Tree rings from a European beech forest chronosequence are useful for detecting growth trends and carbon sequestration

Marco Bascietto, Paolo Cherubini, and Giuseppe Scarascia-Mugnozza

Abstract: Past carbon (C) storage trends were estimated using dendroecological methods in a beech chronosequence in central Germany. Raw-ring-width chronologies, sensitivity curves, and carbon uptake trends were developed for 70-, 110-, and 150-year-old (S70, S110, and S150), even-aged stands. Ecosystem C stock and net ecosystem productivity (NEP$_C$) were computed as the sum of the C stock and fluxes of the soil, the aboveground compartment, and the estimated belowground compartment. The ecosystem C stock ranged from 216 t C·ha^{-1} in S150, to 265 t C·ha^{-1} in S70, to 272 in S110. NEP$_C$ values followed ecosystem C stocks, ranging from 1.7, to 2.4, to 5.1 t C·ha^{-1}·year^{-1} for S150, S70, and S110, respectively. Stem C-stock uptake rate in S110 showed an increase in growth rate over the first 110 years of S150. We estimate that this increase in stem C stock was 6.2%. Given the constancy of forest management among the stands of the chronosequence, we hypothesize that the increase in C stock shown by S110 is due to indirect human-induced effects. We conclude that managed young forests can take advantage of increased resources and counteract the C losses at harvest that are seen in the old forests.

Résumé : Les tendances passées dans le stockage du carbone (C) ont été estimées à l'aide de méthodes dendrochronologiques dans une chronoséquence de hêtre du centre de l'Allemagne. Des chronologies brutes de largeur de cernes, des courbes de sensibilité et des tendances dans le prélèvement du carbone ont été développées pour des peuplements équiennes de 70, 110 et 150 ans. Le stock de C dans l'écosystème et la productivité nette de l'écosystème (PNE$_C$) ont été calculés en faisant la somme des stocks et des flux de C dans le sol, dans la biomasse épigée et dans la biomasse hypogée estimée. Le stock de C dans l'écosystème variait de 216 t C·ha^{-1} dans le plus vieux peuplement à 265 t C·ha^{-1} dans le plus jeune peuplement, à 272 t C·ha^{-1} dans celui de 110 ans. Les valeurs de la PNE$_C$ suivaient celles du C accumulé dans l'écosystème, variant de 1,7 à 2,4 et 5,1 t C·ha^{-1}·an^{-1}. Dans le peuplement de 110 ans, le taux de prélèvement du stock de C dans les tiges montre que celui-ci s'est accru au cours des premiers 110 ans dans le peuplement de 150 ans. Nous estimons à 6,2 % cet accroissement du stock de C dans les tiges. Étant donné la constance de l'aménagement forestier dans les peuplements de la chronoséquence, nous faisons l'hypothèse que l'accroissement du stock de C dans le peuplement de 110 ans est dû à des effets indirects d'origine anthropogénique. Nous concluons que les jeunes forêts aménagées peuvent profiter des ressources accrues et peuvent compenser les pertes de C dues à la récolte qui sont constatées dans les vieilles forêts.

[Traduit par la Rédaction]

Introduction

Forests play a major role in the global carbon (C) cycle (Dixon et al. 1994). The assessment of forest biomass and C pools is vital to meeting Kyoto Protocol commitments. Uncertainty about the response of forests to climatic changes emphasizes the need for information regarding the effects of environmental variability on forest ecosystems.

Uncertainty still surrounds the extent to which tree growth can react to environmental changes, such as rising CO_2,

M. Bascietto[1] and G. Scarascia-Mugnozza. Department of Forest Environment and Resources, University of Tuscia, I-01100 Viterbo, Italy.
P. Cherubini. Swiss Federal Institute for Forest, Snow and Landscape Research, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland.

[1]Corresponding author (e-mail: bask@unitus.it).

N deposition, and increases in temperature and solar radiation. Some studies have indicated that rising CO_2 induces an increase in tree-ring width (e.g., LaMarche et al. 1984; Nicolussi et al. 1995), whereas other data indicate a lack of response (e.g., Kienast and Luxmoore 1988; Briffa et al. 1990). At the stand level, a number of studies have reported an increase in forest biomass over the past 50 years (e.g., Franz et al. 1993; Becker et al. 1995; Spiecker et al. 1996; Bräker 1996; Bert et al. 1997). Recent simulation studies using a two-stage, process-based model have shown that under current climate-change conditions, net annual increments in stem biomass in European forests will further increase, to give an additional 0.9 m^3·ha^{-1}·year^{-1} above that in the current climate scenario, by 2030. By 2050, the increase in increments is reduced to 0.79 m^3·ha^{-1}·year^{-1} (Nabuurs et al. 2002). Tree-ring analysis may be useful for retrospective studies assessing long-term growth changes and C sequestration in forest stands. In the recent past, tree rings have been used more often in ecology as indicators of environmental factors and tree growth. As indicators of tree growth, they provide an estimate of the quantity of biomass produced.

Table 1. Leinefelde forest soil and stand structural features.

	S70	S110	S150
Soil features			
Soil classification	Stagnic Luvisol	Haplic Luvisol	Stagnic Luvisol
Texture	Silty clay	Silty clay	Silty clay
Depth (cm)	55–90	40–75	70–90
Mean pH	4.6	4.4	4.9
Mean organic C content (%)	2.3	3.5	2.7
Structural features and size of samples			
Stand density (trees·ha^{-1})	624	224	64
Stand basal area (m^2·ha^{-1})	33.9	35.2	18.2
Stand mean top height (m)	27.6	36.5	38.2*
Size of sample for C stock analyses (trees/cross sections)	8/154	10/395	8/205
Size of subsample for RW analyses (trees/cross sections)	7/44	8/53	8/5
Year 2000 stem C stock and uptake at the stand scale			
Stock (t C·ha^{-1})	163±12.4	148±8.21	115±7.74
Uptake (t C·ha^{-1}·year^{-1})	2.18±0.562	1.61±0.165	2.12±0.143
Mean uptake over stand life (t C·ha^{-1}·year^{-1})	2.33	1.35	0.767
Year 2000 branch and foliage stock and uptake at the stand scale			
Branch stock (t C·ha^{-1})	14.1	47.1	16.9±2.03
Branch uptake (t C·ha^{-1}·year^{-1})	1.14±0.124	4.46±0.348	1.02±0.117
Foliage uptake (t C·ha^{-1}·year^{-1})	1.65	1.44±0.072	1.25±0.194

Note: Values are means ± 1 SE. RW, ring width; S70, 70-year-old stand; S110, 110-year-old stand; S150, 150-year-old stand. Data for forest soil features are from FAO (1998) and I. Shoening (personal communication 2002); data for stand density, basal area, and mean top height are from M. Mund (personal communication 2001); and data for S70 and S110 branch C stocks are from Masci et al. (2003).

*S150 mean top height evaluated on 64 trees/ha.

Tree rings have already been used to assess aboveground net primary-productivity trends at the stand level (e.g., Graumlich et al. 1989), but only recently have they been used to assess C-sequestration trends (Yanai et al. 2000; Acker et al. 2002; Bond-Lamberty et al. 2002; Mund et al. 2002).

We have investigated trends in tree-ring widths of a forest chronosequence in which harvests and thinning are carried out regularly to fulfil a management plan. The forests include a set of stands of increasing age, within which each stand is usually even aged. The main aim of studying forest chronosequences is to substitute space for time so that one can consider present-day stands as different age stages of the same stand (Foster and Tilman 2000). A complete analysis of C-sequestration trends, however, should provide a full C accounting that includes root productivity and heterotrophic soil respiration.

This study focuses on a European beech (*Fagus sylvatica* L.) forest chronosequence in Leinefelde, Thüringen, Germany. No previous data on ring width and aboveground C stock and uptake trends of even-aged beech chronosequences are available. Forest stands may react differently to exogenous factors as they age. Specifically, younger trees and forest stands are generally considered more responsive than older trees and stands to changes in environmental conditions (Ryan et al. 1997; Mund et al. 2002). Thus, a climate-change-induced increase in ring width and C stock is expected to be greater in younger stands than in older ones. The evaluation of various growth patterns may provide useful insight into whether changing environmental conditions are actually inducing an increase in forest C stocks. The increase in forest productivity could prove to be direct evidence of the increase in photosynthetic activity of terrestrial vegetation and the lengthening of the active growing season, as inferred from satellite data (Myneni et al. 1997). We tested the hypothesis that younger forest stands are growing faster than older ones when they were the age of the younger ones, possibly as a result of recent indirect human-induced effects, such as rising CO_2 and temperatures and N deposition, at both global and regional scales.

