Climate relationships of growth and establishment across the altitudinal range of *Fagus sylvatica* in the Montseny Mountains, northeast Spain[1]

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Abstract: A rise in elevation of the temperate biome has been reported in the mountains of northeast Spain. We aimed to determine the principal climatic factors limiting growth and establishment of the dominant temperate tree, *Fagus sylvatica*, across its altitudinal range and how its climate-response has varied over time. We determined the climate-response of the growth of adult trees and the establishment of juveniles using dendroecological methods at 3 sites along an elevational gradient spanning this species' full altitudinal distribution of approximately 1000–1650 m above sea level. We found strong altitudinal variation in growth and establishment responses to climate. The most common growth response was to high spring and summer temperature (April–July), which promoted growth and establishment at the upper treeline but had the opposite effect at low altitudes. Precipitation was strongly limiting for adult growth at the lower limit of *F. sylvatica* and declined in importance with increasing altitude. Sensitivity of growth to summer temperature increased over the second half of the 20th century. Future increases in summer temperature are likely to have negative consequences for growth and establishment at this species' low altitude, low latitude range-edge, particularly if temperature increase is not matched by increasing precipitation.
Keywords: climate change, geographic range, Mediterranean, tree growth, treeline.

Résumé : Une élévation du biome tempéré a été observée dans les montagnes du nord-est de l'Espagne. Notre objectif était de déterminer les principaux facteurs climatiques limitant la croissance et l'établissement de l'arbre dominant du biome tempéré, *Fagus sylvatica*, le long de sa distribution altitudinale et voir comment sa réponse climatique a varié dans le temps. À l'aide de méthodes dendroécologiques, nous avons déterminé la réponse au climat de la croissance des arbres adultes et de l'établissement des juvéniles dans 3 sites le long d'un gradient d'élévation couvrant l'ensemble de la distribution altitudinale de cette espèce, *i.e.*, approximativement entre 1000 et 1650 m au-dessus du niveau de la mer. Nous avons trouvé de fortes variations altitudinales dans la réponse au climat de la croissance et de l'établissement des arbres. La réponse de la croissance la plus commune était liée à des températures printanières et estivales élevées (avril à juillet) qui favorisaient la croissance et l'établissement à la limite supérieure des arbres mais avaient un effet opposé en basse altitude. Les précipitations étaient un facteur très limitant pour la croissance des adultes *F. sylvatica* à basse altitude et l'importance de ce facteur limitant diminuait avec une augmentation de l'altitude. La sensibilité de la croissance aux températures estivales a augmenté dans la deuxième moitié du 20e siècle. Les augmentations futures des températures estivales risquent d'avoir des conséquences négatives pour la croissance et l'établissement de cette espèce à la limite inférieure de sa distribution altitudinale et latitudinale, particulièrement si l'élévation des températures n'est pas accompagnée d'une augmentation des précipitations.
Mots-clés : changement climatique, croissance des arbres, limite des arbres, méditerranéen, répartition géographique.

Nomenclature: Jalas & Suominen, 1976.

Introduction

There is considerable evidence that contemporary changes in global climate are altering the phenology and distribution of many species (Peñuelas & Filella, 2001; Walther *et al.*, 2002). Climate-change–induced changes in forest growth and distribution are the subject of intense investigation since they impact the distribution and composition of natural communities, the productivity of forestry crops, and the terrestrial carbon balance (Saxe *et al.*, 2001; Grace, Berninger & Nagy, 2002; Geßler *et al.*, 2007). In response to rising temperatures, an altitudinal increase of mountain treelines has been reported from regions including New Zealand (Wardle & Coleman, 1992), Alaska (Lloyd &

Fastie, 2003), Scandinavia (Kullman, 2002; 2003), and the Mediterranean (Peñuelas & Boada, 2003).

Trees record climatic changes in variation in the width of annual growth rings. When long-term trends are removed from the data, this ring-width variation represents changes in the annual growth of the tree in response to changes in its environment (Fritts, 1966; LaMarche, 1974b). Standard dendrochronological techniques allow tree-ring series and corresponding climate reconstructions that extend back many thousands of years to be developed (Ferguson, 1970; Feng & Epstein, 1994). Although climate is the factor most frequently reconstructed from inter-annual variation in ring-width, such variation has been used to study pollution levels (Duchesne, Ouimet & Houle, 2002; Muzika *et al.*, 2004), insect outbreaks (Hogg, Brandt & Kochtubajda, 2002), changes in competition pressure (LeBlanc, 1990), and possible CO_2 fertilization effects (Briffa *et al.*, 1998a; Rolland, Petitcolas & Michalet, 1998).

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Tree-ring chronologies for extant populations allow us to investigate how climate–growth relationships change across species' geographical ranges, and to identify the climatic variables that limit growth at the range edge (Fritts *et al.*, 1965; LaMarche, 1974a; Kienast *et al.*, 1987; Makinen *et al.*, 2002; Takahashi, Azuma & Yasue, 2003; Wilmking *et al.*, 2004; Yadav *et al.*, 2004). Age determination of standing trees can indicate climatic variables that are responsible for variation in the frequency of sapling establishment (Gervais & MacDonald, 2000; Daniels & Veblen, 2004). The longevity of individual trees also provides us with the opportunity to study potential changes in the relationship between climate and growth over the lifetime of the population (Dittmar, Zech & Elling, 2003; Daniels & Veblen, 2004; Wilmking *et al.*, 2004; Yadav *et al.*, 2004). This is particularly important in the context of climatic change, as altered climate–growth relationships, such as a decreased temperature response of growth (Briffa *et al.*, 1998a,b), have been reported for the latter half of the 20th century. Alterations in climate–growth relationships may decrease the accuracy of both past climatic reconstructions and future predictions of tree growth if not taken into account (Briffa *et al.*, 1998a,b; Wilmking *et al.*, 2004; Yadav *et al.*, 2004).

The *Fagus sylvatica* forests of the Montseny Mountains lie at the southern edge of the species' distribution (Figure 1) and constitute the dominant habitat of the temperate biome of these mountains. The forests allow investigation of growth and establishment of *F. sylvatica* across its altitudinal range as well as at the southern edge of its latitudinal distribution in Europe. Mean annual temperatures in the Montseny region have increased by up to 1.65 °C over the last 50 y (Jump, Hunt & Peñuelas, 2006). Significant changes in both the phenology and distribution of a variety

of different organisms have been reported from the same region linked to this temperature increase (Peñuelas, Filella & Comas, 2002; Peñuelas & Boada, 2003). The effects on *F. sylvatica* have included a reduction in population sizes, an elevational rise of the upper treeline, and a long-term reduction in growth and recruitment at the species' low altitude limit (Peñuelas & Boada, 2003; Jump, Hunt & Peñuelas, 2006).

