03	0.61 ± 0.03	0.62 ± 0.03	0.58 ± 0.02
10-30 cm mineral soil	0.54 ± 0.03	0.68 ± 0.04	0.74 ± 0.04	0.66 ± 0.02	0.61 ± 0.05	0.78 ± 0.07	0.66 ± 0.02	0.71 ± 0.04	0.71 ± 0.02	0.72 ± 0.04	0.71 ± 0.03	0.65 ± 0.04
Specific root tip abundance (n mg^{-1})												
Organic layer	29.4 ± 4.4	24.7 ± 5.9	23.9 ± 3.5	23.1 ± 3.3	29.9 ± 3.6	27.4 ± 4.3	30.6 ± 6.5	22.1 ± 2.5	24.3 ± 4.4	26.2 ± 3.2	22.1 ± 2.9	30.7 ± 4.1
0-10 cm mineral soil	36.1 ± 6.1	28.1 ± 4.9	27.5 ± 4.2	25.7 ± 4.1	34.1 ± 6.3	21.4 ± 4.8	31.3 ± 4.8	21.4 ± 3.6	21.3 ± 3.5	26.0 ± 4.2	22.1 ± 3.8	32.9 ± 4.1
10-30 cm mineral soil	33.3 ± 4.7	26.3 ± 4.7	19.2 ± 3.5	28.4 ± 5.2	33.4 ± 5.7	17.2 ± 4.2	24.0 ± 4.9	25.5 ± 4.5	19.1 ± 3.6	29.7 ± 3.6	26.4 ± 3.9	34.1 ± 3.9
Mycorrhizal colonization rate (%)												
Organic layer	76.0 ± 4.8	80.5 ± 4.3	72.3 ± 5.2	76.6 ± 6.1	85.2 ± 3.1	80.5 ± 4.9	81.2 ± 4.2	71.7 ± 5.7	76.4 ± 4.2	75.3 ± 4.6	76.7 ± 4.5	79.0 ± 4.5
0-10 cm mineral soil	77.3 ± 4.5	69.1 ± 6.8	73.1 ± 5.8	73.8 ± 5.6	76.5 ± 4.5	67.2 ± 6.8	73.1 ± 4.9	63.8 ± 6.1	70.4 ± 5.0	74.4 ± 6.0	77.7 ± 4.1	79.1 ± 3.7
10-30 cm mineral soil	73.6 ± 3.7	73.4 ± 5.1	70.0 ± 4.8	65.6 ± 5.0	75.6 ± 3.9	75.5 ± 5.8	68.3 ± 5.3	68.6 ± 5.4	67.4 ± 4.2	75.8 ± 4.5	71.4 ± 4.8	77.8 ± 2.8

Fine root production and turnover

Annual fine root production as estimated in 2010 with the ingrowth core approach ranged from 139 to 479 g m^{-2} yr^{-1} (Table A.5.1) and more than doubled with a decrease in annual precipitation from 820 to 680 mm (R^2 = 0.71, P < 0.001, Table 5.3 and Figure 5.4A). The precipitation effect was larger in the plots on sandy soil when compared with the loam-richer plots as is shown by a larger mean slope of the regression line (increase by 166 g m^{-2} yr^{-1} per 100 mm yr^{-1} of precipitation decrease vs. 83 g m^{-2} yr^{-1} per 100 mm yr^{-1}). In paired plots with equal precipitation, estimated annual fine root production was 35% higher on the sandy soils (mean: 300 ± 44 g m^{-2} yr^{-1}) than on the loam-richer soils (221 ± 27 g m^{-2} yr^{-1}), but the difference was not significant (P = 0.11). Correspondingly, the multiple regression analysis identified the precipitation of the study year as the only significant parameter influencing fine root production (the effect of soil texture was only marginally significant, Table 5.4).

The ratio of annual fine root to leaf production increased significantly with decreasing MAP (Table 5.3) and with decreasing annual precipitation in the study year 2010 (Figure 5.5A). As for annual fine root production, the fine root/leaf mass production ratio showed a steeper increase with decreasing precipitation in stands on sandy than on loam-richer soil (increase by 0.56 vs. 0.27 units per 100 mm decrease in precipitation; R^2 = 0.88 and 0.71). The amount of fine root biomass produced per unit leaf area index revealed a corresponding increase with decreasing precipitation (Figure 5.5B and Table 5.3) with the slope being steeper on sandy soil (27 g m^{-2} yr^{-1} productivity increase per unit LAI with 100 mm yr^{-1} precipitation reduction) than on loam-richer soil (12 g m^{-2} yr^{-1} per 100 mm yr^{-1}).

The stand means of fine root turnover (root biomass produced per standing root biomass) ranged from 0.36 to 0.84 yr^{-1} in the 12 stands (Figure 5.4B, Table A.5.1) and showed a (non-significant) trend of a moderate increase with decreasing precipitation (Table 5.3). The increase in turnover rate with precipitation reduction was marginally significant in the stands on sandy soil (R^2 = 0.39, P = 0.07) when the precipitation of the vegetation period (April to September 2010) was considered (data not shown).
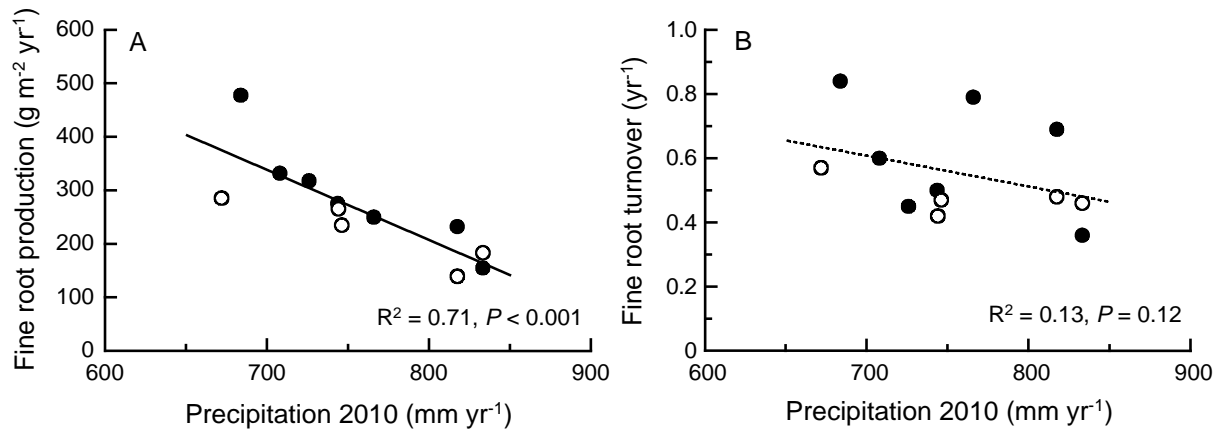
Figure 5.4. Dependence of annual fine root production in 2010 (organic layer and 0-20 cm of mineral soil; ingrowth core data; A) and fine root turnover (B) on annual precipitation in the study year 2010 for the 12 *Fagus sylvatica* stands. Open circles stand for the loam-richer plots, filled circles for the sandy plots.
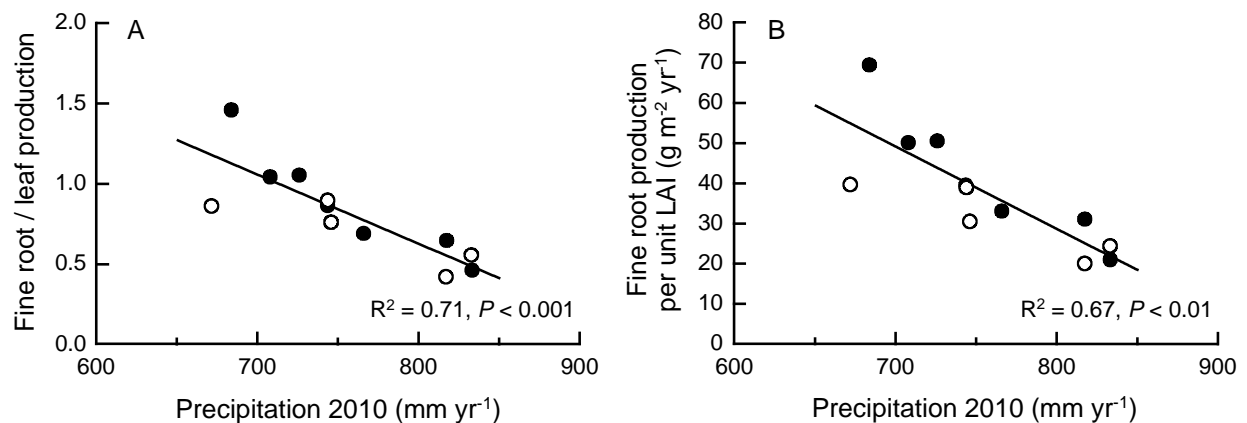
Figure 5.5. (A) Ratio of annual fine root production and annual leaf production in 2010 as a function of annual precipitation in the study year 2010 for the 12 *Fagus sylvatica* stands (B) Relationship between annual fine root production scaled to leaf area index and annual precipitation in the study year 2010 for the 12 *F. sylvatica* stands. Open circles stand for the loam-richer plots, filled circles for the sandy plots.

Discussion

Evidence in support of optimal partitioning theory

With a fine root biomass increase by c. 140 g m^{-2} per precipitation reduction of 100 mm yr^{-1}, our transect data seem to support optimal resource partitioning theory. Fine root biomass and the cumulative surface area of fine roots in the soil (RAI) nearly doubled across the transect with a reduction in MAP by c. 270 mm yr^{-1} (and in precipitation of the study year by c. 190 mm yr^{-1}), while leaf area index and annual leaf production remained unchanged. As a consequence, the ratio of water absorbing to transpiring plant surfaces (RAI/LAI) roughly doubled from the wet to the dry end of the transect as it is predicted by optimal partitioning theory in response to increasing water shortage.

