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Climatic Drivers of Mast Fruiting in European Beech and Resulting C and N Allocation Shifts

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ABSTRACT

European beech shows mast fruiting at intervals of 2–20 years with a 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 4 years, analyzed 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; *Fagus sylvatica*; fruit mass production; leaf area reduction; leaf nitrogen depletion; masting.

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 reproduc-

tive behavior to evolutionary advantages related to predator satiation or increased pollination efficiency (Janzen 1971; Nilsson and Wästljung 1987; Kelly and Sork 2002), comes with difficulties in identifying those factors that immediately trigger fructification events, that is, 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 synchronization over large areas (Wachter 1964; Perrins 1966). This hints at 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 2 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). Because 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 analyzed 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 behavior.

Study aims were (i) to identify climatic variables that 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 analyze 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 (for example, 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 AND METHODS

Study Area and Stands

The study was conducted in the 4 years 2009–2012 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 1). This transect represents the transition from an oceanic to a subcontinental climate with a continuous gradient in precipitation (816–543 mm y^{-1}) and temperature (8.4–9.1°C, Table 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 × 30 m^2 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 more than 80% of the stands' cumulative basal area (24–45 m^2 ha^{-1}) and more than 95% of the canopy cover. The eleven stands originated from natural regeneration. The beech trees reached a height of 24–34 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 1; Figure 1) were not used in this study since beech reached a lower canopy cover here.

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 was 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%).
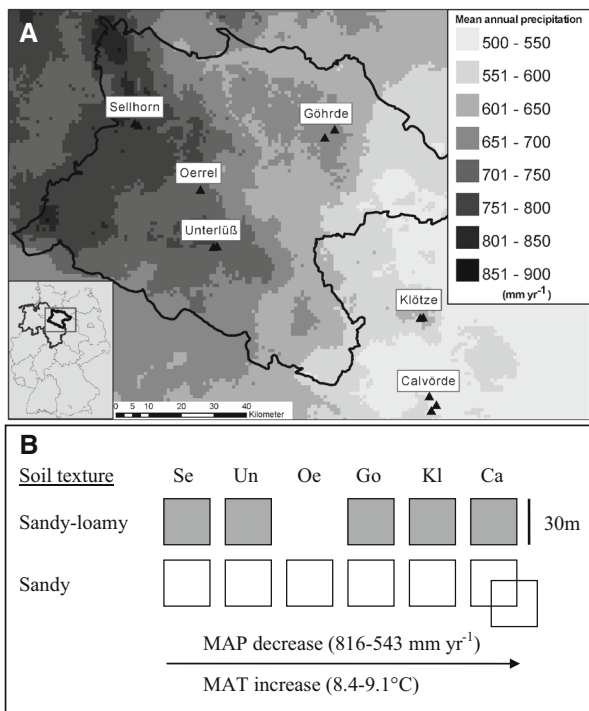
Figure 1. Study plot design: **A** Map of the study area in northern Germany with the six study sites along the precipitation gradient from north-west to southeast (*triangles* location of plots). The *black line* encircles the area of the Lüneburg Heath. Layout by C. Döring. **B** Scheme of the plot 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.

Table 1. Summary of Environmental Conditions and Stand Structural Properties of the 12 Beech Stands in North-western Germany

| 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 (year)	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 (m² 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

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 aluminum; 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 regionalized by C. Döring. Data from plot #5 (Oerrel) was not considered in this study (see "Methods" section).

Carbon and Nutrient Content of Leaves and Fruits

The concentrations of carbon (C) and nitrogen (N) in green leaves were analyzed 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 3 years. On each plot, 4–5 dominant or co-dominant trees were chosen, and leaves from 5 to 8 branches per tree were 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), that is, 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 analyzed in the nuts collected in autumn 2009 in the litter traps. We separated the reproductive material into nuts and cupulae and analyzed 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 analyzer (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 $49.35 \pm 0.57\%$ for C_{mNut} and C_{mCup}, respectively; N: 2.78 ± 0.10 and $0.46 \pm 0.03\%$ 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 1 km $\times$ 1 km grid data set of the German Meteorological Service (Deutscher Wetterdienst, Offenbach, Germany) and averaged the data of 3×3 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) were 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 analyzed in soil pits dug to 1.2-m depth in the center 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) to determine the percentage of particles less than 200-μm diameter (fine sand, silt, clay; ΣfSUT) and of particles less than 63 μm (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 reflectometry probes (TDR, CS616, Campbell Scientific Inc., Logan, Utah, 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):