Previous work on *F. sylvatica* by other authors has demonstrated a diverse range of impacts of climate on the radial growth of this species (Gutierrez, 1988; Biondi, 1993; Biondi & Visani, 1996; Rozas, 2001; Dittmar, Zech & Elling, 2003; Lebourgeois *et al.*, 2005; Piovesan *et al.*, 2005). Altitude has a significant impact on this species' growth response to temperature and precipitation (Gutierrez, 1988; Dittmar, Zech & Elling, 2003; Piovesan *et al.*, 2005), yet a single-site analysis of the change in climate–growth relationships across its full altitudinal range is lacking. A detailed investigation into the effects of climate on the growth and establishment of *F. sylvatica* across its altitudinal range is therefore necessary in order to understand the pronounced distributional changes reported recently for this species (Peñuelas & Boada, 2003). Consequently, in this study we compared the growth and establishment of populations at this species' upper and lower altitudinal limits and in a central area of the forest interior. Specifically, we aimed to determine the principal climatic factors limiting growth and establishment of *F. sylvatica* at its altitudinal range edges and how these factors vary over time. This information is essential in order to understand the changes reported in this species' distribution so far and to better predict changes that may result from future climatic change.
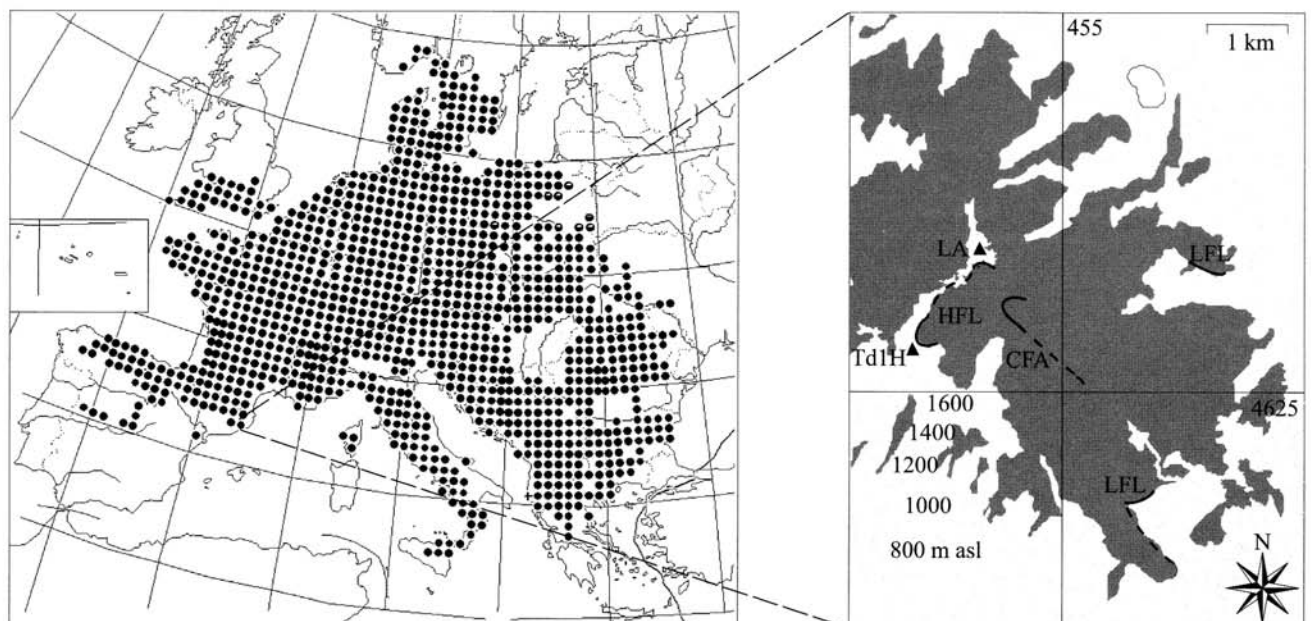

FIGURE 1. Left: native distribution of *Fagus sylvatica* (reproduced from Jalas & Suominen, 1976, by permission of the Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo). Right: location of study sites in relation to *F. sylvatica* distribution in the study area. *Fagus sylvatica* distribution is shown in grey. Study sites: HFL, high *Fagus* limit (upper treeline); CFA, central forest area; LFL, low *Fagus* limit. Dotted lines indicate adult trees, single lines juvenile trees. Principal peaks are marked with a triangle: TdlH, Turó de l'Home; LA, Les Agudes. Grid lines are numbered with UTM coordinates in km.

Methods

STUDY SITES AND SAMPLE PREPARATION

The Montseny Mountains lie 50 km north-northeast of Barcelona and 20 km inland from the Mediterranean Sea. The highest peaks of Turó de l'Home and Les Agudes reach 1712 and 1706 m asl, respectively. *Fagus sylvatica* reaches the southern edge of its European distribution in this region and dominates the temperate zone, which occurs above approximately 1000 m asl (Figure 1). *Fagus sylvatica* forms the treeline on Turó de l'Home and Les Agudes, above which lies a small area of subalpine vegetation dominated by *Juniperus communis* and *Calluna vulgaris*. The lower limit of *F. sylvatica* typically marks the boundary between the temperate zone and the Mediterranean zone (dominated by *Quercus ilex* forest). The *F. sylvatica* forest is naturally occurring, mono-dominant, uneven-aged high forest where establishment occurs via natural regeneration from seed. The forest has been managed at low intensity by the selective removal of large trees; however, the impact of forest management on the upper and lower limits of the *F. sylvatica* forest has been low (Peñuelas & Boada, 2003). Bud burst of *F. sylvatica* occurs in mid to late April at the lower tree line and approximately 2 weeks later at higher altitudes; radial growth continues until the summer drought in August. Soils of the Montseny *F. sylvatica* forest are typically Dystric Regosols and Dystric Cambisols established over schist and granodiorite lithology. The most frequent forest community is the *Luzulo–Fagetum,* with less common areas of *Heleboro–Fagetum.* A detailed description of the vegetation of Montseny and its altitudinal zonation is presented by Bolòs (1983).

We selected 3 sites within the largest area of continuous forest with no evidence of any recent disturbance. These included the upper treeline spanning Turó de l'Home and Les Agudes (HFL site, upper treeline/high *Fagus* limit), an area of the forest interior (CFA site, central forest area), and the lower limit of *F. sylvatica* forest (LFL site, low *Fagus* limit). All 3 sites are on the southeast side of the Turó de l'Home–Les Agudes ridge. It was problematic to sample forests without recent disturbance at the LFL, as forestry plantations and agriculture have a significant impact here. Consequently, it was necessary to split the LFL site between 2 sections of the lower limit of *F. sylvatica* at the boundary of the temperate and Mediterranean zones (Figure 1). Stand characteristics for each site are given in Table I.