One may argue that our root inventory in the organic layer and the mineral soil to 30 cm depth might have missed changes in fine root biomass in deeper soil layers. However, this is not very likely because earlier inventories to a soil depth of 350 cm in beech forests on similar sandy soils in the centre of the transect indicated that more than 75% of the profile total of fine root biomass is located in the upper 30 cm (similarly strong concentrations of the fine root biomass in upper *versus* deeper soil depths were also found in beech stands on different substrate/soil types, Leuschner *et al.* 2004). Moreover, from the wet to the dry stands, we found an increasing, and not a decreasing, proportion of fine root biomass in the uppermost organic layer. The complete fine root biomass inventories further showed that secondary peaks of fine root density in moist subsoil horizons are virtually absent in this Pleistocene substrate which is probably a consequence of its very low nutrient content and high acidity (cation exchange capacity <40 µmol$_c$ g^{-1}, base saturation mostly <15%, pH(H$_2$O) 4.0-4.4). Despite this evidence, we cannot exclude the possibility that a few deep-reaching roots function as 'high capacity roots' in terms of water absorption at the drier sites, i.e. that their functional role is much more important than their biomass.

To our knowledge, our finding of an increase in R:S ratio and in the absolute amount of fine root biomass with decreasing precipitation is the first convincing support of optimal partitioning theory when applied to mature trees under the influence of increasing water shortage. This result contradicts our first hypothesis that referred to the observation of a positive MAP-fine root biomass relation in *F. sylvatica* stands in a transect study on sandstone in central German pre-montane forests (Meier & Leuschner 2008a) as well as on a analysis of literature data (Leuschner & Hertel 2003), thus supporting a type (iii) drought response of the roots (see Introduction). In contrast to the data set of the literature meta-

analysis, the 2 transect studies are well comparable as they consist of 12 or 14 beech stands covering similar precipitation gradients (816 - 543 and 970 - 520 mm yr^{-1} MAP). However, they are located on largely different soils (silicate-poor sandy diluvial deposits vs. silicate-rich Triassic sandstone) with important consequences for the fine root system of *F. sylvatica*. A much higher base saturation in the mineral soil (means of 10 and 40 % in the sand vs. sandstone transects) and pH(H$_2$O) in the organic layer (4.0 vs. 5.0) are probably the cause of more than three times larger fine root biomass and higher fine root necromass in the sand transect (this study, see Table 5.7). Moreover, the thicker organic layers on sand contained a much higher proportion of fine root biomass (37 vs. 9 % of the fine root biomass total on average) indicating that the mineral soil across the sandy soil transect was less favourable for nutrient (and perhaps also water) uptake than the sandstone soils in the study of Meier & Leuschner (2008a). The fine root biomass of *F. sylvatica* and other temperate tree species tends to increase with decreasing nutrient supply, in particular lowered N availability (Aber *et al.* 1985; Vogt *et al.* 1987; Leuschner & Hertel 2003; Leuschner *et al.* 2004), which probably represents a compensatory fine root growth response to low uptake rates. In this context, an important role is probably played by base saturation which was high (>90 %) at the dry end of the sandstone transect but remained low (10-30 %) across the entire sandy soil transect. Thick organic layers on top of the mineral soil obviously are a key requisite for *F. sylvatica* for maintaining large fine root systems. In fact, the fine root biomass in the 12 stands of our study (mean: 482 g m^{-2}) was high compared to the pan-European mean given for *F. sylvatica* by Finér *et al.* (2007). In the drier base-rich stands of the sandstone transect, elevated litter decomposition rates are reducing organic layer depth, thus forcing the roots to abandon this nutrient-rich but dry horizon; this is not the case in the transect on sandy soil.

We assume that a drought-induced increase of fine root biomass as predicted by optimal resource partitioning theory is possible in *F. sylvatica* only, when a thick organic layer is present atop the acidic and nutrient-poor mineral soil, where a dense fine root system can successfully forage for resources. If our results are more generally valid, this would indicate that the fine root biomass response of *F. sylvatica* trees to a precipitation decrease is dependent on additional factors that are not considered in optimal partitioning theory. One such factor seems to be nutrient availability, in particular the supply of base cations, nitrogen or phosphorus, which probably influences the size and structure of tree fine root systems besides water availability. We therefore cannot fully exclude that such effects might have caused the sand vs. loam fine root biomass differences additionally to the differences in soil

water availability between both soil texture types. This, however, would still indicate optimal resource partitioning.

It is also possible that optimal resource partitioning theory cannot adequately predict root system size in forest stands with different water availabilities because root water uptake is not necessarily closely related to the size (biomass or surface area) of the fine root system, but may depend more on differences in the specific uptake rates of the absorbing fine roots as was shown by Leuschner *et al.* (2003). *F. sylvatica* trees growing on sandy soil with low nutrient content and a rapid percolation of infiltrating water could require a larger fine root system to meet their water and nutrient demand when compared with beech trees on the more fertile sandstone soils with higher water retention capacity.

Table 5.7. Summary table comparing selected climatic, stand structural and soil chemical parameters (means, minima and maxima) for the precipitation transects in mature beech forests studied by Meier & Leuschner (2008) and in this study. The transect of Meier & Leuschner (2008) comprised 14 mature beech stands on silicate-rich acid Triassic standstone in the central German uplands, the transect of this study covers 12 mature beech stands on silicate-poor acid Pleistocene sandy deposits in the northern German lowlands. The trends of the parameters along the precipitation gradient from moist to dry is also indicated (+ increase, - decrease, 0 no trend, indicators given in brackets indicate statistically prevalent trends that are not of significant effect size). Please note that the fine root biomas and necromass numbers in the study of Meier & Leuschner (2008) refer to the organic layer plus 0-20 cm mineral soil while the numbers in this study refer to the organic layer plus 0-30 cm mineral soil. Additional data from the sandstone transect were provided by I.C. Meier.

Parameter	Sandstone sites (Meier & Leuschner 2008)				Sandy sites (this study)			
	Mean	Min	Max	Trend with precipitation decrease	Mean	Min	Max	Trend with precipitation decrease
Elevation (m a.s.l.)	320	230	440	-	99	72	130	(-)
MAP (mm yr^{-1})	721	520	970	-	677	543	816	-
MAT (°C)	7.8	7.1	8.3	+	8.8	8.5	9.2	+
Tree age (yr)	126	90	157	0	118	87	142	0
Basal area (m^{-2} ha^{-1})	33	21	49	0	32	24	45	0
Thickness of organic layer (cm)	5.3	3.5	7.2	-	7.3	4.1	9.1	0
pH(H$_2$O) (organic layer)	5.0	4.4	5.9	+	4.0	3.8	4.5	0
C/N (mineral soil) (g g^{-1})	18	15	23	0	19	12	26	-
Base saturation (%) (mineral soil)	47	15	92	+	10	3	24	(-)
Al $_{exch}$ (mmol kg^{-1}) (mineral soil)	30	5	50	-	18	12	29	0
Fine root biomass (g m^{-2})	139	43	288	-	482	289	704	+
Percent root biomass org. layer (%)	9.0	0.02	55	-	37	24	53	0
Fine root necromass (g m^{-2})	287	76	573	0	605	320	1165	0

Does water limitation alter fine root morphology?

Trees may adapt to reduced water availability not only by adjusting the size and positioning of their absorbing root surface area, but also by modifying root morphology and physiology in order to increase uptake efficiency under unfavourable conditions (Lõhmus *et al.* 1989; Eissenstat *et al.* 2000; Hertel & Wesche 2008; Ostonen *et al.* 2011). Producing thinner fine roots with larger surface area and greater length per unit carbon invested may help to optimise the cost-benefit ratio of fine root operation of a tree (Eissenstat and Yanai 1997; Eissenstat *et al.* 2000; Pregitzer *et al.* 2002; Ostonen *et al.* 2007). Thus, root morphological plasticity would represent one strategy of trees to respond to increasing water limitation (Eissenstat 1992; West *et al.* 2004). One of the few reports from adult trees is the observation by West *et al.* (2004) of a decreasing mean fine root diameter with increasing soil water limitation in *Pinus palustris* trees. In their comparison of five mature stands of *F. sylvatica* differing in precipitation and soil chemistry, Leuschner *et al.* (2004) did not find marked alterations in fine root morphology, while Meier & Leuschner (2008a) reported an increase in specific fine root area (SRA) and a corresponding decrease in mean fine root diameter with decreasing rainfall in their transect study.

We did not find consistent adaptive modifications in fine root morphological properties with decreasing precipitation, but a specific response that was restricted to the drier beech stands on sandy soil and that only occurred in the uppermost organic soil horizon. Similar to the transect of Meier & Leuschner (2008a), specific root length and root area (SRL and SRA) increased and average fine root diameter decreased with decreasing precipitation in this subset of plots. However, no modification was observed in the loam-richer soils with higher water storage capacity, which supports our hypothesis (v) about the soil texture effect on rooting patterns. Since periderm thickness and the number of suberin-coated cell layers typically increase in parallel with root diameter in ageing tree fine roots (e.g. Leuschner *et al.* 2003), thinner roots should in general be more drought-sensitive than thicker ones (van Hees 1997; Enstone *et al.* 2002; Metcalfe *et al.* 2008; Schreiber & Franke 2011). If applied to the *F. sylvatica* transect, this assumption implies that the trees in the drier stands are suffering from a higher drought-induced mortality of their fine absorbing roots and thus experience a reduction in mean fine root age, because rootlets are replaced by new ones with thinner diameter and larger surface area. Thus, soil desiccation may rejuvenate the fine root system of a tree with a possible positive effect on root relative growth rate and water absorption capacity at the cost of a higher carbohydrate demand for root growth because turnover is increased.