Materials and methods

Site description

The study was carried out in an even-aged beech chronosequence in the Leinefelde forest, Thüringen, Germany (51°20′N, 10°22′E). We analyzed trends in growth of three even-aged monospecific stands 70, 110, and 150 years old as of 2000 (S70, S110, and S150). The forest lies in a flat area at 420–450 m a.s.l. (above sea level). The mean annual precipitation is 750–800 mm, and mean annual temperature ranges from 6.5 to 7.0 °C (long-term averages of the forest district Wuchsbezirk Hainich-Dün). The Leinefelde forest soil is a uniform, fertile, silty clay loam Brown Luvisol (FAO 1998). Mean soil depth reaches a minimum of 60 cm in S110 and a maximum of 80 cm in S150. The pH is reasonably uniform among the stands, ranging from 4.4 to 4.9. Nitrogen (N) deposition in the forest averages 9 kg·ha^{-1}·year^{-1}.

The forest is intensively managed, and all silvicultural treatments are strictly planned. The forest includes a number of even-aged plots that are all managed in the same way: through shelterwood cutting (Table 1). The rotation period is 150 years, with a regeneration interval of 15 years. Natural

regeneration has always been abundant. Thinning is performed "from above", and this includes removing dead or damaged trees and some codominant trees to favour the best individuals of dominant classes. No pruning policy is in operation in these forest stands.

Tree sampling and dendrochronological analysis

Trees were sampled in December 2000 (S110), June 2001 (S70), and December 2001 (S150). Eight to 10 sample trees (Table 1) were felled in each stand. Trees were chosen to represent stand structural features, diameter and height distribution, and social classes (i.e., dominant, codominant, and suppressed trees). To avoid bias on ring width due to competition constraints on crown development, ring-width chronologies were built using cross sections from dominant and codominant trees. Particular care was taken to select trees with canopies spaced far from each other. This would ensure the independence of tree-ring data. Because of the high commercial value of beech timber, the main stems were cut into logs of different length, according to market need. A cross-sectional disk was taken from the end of each log (six or seven cross sections per tree), and an increment core was taken at breast height (1.30 m). Furthermore, for stem C-stock estimation at the stand level, a number of cross sections were taken from the bifurcations originating at each stem. Because bifurcated trees have no commercial value, cross sections were taken regularly every 2 m. Bifurcation occurred when the diameters of both stems at their stump were >7 cm. The cross sections of the bifurcated stems are not included in the subsample for sensitivity analysis, chronology development, or assessment of the basal-area increment. Therefore, C-stock assessment was accomplished on the sample of all cross sections from the felled trees, and ring-width analyses were performed on a subsample of cross sections taken from the stem of dominant and codominant trees.

Cross sections and cores were stored in a fresh-air drying chamber and sanded a few months later, before ring-width measurements were carried out. Ring-width measurements were made to the nearest 0.0025 mm on two radii on each of the cross sections, using LINTAB measurement equipment (Frank Rinn, Heidelberg, Germany), fitted with a Leica MS5 stereomicroscope, and analyzed with the TSAP software package. The ring-width series were plotted and visually synchronized for identification of errors during the measurements and of potential missing or double rings (Fritts 1976; Schweingruber 1996). The corrected time series were averaged into a mean stand chronology, and synchrony was checked by means of Pearson's correlation coefficient and Student's t test, to determine the significance of the r value (H_0: $r \neq 0$, $\alpha_2 = 0.05$).

Mean stand sensitivity curves were computed from raw-ring-width curves. Mean sensitivity is a measure of variability and expresses the difference between two successive values in a series by means of percentages:

[1] $$S_{i+1} = 100 \frac{2(x_{i+1} - x_i)}{x_{i+1} + x_i}$$

where x_i is the width of the ith ring in the series, and x_{i+1} is the width of the successive ring. The use of sensitivity curves gives insight into the extent to which the growth of an individual species is influenced by environmental factors and into the periodic variability of growth conditions (Fritts 1976). The interval trend was analyzed for all the raw-ring-width series. The interval trend shows how many of the intervals from the same data display the same tendency in several curves (Schweingruber 1988).

In addition, 5-year window pointer years were analyzed (Cropper's values; Cropper 1979) and used to build skeleton plots. These skeleton plots were used to cross-date stand chronologies. Although standardization techniques effectively minimize the effects of low-frequency disturbances on ring-width series (such as those induced by stand dynamics), they were not used, because they also remove other low-frequency signals, such as evidence of pollution or long-term climate change (Briffa et al. 1996).

The means of ring widths of the sample trees from the three stands at different time intervals were tested to verify the null hypothesis of no significant difference in the mean ring width. Probability of type I error was 0.05. Variance analysis was performed using Duncan's multiple range test of differences between means. For each stand, an average cumulative basal area curve was computed and plotted against cambial age (the age of the section of the stem) and calendar year. The stand cumulative basal area was analyzed to test the null hypothesis of no significant differences in basal area for the same time interval among the three stands. Probability of type I error was 0.05. Variance analysis was performed using a two-tailed Wilcoxon rank-sum test.

Both tests were carried out on the average radius of the cross section at stump height. Sample size for the tests was the number of dominant and codominant trees (Table 1): seven for S70 and eight for S110 and S150. Variance analyses were carried out using the SAS software package (SAS Institute Inc. 1989).

Stem C-stock trend at the stand level

The stem C stock sampling scheme used a one-stage randomized branch sampling (RBS) elaboration (Gregoire et al. 1995). RBS is a probabilistic sampling scheme that yields unbiased estimators for several biomass parameters. The diameter at breast height (DBH) elevated to the power of 2.5 (DBH$^{2.5}$) was used as proxy variable to estimate stem C stock. The DBH$^{2.5}$ correlates well with stem biomass (Westoby 1984) and therefore to stem C stock. The sampling probability at the stand level (P_{t_j}) of the jth tree was computed as

[2] $$P_{t_j} = \frac{A_{t_j}}{\sum\limits_{j=1}^{q} A_{t_j}}$$

where q is the number of trees in the stand, and A_{t_j} is the proxy variable (DBH$^{2.5}$) of the jth tree.

Stem analysis was performed on each stem. Tree-height growth pattern was interpolated using Carmean's equations (Carmean 1972), and stem volume was computed using Smalian's formula, which is based on the mean of the two end cross-sectional areas and the distance between them

(Corbyn et al. 1988). Tree age was computed by dating the innermost ring of the cross section at stump height.

Dry-wood density was used to convert stem volume to stem dry mass. Wood density was calculated as the ratio of dry mass to dry volume. Three subsamples for stem dry-wood density were taken per tree: at stump height, halfway through the stem length, and close to the tree top. Wood samples were oven-dried at 80 °C to constant mass. Wood volume was measured by water displacement to the nearest 10 mL; wood mass was measured to the nearest 0.01 g.

The ratio of carbon to dry-wood mass was used to convert stem dry-wood mass to C mass. Three stem subsamples per tree and 10 branch subsamples per stand were analyzed for C content.

Every jth tree yields an unbiased estimator of the stem C stock of the stand:

$$[3] \qquad \hat{V}_{S_j} = \frac{W_{C_j}}{P_{t_j}}$$

where W_{C_j} is the C stock of the stem and its bifurcations of the jth tree.

The unbiased mean and the variance of the estimator are therefore as follows:

$$[4] \qquad \hat{V}_S = \frac{1}{n} \sum_{j=1}^{n} \hat{V}_{S_j}$$

$$[5] \qquad \sigma^2(\hat{V}_S) = \frac{\sum_{j=1}^{n} (\hat{V}_{S_j} - \hat{V}_S)^2}{n(n-1)}$$

where n is the number of sampled trees per stand ($n = 8$ for S70 and S150; $n = 10$ for S110). Stem C yearly uptake was upscaled at the stand level on the same computational basis.

To compare stem C-stock growth patterns between chronosequence stands, the history of stem C uptake was computed. Tree-sampling probabilities (P_{t_j}) were recalculated on estimated DBH distributions for any given year in the past. Past DBH distributions of stands were estimated from the DBH distributions measured in the field. The rate of DBH growth of sampled trees was used to estimate the stand rate of DBH growth. For any given year in the past, the stem C stock and yearly uptake of each sample tree were upscaled at the stand level using the sampling probabilities (P_{t_j}) recalculated for that year in the past. RBS unbiased estimators for stem C stock and uptake were finally computed.