$$REW = (W - W_m)/(W_F - W_m) \tag{1}$$

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

Unlike the soil physical parameters, the soil chemical characterization 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_4Cl-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 4 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 analyzed using monthly weather data from the 2 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* (for example, differences in the timing of bud burst), we used moving averages of 2 months in width, for example, '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 × 32 time windows) was used for analyzing 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 2 years pooled. Second, the entire 4-year observation period was analyzed 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 co-varying factor in these analyses.

For analyzing 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) 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 analyzed 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 ($P \leq 0.05$). 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 (810–509 mm y^{-1}); it was associated with particularly low precipitation at the dry end of the transect (Table 1). The trends of decreasing precipitation and increasing temperature and solar radiation existed also during the vegetation period (April–October) in the 4 years (Figure 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).
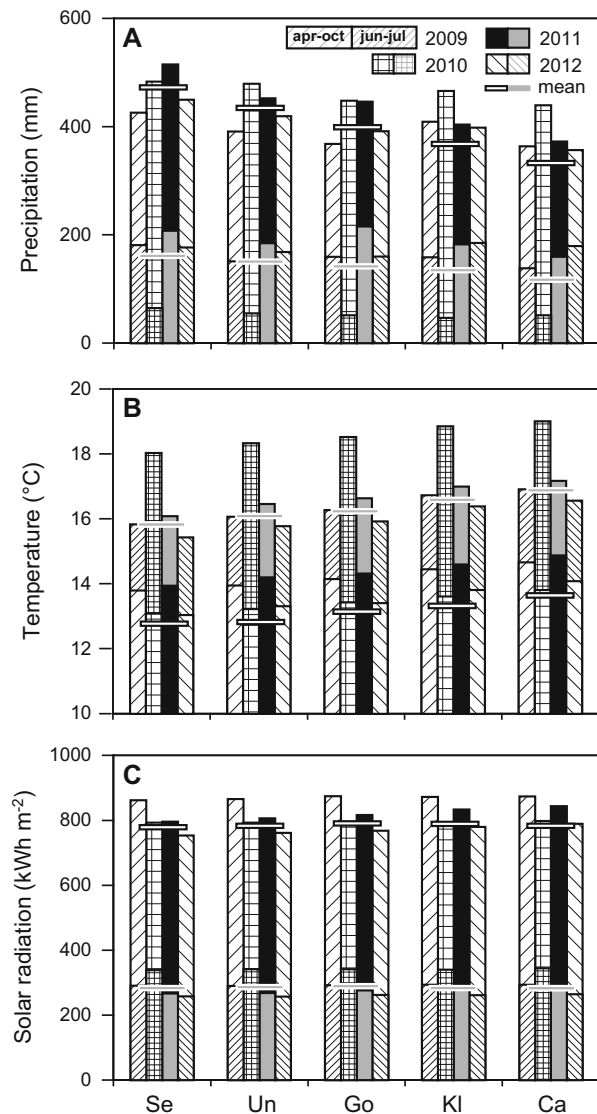
Figure 2. Precipitation **A**, temperature **B** and solar radiation **C** in 2009–2012 at the five study sites. Values shown refer to two periods: 'growing season' (April–October: P_{4-10}, T_{4-10}, Rad_{4-10}) and 'early summer' (June–July: P_{6-7}, T_{6-7}, Rad_{6-7}). *Horizontal bars* indicate long-term means (*black bars* weather conditions$_{4-10}$; *gray 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.