This hypothesis needs testing by direct observation of root longevity with rhizoscopes, a task that has recently been started in our plots on sandy soil.

Other root morphological traits such as root tissue density (RTD) and specific root tip abundance remained invariant across the precipitation gradient and were not influenced by soil texture. Similarly, the colonization rate of the tips by ectomycorrhizal fungi did not vary systematically from the wet to the dry end of the transect and was apparently unrelated to the decrease in mean fine root diameter in the stands on sandy soil. Since we did not investigate the fungal communities that formed ectomycorrhizae with the roots of *F. sylvatica*, we do not have information on possible functional changes in the root symbiosis along the precipitation gradient as it was assumed in earlier studies (e.g. Espeleta *et al.* 1999; Eissenstat *et al.* 2000).

Stimulation and inhibition of tree root growth by water shortage

Given the widely acknowledged importance of tree fine root production for the global C cycle (Nadelhoffer & Raich 1992; Vogt *et al.* 1996; Jackson *et al.* 1997; Gill & Jackson 2000), our limited understanding of the controls of fine root growth and mortality in forests is unsatisfactory. Stimulation of root growth would match with the predictions of optimal resource partitioning theory, but such a response depends on the availability of carbohydrates that may be short in supply when photosynthetic C gain declines due to drought-induced reductions in leaf conductance and/or leaf area. Thus, resource partitioning according to theory might not occur when water limitation or other stressors result in C source limitation of growth. Consequently, water limitation may either stimulate or reduce the fine root production of trees with largely different consequences for above-ground productivity and stem growth, and the C cycle in forests (Eissenstat *et al.* 2000; Norby & Jackson 2000). The 'tipping point' between increased or reduced C allocation to root growth is most likely species-specific and may depend on the soil environment and the stress history of the trees.

Besides precipitation, soil texture and the water storage capacity of the soil were identified as additional, but only secondary, influential factors of fine root productivity in our study; this is evident from the much more pronounced precipitation effect on productivity observed on sandy as compared to loam-richer soils. In fact, the estimated productivity was 35% higher on sandy soils than on loam-richer soils in our study. It could be that a stimulation of root growth by soil desiccation is more prominent in stands on infertile and acidic soils where the trees are producing large and more dynamic fine root systems; this would also offer an explanation for the lacking stimulation effect on root growth in the transect study on sandstone of Meier &

Leuschner (2008a) where both standing fine root biomass and root productivity were considerably smaller than in this study.

Soil drought has been found in short-term experiments to accelerate fine root turnover due to reduced root longevity (Eissenstat *et al.* 2000; Gaul *et al.* 2008). However, it is not clear whether mature trees are responding with compensatory root growth when exposed to reduced water availability for years or the entire life, and as to whether short-term acclimation and long-term adaptation lead to similar plant responses. In a literature review of tree fine root productivity data, Finér *et al.* (2011b) found only a weak effect of annual precipitation on the tree fine root production in boreal, temperate and tropical forests. This conclusion matches the findings of Vogt *et al.* (1996) in an earlier review. However, both studies found that the explanatory power of precipitation and other climate factors for the variation in fine root productivity increased when individual species or species groups instead of the whole data set were analysed. In the few studies, where the root productivity of a tree species or a forest type was compared at sites with contrasting water availability, higher productivities at drier sites were observed (Santantonio & Herman 1985; Comeau & Kimmins 1989; West *et al.* 2004).

In *F. sylvatica*, the results from short-term drought studies and long-term site comparisons are also not fully consistent. Leuschner *et al.* (2001a) found a stimulation of beech fine root production on sandy soil after a severe summer drought period while Mainiero & Kazda (2006) detected no effect on root productivity of a severe summer drought on loamy soil and Meier & Leuschner (2008a) found no growth stimulation toward drier beech stands in the transect on sandstone.

With respect to fine root turnover (root production per standing root biomass, or the inverse of root longevity), mature beech trees either showed higher rates in drier soil or exhibited no precipitation sensitivity. While Mainiero & Kazda (2006) did not observe a significant change in fine root turnover of mature trees in an exceptionally dry summer in 2003, Leuschner *et al.* (2001a) reported a compensatory increase in fine root production of *F. sylvatica* trees after a period of drought-induced higher fine root mortality in a mature stand.

Global meta-analyses of literature data by Gill & Jackson (2000) and Lauenroth & Gill (2003) indicate only a weak or no precipitation effect on the turnover rate of tree fine roots. Increased turnover of tree fine roots has been observed as a response to single drought events when root mortality increased and was followed by compensatory regrowth of fine roots (Leuschner *et al.* 2001a; Konopka *et al.* 2005; Gaul *et al.* 2008). In contrast, West *et al.* (2004) and Mainiero & Kazda (2006) did not find a significant alteration in fine root turnover

in periods of soil desiccation. We observed a rise in turnover rate, or a reduction in mean root lifespan, with decreasing precipitation only in the *F. sylvatica* stands on sandy soil (marginally significant, $P = 0.07$), but not in those on loam-richer soil. In the beech gradient study of Meier & Leuschner (2008a) on sandstone, turnover also increased with a precipitation decrease. Root turnover would remain constant with a reduction in precipitation when the stimulation of root production as a response to increased mortality results in a proportional increase in standing root biomass. This seems to have happened in the beech stands on loam-richer soil, where no increase in turnover with decreasing precipitation was found, while the stimulation of production apparently was larger in the sandy soils where both productivity and mortality increased in excess of the increase in standing biomass toward the drier stands, and thus fine root turnover tended to be faster. The fact that mean fine root diameter decreased towards the drier stands on sandy soil in our transect fits into this picture. Thinner, less costly fine roots with a putative higher specific water absorption rate are more rapidly substituted by newly grown roots at the drier sites which may optimise the cost/benefit ratio of root construction and maintenance (Eissenstat *et al.* 2000; Eissenstat and Yanai 2002) and reduce the respiration costs when soil conditions are unfavourable during drought (Bryla *et al.* 1997). Our data further indicate that the carbon transfer to the soil via root growth and death increases in *F. sylvatica* forests with decreasing precipitation, and that soils with low water storage capacity further enhance this flux.

Conclusions

This precipitation transect study about the adaptive response of the fine root system of *F. sylvatica* produced convincing evidence that optimal resource partitioning theory can also explain the below-ground response of mature trees to water limitation. The strong increase in standing fine root biomass and fine root productivity with decreasing precipitation demonstrates the high degree of allocational plasticity in mature *F. sylvatica* trees which certainly is a key functional trait enabling this species to be competitive in both high- and low-precipitation environments and to occupy an extraordinarily broad climatic and edaphic niche space (Leuschner *et al.* 2006; Ellenberg & Leuschner 2010). Plasticity in root morphology was found to be a secondary factor but it increases the below-ground adaptive potential of beech in particular on the more extreme sandy soils. Not much is known about the plasticity of root physiological traits in mature trees as water availability changes. Rewald *et al.* (2011) discuss several adaptive mechanisms including osmotic adjustment of root tissue,

changes in specific water absorption rates due to differential aquaporin activity, and hydraulic adaptation that could improve root performance under exposure to water limitation, but the significance of these mechanisms in mature forests is not known.

However, comparison with other studies on the topic shows that the below-ground response of *F. sylvatica* to water limitation is not fully explained by optimal partitioning theory alone. Rather, fine root system adaptation seems to depend largely on the local growing conditions, in particular the severity of water limitation. Further, root responses appear to be modified by plant age and may even be over-ruled by drought-induced carbon limitation of growth. There is a need for additional studies on root system adaptability in mature trees that cover a broader range of site conditions in order to develop a valid picture of the whole-tree drought response of *F. sylvatica* and other tree species.

Our data confirm the perception that the impact of water limitation on plant vitality and growth may be traced to independent climatic (precipitation) and edaphic components (water storage capacity). By including soil texture and the related WSC as an independent variable in the study design, we were able to show that water limitation is acting on the beech root system mainly through the climatic pathway, but that soil texture has a significant, yet secondary, influence as well. Consequently, predictions about the possible climatic change impact on the vitality of *F. sylvatica*, and also of other tree species, cannot solely rely on the modelling of future precipitation regimes, but also have to consider water storage capacity. This is equally valid for forestry planning. From this study in mature stands, we conclude that *F. sylvatica* has a remarkable potential for permanently modifying the size and structure of its fine root system to cope with precipitation amounts <600 mm yr^{-1} and to explore soils with unfavourable water storage properties, but the existence of an intact thick organic layer seems to be of paramount importance at such sites.