Stem C stock and uptake at the stand level provide a clear image of forest-growth capability, although different tree densities make the comparison of C stock trends among stands difficult. We modeled the effect of S150 thinning mortality on S110 to compare the C stock of its surviving trees to S150 C stock at the same cambial age. We forced S110 tree density to S150 tree density, modeling the effect of future thinning (removing dominated individuals) and the effect of future regeneration cut (removing half of the dominant and codominant individuals). S110 C stock was recalculated, taking into account only the surviving trees, and compared with the C stock of S150 at cambial age 110 (1960). The two stand C stocks were tested for homogeneity

of variances (H_0: $\sigma^2_{110} = \sigma^2_{150}$, $n_{110} = 10$, $n_{150} = 8$, $\alpha = 0.05$). A t test was then performed on the means (H_0: μ_{110}, μ_{150}, $n_{110} = 10$, $n_{150} = 8$, $\alpha = 0.05$).

The purpose of the model was to compare S150 C stock at age 110 years (1960) and S110 C stock at age 110 years (2000), based on S150 tree density. The simulation was carried out solely on S110 and S150 and relied on two assumptions: (*i*) thinning practices are carried out in the same way across stands, and (*ii*) S110 tree density will converge to S150 tree density in 40 years (the difference between the mean ages at S150 and at S110). The fact that management practices in the Leinefelde forest have been constant and regular at S110 and S150 prevents these assumptions from being arbitrary. The simulation removed the smallest diameter trees from S110 because those are likely to be cut during thinning in the next 40 years.

Results

Age structure and diameter growth

Leinefelde forest stands are growing rapidly. Height growth, estimated using stem-analysis techniques, was about 0.3–0.4 m·year^{-1} for all stand ages. Although the cross section at the base of the tree is seldom taken at actual ground level, rapid tree-height growth enables us to reasonably assume that the age of the innermost ring of the lowest cross section approximates tree age.

The age of the sampled trees was concentrated in a narrow range, indicating that stands are even aged. According to the age of the sample trees, stands regenerated between 1925 and 1940 (S70), 1883 and 1899 (S110), and 1838 and 1851 (S150). Most S150 trees were actually established between 1844 and 1851. Thus, we conclude that the regeneration period has been fairly constant over the past two centuries. The mean germination year of sample trees was defined as the establishment year of the stand.

Changes in social status in even-aged stands are believed to occur less frequently than in uneven-aged stands (Badeau et al. 1996). Nevertheless, there is evidence of social-status changes in even-aged forests (Kramer and Kätsch 1994; Cherubini et al. 1998). To test the hypothesis that trees did not change their social status, we ranked sampled trees according to their reconstructed DBH values every 10 calendar years. Tree DBH growth proved to be extremely regular, revealing that trees did not tend to change social status. As a result, a sample of the current dominant trees in a stand of Leinefelde forest can be considered a sample of dominant trees in the past (Bascietto et al. 2003). This result is important and enables us to reconstruct past growth trends.

Tree-ring-width chronologies

Tree rings were clear and readily detectable, and neither false nor missing rings occurred. Dating of tree rings was confirmed by the synchronous occurrence of pointer years between stands. Pointer years indicate the trees' reaction to extreme environmental conditions (Schweingruber et al. 1990). A higher frequency of pointer years after 1992 is shown by S110 and S150, possibly as a result of an increased sensitivity to climate. The cross-dating process among ring-width series in the stands was successful for S110 and S150 but proved difficult for S70. A number of

Fig. 1. Mean tree-ring-width chronologies plotted against calendar date. Standard error bars omitted for clarity. Chronologies end at 2000. S70, 70-year-old stand; S110, 110-year-old stand; S150, 150-year-old stand.
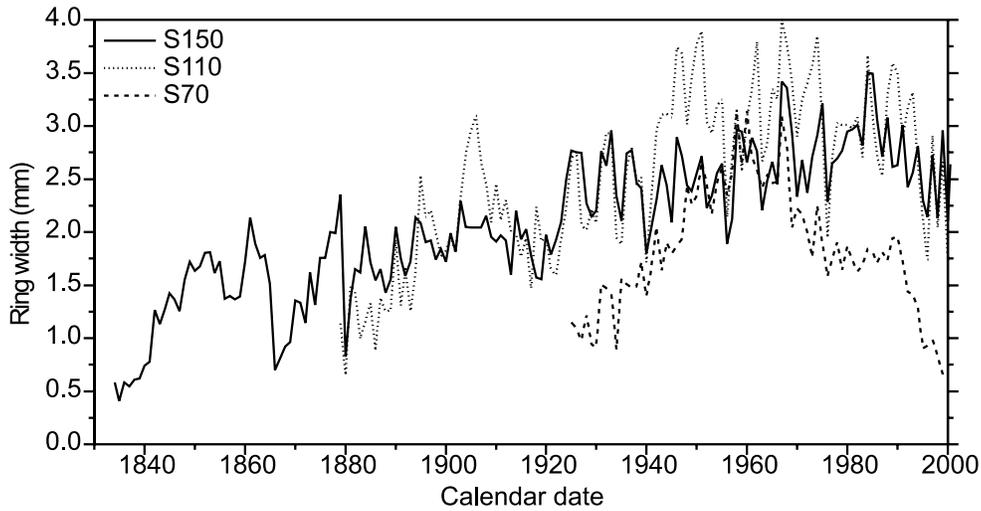

Fig. 2. Mean tree-ring-width chronologies plotted against stand age. Chronologies end at 2000. The establishment year of the stands is spread over the 15-year regeneration period and was thus marked as the mean regeneration year of sample trees. S70, 70-year-old stand; S110, 110-year-old stand; S150, 150-year-old stand.
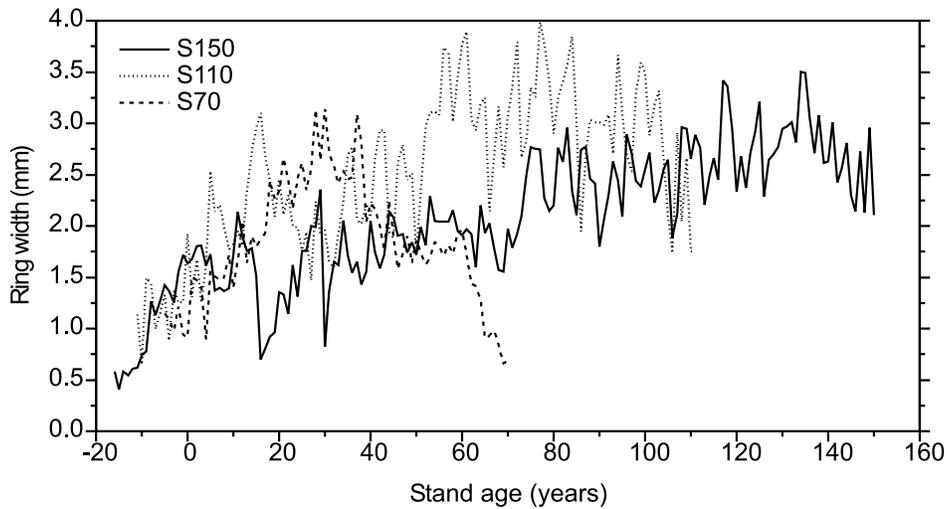
S70 ring-width series (40%) did not consistently synchronize with stand mean chronology. This result shows higher individual variability in response to environmental conditions in this stand.

Stand mean chronologies from ring-width series of cross sections at stump height were built and plotted with respect to year (Fig. 1) and cambial age (Fig. 2). The S70 chronology starts in 1925 (spanning 75 years); S110, in 1879 (121 years); and S150, in 1834 (166 years). Mean ring width in S70 (±1 SE) is 1.84 ± 0.596 mm; in S110, 2.51 ± 0.758 mm; and in S150, 2.07 ± 0.664 mm.

Mean chronologies for S110 and S150 reveal good synchrony as far as growth trends and Cropper's values are concerned, particularly from 1900 onward, probably as a result of the increase in the S110 sample size.

The mean chronology of S70 differs from those of S110 and S150, not only in diameter growth pattern but also in synchrony. The S70 diameter growth pattern varies between

trees and, as a result, the mean stand chronology for S70 does not respond to external factors in the same way as those for S110 and S150 do. Furthermore, S70 shows a peculiar growth trend in which two main growth periods can be detected: enhanced growth between 1940 and 1960 and a decline up to 2000. The declining growth phase has affected the mean stand ring width such that S70, on average, shows the lowest mean increment among the three sampled stands in the Leinefelde forest.