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 + approximately 20%, respectively.
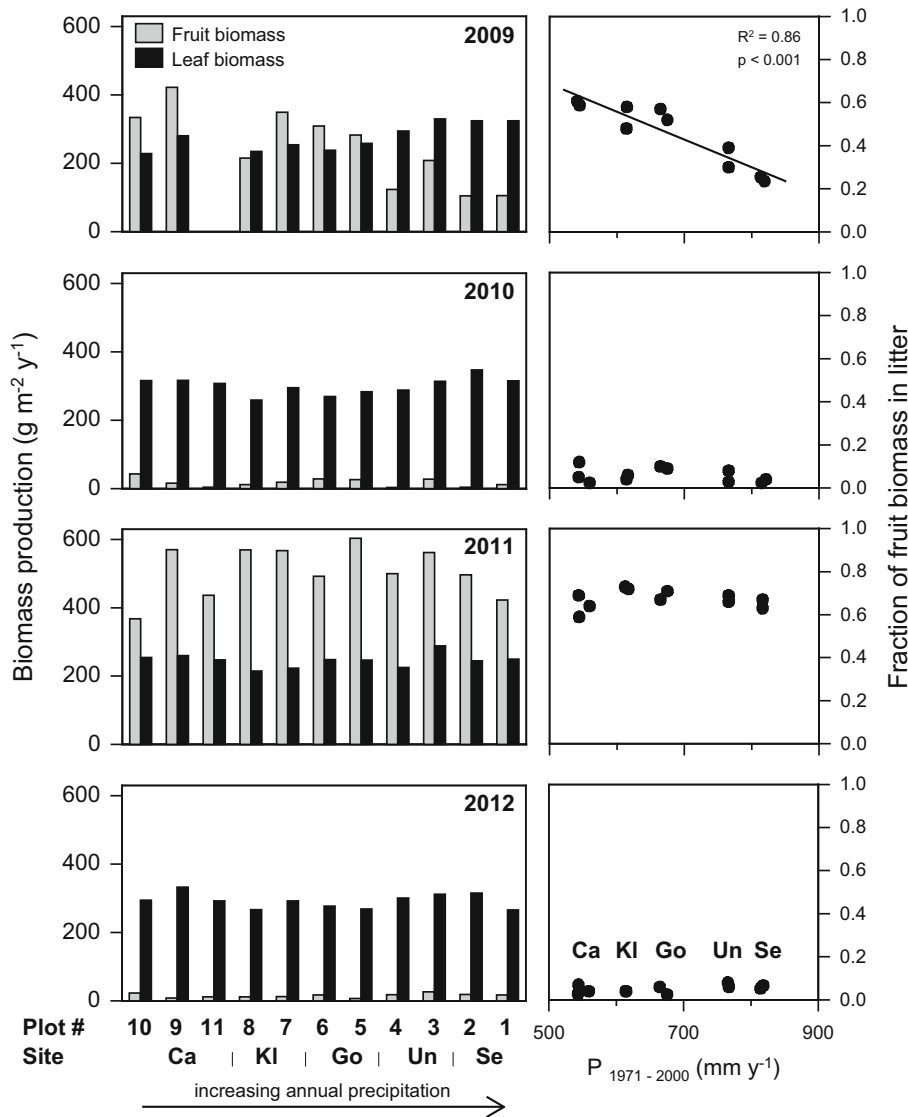
Leaf and Fruit Mass Production

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} y^{-1} on the two plots at the moistest site Sellhorn to 422 g m^{-2} y^{-1} on the loamy-sandy plot at the driest site Calvörde (335 g m^{-2} y^{-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 3). In 2011, heavy masting occurred throughout the transect with no dependence on precipitation means (368–603 g m^{-2} y^{-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} y^{-1}).

Leaf mass production averaged at 290 g m^{-2} y^{-1} in the eleven stands during the 4 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 2). LAI varied between 5.3 and 8.8 in the eleven stands during the 4 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 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 summarized in Table A1 in Appendix in electronic supplementary material.

Climatic Drivers of Mast Fruiting

The analysis of the whole data set (4-year 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 3: last three columns). Similar results were obtained with linear regression analyses considering only the two mast years (2009 and 2011; Table 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

Figure 3. Annual production of leaf mass (*black bars*) and fruit mass (*gray 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 2. Production of Leaf and Fruit Mass

Year	Leaf mass production (g m^{-2} y^{-1})	LAI (m^2 m^{-2})	Fruit mass production (g m^{-2} y^{-1})	Total litter production (g m^{-2} y^{-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)
2009–2012	289.8	6.9	195.5	485.3

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.

positive effect on masting, but the radiation influence was weaker than in the year-1 (see also Beta weights in Table 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