Acknowledgements

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Appendices
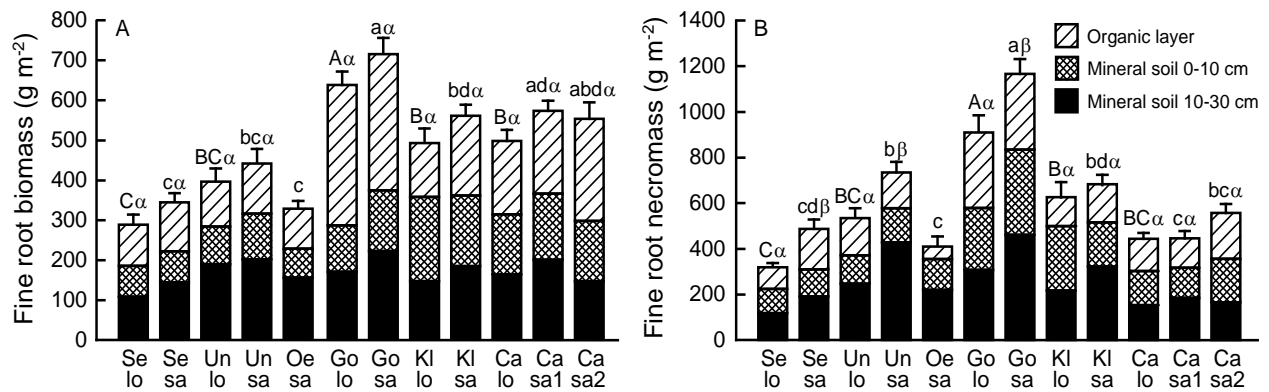
Figure A. 5.1. Fine root biomass (A) and fine root necromass (B) in the organic layer and the upper 30 cm of the mineral soil in the 12 *Fagus sylvatica* stands. Given are means and standard errors from two inventories (June and September 2009) the data of which were averaged. Different capital Latin letters indicate significant differences among the loam-richer ('lo') plots, different small Latin letters indicate significant differences among the sandy ('sa') plots, and different small Greek letters indicate significant differences between the pairs of sandy and loam-richer at a site ($P < 0.05$).
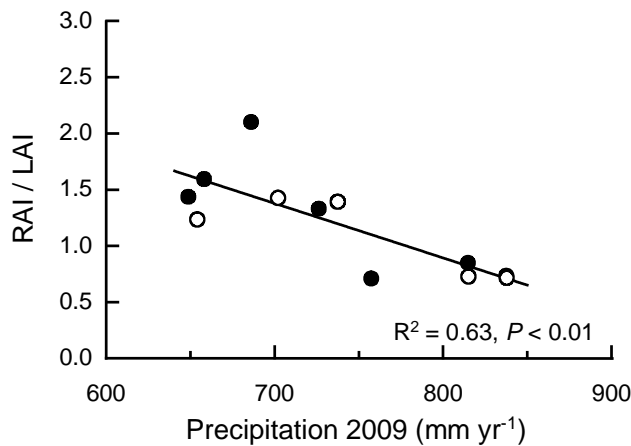
Figure A. 5.2. Change in the ratio of root area index (RAI) and leaf area index (LAI) as a function of annual precipitation in the study year 2009 for the 12 *Fagus sylvatica* stands. Open circles stand for the loam-richer plots, filled circles for the sandy plots.

Table A. 5.1. Annual fine root production and turnover (organic layer and 0-20 cm of mineral soil) in the 12 *Fagus sylvatica* stands in the year 2010 (means ± SE). The loam-richer plots are marked by 'lo', the sandy plots by 'sa'. Different Latin capital letters mark significant differences among the loam-richer plots; different small Latin letters differences among the sandy plots, and different small Greek letters significant differences the paired sandy and loam-richer plots at a site ($P < 0.05$).

Plot No.	1	2	3	4	5	6	7	8	9	10	11	12
Site code	Se	Se	Un	Un	Oe	Go	Go	Kl	Kl	Ca	Ca	Ca
Substrate	lo	sa	lo	sa	sa	lo	sa	lo	sa	lo	sa1	sa2
Fine root production ($g\ m^{-2}\ yr^{-1}$)	139 ± 11 B α	234 ± 11 bc β	183 ± 20 AB α	156 ± 24 c α	251 ± 33 bc	265 ± 36 A α	319 ± 21 B α	234 ± 24 AB α	277 ± 28 bc α	285 ± 24 A α	479 ± 38 a β	333 ± 31 ab α
Fine root turnover (yr^{-1})	0.48 ± 0.04 A α	0.69 ± 0.07 ab β	0.46 ± 0.05 A α	0.36 ± 0.05 b α	0.79 ± 0.10 a	0.42 ± 0.06 A α	0.45 ± 0.03 b α	0.47 ± 0.05 A α	0.50 ± 0.05 ab α	0.57 ± 0.05 A α	0.84 ± 0.07 a β	0.60 ± 0.06 ab α

Chapter 6

Synthesis

Climatic and hydrologic influences on growth and partitioning in mature beech forest stands on Pleistocene soils in Northern Germany

With predicted decreases in summer rainfall over wide parts of central Europe, limited water availability is assumed to increasingly constrain the vitality and productivity of *Fagus sylvatica* (Manthey and others 2007; Sutmöller and others 2008). This relationship is in general attributed to a drought-sensitive stomatal reaction in beech (Epron and others 1995; Backes and Leuschner 2000; Granier and others 2000, 2007; Geßler and others 2004). However, the majority of estimations on climate-productivity relationships are derived from investigations of only single aspects of biomass production, mostly from dendro-ecological analyses of stem increment. The present study attempts to develop a more comprehensive understanding of growth responses of *F. sylvatica* to long-term alterations in water availability and varying climatic growing conditions by including all components of biomass production (except coarse root growth) of mature beech trees in closed forest stands. For this purpose, the entire aboveground biomass production of 12 mature beech stands on similar geological substrate but differing in the exposure to climatic and edaphic drought was recorded in detail during 3 study years (2009-2011; Chapter 3). In order to assess the biomass production and nutrient allocation within the forest canopy in reaction to short-term climatic variations, litter production of 4 years (2009-2012) was examined (Chapter 4). In addition, fine root biomass and morphology as well as fine root production was investigated in 2009 and 2010, respectively (Chapter 5).

Is the productivity of mature beech forest stands controlled by precipitation and soil water availability?

In this study, the sensitivity of growth responses to variations in water availability was shown to largely differ between aboveground and belowground components of biomass production. As shown in Chapter 3, the annual production of wood, leaf and fruit biomass was not found to be markedly influenced by current year precipitation parameters. Nevertheless, on average within the 3 study years, wood mass production (and $RSVI_a$) significantly decreased with decreasing MAP (by ~ 40 g m^{-2} y^{-1} and 0.26 % y^{-1} per 100 mm decline in annual precipitation, respectively; Table 6.1). Likewise, leaf mass production (and LAI) decreased toward the dry end of the transect when averaged over the 3 study years, however this trend was less pronounced than the trend for wood production (decreases by ~ 16 g m^{-2} y^{-1} and 0.35 m^2 m^{-2} per 100 mm rainfall decline, respectively). The reduction of leaf mass and LAI was predominantly induced by a reduction in leaf number towards the drier sites; the

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latter result was also found in a former transect study in *F. sylvatica* (Meier and Leuschner 2008b). As beech exhibits a pronounced masting behaviour, the production of fruit biomass showed a very high inter-annual variability between mast years (2009 and 2011; mean = 360 $\pm$ 35 g m^{-2} y^{-1}) and non-mast years (2010 and 2012; mean = 16 $\pm$ 2 g m^{-2} y^{-1}), whereas masting appeared synchronously at all sites. Contrary to vegetative growth, the production of fruit biomass over the total observation period significantly increased towards the drier and warmer sites (Table 6.1).

Regarding the total aboveground biomass production (NPP$_a$; sum of wood, leaf and fruit biomass production), only little evidence was found for a precipitation control of productivity along the studied rainfall gradient. During the 3-year observation period, intra-annual variation of NPP$_a$ across the transect was low and showed no correlation with annual rainfall (or precipitation totals for the growing season). Even when averaged for the entire observation period, NPP$_a$ in the 12 study stands (875 $\pm$ 27 g m^{-2} y^{-1}) remained fairly unaffected by alterations of the long-term precipitation regimes (Table 6.1). The inter-annual comparison of biomass production and weather conditions in this study suggested that the time of occurrence of water shortage during the phenological cycle might be more influential to the aboveground productivity than the hydrologic regime during the entire growing season. In spite of comparable rainfall patterns between the study years, the aboveground biomass production in 2010, when water shortage emerged during the early-summer, was reduced by ~ 25% on all sites compared to 2009 (late-summer drought) and 2011 (late-spring drought). This is in line with results of many dendro-ecological studies, in which precipitation or water availability during early summer was identified as the most crucial climatic parameter for stem increment (Dittmar and others 2003; Lebourgeois and others 2005; Friedrichs and others 2009; Scharnweber and others 2011; Michelot and others 2012; van der Maaten 2012).

In contrast to the aboveground biomass components, belowground biomass and productivity were found to be highly responsive to variations in current hydrologic conditions as shown by results presented in Chapter 5. Both fine root biomass and annual fine root production doubled from the moist to the dry end of the transect, increasing by ~140 g m^{-2} and ~130 g m^{-2} y^{-1} per 100 mm decline in annual precipitation, respectively (Table 6.1). These findings contradict observations of a positive precipitation effect on the productivity of fine root biomass in *F. sylvatica*, obtained in a rainfall gradient study (520-970 mm y^{-1}) on sandstone in Central German pre-montane forests (Meier and Leuschner 2008a) and also in a pan-European analysis of published root studies from beech forests (Leuschner and Hertel 2003).

In spite of such significant response in belowground biomass growth, the approximation of total NPP in 2010 along the rainfall gradient revealed that the overall productivity of beech on Pleistocene sands is mostly independent from annual precipitation parameters. NPP varied surprisingly little between the 12 stands (mean = 965 ± 27 g m^{-2} y^{-1}; Figure 6.1), and no tendency of decline in total biomass production was found in relation to a reduction in MAP (by c. 270 mm y^{-1}) or to the rainfall decrease in the study year (by c. 190 mm y^{-1}). This result was particularly unexpected as the dry end of the studied precipitation gradient (543-816 mm y^{-1}) comes close to the natural drought-induced distribution limit of *Fagus sylvatica* in Central Germany (Kölling and others 2007; Leuschner 2009).