Plotting chronologies versus their cambial age enabled us to make qualitative comparisons between growth rates of the stands. In the first 20 years, the three stands showed similar growth rates and absolute ring-width values. Subsequently, S110 and S150 alternated short slow-growing phases with longer fast-growing ones, with S110 showing, at all times, greater ring-width values. In contrast, S70 extended its active growth period for a further 20–30 years, but its radial increment abruptly declined after cambial age 40–50 years.

Table 2. Duncan's multiple range test for mean ring width.

Interval	S70		S110		S150	
	Rank	Value	Rank	Value	Rank	Value
1–10	A	1.16	A	1.17	B	0.726
1–20	A,B	1.40	A	1.48	B	1.14
1–30	A	1.68	A	1.78	B	1.30
1–40	A	1.93	A	1.84	B	1.28
1–50	A	2.01	A	1.89	B	1.36
1–60	A	1.96	A	1.98	B	1.41
1–70	B	1.92	A	2.12	B	1.49

Note: S70, 70-year-old stand; S110, 110-year-old stand; S150, 150-year-old stand. The value column provides the mean ring width (mm) for each period. The rank column attributes a letter to each mean ring width. In the same row, means with the same rank letter are not significantly different at $\alpha = 0.05$. Time intervals from 1–80 to 1–110 are not in the table; S110 is always significantly different from S150.

These growth trends were confirmed by statistical analysis. Duncan's multiple range test of mean tree-ring widths by decade (Table 2) indicates that S110 and S150 mean tree-ring widths are at all times significantly different, with S110 values always being higher. In contrast, S70 mean tree-ring width prematurely decreases after the first 50 years. This mean tree-ring width never significantly diverges from that of S110. In fact, on consideration of the entire S70 life span (period 1–70), S70 mean tree-ring width is significantly lower than that of S110 (Table 2).

Stand sensitivity through time

Figure 3 shows the variation in stand sensitivity through time. The plots are quite irregular in their early years, probably as a result of low sample size and lack of an average smoothing effect. After this phase, the curves become smoother, as a result of a very regular growth trend. In agreement with the mean chronologies trend, sensitivity curves for S110 and S150 are similar. Both curves also show a relevant increase in variability in the last 20 years. The S70 sensitivity curve had at all times less variability than either the S110 or the S150 one.

Cumulative basal-area increment

To assess long-term stand growth patterns, we computed the basal-area (G) cumulative data against cambial age (Fig. 4). The basal area of the stands takes the usual form of the first part of a sigmoidal curve, in which the change in concavity is yet to be reached. Trees in S110 grew faster than those in either S70 or S150. S70 had a slightly higher growth rate than S110 for the first 50 years, after which time the growth rate reduced dramatically, reaching a negative peak in the last decade.

This trend was confirmed by statistical analysis (Table 3). S70 G is never significantly different from S110 G, but it was higher than S150 G only in the 1–40 and 1–50 periods. S110 G rises at a higher rate than S150 from the 1–30 period onward.

Stem C-stock trend at the stand level

In 2000, the S70 standing-stem C stock (± 1 SE) reached 163 ± 12.4 t C·ha^{-1}; that of S110 reached 148 ± 8.21 t C·ha^{-1}; and that of S150 reached 115 ± 7.74 t C·ha^{-1} (Table 1). Tra-

ditional biomass sampling was also carried out in S70 and S110 (Masci et al. 2003). The upscaling on an allometric basis yielded C stock values not significantly different from the estimates. As a result, tree-ring measurements can be confidently coupled to the stem analysis technique to yield estimates of biomass and C stocks. The three stands of the chronosequence stocked a similar amount of C in their stems, although their stand-maturity stage differed in a remarkable way. Furthermore, at the same cambial age, S70 always stocked the highest amount of C, whereas S150 stocked the lowest amount of C (Fig. 5a). Possibly as a result of full stocking of S70, its last decadal increment (from year 60 to year 70) is much lower than that of the previous decade (Fig. 5b). S110 and S150 decadal increments are lower than that of S70 and steadily growing.

Stem C-stock estimations are based on tree densities in 2000 (Table 1). Thinning practices usually withdraw a substantial number of trees, which affects the standing C stock. No information about past thinning of the stands of the chronosequence was available. As a consequence, the intermediate yields are not accounted for in the estimations of standing C stock.

To allow a comparison of stand C stocks of the same cambial age, we modeled the effect of possible future thinning on S110. The model yielded a C stock for S110 surviving trees (± 1 SE) of 54.0 ± 2.99 t C·ha^{-1} (2000). In 1960, the S150 C stock was 44.0 ± 2.50 t C·ha^{-1}. Variances of the two C stocks were similar (H_0 retained, $F = 1.79$). A t test showed no significant differences between the means ($t = 2.56$). In the period from stand regeneration to the 110th year, the C stock of S110 increased 9.99 ± 3.90 t C·ha^{-1} more than that of S150. The annual mean C increment of S110 over S150 (0.083 t C·ha^{-1}·year^{-1}) is 6.2% of the S110 mean increment (Table 1). However, it is difficult to clearly mark the initial year of stand growth, because of the range in stand regeneration period (15 years). As a consequence, the age of sample trees within the same stands may differ. This might lead to a potential difference in growth responses of trees to external factors.

The total C stock at the ecosystem level should be calculated taking into account the above- and below-ground (roots) C stock of the trees and C stocked in the soil. We consider the C stocked in shrubs to be negligible in the Leinefelde stands. The net difference between the C net primary productivity and heterotrophic soil respiration (here called C mineralization) is a measure of C net ecosystem production (NEP$_C$). To present a more complete picture of C cycling in the Leinefelde stands, we used literature data to estimate the belowground C stock and increment, the C mineralization rate, and the soil C stocks.

Belowground C stocks and uptake rates in the Leinefelde stands were estimated by applying the same root/shoot (R/S) ratio as that showed by a beech forest in the Solling plateau (Germany) (Ellenberg 1981, cited in Cannel 1982). Fine root stock and uptake were not included in the assessment of the belowground compartment of Leinefelde stands, although it is not clear whether they were in the Solling forests. The R/S ratios were computed from the above- and belowground stock and uptake rates of the 59-, 80-, and 122-year-old stands. Although major errors could be introduced by using

Fig. 3. Stand sensitivity curves. From top to bottom, the periods are 1830–1880 (only S150 shown), 1880–1930 (only S120 and S150 shown), and 1930–2000. S70, 70-year-old stand; S110, 110-year-old stand; S150, 150-year-old stand.
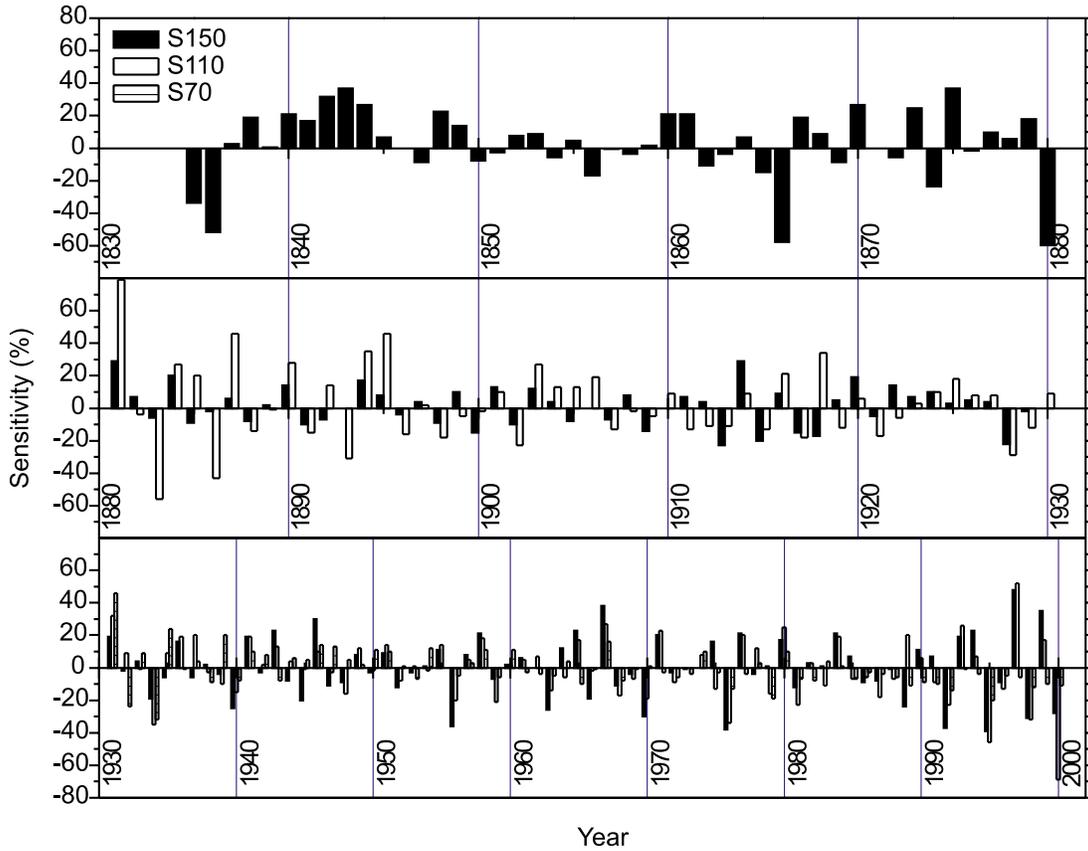