At each of the 3 study sites we sampled 15 of the largest adult, single-stemmed, dominant or co-dominant trees, avoiding those that had obvious damage or die-back of major limbs. We also sampled 70 juvenile trees. Adult trees were sampled over 1 km of forest and juvenile trees over 2 km (Figure 1). Juvenile trees were spaced as evenly as establishment patterns allowed and selected according to the criteria that they were straight, single-stemmed individuals estimated to be under 40 y old. The maximum-age criterion was based on a maximum diameter of 8 cm at 15 cm height above ground level, which was identified in a pilot study. This maximum age was intended to confine establishment–growth relationships to current climatic conditions, given the potential alterations in climate growth relationships mentioned above. All juvenile trees were assumed to originate from seed as we found no evidence for vegetative reproduction from root sprouts.

Increment cores were taken using a 4.3-mm increment borer at breast height (1.3 m) from adult trees to assess growth and at 15 cm from juvenile trees to assess establishment. Two or three cores were taken from each tree, depending on the quality of the cores. Multiple cores were sometimes necessary in juvenile trees to ensure that one core passed through the centre of the tree. Juvenile trees that were too small to permit the removal of an increment core were felled at a height of 15 cm and a stem disc removed. Samples were dried, mounted on wood supports, and sanded to prepare them for tree-ring analysis using standard dendroecological methods. Prepared samples were then scanned at 1600 dpi using a flatbed scanner and saved as jpg files.

CLIMATE DATA

Climate data used for analyses in this study are from the Turó de l'Home meteorological station (1712 m asl), located on top of the mountain, directly above our HFL study site. Data were available from this station for the periods 1961–2004 (mean monthly temperature) and 1933–1938 and 1951–2004 (total monthly precipitation) (Figure 2). Data were also available from Fabra observatory for 1914–2003 (413 m asl, 48 km south-southeast of Turó de l'Home) and Roquetes, 1914–1994 (55 m asl, 194 km west-southwest).

Mean monthly temperature and total precipitation were estimated for Turó de l'Home for the periods missing from this station between 1914 and 2004 by using the MET routine of the Dendrochronology Program Library (Holmes, 2001) to interpolate data from nearby meteorological stations (Figure 3). We assessed meteorological data from other stations for their suitability in estimating the Turó de l'Home climate by cross-correlation of the monthly climate values for the period 1961–1994 common to all stations. Mean correlation of temperature at Turó de l'Home was 0.898 with Fabra and 0.801 with Roquetes. Mean correla-

TABLE I. Summary information for *Fagus sylvatica* samples used in this study.

Site	Stand details		Mature tree samples			Juvenile tree samples		
	Stand basal area (m²·ha⁻¹)	LAI	Altitude	n	DBH (cm)	Altitude	n	Age (y)
Upper treeline (HFL)	23.98	4.06	1640	15	56.6 (28.2–118.4)	1600	66	16.2[b] (3–40)
Central forest area (CFA)	25.24	4.30	1127	14	47.3 (25.8–66.2)	1179	49	25.0[a] (11–40)
Low *Fagus* limit (LFL)	20.62	4.09	992	14	51.3 (33.3–68.1)	1015	46	24.6[a] (12–38)

LAI: leaf area index; Altitude: mean sample altitude (m asl); *n*: final number of trees analyzed; DBH: diameter at breast height. Mean values for DBH and Juvenile age are followed by the range in parentheses. Mean juvenile ages followed by the same letter do not differ significantly (Mann–Whitney *U*-test comparisons, *P* > 0.05).
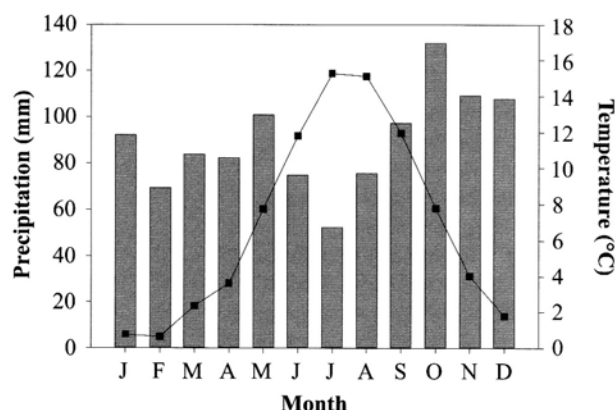
FIGURE 2. Mean monthly precipitation (bars) and temperature (line) from Turó de l'Home meteorological station for the period 1961–2003. Months are indicated by the initial letter of each month.
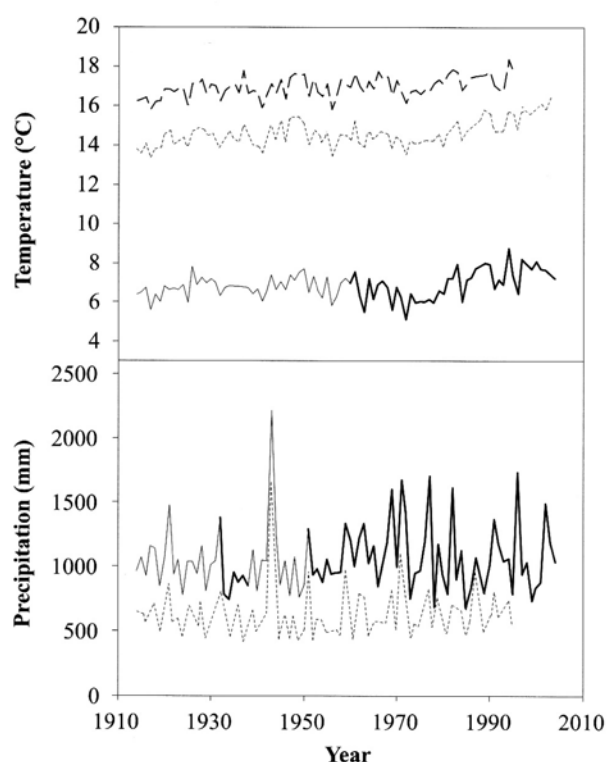

FIGURE 3. Mean yearly temperature and total yearly precipitation 1914–2003 for Turó de l'Home (bold solid lines: data from climate records; non-bold solid lines: estimated data), Fabra (short-dashed lines), and Roquetes (long-dashed line, temperature only).

tion of precipitation at Turó de l'Home was 0.769 with Fabra and 0.614 with Roquetes (Pearson's *r*, mean of 12 monthly values). As correlation between precipitation at Roquetes and Turó de l'Home was poor, this station was not used to estimate precipitation data. The mean annual deviation of original data of Turó de l'Home agrees well with the mean annual deviation of data estimated from Fabra for the same periods: temperature, original: 7.9 °C (range: 7.1–8.6); estimated: 7.8 °C (6.9–9.0); precipitation, original: 35.4 mm (6.0–74.9); estimated: 35.2 mm (6.0–74.9). It was not appropriate to use the Fabra data directly in climate-

growth analyses as the mean monthly deviation of climate at Turó de l'Home from Fabra is not consistent throughout the year, being greater in the summer for temperature and in the winter for precipitation.