In addition, the sensitivity of growth response to variations in water holding capacity of the soils was found to differ between above- and belowground biomass growth. While the results suggested that soil texture shows little influence on the aboveground biomass growth, both root biomass and fine root production were significantly higher on drier plots with sandy soils in comparison to the loam-richer sites (Table 6.1).
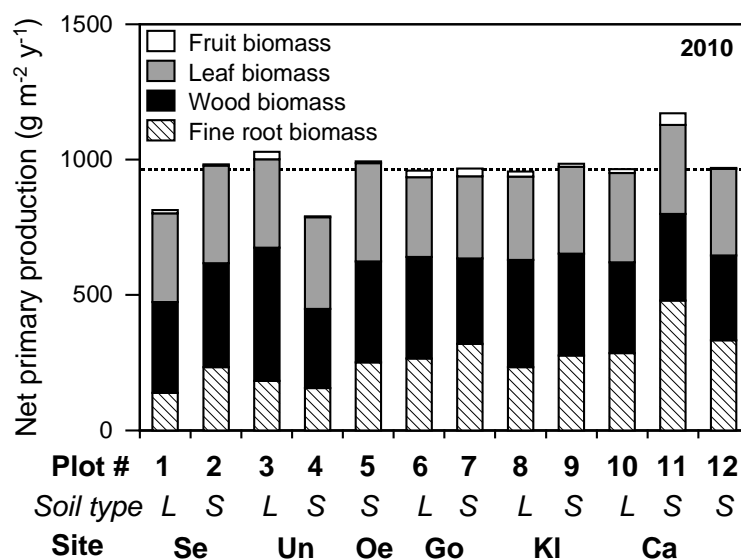
Figure 6.1. Net primary production (NPP) of 12 mature beech forests in Northern Germany in 2010. Study plots arranged following to decreasing MAP. Dotted line illustrates mean value for all study plots (mean = 965 ± 27 g m^{-2} y^{-1}). Soil type codes are 'L' for loam-richer soils, and 'S' for sandy soils.

Table 6.1. Parameters of aboveground and belowground biomass and production across the studied matrix of climatic and edaphic drought. Given are the mean and the range (min-max) and, in case of significance, the alteration per 100 mm precipitation decrease (MAP or annual precipitation figures) obtained from simple linear regression analysis. Supercript 'a' indicates a significantly steeper precipitation-effect on sandy compared to loamy sites (according to type-III sum of squares). Influence by different substrate classes 'loamy-sandy' (L) and 'sandy' (S) was tested applying paired t-tests for paired plots with equal precipitation (after testing for normal distribution and homoscedasticity). Significance levels: $^{+}P < 0.1$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

Parameter	Unit	Mean	(Range)	Variation per 100 mm precipitation decrease	Substrate class comparison
Aboveground biomass 2009 - 2011				with MAP	
Timber volume	$m^3\ ha^{-1}$	414.8	(227-758)	n.s.	
NPP_a	$g\ m^{-2}\ y^{-1}$	875.1	(785-1103)	n.s.	
Wood mass production	$g\ m^{-2}\ y^{-1}$	336.1	(256-512)	-41.0 *	
RSVI	$\%\ y^{-1}$	1.24	(0.63-1.95)	-0.26 *	L<S *
Leaf mass production	$g\ m^{-2}\ y^{-1}$	296.9	(267-334)	-16.3 **	
LAI	$m^2\ m^{-2}$	6.97	(6.2-7.9)	-0.35 *	
Leaf number	$n\ m^{-2}$	3780	(3141-4301)	-295.88 **	
Leaf size	cm^2	18.1	(16.0-19.9)	0.25 $^{+}$	
SLA	$kg\ m^{-2}$	23.7	(22.3-24.7)	n.s.	
Fruit mass production	$g\ m^{-2}\ y^{-1}$	242.2	(56-336)	42.29 *	L>S *
<u>Fractions of NPP_a</u>					
Wood biomass	%	39.2	(32.0-50.4)	-3.46 *	
Leaf biomass	%	35.4	(30.3-42.5)	n.s.	
Fruit biomass	%	25.4	(7.1-33.1)	4.71 **	L>S *
Belowground biomass 2009				with P_{2009}	
Fine root biomass	$g\ m^{-2}$	482	(290-705)	139.2 **	L<S ***
Fine root necromass	$g\ m^{-2}$	605	(320-1165)	n.s.	L<S *
RAI	$m^2\ m^{-2}$	8.32	(4.97-13.2)	3.01 ***	
RAI:LAI	$m^2\ m^{-2}$	1.19	(0.71-2.10)	0.48 **	
Fine root diameter	mm	0.39	(0.35-0.45)	n.s.	
SRA	$cm^2\ g^{-1}$	201	(168-259)	n.s.	
SRL	$m\ g^{-1}$	17.3	(12.5-24.7)	n.s.	
Above- and belowground biomass production 2010				with P_{2010}	
Fine root production	$g\ m^{-2}\ y^{-1}$	263	(139-479)	130.8 *** ^{a}	L<S *
Root turnover	y^{-1}	0.55	(0.36-0.84)	n.s.	
NPP	$g\ m^{-2}\ y^{-1}$	965	(790-1170)	89.3 *	
Root:leaf production	$g\ g^{-1}$	0.81	(0.42-1.46)	0.43 * ^{a}	
Stem:root production	$g\ g^{-1}$	1.53	(0.67-2.69)	-0.89 ***	L>S **
<u>Fractions of NPP</u>					
Wood biomass	%	37.4	(27.4-47.8)	-6.69 **	L>S *
Leaf biomass	%	34.2	(28.0-42.8)	-4.79 * ^{a}	
Fruit biomass	%	1.65	(0.39-3.67)	n.s.	
Fine roots	%	26.8	(17.1-40.9)	10.84 ***	L<S **

Allocational and morphological acclimation responses in mature beech to varying climatic and hydrologic conditions

While the productivity of mature beech was found to be largely unaffected by hydrologic conditions, patterns of biomass production exhibited a high degree of allocational plasticity and – to a lesser extent – also morphological plasticity in response to changes in water availability and climatic growing conditions. Aboveground partitioning between wood, leaves and fruit biomass showed a significant alteration along the studied gradient. These shifts, as well as inter-annual variability between these three fractions, were not primarily due to changes of the precipitation regimes but instead induced by fluctuating fruit production.

The fraction of wood production to total aboveground productivity was c. 40 % on average during the entire study period (44 % vs. 36 % of NPP_a on sites with MAP > 700 and MAP < 700 mm y^{-1}, respectively; Table 6.1) and continuously decreased with declining precipitation (Figure 6.2a). Results of a separate study on xylem anatomy in dominant beech trees on only the sandy sites of this transect also showed morphological adaption in the hydraulic architecture of the trees to climatic drought: with declining annual rainfall, vessel diameters in branchlets of the sun canopy were shown to decrease, probably as a prevention to avoid drought stress-induced xylem embolism, but simultaneously reducing conductivity for water to the transpiring leaf surfaces (Schuldt and others, in prep.).

Only little evidence was found for adaptive responses to drought stress of leaf growth. The fraction of leaf biomass production showed only small inter- and intra-annual variation along the gradient (2009-2011: 35.4 ± 1.1% of NPP_a) and only a slight increase toward the moister sites. In accordance with former gradient studies on leaf production and leaf morphology of beech (Leuschner and others 2006; Meier and Leuschner 2008b), an adaption of the transpiring surfaces to shifting hydrologic regimes was not observed in this study. A strong influence on leaf production and leaf morphology was found for resource competition between fruits and leaves, resulting in smaller and, moreover, lighter leaves in mast years (see below). In contradiction to an expected drought adaption, leaf size was found to slightly increase toward the dry end of the transect (Table 6.1). This confirms results obtained in former rainfall gradient studies in which increasing leaf size was related with rising LAI towards the drier sites (Hertel and others 2004; Meier and Leuschner 2008b). This effect is presumably explained by influences of co-varying increases in temperature (and possibly N availability) during the phase of leaf growth, which usually takes place before summer drought periods emerge. In line with Meier and Leuschner (2008b), leaf size in non-mast

years was most positively correlated to the mean temperature in the current year's spring (April and May, $R^2 = 0.60$, $p < 0.001$).
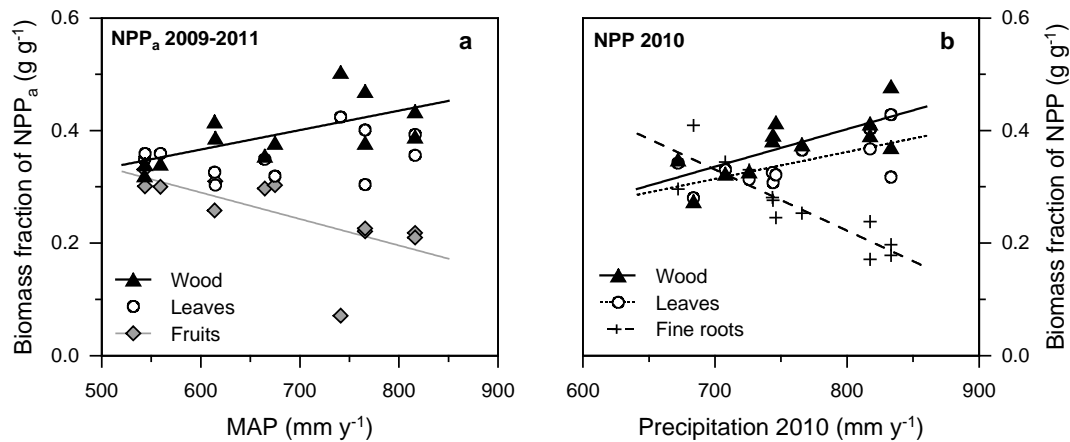
Figure 6.2. Biomass partitioning in relation to precipitation parameters for aboveground productivity (NPP$_a$) in the years 2009-2011 (a), and for total above- and belowground productivity (NPP) in 2010 (b). a) Wood, leaf and fruit production as fractions of NPP$_a$ (averaged for the years 2009-2011) in relation to MAP. Fraction of NPP$_a$ as a function of MAP for wood production: y = 15.9 + 0.03x, $R^2 = 0.42$, $p = 0.01$; for leaf production: n.s.; for fruit production: y = 57.3 - 0.05x, $R^2 = 0.46$, $p < 0.01$. b) Wood, leaf and fine root production as fractions of NPP in relation to annual precipitation 2010. Fraction of NPP as a function of annual precipitation for wood production: y = -0.132 + 0.001x, $R^2 = 0.53$, $p < 0.01$; for leaf production: y = -0.021 + 0.0005 x, $R^2 = 0.42$, $p = 0.01$; for fine root production: y = 1.03 – 0.001x, $R^2 = 0.76$, $p < 0.001$. Figures of fruit production (insignificant throughout the transect in 2010) omitted for clarity.