Fig. 4. Mean cumulative basal-area curves for three Leinefelde stands. The inset shows stand growth during the first 70 years. Stand age is given as in Fig. 2. Values are means ± 1 SE (n = 8 for S70 and S150; n = 10 for S110). S70, 70-year-old stand; S110, 110-year-old stand; S150, 150-year-old stand.
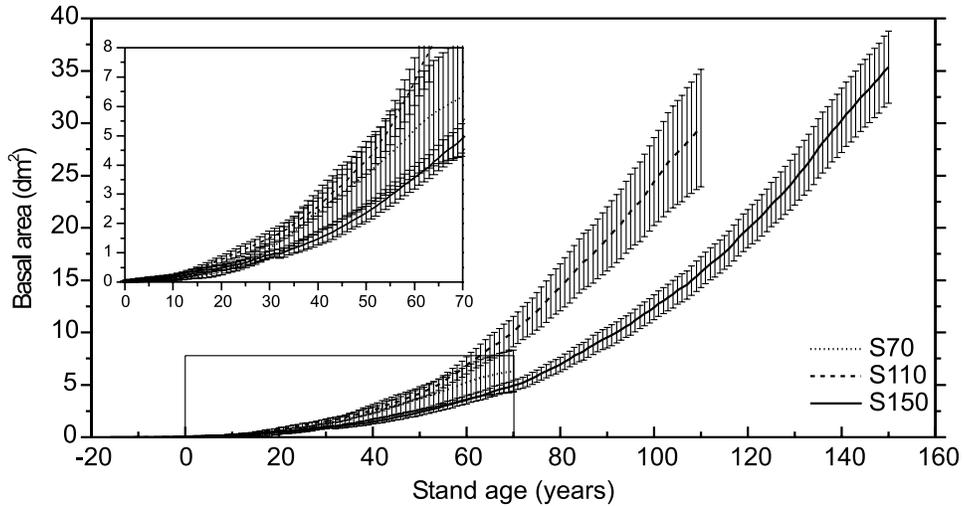
R/S ratios or regressions developed off site (Clark et al. 2001), the ecological conditions and limitations to tree growth should be similar in the two forests. Belowground C stocks in Leinefelde were estimated as 22.7, 22.0, and 15.3 t C·ha^{-1} (from the youngest to the oldest stand), whereas belowground C uptake rates were 0.52, 0.46, and 0.26 t C·ha^{-1}·year^{-1}.

Soil C stocks (L layer 30 cm, T. Persson, personal communication) were 62, 54, and 68 t C·ha^{-1} (from the youngest to the oldest stand). The C stock of the soil was summed

Table 3. Wilcoxon's two-sample test for difference in cumulative basal-area increment, expressed as *p* values.

Interval	S70–S110	S70–S150	S110–S150
1–10	0.835	0.144	0.144
1–20	0.954	0.591	0.564
1–30	0.793	0.203	0.034*
1–40	0.958	0.028*	0.010*
1–50	0.875	0.027*	<0.010*
1–60	0.637	0.076	<0.010*
1–70	0.318	0.158	<0.010*

Note: S70, 70-year-old stand; S110, 110-year-old stand; S150, 150-year-old stand. Time intervals from 1–80 to 1–110 are not in the table; S110 is always significantly different from S150 from the third decade onward. An asterisk indicates significant *p* values at $\alpha = 0.05$.

with the tree above- and below-ground C stocks to provide the ecosystem C stock of the three Leinefelde stands. The estimated total ecosystem C stocks in S70, S110, and S150 corresponded to 265, 272, and 216 t C·ha^{-1}, respectively. The belowground component accounted for 7%–9% of the total C stock, whereas the aboveground part accounted for 62%–72% of the total C stock (Fig. 6).

The observed C-mineralization rates (L layer 30 cm, T. Persson, personal communication) were 3.1 t C·ha^{-1}·year^{-1} in S70 and S110 and 3.0 t C·ha^{-1}·year^{-1} in S150. No significant trends in C mineralization were observed among the chronosequence stands. The total NEP$_C$ values of S70, S110, and S150 were estimated as 2.4, 5.1, and 1.7 t C·ha^{-1}·year^{-1}, respectively. The contribution of belowground C uptake to the NEP$_C$ was negligible compared with that of the aboveground component (Fig. 7).

Discussion

Growth trend of S70

S70 has "complacent" long-term radial growth, with low annual variability in sensitivity (Fig. 3). Its cumulative basal-area growth (Fig. 4) was higher until the period 1960–1970. Sensitivity is affected by environmental factors that influence the interannual variability of tree-ring width. This variability might be due to a number of factors, including short- and long-term variations in climate; forest-management practices; soil fertility; occurrence of pests and diseases; changes in fertilization practices; atmospheric deposition; or damage caused by fires, storms, and snow. In the long term, the major factors influencing tree radial growth are climate or stand intrinsic factors, such as forest management or disturbances. Neither biotic nor abiotic disturbances have been recorded in Leinefelde. The Leinefelde forest stands lie in the same microclimatic region; consequently, climate triggers the same growth responses in trees belonging to the three stands. The difference in stand sensitivity and growth, particularly evident between S70 and the other two stands, cannot be satisfactorily explained by climate.

Effects of climatic variability on basal-area increment vary according to level of competition (Piutti and Cescatti 1997). As a result, the S70 declining growth trend may be related to excessive stocking. Trees under competition pressure tend to allocate resources to primary growth in height, rather than to secondary growth in diameter, and tend to in-

crease leaf number within the apical part of the canopy in an effort to seek light. This is corroborated by the forest-management history (S. Mayer and M. Mund, personal communication). Because of economic problems in former East Germany and the permanent high demand for timber harvest, only the oldest stands were thinned in the recent past. Thinning younger stands (e.g., S70) would not yield a positive income, so thinning has not been carried out since the 1970s, when a new thinning policy became effective.

Although thinning does not have a large effect on the total yield of a stand, it reduces competition pressure for the remaining trees, allowing crowns to grow to meet maintenance and growth requirements of the woody parts (Mäkelä 1986). When thinning is carried out on a regular basis, the influence of climate on radial increment is stronger. Values for stand mean C uptake of stems in 2000 (Table 1) suggest that the youngest and oldest stands are growing at a comparable rate. Comparing yearly stand C uptake figures can be misleading if one relies solely on such data to assess forest response to climatic variability, because they do not take into account management practices in the forest itself. On a decadal time scale, stand C uptake is barely affected by positive or negative growth pulses (Fig. 5*b*), and long-term effects of forest practices (or a lack of thinning) can be readily revealed.

Growth trends of S110 and S150

S110 and S150 show similar sensitivity to long-term climatic patterns. Their long-term growth trend (measured as cumulative basal-area trend, Fig. 4) reveals that the younger stand (established between 1879 and 1894) is growing at a significantly higher rate than the older stand. This result led us to reject the null hypothesis of no long-term growth pattern differences between stands. Neither S110 nor S150 shows an age-related decrease in growth, and the mean height of their tallest trees is particularly elevated (Table 1). Differences in stand growth patterns are likely to be related to external factors, such as environmental conditions, because forest management was constant and similar between the two stands.

Peak periods of sensitivity (1910s, 1928–1935, 1960s) often occur synchronously in comparison with a Lower Saxony mean sensitivity trend (Makowka et al. 1992). Agreement was particularly good in 1976 (one of the years of extreme summer drought throughout Europe); the Leinefelde forest demonstrated strong sensitivity (S110 and S150 values are –0.34 and –0.38), whereas Lower Saxony had the highest sensitivity in the entire sensitivity curve (~0.80 in absolute values). Repeated growth disturbances in connection with crown-damage symptoms since the late 1970s and an increase in sensitivity were found by Dittmar et al. (2003) in beech forests growing in central Europe at altitudes above 800 m a.s.l. The Leinefelde trees have increased sensitivity from the late 1980s onward but no decreases in radial increment.