DATA ANALYSIS: ADULT TREES

Using CooRecorder v2.3.13 (Larsson, 2003b), ring boundaries were delimited manually on jpg images and ring-width was measured to an accuracy of 0.001 mm. Any suspect core sections were examined on the original sample with the aid of a binocular microscope. Preliminary matching of cores taken from the same tree was performed in CDendro v4.1.1. (Larsson, 2003a). The data files were then converted into decadal format using the FMT and EDRM routines of the Dendrochronology Program Library (Holmes, 2001). Cross-dating accuracy was checked using COFECHA v6.06P (Grissino-Mayer, 2001; Holmes, 2001), and sections of any core that were a poor match with the COFECHA master series for each site were identified. Where poor matching of correctly dated segments resulted from twisted, compressed, or decayed wood, these were excluded from the analysis.

To assess climate–growth relationships it is necessary to treat ring-width series statistically to remove long-term growth variations and serial autocorrelation and to amplify the common climatic signal (Cook & Peters, 1981; Cook *et al.*, 1990). Standardization was performed using ARSTAN v6.05P (Holmes, 2001) using a double de-trending process based on an initial negative exponential or linear regression followed by the fitting of a cubic smoothing spline with a base length of 40 y (Cook & Peters, 1981; Cook *et al.*, 1990). Standardized tree-ring data were summarized to a single chronology for each site.

The residual chronology for each site was used for the response function and correlation analyses (Fritts, 1976). This is the chronology obtained after double de-trending, autoregressive modelling, and calculation of the single series, using a bi-weight robust mean, which is used to remove the effects of outliers in the data, which are common in closed canopy forests (Cook *et al.*, 1990). Response function and correlation analyses were performed using the program DENDROCLIM2002 (Biondi & Waikul, 2004). The analyses were conducted for a 14-month period, beginning with June of the previous year and ending in July of the current year, after which the summer drought halts growth. Correlation coefficients are univariate estimates of Pearson's product moment correlation, whilst the response function coefficients are multivariate estimates derived from a principal component regression model; full details of their calculation are given by Biondi and Waikul (2004). The statistical significance of the coefficients was determined in DENDROCLIM2002 by calculating 95% quantile limits based on 1000 bootstrap re-samples of the data. The residual chronology was analyzed against total monthly precipitation and mean monthly temperature from the Turó de l'Home meteorological station for the period 1961–2003.

To assess the temporal stability of climate–growth relationships for the trees in our study, we conducted a moving-window analysis of climate–growth relationships (Biondi & Waikul, 2004) using DENDROCLIM2002. We used climate

data for Turó de l'Home covering the period 1914 to 2003, including data interpolated from nearby meteorological stations as described above. To assess potential effects of estimating climate data for Turó de l'Home, the results were compared with those from an identical analysis performed using the climate data for the Fabra meteorological station. The moving window analysis was performed by moving a 50-y analysis window progressively along the residual chronology in 1-y steps. The analysis started with the window for the period 1914–1964 and ended with the window for the period 1953–2003, giving a total of 40 analyses of the 50-y relationship between growth and climate.

DATA ANALYSIS: JUVENILE TREES

AGE DETERMINATION

Juvenile trees were dated from jpg images of scanned cores and discs by ring counting using CooRecorder, with additional reference to the original sample using a binocular microscope as noted for adult trees above. Images of scanned samples generally gave very clear ring boundaries; however, it was not possible to cross-date samples as most of the trees were sampled under a closed canopy and exhibited a large proportion of narrow rings as a consequence of light limitation. Age at 15 cm was estimated from each core for each tree separately or from several radii from each stem disc. The modal value of the number of annual terminal bud scars at 15 cm, counted on a sample of 30 saplings at each site, was added to the age at 15 cm derived from ring counts to give total age for each juvenile tree.

Age estimation accuracy was estimated by comparison of individual ring counts for each tree and re-counts made on a random selection of 10 percent of cores and discs and from the variability of terminal bud counts. Trees were assigned to establishment years based on their age, as calculated above. A 3-y running average of establishment was then calculated for each site, based on our assessment of the mean accuracy of tree age measurement of ± 1 y (calculated based on age error estimates of ± 1 y at 15 cm and ± 0 y age estimation from cores/discs). This 3-y running average of tree establishment data was used in subsequent climate–establishment analyses. In order to confine the investigation to the assessment of current climate–establishment relationships and to reduce bias caused by a decreasing probability of sampling older trees given our maximum size criterion, individuals over 40 y old were excluded from the data set.

CLIMATE–ESTABLISHMENT ANALYSIS

Using climate data from Turó de l'Home for the period 1963–2003, Pearson correlation coefficients and their bootstrapped significance values were calculated between 3-y running averages of establishment and climate variables using DENDROCLIM2002. The time period of current year January–December was used in this analysis to allow for potential effects of snow pack at the upper treeline. Similar methods for assessment of temporal variation in tree establishment and climate–establishment relationships were used by Gervais and MacDonald (2000) and Daniels and Veblen (2004). A major limitation of using mean monthly values of temperature is that extreme events are not described by the data (Makinen et al., 2002). As extreme events rather than average conditions are likely to have the biggest influence on seedling survival, we analyzed establishment patterns using mean monthly precipitation and maximum and minimum monthly temperatures.

Additional statistical analysis was performed using SPSS for Mac v11.0.2 (SPSS Inc., Chicago, Illinois, USA). As juvenile tree sample size and sample variance differed between sites, the Kruskal–Wallis test and subsequent Mann–Whitney U-tests were used to test differences between mean juvenile tree age at each site (Table I).

Results

DATA SUMMARY INFORMATION

Of the 70 juvenile trees sampled at each sampling area, 46 (LFL), 49 (CFA), and 66 (HFL) met our criterion for being dateable at 40 y old or less and were used in this study. Mean age of juvenile trees was 16.2 at the HFL, 25.0 at the CFA, and 24.6 at the LFL. Mean age differed significantly between sample sites (Kruskal–Wallis test, $\chi^2 = 29.54$, $P < 0.001$); the juvenile trees were significantly younger at the altitudinal treeline than those at lower elevations (Table I). Modal tree age at 15 cm calculated from terminal bud counts was HFL: 2 (range 1–4); CFA: 4 (2–4); and LFL: 4 (2–5). Variability of age estimates from different cores taken from the same juvenile or counts made on different radii from the same stem disc were HFL, mode: ± 0 y (range ± 0–3 y); CFA, 1 (0–4); and LFL, 0 (0–5).