With high inter-annual variability (0.5-57.2 % of NPP$_a$), the fraction of fruit biomass in total aboveground productivity increased significantly toward the drier sites of the transect (Figure 6.2a). In Chapter 4, the role of different climate parameters for the proximate control of masting patterns was analysed in detail. Contrary to common assumption, the pattern of fruit production in beech was shown to be largely independent of hydrologic regimes and unaffected by the experience of increased drought and heat stress. The results of this analysis strongly suggest that above-average levels of solar radiation during early summer trigger floral induction and thus strongly determine the fructification response in the following growing season. A sudden increase in fruit production beyond a certain radiation level suggests fructification as a threshold-controlled reaction to enhanced levels of canopy carbon gain. Besides climatic influences, a key role for the plant-internal N level as the potential driver for the temporal pattern of masting events was derived from resource dynamics upon masting observed in this study. The climate-controlled induction of fruiting was found to be the most influential factor for aboveground biomass partitioning along the climate gradient. In line with results of former studies on C allocation in woody plants, vegetative growth was

suppressed upon masting by the high sink strength of reproductive structures (Koenig and Knops 1998; Drobyshev and others 2010). Among the aboveground biomass components, especially stem increment was shown to be sensitively affected by simultaneous fruit growth. Detailed examination of resource competition between leaf and fruit growth showed that the utilization of nutrients and photosynthates for fruit production resulted in impaired development of leaf mass and leaf area, and furthermore, considerably lowered the foliar N content in the mast and even in the post-mast year. Accordingly, reproductive growth did not only impose direct costs (i.e., the export of photoassimilates toward developing fruits), but also indirect costs on aboveground vegetative growth, as both a reduction in leaf area and a lowered foliar N content probably led to a reduction in carbon gain (Jarvis and Leverenz 1983; Evans 1989). Owing to an ample plasticity in SLA, the reduction in LAI with increasing resource allocation to fruit growth was somehow attenuated compared to the decrease in leaf mass production.

Several adaptive responses of tree fine root systems to water shortage are known. According to the optimal resource partitioning theory, increased drought exposure should stimulate the plants to allocate relatively more carbon and nutrients to fine root growth in order to optimise their capacity for resource acquisition (Poorter and Nagel 2000). Besides an adjustment of the size of the fine root system (biomass or surface area), growth responses may also entail modifications regarding the morphology and the spatial distribution of fine roots (Lõhmus and others 1989; Lynch 1995; Eissenstat and others 2000; Hertel and Wesche 2008; Ostonen and others 2011). Results of this study revealed a substantial response in aboveground vs. belowground partitioning in reaction to both investigated factors of water availability – precipitation and soil water storage. With almost unvarying total biomass production (NPP) over the 12 study sites (and negligible fruit production) in 2010, the portions of wood and leaf mass production significantly decreased ($R^2 = 0.53$, $p < 0.01$ and $R^2 = 0.42$, $p = 0.01$; Figure 6.2b), while the fraction of fine root production significantly increased with decreasing annual precipitation ($R^2 = 0.76$, $p < 0.001$). Correspondingly, the ratio of fine root:leaf production (in terms of dry mass as well as surface area) increased significantly toward the drier sites, which, in line with Linder and others (1985) and Cannell (1989), was strongly related to decreasing allocation of resources toward wood production (Figure 6.3). In addition to allocational adaption processes, it was shown in Chapter 5 that mature beech trees may also react to increasing water deficit by a distributional shift and by adjusting the fine root morphology. With decreasing rainfall, absorbing root surface area increasingly concentrated in the thick organic layers, which thereby gained importance for the acquisition of water and nutrients at

the drier sites. Also specific root area and root length (SRA and SRL) were found to increase with decreasing precipitation, but this response was restricted to drier beech stands on sandy soils. These results partly contradict findings reported by Meier and Leuschner (2008a) who observed that with declining annual rainfall, the ratio of fine root area to leaf area was significantly shifted to the disadvantage of the root surface and that the fine root abundance in the organic layer decreased on drier sites. Instead of a size adjustment of the fine root system in response to increasing water deficit, the cited study reports an acceleration of fine root turnover and – in line with observations of the present study – morphological alterations which are suited to enhance root water uptake per unit carbon invested.
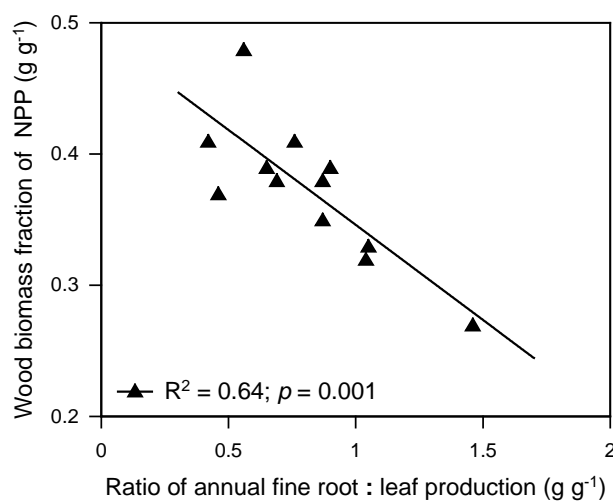
Figure 6.3. Wood production as fraction of NPP as dependent on the ratio of annual fine root:leaf production in 12 mature beech forest stands in Northern Germany in 2010.

Besides precipitation, soil texture was also shown to affect above- vs. belowground partitioning; on paired plots with equal precipitation, belowground biomass production was elevated (by 57.2 ± 11.3 g m^{-2} y^{-1}, marginally significant) and aboveground production was reduced (by 42.6 ± 20.9 g m^{-2} y^{-1}, not significant) on plots with sandy soils in comparison to the loam-richer sites (Table 6.1). Moreover, the water holding capacity of the soils notably influenced the precipitation effect on above- vs. belowground partitioning: over the entire rainfall gradient, the study plots with a more fine-grained soil texture showed an elevated wood mass fraction and a smaller fine root fraction of total NPP (Figure 6.4a, b). Hence, a significantly higher stem:root ratio in production was found for the beech stands on loam-richer soils along the transect (Figure 6.4c). According to linear regression analysis, the deviation in stem:root ratios which was induced by different water storage capacities between the two substrate classes corresponded to a difference in annual precipitation of c. 40-60 mm.

These findings on allocational responses to variations in the two main factors of water availability provided convincing evidence that adaption of mature beech trees to increasing water shortage occurs in accordance with the optimal partition theory. It is most likely that this high degree of plasticity in biomass partitioning is one key factor for the ample tolerance of this tree species toward a wide range of climatic growing conditions (Ellenberg and Leuschner 2010).
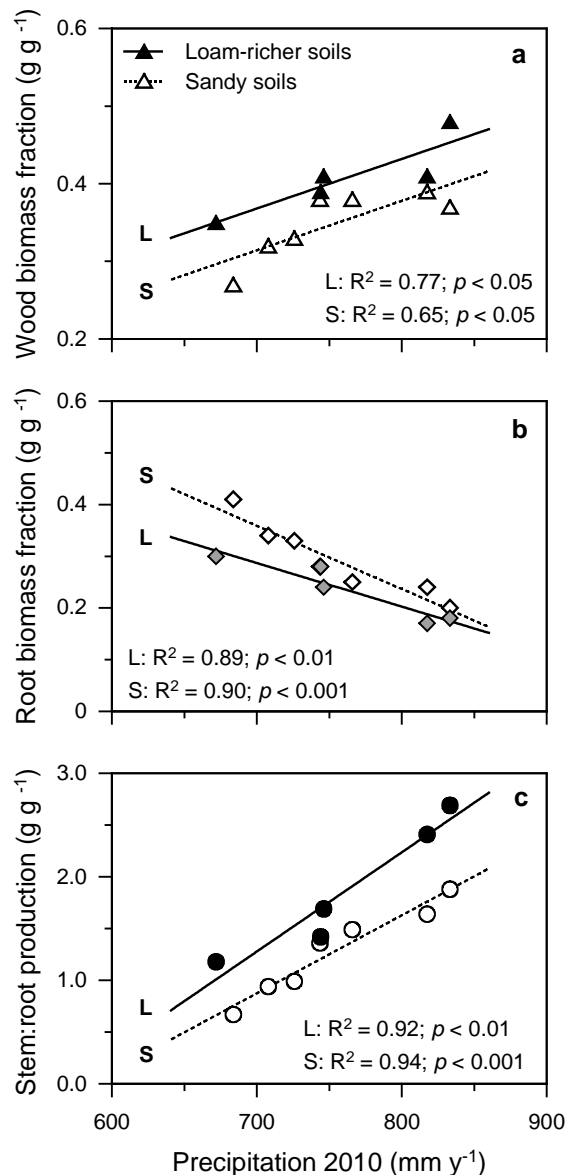
Figure 6.4. Aboveground and belowground partitioning of biomass in response to precipitation and soil texture in 12 mature beech forest stands in Northern Germany in 2010. Production of wood biomass (a) and fine root biomass (b) as fraction of NPP, and ratio of annual stem:root production (c), for sites on loam-richer (N=5) and sandy soils (N=7), separately.