Canopy and stem growth can be increased by the uptake of additional N. Atmospheric N deposition in Germany has increased over the last 110 years (Schulze et al. 1989). Furthermore, the Earth's climate has warmed by about 0.6 °C in the past 100 years (Walther et al. 2002), the length of the growing season has increased in some European areas by up

Fig. 5. Growth trend for stem C stock (*a*) and uptake (*b*) at the stand level of three Leinefelde stands. Charts do not take into account C removed by thinning practices. C uptake is a decadal sum of yearly C increments. Error bars are 95% confidence intervals (*n* = 8 for S70 and S150; *n* = 10 for S110). S70, 70-year-old stand; S110, 110-year-old stand; S150, 150-year-old stand.
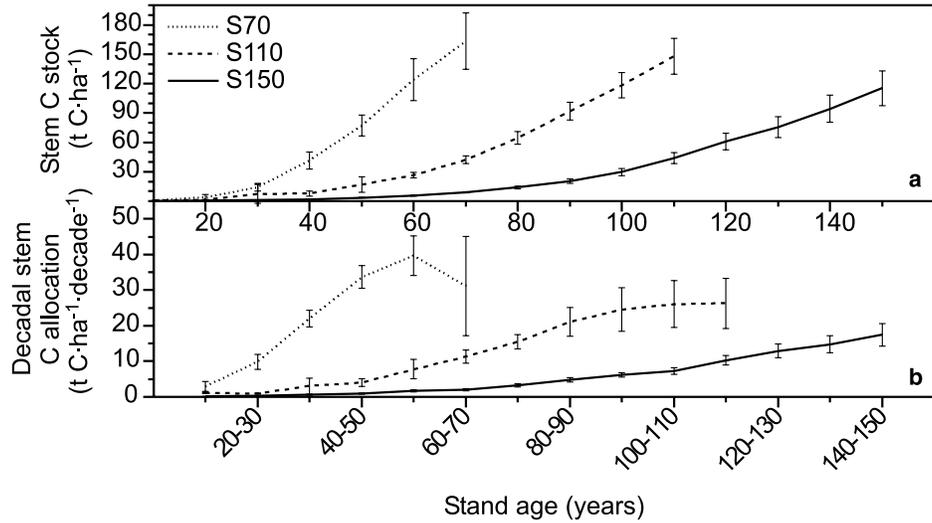

Fig. 6. Ecosystem C stock in the three Leinefelde stands. Root stock was estimated from literature data. S70, 70-year-old stand; S110, 110-year-old stand; S150, 150-year-old stand.
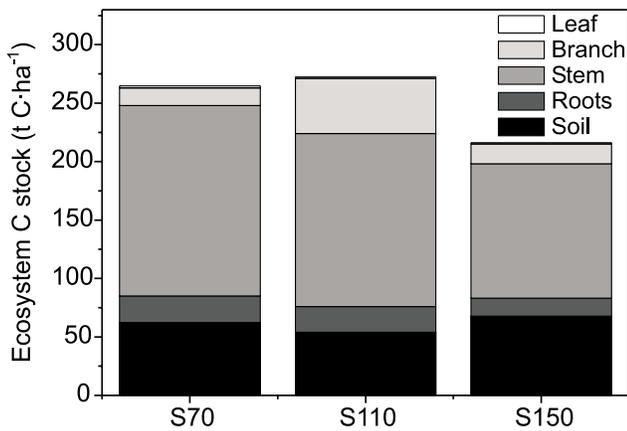
Fig. 7. Carbon uptake by the major ecosystem components. The presence of shrubs was negligible in the three stands, and their contribution to NEP$_C$ was ignored. Root C uptake was estimated from literature data. NEP$_C$, C net ecosystem production; S70, 70-year-old stand; S110, 110-year-old stand; S150, 150-year-old stand.
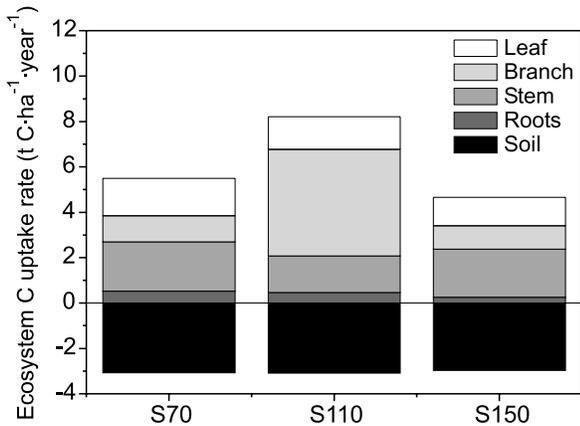
to 3.6 days·decade^{-1} over the past 50 years (Menzel and Fabrian 1999), and the seasonal cycle has advanced by 7 days since the early 1960s (Keeling et al. 1996). Oren et al. (2001) claimed that low soil fertility can restrain the response of wood C uptake to increased atmospheric CO_2 but that high nutrient concentrations can increase C gain. Although the Leinefelde soil is no deeper than 90 cm (Table 1), no nutrient or water deficits have been reported, and the site is characterized by optimum ecological conditions for European beech. As a result, the Leinefelde forest stands could take advantage of added N deposition to soil, supporting the increased growth rate due to increased CO_2, without incurring a nutrient imbalance (Schulze 1989). The concomitant occurrence of proper forest management and more favourable environmental conditions might result in faster forest growth and C uptake.

Carbon sequestration is an important function at the whole ecosystem scale, it includes not only the aboveground stock but also the belowground component, root turnover, C respiration, and C stock in the soil. However, very little is known about the belowground C stock and turnover in forests (Bauer et al. 2000; Persson et al. 2000; Le Goff and Ottorini 2001). In the three Leinefelde stands, the tree above- and below-ground C stocks account for nearly 75% the total ecosystem C stock, and the tree aboveground C uptake is the main C uptake component, although the estimate of the fine-root uptake is uncertain.

To distinguish between the effect of management practices and the effect of changing environmental conditions, we estimated S150 stem C stock at age 110 and compared it with current S110 stem C stock at S150 tree density. In other words, if we let tree density be the same for the two stands, the growth pattern of the stand will be affected solely by the growth patterns of sample trees. Because thinning practices have remained constant across the stands, the comparison of stem C stocks at similar tree densities should yield an estimate of forest growth reaction to changing environmental conditions. The difference between S110 C stock allocated by its 64 most probable surviving trees per hectare and S150

stem C stock allocated by its 64 trees/ha in their first 110 years was 9.99 ± 3.90 t C·ha^{-1} (0.083 t C·ha^{-1}·year^{-1}). Although not significant, the net C gain of S110 (i.e., in the period 1890–2000) over the first 110 years of S150 (i.e., in the period 1850–1960) provides insight into how more favourable growth conditions may affect C-uptake trends.

A number of studies have shown increased growth at the tree, stand (Kauppi et al. 1992; Spiecker et al. 1996; Valentini et al. 2000; Schimel et al. 2000; Read and May 2001; Mund et al. 2002), and continental scales (Nabuurs et al. 2003; Nemani et al. 2003). Additionally, changes in land use and in land management are leading to increasing net C uptake by terrestrial ecosystems in the Northern Hemisphere. Indirect human-induced effects (including effects of increased growth due to CO_2 fertilization, climate change, and N deposition) are not eligible under article 3.4 of the Kyoto Protocol (UNFCCC 1997) and should not be incorporated in a country's emission targets. The Intergovernmental Panel on Climate Change claims that distinguishing the indirect human-induced effects from the observed stock change is difficult (IPCC 2000). Furthermore, analysis of data series and models for the United States suggests that these effects are smaller than direct human-induced effects, of the order of 5%–30% (Valentini et al. 2000). The Conference of the Parties Sixth Session Part 2 (COP6bis) applied an 85% discount to national reports under article 3.4 to account for indirect human-induced effects and forest practices before 1990 (Schulze et al. 2002).