Table 3. Relationships Between Annual Fruit Mass Production and Two-monthly Means of Climatic Conditions

2-Month period	Mast years 2009 and 2011 Pearsońs R			Total period 2009–2012 Beta weight		
	Prec	T max	Rad	Prec	T max	Rad
Mast year-2						
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

Results of regression analyses between annual fruit mass production and two-monthly means of climatic conditions in the mast year and the 2 years prior to masting. The pooled data of the two masting years (2009 and 2011) were analyzed 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).
Prec = precipitation, T max = maximum temperature, Rad = solar radiation.
Significance levels: *P < 0.05; **P < 0.01; ***P < 0.001 (in bold).

of the pooled data (Table A2 in Appendix in electronic supplementary material). 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 3: last column).

Fruit mass production increased linearly with the June–July solar radiation total in year-1 when a threshold of about 300 kWh m^{-2} was passed (Figure 4A) or when the long-term radiation mean in mid-summer (285–291 kWh m^{-2}) was exceeded

by more than 5% (or 10–15 kWh m^{-2}) (Figure 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 ($\sim$ +1.5 and +1.0 K; Figure 4C–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 (Figure 4G, H).

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
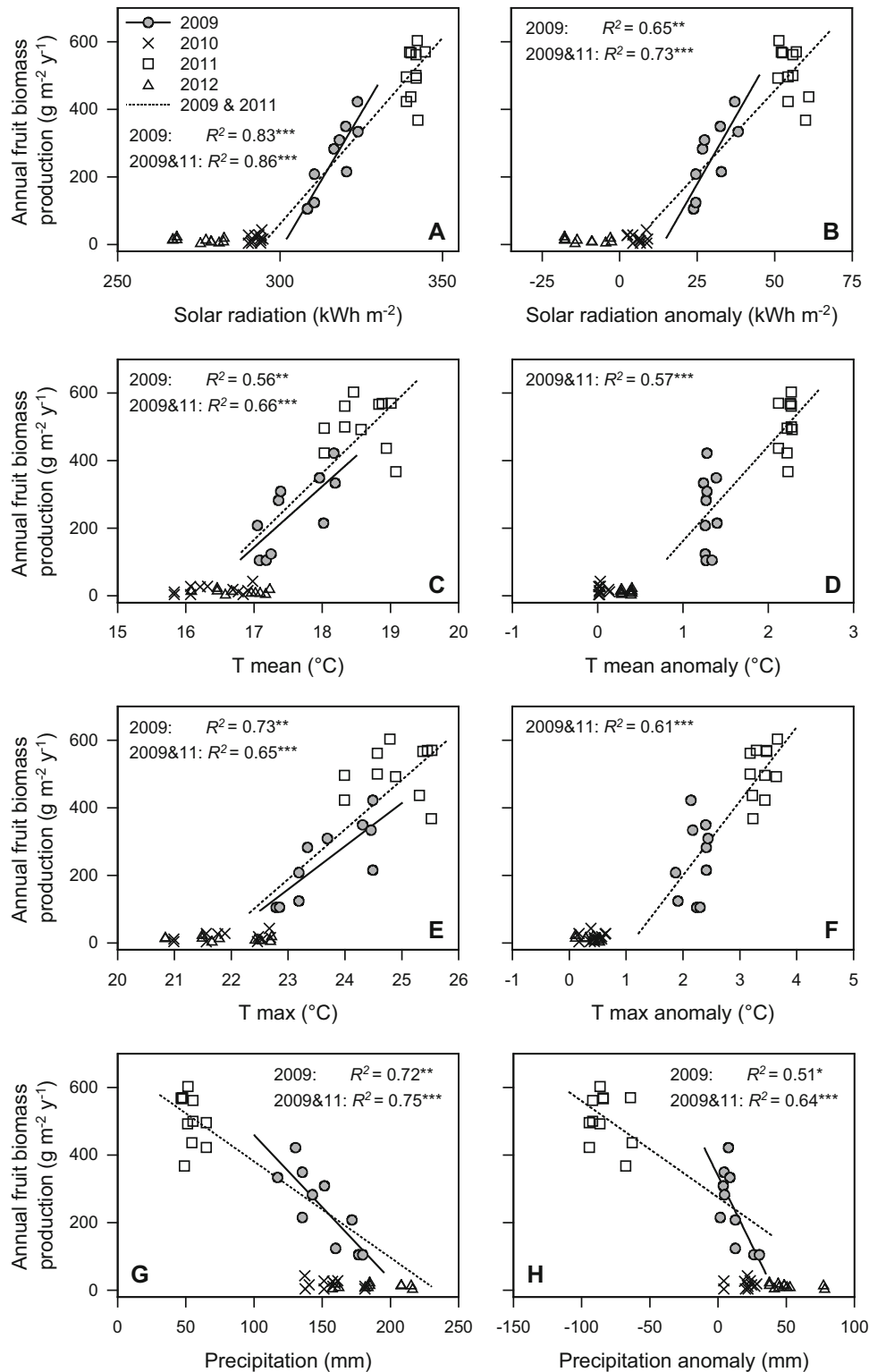
climatic variable radiation in JJ_{-1} (Table 4). However, in 2011 with very high fruit production, the model fit was better when the proportion of fine-grained soil particles ($\Sigma fSUT$ and ΣUT: 2011), water storage capacity (AWSC: 2009/2011), soil N content, stand age (all positive effects), or stem density (negative effect) were included; this was also valid for the combined data set of 2009 and 2011.