Future threats to productivity and vitality of beech by climate change

Facing a predicted increase in summer drought events for large parts of Central Europe, the future role of beech for forestry is estimated very differently. Some studies concluded that beech may lose its competitive superiority toward more drought tolerant tree species (Rennenberg and others 2004; Geßler and others 2007), whereas other authors emphasize a high drought tolerance and high resilience in succession to severe drought events (Ammer and others 2005; Kölling and others 2007, 2010). In any case, the drought resistance of this species is assumed to play a decisive role for its presence and persistence at lower altitudes in Central Europe.

Recent dendro-ecological studies report a decline in productivity of beech stands on dry sites in Northern and Central Germany and identify critical precipitation thresholds of ~ 600 mm y^{-1} (annual precipitation) or ~ 190 mm (summer precipitation; June-August) on sandy or loamy soils (Scharnweber and others 2011, Zimmermann and others in prep.). Based on projections on summer precipitation decreases by 10-30 % (depending on region, scenario and model approach) until the end of this century compared to 1971-2000 (Spekat and others 2007; Jacob and others 2008; Moseley and others 2012), successful cultivation of *F. sylvatica* could be threatened by future shortfalls in water availability at many current beech forest sites.

From the findings in this study, a more detailed picture on growth responses of beech to decreasing water availability emerges. The present results confirm a constrained stem wood production on sites with long-term annual rainfall amounts < 600 mm y^{-1} (~260 g m^{-2} y^{-1}; averaged for 2009-2011) in comparison to the sites with a more favourable water balance (~360 g m^{-2} y^{-1}). However, limited wood production was not related with a decrease in total productivity, but resulted solely from altered resource allocation in response to low water availabilies. Neither belowground productivity nor total biomass production declined at the dry end of the rainfall gradient used in this study (543-816 mm y^{-1}) and – contrary to thresholds derived from ring width studies – no evidence was found for limitation of productivity with annual (or summer-) precipitation even below 510 mm y^{-1} (or 160 mm, June-August). This is convincing indication that long-term adaption processes enable mature beech trees to tolerate such low rainfall regimes without exceeding early stages of drought stress. In particular, investigations of the belowground biomass production revealed a remarkable potential to absorb long-term water shortage and to cope with annual rainfall regimes < 600 mm y^{-1} by permanent modification of size and structure of the fine root system. A high plasticity in resource partitioning might constitute a crucial trait for an effective

adaptability of beech and for a lowered climate-sensitivity of beech stands on dry as compared to moderate-dry sites (Friedrichs and others 2009; Scharnweber and others 2011; Weber and others 2012). However, in connection with pronounced early summer drought (50-60 mm in June-July), aboveground productivity was significantly reduced, which might in parts be explained by enhanced resource partition to belowground production.

Especially stem increment was found to be affected by allocation shifts, as this biomass fraction varied most widely under the influence of resource dedication towards fruit- and root growth (wood production took up 16-60 % of NPP_a between mast and non-mast years; 27-47% of NPP in a non-mast year). This reflects the low priority of wood growth among competing life-history traits (Epron and others 2012; Sala and others 2012). As silviculture is also geared toward the optimization of timber yield, an economic assessment of future beech cultivation will differ from forest-ecological evaluations.

The lowest proportion of wood production and lowest stem:root ratios were found at the sites with the highest climatic drought, but also at sites with moderate precipitation regimes in combination with low water storage capacities of the soils. This illustrates that climatic thresholds can only serve as an approximation and that, among other site factors, especially soil physical properties should be considered in estimations of possible climate change impacts on the vitality of *F. sylvatica* and other tree species (Betsch and others 2011). The water-holding capacity of the soils will even gain in importance for future water availability, as a decrease of summer rainfall is projected to occur in company with increasing summer dry spell duration, like already found in Northern Germany by 36 % for the period 1951-2005 (Haberlandt and others 2010).

Decreasing summer precipitation, increased air temperature and increases in frequency and intensity of heat waves and dry spell periods will contribute in varying degree to local drought stress in forest ecosystems. In addition, further stresses for forest ecosystems are likely to derive from increases in, e.g., atmospheric CO_2 concentration, N availability and length of the growing period, as also from increasing intensities of infestation by insect pests and pathogens, storms and severe rainfall events. For the period 1881-2010, an increase in sunshine duration during summer by 5 % was recorded for Northern Germany (Moseley and others 2012). The findings on climatic control of reproduction behaviour in this study illustrate that already small variations in solar radiation have the potential to provoke great effects on the allocation behaviour of beech and to substantially alter forest productivity and forest biogeochemical cycles. Hence, if radiation-rich summer conditions and high

atmospheric N depositions further result in an increased frequency of masting as recorded over the last three decades in central and northern Europe, fructification might be another source of limitation for vegetative growth of beech in future.

The presented findings were obtained in beech forests on lower Pleistocene sandy (or sandy-loamy) soils which are common over the Northern German lowlands. Therefore, growth reactions of beech depicted here can be assumed to be representative for this region. During this study period, drought emerged at different intensity and seasonality. However, growth reactions to extreme drought conditions, as they occurred in Central Europe in 1976 or in 2003, could not be investigated in this study. Therefore, the present findings do not allow for the identification of critical thresholds related to reductions in rainfall or soil moisture but rather are suited to analyse basic mechanism of a long-term drought response in this drought-susceptible tree species. When applying these mechanisms to regionalised precipitation scenarios, it must therefore be considered that future vitality of beech might be to a large extent determined by the frequency of severe drought events.

Conclusions

From this study on above- and belowground productivity and allocation in mature *Fagus sylvatica* stands under varying exposure to climatic and edaphic drought, the following conclusions can be drawn:

-   Annual (or growing season) measures of water availability exert no or little influence on productivity in the beech forests in the Northern German lowlands. Instead, NPP_a and stem wood production were found to be primarily controlled by water availability in the peak growing period (June and July).

-   In reaction to varying water availabilities, beech exhibits a high plasticity in aboveground vs. belowground resource allocation, which proves drought adaption of mature beech trees to comply with the optimal partition theory.

-   Highly drought-sensitive modification of the size and the structure of the fine root system indicate an effective long-term adaptation to low water availability which enables *Fagus sylvatica* to maintain undiminished productivity under annual rainfall regimes < 600 mm y^{-1} on sandy soils.

-   Leaf production and leaf morphology in beech are fairly unresponsive to long-term alterations in the local climatic water balance.

-   Floral induction in beech is very likely triggered by enhanced photosynthetic carbon gain in early summer (June and July) preceding a mast year; large shifts of C and N allocation towards developing fruits impair aboveground vegetative growth and reduce the assimilation capacity in the mast year and the following year.

-   Stem increment is not a reliable measure of productivity in beech, as varying resource allocation toward fruit and fine root growth largely alters the proportion of wood production to NPP.

-   Biomass partitioning in beech is highly responsive to both climatic and edaphic influences on water availability; therefore, assessments of future regional-scale drought impacts on tree vitality should include local water storage capacities of the soil.

Especially the high degree of allocational plasticity in mature trees, as shown in this study, certainly is a key functional trait enabling *Fagus sylvatica* to be competitive under high to low-precipitation conditions and to occupy a broad climatic and edaphic niche breadth.

Further research recommendations

To evaluate the importance of long-term adaptation for current drought-resistance and sensitivity in short term reactions to severe water deficits, studies along natural precipitation gradients should be combined with artificial rainfall exclusion.

In order to develop a more comprehensive picture of the whole-tree drought response, research on safety margins in the hydraulic system and on responses of C assimilation and plant respiration to drought periods in adult beech stands should be intensified.

To elucidate reasons for contrasting findings on the behaviour of fine root growth with decreasing water availability in different studies, the influence of soil acidity and nutrient availability on belowground C partitioning patterns should be investigated under a broader range of site conditions.

In order to deepen the understanding on the masting behaviour of *F. sylvatica* and to refine models of future forest productivity, detailed observations of C assimilation und fluctuation of NSC and N compounds in trees between mast years and non-mast years should be conducted at sites differing in nitrogen and water availability.

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Chapter 7

Summary

Summary

European beech (*Fagus sylvatica* L.) is by far the most abundant tree species of Central Europe's natural forest vegetation and one of the economically most important trees in Germany. Although this late-successional tree species shows a wide physiological tolerance toward a broad range of climatic and edaphic growing conditions, beech is known to be relatively drought sensitive when compared to other broad-leaved temperate forest trees. As man-made climate change is likely to impair the climatic water balance during the growing season and to increase the frequency of severe drought events over large parts of Central Europe, the future role of beech in forestry is under current debate. Thus, this study aimed at investigating the influence of hydrologic and climatic conditions on the productivity and vitality of beech and to identify basic mechanisms of a long-term adaption to water deficits in this drought-susceptible tree species. For this purpose, above- and belowground biomass production was studied in 12 mature beech forest stands along a natural rainfall gradient (543-816 mm y^{-1}) on uniform sandy geological substrate in the Northern German Lowlands. To consider the potential effect of soil water storage on the precipitation-response, this study was carried out in paired beech stands with similar climatic conditions but growing on sites with contrasting soil texture (sandy vs. sandy-loamy). Influences of water availability and climatic variations on growth patterns were investigated by monitoring (i) total above- and belowground biomass production, (ii) carbon partitioning and resource allocation dynamics, and (iii) morphology of the water absorbing and transpiring surfaces in response to climatic alterations.