Mund et al. (2002) compared the current growth of four spruce chronosequence stands with their foreseen growth predicted by yield tables representing growing conditions before 1960. They found a mean increase of current mean annual uptake of 0.24 t C·ha^{-1}·year^{-1} over the annual uptake predicted using the yield tables. On this basis, it is difficult to discriminate between indirect human-induced effects and effects of forest-management improvements. The model we applied exploits a chronosequence that enables us to substitute space for time. It does not compare the pattern of growth of the same stand under current and predicted growth conditions; instead, it makes a comparison between stands of the chronosequence itself. Comparing stands that have undergone similar forest management enhances the effects of changing environmental conditions, despite changes in forest practices. Our estimate of the increase in mean annual increment due to climate change (0.083 t C·ha^{-1}·year^{-1}) accounts for a 6.2% increase in standing C stock. This figure does not agree with the findings of Nabuurs et al. (2002), who modeled an 18% peak year increment in stem wood for European forests under climate change and increased thinning. It should be noted, however, that this modeled increase in stem wood increment is estimated on a yearly basis and referred to 2030, which they considered the most productive growing season in their simulation. Reformulating the mean Leinefelde increase in C stock for a shorter time interval and closer to postindustrial times would most certainly lead to a larger estimate of mean C stock increment, closer to the modeled estimates of Nabuurs et al. (2002).

Major uncertainties surround estimates of the increase in standing C stock that is due to indirect human-induced effects, especially lack of data on the amount of C removed by thinning and high natural variability in biomass estimates at the tree level (resulting in major sampling bias; Fig. 5). Forest records and yield tables can be used to reconstruct the history of stand growth, and sampling bias can be reduced such that natural variability in stem architecture is lower (e.g., spruce chronosequences in conifer stands). Furthermore, an assessment of uncertainty introduced by estimating past DBH distribution and by errors in field measurements must to be accounted for in future models.

At Leinefelde, the older stands are far from being natural stands in dynamic equilibrium. However, it should be noted that forest-management practices in several areas of Europe are shifting from preferring monospecific even-aged stands toward preferring mixed ones. This policy aims to develop the structural and functional characteristics of old-growth forests (Kenk and Guehne 2001; Spiecker 2002; Nyland 2003). It has been pointed out that harvesting old-growth forest leads to C losses to the atmosphere as a result of replacing a large C pool with a small C pool of regrowth and reduces the flux into a permanent pool of soil organic matter (Schulze et al. 2000). Our results indicate that the increase in C uptake of younger stands over older ones could partially counteract C losses on harvest in old forests.

Conclusions

Forest-management treatments strongly influence tree growth in diameter and height and canopy architecture. Ring-width chronologies from trees should take into account the management practices to which the trees have been exposed. In forests in which silvicultural history and biotic and abiotic factors have affected trees in the same manner, it can reasonably be expected that trees will react with the same sensitivity to environmental conditions, including climate.

S70 had rapid growth in the first 40–50 years and slower growth in the last 30 years. This is a result of a new thinning policy that became operative in the 1970s and left S70 unmanaged. Thus, a comparison with the older stands is difficult. It seems reasonable to conclude that if the new thinning regime had not become operative, the youngest stand would have taken better advantage of the availability of resources. Management practices have a large effect on the capacity of forests to take advantage of climate scenarios effected by human-induced modifications of the environment. Absence of carefully planned thinning practices may actually lead to a decrease in active C uptake by trees.

At Leinefelde, S110 and S150 appeared to be largely homogeneous. Our data reveal that the younger stand is growing at a 6.2% faster rate than the older one. This is caused by a mean age difference of 40 years, which allows the younger stand to take advantage of recently improved growing conditions. The 6.2% estimate for the increase in C uptake due to indirect human-induced effects is not eligible under article 3.4 of the Kyoto Protocol. As a consequence, it should be subtracted from national sink reports. Higher C uptake rates in younger stands can counteract the C losses on harvesting of old stands.

Acknowledgements

References

Acker, S.A., Halpern, C.B., Harmon, M.E., and Dyrness, C.T. 2002. Trends in bole biomass accumulation, net primary production and tree mortality in *Pseudotsuga menziesii* forests of contrasting age. Tree Physiol. **22**: 213–217.

Badeau, V., Becker, M., Bert, D., Dupouey, J., Lebourgeois, F., and Picard, J. 1996. Long term growth of trees: ten years of dendrochronological studies in France. *In* Growth trends in European forests. *Edited by* H. Spiecker, K. Mielikäinen, M. Köhl, and J.P. Skovsgaard. Springer-Verlag, Heidelberg, Germany. pp. 167–181.

Bascietto, M., Masci, A., Hajny, M.T., and Matteucci, G. 2003. Long-term stem biomass growth trend of an even-aged beech (*Fagus sylvatica* L.) forest in Thüringen (Germany). *In* Alberi e Foreste per il Nuovo Millennio. Proceedings of the 3rd Meeting of the Italian Society of Forest Management and Ecology, 15–18 September 2001, Viterbo, Italy. IP office, Viterbo, Italy. pp. 389–396.

Bauer, G.A., Persson, H., Persson, T., Mund, M., Hein, M., Kummetz, E., Matteucci, G., Van Oene, H., Scarascia-Mugnozza, G., and Schulze, E.-D. 2000. Linking plant nutrition and ecosystem processes. *In* Carbon and nitrogen cycling in European forest ecosystems. *Edited by* E.-D. Schulze. Springer-Verlag, Berlin and Heidelberg, Germany. pp. 63–98.

Becker, M., Bert, G., Bouchon, J., Dupouey, J., Picard, J., and Ulrich, E. 1995. Long-term changes in forest productivity in northeastern France: the dendroecological approach. *In* Forest decline and atmospheric deposition effects in the French mountains. *Edited by* G. Landmann and M. Bonneau. Springer-Verlag, Heidelberg, Germany. pp. 143–156.

Bert, D., Leavitt, S.W., and Dupouey, J. 1997. Variations of wood $\delta^{13}C$ and water-use efficiency of *Abies alba* during the last century. Ecology, **78**: 1588–1596.

Bond-Lamberty, B., Wang, C., Gower, S.T., and Norman, J. 2002. Leaf area dynamics of a boreal black spruce fire chronosequence. Tree Physiol. **22**: 993–1001.

Bräker, O.U. 1996. Growth trends of Swiss forests: tree ring data. Case study Toppwald. *In* Growth trends in European forests. *Edited by* H. Spiecker, K. Mielikäinen, M. Köhl, and J.P. Skovsgaard. Springer-Verlag, Heidelberg, Germany. pp. 199–217.

Briffa, K.R., Bartholin, T.S., Eckstein, D., Jones, P.D., Karlén, W., and Schweingruber, F.H. 1990. A 1400-year tree-ring record of summer temperatures in Fennoscandia. Nature (London), **346**: 434–439.

Briffa, K.R., Jones, P.D., Schweingruber, F.H., Karlén, W., and Shiyatov, S.G. 1996. Tree-ring variables as proxy-climate indicators: problems with low-frequency signals. *In* Climatic variations and forcing mechanisms of the last 2000 years. *Edited by* P.D. Jones, R.S. Bradley, and J. Jouzel. Springer-Verlag, Berlin, Germany. pp. 9–41.

Cannel, M.G.R. 1982. World forest biomass and primary production data. Academic Press, London.

Carmean, W.H. 1972. Site index curves for upland oaks in the central states. For. Sci. **18**: 109–120.

Cherubini, P., Dobbertin, M., and Innes, J.L. 1998. Potential sampling bias in long-term forest growth trends reconstructed from tree rings: a case study from the Italian Alps. For. Ecol. Manage. **109**: 103–118.

Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., and Ni, J. 2001. Measuring net primary production in forests: concepts and field methods. Ecol. Appl. **11**: 356–370.

Corbyn, I.N., Crockford, K.J., and Savill, P.S. 1988. The estimation of the branchwood component of broadleaved woodlands. Forestry, **61**(3): 193–204.

Cropper, J.P. 1979. Tree-ring skeleton plotting by computer. Tree-Ring Bull. **39**: 47–60.

Dittmar, C., Zech, W., and Elling, W. 2003. Growth variations of common beech (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe — a dendroecological study. For. Ecol. Manage. **173**: 63–78.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., and Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. Science (Washington, D.C.), **263**: 185–190.

Ellenberg, H. 1981. *In* Dynamic properties of forest ecosystems. *Edited by* D. Reichle. Cambridge University Press, Cambridge, U.K. pp. 666–668.

FAO. 1998. World reference base of soil resources. Food and Agriculture Organization of the United Nations, Rome, Italy. Rep. 84.

Foster, B.L., and Tilman, D. 2000. Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. Plant Ecol. **146**: 1–10.