We excluded 1 mature tree from both the LFL and CFA samples due to low correlation with the other trees sampled at the same site. Summary statistics for the standard *F. sylvatica* chronologies (Table II) indicate good data quality (see Grissino-Mayer, 2000 and Dittmar, Zech & Elling, 2003), similar for the 3 sample sites and comparable with other published *F. sylvatica* chronologies (Gutierrez, 1988; Biondi, 1993; Rozas, 2001; Dittmar, Zech & Elling, 2003; Lebourgeois et al., 2005). Although we expected the trees in the central forest area to provide a more complacent chronology (Fritts et al., 1965; LaMarche, 1974b), this was not the case, as evidenced by the similar mean sensitivity and

TABLE II. Summary statistics of standard chronologies for *Fagus sylvatica*.

Site	Complete series					Common Interval Analysis				
	NT/C	CS	MS	SD	AC	CIS	NT/CCI	CBT	SNR	EV
HFL	15/29	1878–2003	0.2	0.24	0.47	1942–2003	9/18	0.49	8.67	53.77
CFA	14/28	1869–2003	0.21	0.23	0.35	1952–2003	13/25	0.38	7.84	42.5
LFL	14/28	1900–2003	0.2	0.22	0.38	1944–2003	13/22	0.32	6.09	37.47

Sites as Table I; NT/C, no. trees/cores; CS, chronology span (y); MS, mean sensitivity; SD, standard deviation; AC, first order autocorrelation; CIS, common interval span; NT/CCI, no. trees/cores in common interval; CBT, mean correlation between trees; SNR, signal to noise ratio; EV, variance in first eigenvector (%).

standard deviation for each chronology. The mean inter-tree correlation, the signal to noise ratio, and the percentage of environmental variance explained by the first eigenvector in the analysis all increased with increasing altitude, suggesting that the common environmental signal recovered from the ring width data was stronger at higher elevations.

RESPONSE OF TREE GROWTH TO TEMPERATURE AND PRECIPITATION

Trees at the upper treeline (HFL), central forest area (CFA), and low *Fagus* limit (LFL) showed a contrasting response of radial growth to climate (Figure 4) (we refer only to significant [$P < 0.05$] correlation and response function coefficients throughout). Radial growth of LFL and CFA trees showed a similar negative correlation with sum-

mer temperatures, although this effect is greater at the LFL (Figure 4). This weaker response to climate is also seen in the precipitation response of the CFA trees when compared with those at the LFL. LFL ring width was positively correlated with precipitation in June and September of the previous growing season and April, May, and June of the current growing season, whereas CFA ring-width showed a positive correlation only with previous-season June precipitation. The limiting effect of low precipitation on tree growth was thus much more evident at the LFL. In contrast with the growth response shown at lower altitudes, radial growth at the HFL was not correlated significantly with precipitation in any month but showed a positive correlation with current summer temperatures. A negative
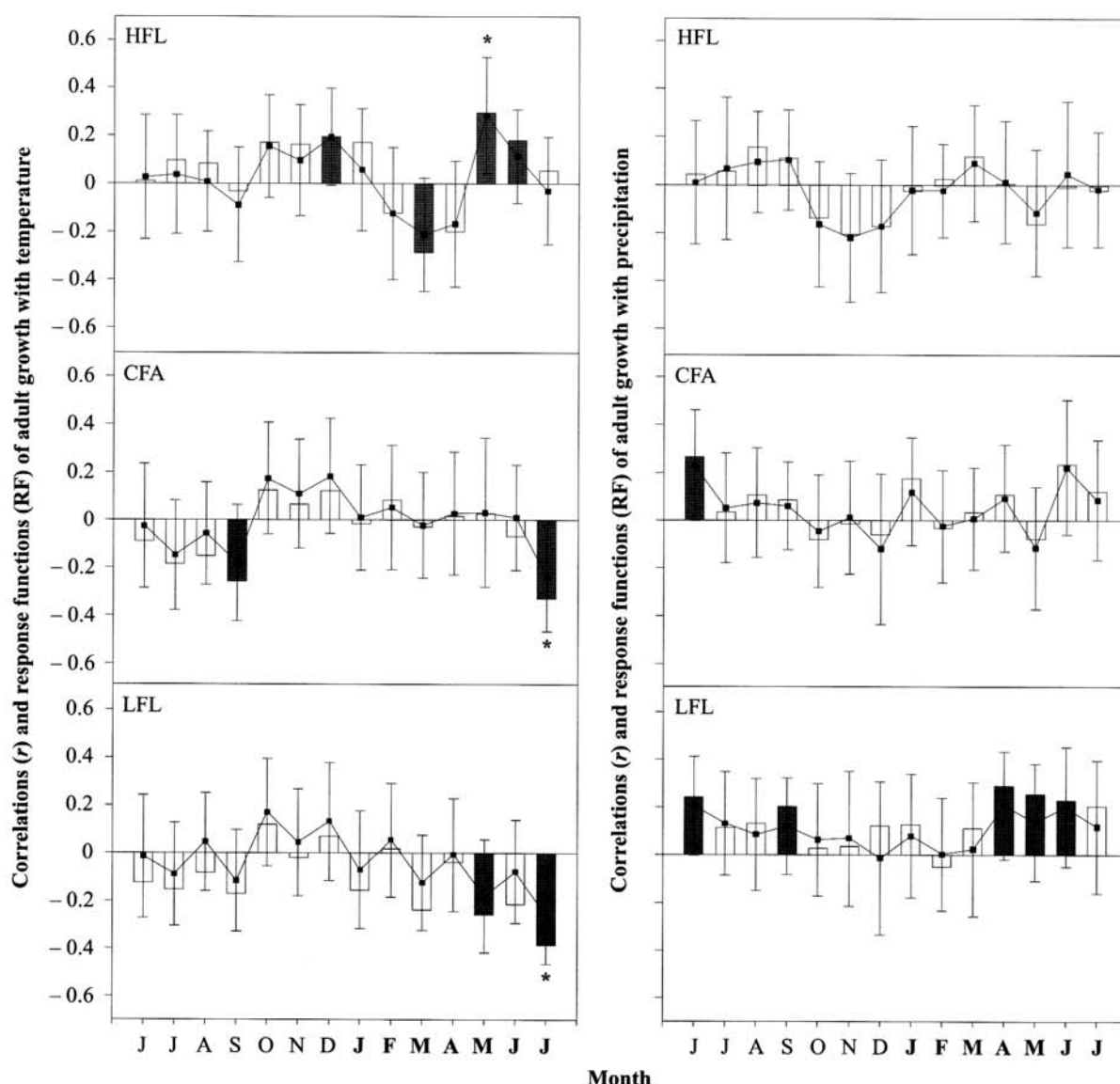

FIGURE 4. Correlations (*r*) and response functions (RF) of *Fagus sylvatica* residual chronologies with mean monthly temperature and precipitation for the period previous year June to current year July. Months are indicated by the initial letter of each month. Current year months are in bold. Correlations (bars) and response functions (lines) are plotted on the same axis. Significant correlations ($P < 0.05$) are indicated by filled bars. Error bars for response functions represent the 95% quantile limits derived from 1000 bootstrapped samples. Significant response functions (indicated by an asterisk) are those where the error bars do not include 0.

correlation between HFL radial growth and current March temperatures was also detected.