Quite unexpectedly, differences of annual (or growing season) water availability across the climatic gradient were found to exert only little influence on the productivity of mature beech stands, as neither aboveground NPP (NPP$_a$) nor total NPP showed a decrease towards the dry end of the transect. However, NPP$_a$ and stem wood production were found to be primarily controlled by hydrologic conditions in the current peak growing period (June and July). Along the precipitation gradient, a pronounced continuous shift in the patterns of biomass partitioning emerged, resulting in higher fine root production and decreased aboveground:belowground productivity at the drier sites. Unlike aboveground biomass components, fine root production in mature beech was shown to react highly responsive toward changes in water availability. In line with the optimal partitioning theory, this allocational behaviour could be observed in response to decreasing precipitation but also with decreasing soil water storage capacity. Such allocational adaption processes to water shortage

were complemented by morphological plasticity (increased surface:biomass ratio) and adjustment of the positioning (increasing concentration of fine roots in the organic layers) of the fine root system. Leaf morphological alterations, however, were not found as a part of long-term adaption to changing hydrologic regimes in mature beech.

Fructification was found to be a second important factor for allocational shifts in beech, as a large C allocation toward fruit growth strongly impaired aboveground vegetative growth, especially stem wood increment. For a high sink strength for C and N, fruit growth caused decreases in the weight and size of single leaves and thereby reduced a production of leaf biomass and LAI. Besides decreases in leaf area, pronounced foliar N depletion upon masting assumably lowered the canopy C assimilation in the mast and even in the post-mast year. Observed patterns in the fructification response to solar radiation suggest that floral induction in beech is a threshold controlled reaction to enhanced levels of canopy carbon gain in early summer (June-July) preceding the mast year. By these findings, the temporal pattern of a masting response to climatic cues in beech appears to be feedback-controlled by plant-internal N dynamics and, with continuing high N deposition loads, from this mechanism may arise additional burden for future vegetative growth in beech.

A high degree of allocational plasticity in mature trees certainly constitutes an integral part of long-term adaptability of *Fagus sylvatica* to a wide range of hydrologic regimes which may also support resistance and resilience to single severe drought events.

Zusammenfassung

Die Rotbuche (*Fagus sylvatica* L.) ist die bestimmende Baumart der potentiell natürlichen Vegetation in den Wäldern Mittel- und Westeuropas die ökonomisch bedeutsamste Laubbaumart Deutschlands. Obwohl diese spät-sukzessionelle Baumart über eine hohe physiologische Toleranz gegenüber einem weiten Spektrum klimatischer Wuchsbedingungen verfügt, wird die Buche gegenüber anderen temperaten Laubbaumarten als relativ trockensensitiv eingeschätzt. Da im Zuge des globalen Klimawandels mit einer Verschlechterung der klimatischen Wasserbilanz und mit einer Zunahme sommerlicher Trockenperioden gerechnet wird, wird die zukünftige Rolle der Rotbuche in der europäischen Forstwirtschaft derzeit intensiv diskutiert. Diese Studie hatte zum Ziel, hydrologische und klimatische Einflüsse auf die Produktivität und die Vitalität der Rotbuche zu untersuchen. Hierdurch sollen grundlegende Mechanismen der Trockenstressantwort bei dieser trocken-sensitiven Art identifiziert, und Rückschlüsse auf zukünftige Klimaantworten von Buchenbeständen ermöglicht werden. Zu diesem Zweck wurde die ober- und unterirdische Biomasseproduktion von 12 Buchenaltbeständen im Norddeutschen Tiefland entlang eines natürlichen Niederschlagsgradienten (543-816 mm a^{-1}) auf einheitlichem geologischen Substrat ermittelt. Um den zusätzlichen Einfluss der Wasserspeicherkapazität der Böden zu berücksichtigen, wurden Paare von Buchenbeständen untersucht, die unter nahezu identischen klimatischen Bedingungen, jedoch auf Böden unterschiedlicher Textur (sandige versus lehmig-sandige Böden) stockten. Einflüsse der Wasserverfügbarkeit und klimatischer Variationen auf das Wachstum wurden untersucht unter Berücksichtigung (i) der gesamten ober- und unterirdischen Biomasseproduktion, (ii) der Dynamik von Ressourcen-Allokation und Kohlenstoff-Partitionierung, sowie (iii) der Morphologie wasseraufnehmender und -abgebender Oberflächen.

Unerwarteterweise zeigte sich die gesamte Produktivität von Buchen-Altbeständen nur geringfügig von Veränderungen der hydrologischen Regime entlang des Gradienten beeinflusst. Trotz deutlicher Unterschiede in der jährlichen Wasserverfügbarkeit nahmen die oberirdische und die gesamte Biomasseproduktion auf den trockeneren Flächen des Transektes nicht ab. Allerdings führten ausgeprägte früh-sommerliche Wasserdefizite (in den Monaten Juni und Juli) zu deutlichen Einbußen der oberirdischen Biomasseproduktion, und insbesondere der Stammholzproduktion. Entlang des untersuchten Gradienten konnte eine ausgeprägte, kontinuierliche Verschiebung der Allokationsmuster festgestellt werden: Mit abnehmender Wasserverfügbarkeit nahm die Feinwurzelproduktion zu und das Verhältnis von

oberirdischer:unterirdischer Biomasseproduktion ab. Anders als oberirdische Komponenten zeigte die Feinwurzelproduktion eine hohe Sensibilität gegenüber Unterschieden hinsichtlich hydrologischer Regime. In Übereinstimmung mit der Optimalitätstheorie der pflanzlichen Ressourcennutzung konnte dieses Allokationsverhalten in sowohl in Reaktion auf veränderte Niederschläge, als auch in Antwort auf auch veränderte Wasserspeicherkapazitäten beobachtet werden. Allokative Anpassungsmechanismen an Wassermangel wurden im Feinwurzelbereich zusätzlich durch morphologische Plastizität (Zunahme im Verhältnis von Oberfläche: Biomasse) und durch Regulierung der räumlichen Verteilung (zunehmende Konzentrierung von Feinwurzeln in der organischen Auflage) komplementiert. Im Gegensatz zu diesen komplexen unterirdischen Trockenheits-Antworten konnten keinerlei Anpassungen der Blattmorphologie an veränderte hydrologische Bedingungen festgestellt werden.

Neben Reaktionen auf Wasserverfügbarkeit wurde die Fruchtbildung als zweiter wesentlicher Einfluss auf das Allokationsverhalten der Buche erkannt. Eine deutliche Ressourcen-Allokation zu Gunsten der Fruchtentwicklung beeinträchtigte maßgeblich das oberirdische vegetative Wachstum, insbesondere den Stammholzzuwachs. Auf Grund einer hohen Attraktionsstärke der Früchte gegenüber C und N führte zunehmende Fruktifizierung auch zu einer Gewichts- (und Größen-) Abnahme der Einzelblätter und somit zu reduzierter Bildung von Blattmasse und Bestandesblattfläche (LAI). Neben dieser Abnahme an assimilierender Blattoberfläche führte auch eine deutliche Senkung der Blatt-Stickstoffgehalte in Folge der reproduktiven Ressourcenwidmung mutmaßlich zu einer Verschlechterung der C-Bilanz, sowohl im Mast- als auch im Folgejahr. Eine Analyse klimatischer Einflussfaktoren auf das Mastverhalten legt nahe, dass die Blütenbildung der Buche durch Überschreitung eines Schwellenwertes der Kohlenstoffassimilation im Frühsommer (Juni-Juli) induziert wird.

Sofern diese Schlüsse zutreffen, unterliegt das zeitliche Muster der Fruktifikations-Antwort auf Witterungsauslöser einer Rückkopplungskontrolle durch pflanzliche Stickstoff-Dynamik. Vor dem Hintergrund anhaltend erhöhter Stickstoffdepositionen ergäbe sich aus diesem Mechanismus eine zusätzliche Belastung für das zukünftige vegetative Wachstum der Buche.

Es ist anzunehmen, dass die in dieser Studie belegte hohe allokative Plastizität in Altbäumen *Fagus sylvatica* dazu befähigt, ihre hohe Konkurrenzkraft in einem breiten Spektrum hydrologischer Regime zu entfalten. Darüber hinaus werden die hier dargestellten Mechanismen einer langfristigen Trockenheitsanpassung mutmaßlich zu einer gesteigerten Resistenz und Resilienz von Buchen-Altbeständen gegenüber Ereignissen extremer Sommertrockenheit beitragen.

Chapter 8

Appendix

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Viele helfende Hände, Geister und Herzen haben diese Arbeit in ihrer Form ermöglicht. Obwohl der Versuch, alle diese Beiträge dankend zu berücksichtigen, unvollständig bleiben muss, möchte ich es dennoch hiermit versuchen:

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Declaration of originality and certificate of ownership

I, Hilmar Müller-Haubold, hereby declare that I am the sole author of this dissertation entitled 'CLIMATE RESPONSE OF ABOVE- AND BELOWGROUND PRODUCTIVITY AND ALLOCATION IN EUROPEAN BEECH'. All references and data sources that were used in the dissertation have been appropriately acknowledged. I furthermore declare that this work has not been submitted elsewhere in any form as part of another dissertation procedure.

Göttingen, May 29, 2014   _____

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