In contrast, soil water content (VWC, REW) in the early summer of year-1 (or of other periods) as

◀ **Figure 4.** Relationship between annual fruit mass production and the weather conditions during early summer 1 year prior to the masting (June and July of year -1) across the 11 stands in 4 years (2009–2012). **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** Solar radiation expressed as the absolute 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 and 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 and 2011: $y = -3183.9 + 197.04x$, $R^2 = 0.66$, $P < 0.001$. **D** Mean temperature deviation from the long-term mean (1971–2000); Fruit production 2009 and 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 and 2011: $y = -3185.1 + 146.72x$, $R^2 = 0.65$, $P < 0.001$. **F** Maximum temperature deviation from the long-term mean (1971–2000); Fruit production 2009 and 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 and 2011: $y = 666.2 - 2.85x$, $R^2 = 0.75$, $P < 0.001$. **H** Rainfall deviation from the long-term mean (1971–2000); Fruit production 2009: $y = 338.5 - 8.26x$, $R^2 = 0.51$, $P < 0.05$; 2009 and 2011: $y = 274.8 - 2.85x$, $R^2 = 0.64$, $P < 0.001$.

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 5; visible in the mast years 2009 and 2011 and also in the 4-year 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-year data set (see also Table A3 in Appendix in electronic supplementary material). 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.

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: $N_{mNut} = 2.78 \pm 0.10\%$; $N_{mCup} = 0.46 \pm 0.03\%$; $C_{mNut} = 49.93 \pm 0.39\%$; $C_{mCup} = 49.35 \pm 0.57\%$; 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 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 6) as a consequence of both decreased leaf mass production (Table 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 ($\sim$0.50 g N withdrawn from leaf production per g N invested in fruit mass vs. $\sim$0.25 g C per g C; Figure 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 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 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.

Table 4. The Influence of Edaphic and Stand Structural Parameters on Fruit Mass Production

Type of regression model			2009		2011		2009 and 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	–	–

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 and 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 < 200 μm/< 63 μm; 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.*
[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.

Table 5. Relationships Between Annual Fruit Mass Production and Several Leaf Mass and Leaf Morphology Traits

		Leaf biomass	LAI	SLA	Leaf size	Leaf mass	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 and 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 and 2012	−0.18	0.29	**0.33***	−0.70	−0.55	0.25 (0.43)

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

Table 6. C and N Allocation Between Leaf and Fruit Mass Production

	N	Carbon				Nitrogen			
		C_m	C_a	C_{leaf}	$C_{Leafmass}$ (b)	N_m	N_a	N_{leaf}	$N_{Leafmass}$ (b)
Relations within mast years									
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)

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 characterized by Pearsoń'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.

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 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.