Response functions for the period 1961–2003 indicate that the principal growth-responses to climate were negative responses to current-season July temperatures at the LFL and CFA and a positive response to current May temperatures at the HFL. Radial growth showed no significant response functions to precipitation at any of the 3 sampling areas.

VARIATION IN CLIMATE-RESPONSE OVER TIME

In the moving-window analysis (Figure 5) only the results for the principal months identified in the response function analysis (Figure 4) are shown, in all cases cor-
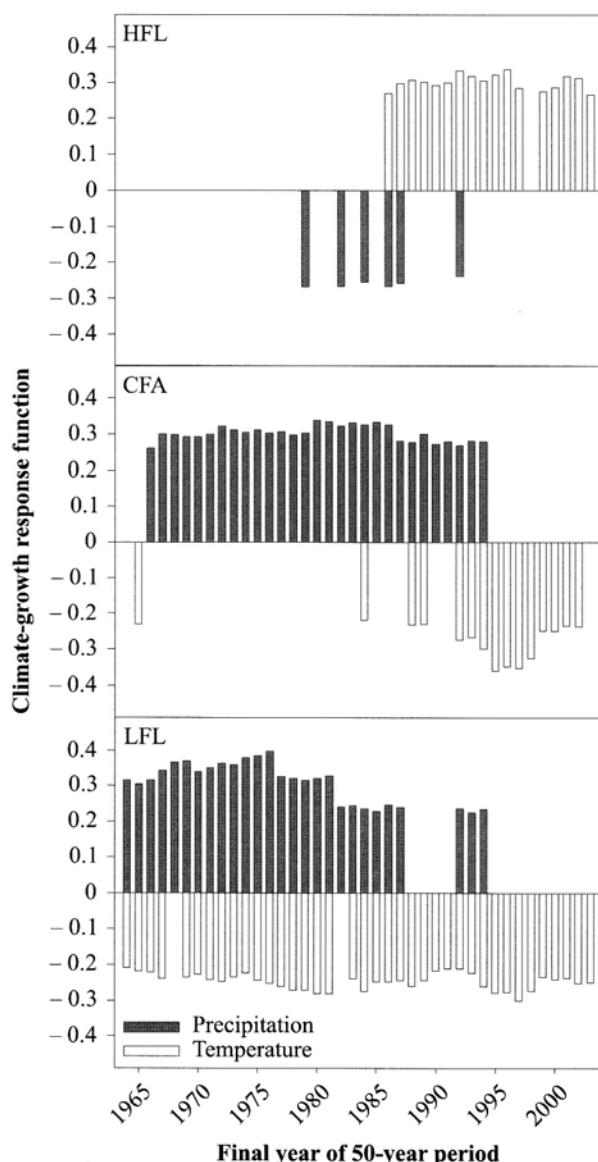
responding to the summer months of growth. The LFL and CFA climate-response function (July 1951–2003) was not stable over time. LFL and CFA trees responded strongly to climate during the months of June, July, or both in different years; consequently, the highest response function coefficient for these two months is presented for the LFL and CFA trees. The response identified for the HFL trees (May) was stable and no significant response function occurred in either neighbouring month during the analysis periods between 1914 and 2003 (data not shown).

Significant responses of radial growth to temperature were almost absent at the HFL and CFA in the 50-y periods ending before 1986 (Figure 5). However, in recent years (the periods ending after 1985 at the HFL and after 1991 in the CFA), temperature dominates the climate response of these trees. In contrast, negative effects of high summer temperatures have been a consistent factor in limiting the growth of *F. sylvatica* at the LFL. The once-positive effects of precipitation at the CFA and LFL do not occur during the 50-y periods ending in the last 2 decades. HFL growth showed a response to precipitation during only 6 of the forty 50-y periods analyzed. These patterns are evident if this analysis is repeated using the Fabra climate records, thereby removing any potential confounding effects of estimating missing climate data for Turó de l'Home in the first half of the last century (data not shown).

RESPONSE OF TREE ESTABLISHMENT TO TEMPERATURE AND PRECIPITATION

Tree establishment was most strongly correlated with maximum temperature and least impacted by precipitation at all sites. In agreement with the growth response seen in adult trees, there was increased establishment of seedlings at the upper treeline but reduced establishment at lower elevations during periods of high maximum temperature (Figures 6 and 7). The correlation between temperature and establishment appears to be stronger in the CFA than at the LFL and occurred in the CFA also during the months of February and October. Similarly, negative relationships with minimum temperature occurred during the months of March and November at the CFA and LFL, although positive correlations also occurred during December at the LFL and February and December at the CFA (Figure 6). In contrast to patterns seen at lower altitudes, HFL establishment showed positive correlations with maximum temperature and with minimum temperature during the month of March (a negative correlation with minimum temperature was seen during September). Only the HFL showed a significant relationship between precipitation and establishment, in this case a negative correlation during February. An example of the relationship between establishment and climate is given in Figure 7.

Discussion

ADULT GROWTH AND JUVENILE ESTABLISHMENT

Growth and establishment of *F. sylvatica* are strongly impacted by temperature across the altitudinal range of this species. High growing season temperatures promote growth and establishment at the upper treeline but limit growth and establishment at low altitudes (Figures 4, 6, and 7). Precipitation is also a strong limiting factor of *F. sylvatica*