Franz, F., Röhle, H., and Meyer, F. 1993. Wachstumsgang und Ertragsleistung der Buche (120jährige Beobachtung des Buchen-Durchforstungsversuches Fabrikschleichach 15). Allg. Forstz. **6**: 262–267.

Fritts, H.C. 1976. Tree rings and climate. Academic Press Inc. Ltd., London.

Graumlich, L.J., Brubaker, L.B., and Grier, C.C. 1989. Long-term trends in forest net primary productivity: Cascade Mountains, Washington. Ecology, **70**: 405–410.

Gregoire, T.G., Valentine, H.T., and Furnival, G.M. 1995. Sampling methods to estimate foliage and other characteristics of individual trees. Ecology, **76**: 1181–1194.

IPCC. 2000. Land use, land-use change, and forestry. Cambridge University Press, Cambridge, U.K. Spec. Rep.

Kauppi, P.E., Mielikäinen, K., and Kuusela, K. 1992. Biomass and carbon budget of European forests, 1971 to 1990. Science (Washington, D.C.), **256**: 70–74.

Keeling, C.D., Chin, J.F.S., and Whorf, T.P. 1996. Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. Nature (London), **382**: 146–149.

Kenk, G., and Guehne, S. 2001. Management of transformation in central Europe. For. Ecol. Manage. **151**: 107–119.

Kienast, F., and Luxmoore, R.J. 1988. Tree-ring analysis and conifer growth responses to increased atmospheric CO_2 levels. Oecologia, **76**: 487–495.

Kramer, H., and Kätsch, C. 1994. Individuelles Wachstum von Waldbäumen in Abhängigkeit von natürlichen und anthropogenen Einflüssen. Schriftenr. Forstl. Fak. Univ. Göttingen, **117**: 1–148.

LaMarche, V.C., Graybill, D.A., Fritts, H.C., and Rose, M.R. 1984. Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural vegetation. Science (Washington, D.C.), **225**: 1019–1021.

Le Goff, N., and Ottorini, J.-M. 2001. Root biomass and biomass increment in a beech (*Fagus sylvatica* L.) stand in north-east France. Ann. For. Sci. **58**: 1–13.

Mäkelä, A. 1986. Implications of the pipe model theory on dry matter partitioning and height growth in trees. J. Theor. Biol. **123**: 103–120.

Makowka, I., Riemer, T., Stickan, W., and Worbes, M. 1992. Dendroclimatological studies on beech-trees (*Fagus sylvatica* L.) and the changing influence of climate on radial growth. *In* Tree Rings and Environment. Proceedings of the International Dendrochronological Symposium, 3–9 September 1990, Ystad, Sweden. Department of Quaternary Geology, Lund University, Lund, Sweden. Rep. 34. pp. 217–221.

Masci, A., Hajny, M.T., Bascietto, M., and Matteucci, G. 2003. Biomassa epigea in una cronosequenza di faggio della Turingia (Germania). In Alberi e Foreste per il Nuovo Millennio, Proceedings of the 3rd Meeting of the Italian Society of Forest Management and Ecology (SISEF), 15–18 September 2001, Viterbo, Italy. IP office, Viterbo, Italy. pp. 511–516.

Menzel, A., and Fabrian, P. 1999. Growing season extended in Europe. Nature (London), **397**: 659.

Mund, M., Kummetz, E., Hein, M., Bauer, G.A., and Schulze, E.-D. 2002. Growth and carbon stocks of a spruce forest chronosequence in central Europe. For. Ecol. Manage. **171**: 275–296.

Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G., and Nemani, R.R. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. Nature (London), **386**: 698–702.

Nabuurs, G.-J., Pussinen, A., Karjalainen, T., Erhard, M., and Kramer, K. 2002. Stemwood volume increment changes in European forests due to climate change — a simulation study with the EFISCEN model. Glob. Change Biol. **8**: 304–316.

Nabuurs, G.-J., Schelhaas, M.J., Mohren, G.M.J., and Field, C.B. 2003. Temporal evolution of the European forest sector carbon sink from 1950 to 1999. Glob. Change Biol. **9**: 152–160.

Nemani, R.R., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J., Myneni, R.B., and Running, S.W. 2003. Climate driven increases in global terrestrial net primary production from 1982 to 1999. Science (Washington, D.C), **300**: 1560.

Nicolussi, K., Bortenschlager, S., and Körner, Ch. 1995. Increase in tree-ring width in subalpine *Pinus cembra* from the central Alps that may be CO_2-related. Trees, **9**: 181–189.

Nyland, R.D. 2003. Even- to uneven-aged: the challenges of conversion. For. Ecol. Manage. **172**: 291–300.

Oren, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maler, C., Schäfer, K.V.R., McCarthy, H., Hendrey, G., McNulty, S.G., and Katul, G.G. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. Nature (London), **411**: 469–472.

Persson, T., Karlsson, P.S., Seyferth, U., Sjöberg, R.M., and Rudebeck, A. 2000. Carbon mineralization in European forest soils. *In* Carbon and nitrogen cycling in European forest ecosys-

tems. *Edited by* E.-D. Schulze. Springer-Verlag, Heidelberg, Germany. pp. 257–275.

Piutti, E., and Cescatti, A. 1997. A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. Can. J. For. Res. **27**: 277–284.

Read, D.J., and May, R. 2001. The role of land carbon sinks in mitigating global climate change. The Royal Society of London, London. Rep. 10/01.

Ryan, M.G., Binkley, D., and Fownes, J.H. 1997. Age-related decline in forest productivity. Adv. Ecol. Res. **27**: 213–262.

SAS Institute Inc. 1989. SAS/STAT® user's guide. Version 6.4 ed. [computer program]. SAS Institute Inc., Cary, N.C.

Schimel, D.S., Melillo, J.M., Tian, H., McGuire, A.D., Kicklighter, D.W., Kittel, T., Rosenbloom, N., Running, S.W., Thornton, P.E., Ojima, D., Parton, W., Kelly, R., Sykes, M., Neilson, R., and Rizzo, B. 2000. Contribution of increasing CO_2 and climate to carbon storage by ecosystems in the United States. Science (Washington, D.C.), **287**: 2004–2006.

Schulze, E.-D. 1989. Air pollution and forest decline in a spruce (*Picea abies*) forest. Science (Washington, D.C.), **244**: 776–783.

Schulze, E.-D., Oren, R., and Lange, O.L. 1989. Processes leading to forest decline: a synthesis. *In* Forest decline and air pollution: a study of spruce (*Picea abies*) on acid soils. *Edited by* E.-D. Schulze, O.L. Lange, and R. Oren. Springer-Verlag, Heidelberg, Germany. pp. 459–468.

Schulze, E.-D., Wirth, C., and Heimann, M. 2000. Managing forests after Kyoto. Science (Washington, D.C.), **289**: 2058–2059.

Schulze, E.-D., Valentini, R., and Sanz, M.-J. 2002. The long way from Kyoto to Marrakesh: implications of the Kyoto Protocol negotiations for global ecology. Glob. Change Biol. **8**: 505–518.

Schweingruber, F.H. 1988. Tree rings. Basics and applications of dendrochronology. D. Reidel Publishing Co., Dordrecht, Netherlands.

Schweingruber, F.H. 1996. Tree rings and environment dendroecology. P. Haupt Publishers, Stuttgart, Germany.

Schweingruber, F.H., Eckstein, D., Serre-Bachet, F., and Bräker, O.U. 1990. Identification, presentation and interpretation of event years and pointer years in dendrochronology. Dendrochronologia, **8**: 9–39.

Spiecker, H. 2002. Tree rings and forest management in Europe. Dendrochronologia, **20**: 191–202.

Spiecker, H., Mielikäinen, K., Köhl, M., and Skovsgaard, J.P. 1996. Growth trends in European forests. Springer-Verlag, Heidelberg, Germany.

UNFCCC. 1997. The Kyoto Protocol. United Nations Framework Convention on Climate Change, Bonn, Germany.

Valentini, R., Dolman, H., Ciais, P., Schulze, E.-D., Freibauer, A., Schimel, D.S., and Heimann, M. 2000. Accounting for carbon sinks in the biosphere, European perspective. CarboEurope European Office, Jena, Germany.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological responses to recent climate change. Nature (London), **416**: 389–395.

Westoby, M. 1984. The self-thinning rule. Adv. Ecol. Res. **14**: 167–225.

Yanai, R.D., Arthur, M.A., Siccama, T.G., and Federer, C.A. 2000. Challenges of measuring forest floor organic matter dynamics: repeated measures from a chronosequence. For. Ecol. Manage. **138**: 273–283.