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 1 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 and others 2009). Switching reproduction behavior in response to continuous variation in climatic factors 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 around 300 kWh m^{-2} in these 2 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. Although Kelly and others (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 A1 in Appendix in electronic supplementary material). 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 1.2 K
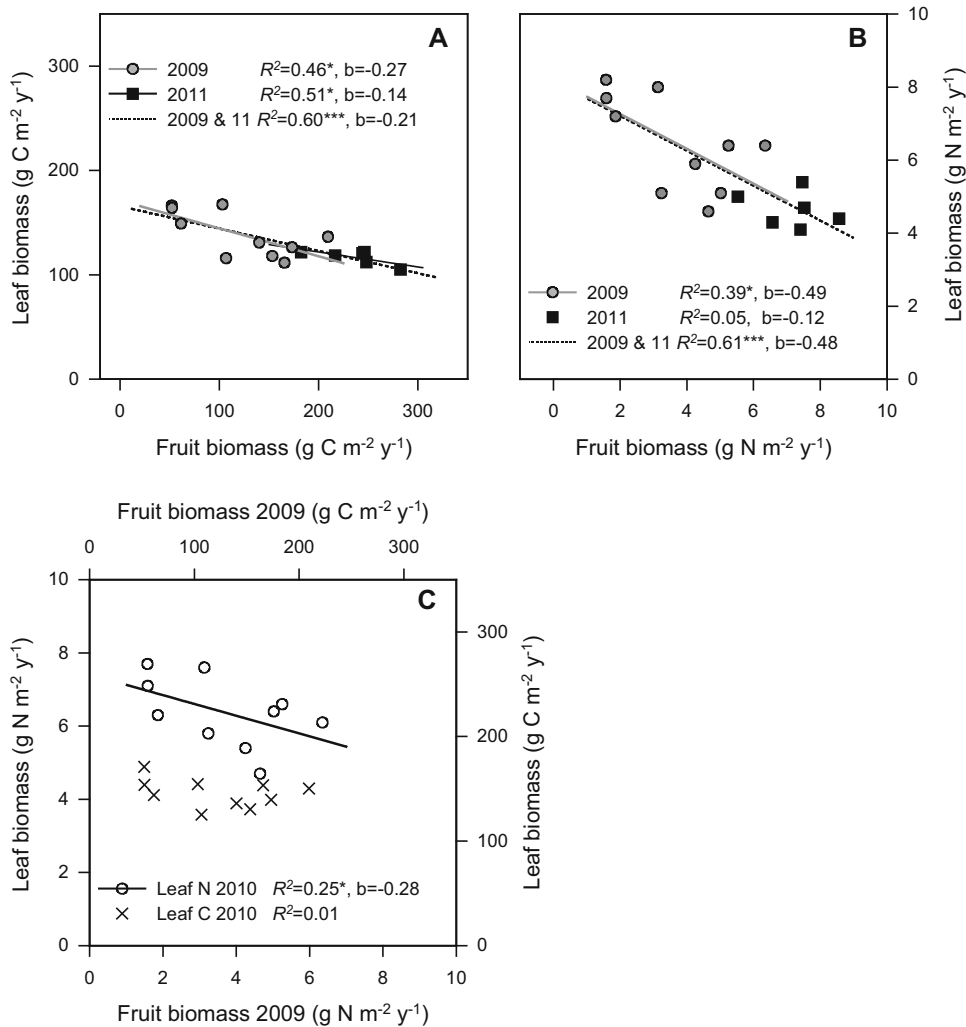
Figure 5. Amount of C (**A**) and N (**B**) in the stand leaf litter in relation to the C and N amount in the corresponding fruit mass produced in the mast years 2009 or 2011 across the 11 stands. **C** C or N in the leaf biomass of the non-mast year 2010 in relation to C and N in fruit mass in the preceding masting in 2009 across the 11 stands.

(1.3 K for maximum temperature), presumably because solar radiation was 10–20 kWh m^{-2} below the long-term mean (Figure A2 in Appendix in electronic supplementary material). Second, very low beech fruit production was recorded in all study years in a stand in which the beeches 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, 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 and others (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 *Cryptomeria 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 (for example, 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 fruit dry 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 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 neighboring 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 and 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 1 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 non-linear 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 (for example, Smaill and others 2011). Apart from these alternative 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 (for example, 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. In-

creased 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 *C. 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. Although 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 is likely inhibited in a current mast year due to resource allocation toward fruit growth by three mechanisms. They are (i) 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) 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 synchronizing 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, 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. Because 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.

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