FIGURE 5. Temporal change in principal significant ($P < 0.05$) response functions of *Fagus sylvatica* residual chronologies for temperature and precipitation during the growing season (HFL: May; LFL and CFA: June/July). Response functions are calculated for 50-y analysis periods. The x axis represents the last year of each analysis period.
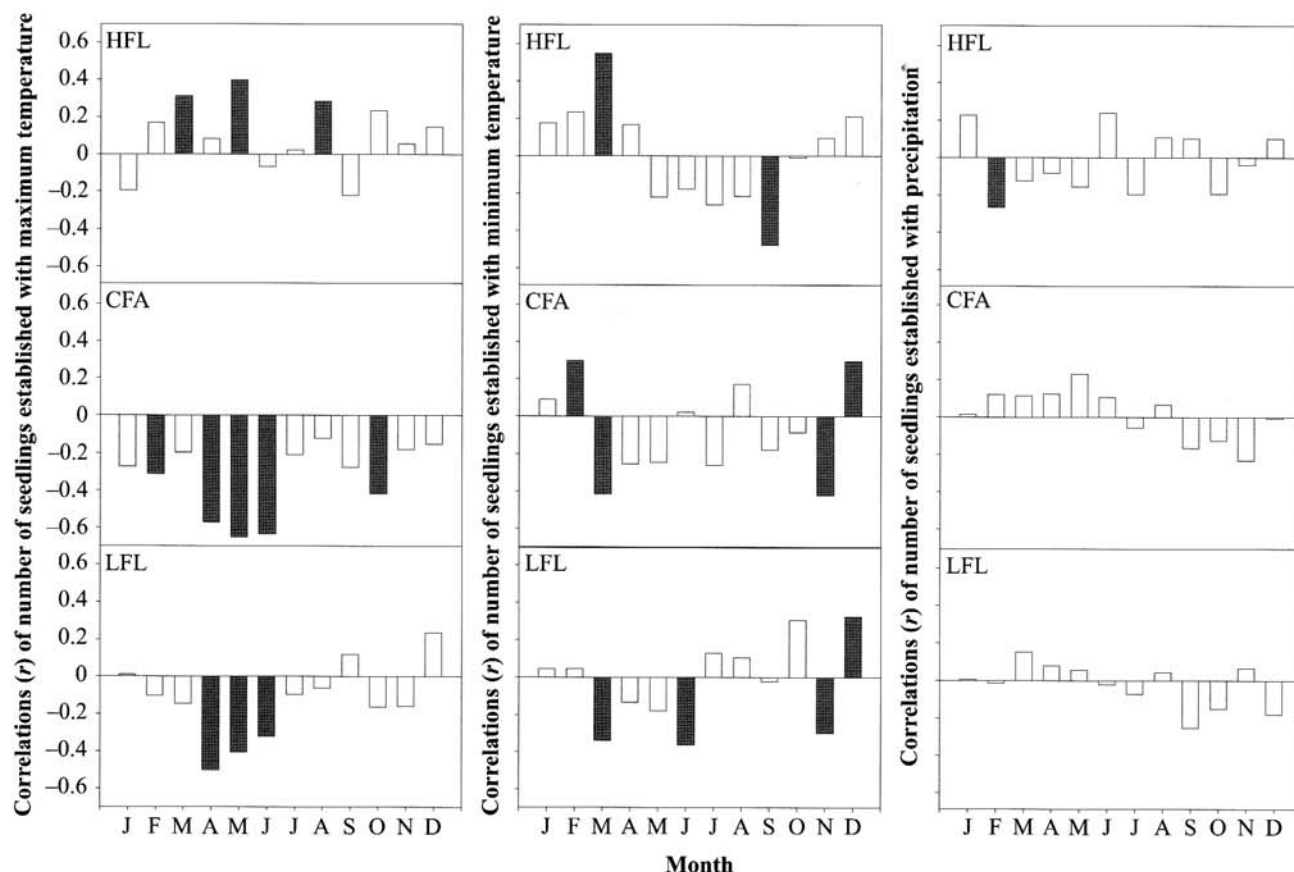
FIGURE 6. Correlations between number of *Fagus sylvatica* seedlings established per year and monthly climatic variables. Months are indicated by the first letter of each month. Significant correlations ($P < 0.05$) are represented by filled bars.

growth at its lower altitudinal limit, although this limiting effect declines with increasing altitude such that precipitation is not currently limiting at the upper treeline (Figure 4).

The growth of *F. sylvatica* at Turó de l'Home is most strongly related to the climate of the current growing season (Figure 4). However, correlations with climatic conditions of the previous season also occur. Such preconditioning of current season growth is a common phenomenon in dendroecological studies and can be explained by the impact of previous season climatic conditions on bud formation (Power, 1994; Tardif, Brisson & Bergeron, 2001) and the balance of stored carbohydrate reserves (LaMarche, 1974b; Fritts, 1976; Dittmar, Zech & Elling, 2003; Savva *et al.*, 2006).

A diverse range of effects of temperature and precipitation are reported on the radial growth of *F. sylvatica* during summer of the current growing season (Gutierrez, 1988; Biondi, 1993; Biondi & Visani, 1996; Rozas, 2001; Dittmar, Zech & Elling, 2003; Lebourgeois *et al.*, 2005; Piovesan *et al.*, 2005). Altitude has a significant effect on the growth response of *F. sylvatica* to climate, as we demonstrate, although only Gutierrez (1988), Dittmar, Zech, and Elling (2003), and Piovesan *et al.* (2005) take this into account explicitly in their sampling strategy. These studies demonstrate that high temperatures and low precipitation are frequent limiting factors for the growth of this species across southern Europe, in agreement with the observation that drought stress is particularly important in determining the
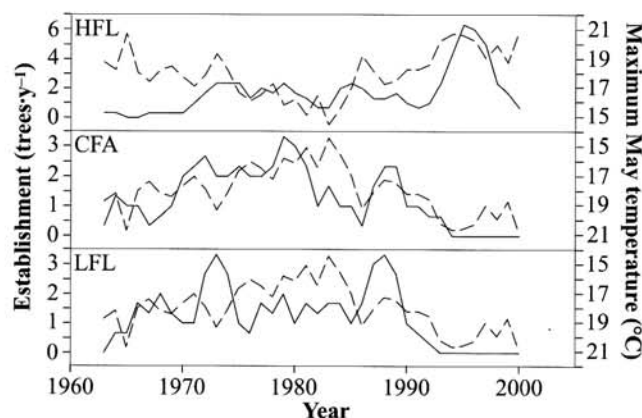

FIGURE 7. Establishment chronologies for *Fagus sylvatica* (solid lines) and maximum May temperature (dashed lines), a climate signal common to all 3 chronologies (see Figure 6). Note: Temperature is plotted on inverted axis for the CFA and LFL sites to facilitate comparison with establishment.

southern European limit of temperate deciduous tree species (Pigott & Huntley, 1978). The pattern of a positive temperature response of tree growth at high-altitude sites and negative response at lower altitudes may be a more general pattern (Brubaker, 1986 and references therein; LaMarche, 1974a; Block & Treter, 2001; Makinen *et al.*, 2002; Dittmar, Zech & Elling, 2003; Piovesan *et al.*, 2005; Wang, Ren & Ma, 2005; Savva *et al.*, 2006). Declining importance of

precipitation with increasing altitude is reported in studies assessing the growth response of *Picea abies* (Norway spruce) (Makinen *et al.*, 2002) and *F. sylvatica* (Dittmar, Zech & Elling, 2003) over broad regions of Europe, although drought stress may also limit growth at high elevation (Kusnierczyk & Ettl, 2002; Wilmking *et al.*, 2004; Wang, Ren & Ma, 2005).

Factors promoting radial growth in adult trees are frequently similar to those promoting seedling establishment (Kullman, 1987; Szeicz & Macdonald, 1995; Camarero & Gutierrez, 1999; Gervais & MacDonald, 2000), although Daniels and Veblen (2004) report much less agreement. The contrasting effects of high temperatures on juvenile establishment at the HFL compared with the lower altitude sites (Figures 6 and 7) mirror the patterns seen in adult growth (Figure 5). The data for establishment at the upper treeline include the only significant correlation between precipitation and establishment found in this study: in this case, a negative response during February, possibly as a consequence of high early season snow accumulation inhibiting germination or subsequent seedling growth. The general absence of precipitation correlations suggests that temperature is the most important limiting factor for seedling survival in this area. The younger mean age of juvenile trees reported for the HFL in comparison with the CFA and LFL sites (Table I) is likely to reflect the recent increase in establishment of this species at the upper treeline linked to rising temperatures, reported by Peñuelas and Boada (2003).

Fagus sylvatica is a masting species that does not form a persistent seed bank (Grime, Hodgson & Hunt, 1989). The trigger for masting in this species is strongly climatic and linked to an early summer drought following a cool wet summer in the previous year (Piovesan & Adams, 2001). However, we found no evidence of correlations of establishment with consistent climatic factors in previous growing seasons (data not shown), and the climate–establishment response varies on a local scale (< 5 km), which suggests our data reflect the climatic conditions of the establishment period itself rather than being related simply to masting frequency. The establishment of experimental plots to assess seedling mortality and survival throughout the altitudinal range of *F. sylvatica* will facilitate further investigation of recruitment in this species.

CHANGING RESPONSE TO CLIMATE OVER TIME

The results of the response function moving-window analysis displayed in Figure 5 indicate an increase in the impact of high summer temperatures in the latter half of the 20th century. Furthermore, this analysis suggests that the negative effect of high summer temperature is now of greater importance than any positive effect of summer precipitation at either the LFL or CFA. Like the single period analysis shown in Figure 4, this analysis demonstrates clear altitudinal variation of the importance of temperature and precipitation for tree growth.

The change in climate–growth relationships shown by the moving-window analysis explains the disparity between our results and those of Gutierrez (1988), who reported a much greater importance of precipitation for the growth

of *F. sylvatica* at Montseny over a restricted altitudinal range. Taken together, these 2 studies show a recent alteration in the climate–growth relationships of *F. sylvatica* at Montseny, a finding that has been reported for other species elsewhere (Briffa *et al.*, 1998a,b; Wilmking *et al.*, 2004; Yadav *et al.*, 2004). This change in climate–growth relationships of *F. sylvatica* is likely to be related to the diverging trends of temperature and precipitation in this region.

CONSEQUENCES OF CLIMATE CHANGE

The altitude-dependent relationship between climate and the growth and establishment of *F. sylvatica* that we report provides a significant insight into the climatic factors that limit the altitudinal distribution of this species in this region. The intensity of summer drought is an important factor limiting the distribution of temperate forest at the boundary of the Mediterranean zone (Pigott & Huntley, 1978). Low soil water availability increases the susceptibility of *F. sylvatica* to extreme temperatures (Lebourgeois *et al.*, 2005). Previous work has shown a 1.2–1.65 °C increase in annual average temperature over the last half of the 20th century that was not accompanied by any increase in precipitation (Peñuelas, Filella & Comas, 2002; Peñuelas & Boada, 2003; Jump, Hunt & Peñuelas, 2006), thereby exacerbating the summer drought that is a feature of the climate of this region (see Figure 2 and Gutierrez, 1988). In agreement with suggestions made by Bolòs (1983) and Pigott and Huntley (1978) and the previous studies of Gutierrez (1988) and Jump, Hunt, and Peñuelas (2006), our data show that high temperature and low precipitation are important in limiting both the growth and reproduction of this species at lower elevations.

When viewed together with the current climate-response of this species (Figures 4 and 6), the moving-window analysis (Figure 5) indicates that the positive effects of high levels of precipitation at the CFA and LFL have diminished. This does not suggest that water availability is now less limiting for this species; rather, it suggests that the higher temperatures experienced in recent years are having a dominant effect in limiting growth. As positive growth responses to high precipitation still occur at both sites, the increasing impact of high temperatures on growth is likely to be a consequence of their exacerbation of drought, which is reduced when precipitation is high in the current or previous year (Figure 4). However, the absence of a positive response of establishment to precipitation suggests that a direct effect of high temperatures on physiological processes cannot be ruled out (Bassow, McConnaughay & Bazzaz, 1994; Leverenz, Bruhn & Saxe, 1999; Grace, Berninger & Nagy, 2002).

Precipitation affects water availability to *F. sylvatica* both by immediate supply for current growth and replenishment of soil water depleted during the summer drought (Gutierrez, 1988). Lebourgeois *et al.* (2005) demonstrate that soil water deficits play an important role in limiting the growth of *F. sylvatica*. If precipitation remains constant over time but temperature increases, increased transpirational demand may cause water availability to become insufficient to allow the persistence of *F. sylvatica* at its south-

ern European low-altitude range-edge. Lebourgeois *et al.* (2005) state that only a slight increase in drought would be necessary for *F. sylvatica* to be out-competed by more drought-tolerant species in many of the sites they studied in France, a finding that may be common to many deciduous temperate tree species at their Mediterranean boundary (Pigott & Huntley, 1978). Investigation of the effects of recent warming on soil hydrology in Montseny would determine whether an exacerbation of summer drought could be contributing to the observed reduction of *F. sylvatica* forest at low altitudes in this region.

Conclusion

Growth and establishment of *F. sylvatica* show a very similar response to growing season temperatures. At high altitudes, high temperatures promote growth and seedling establishment, whereas at low altitudes the opposite pattern is seen. Precipitation becomes increasingly limiting for the growth of this species toward its lower altitudinal limit. We show that the sensitivity of *F. sylvatica* growth to growing season temperatures has increased over the latter half of the 20th century. In the region we investigated, rising temperatures are not matched by an increase in precipitation, which may explain why temperature is becoming more important in determining the growth of this species. At high altitudes, the positive response to temperature will encourage the expansion of this species in response to increasing temperatures. At low altitudes, increasing temperatures will have negative consequences for the persistence of this species by increasing the severity of summer drought. This risk may be common to many temperate deciduous tree species at their low-altitude southern range-edge in Europe. Our data advance our understanding of the distributional changes of *F. sylvatica* that have occurred over recent decades and show that these changes will continue as the climate continues to warm.

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