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Growth and nutrition of *Quercus petraea* underplanted in artificial pine stands under conversion in the northeastern German Lowlands

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Abstract

This study presents results on the growth and nutritional status of *Quercus petraea* trees underplanted in an artificial pine stand as a conversion strategy. A total of 162 plots of 400 to 800 m^2 were established in underplanted pine stands (130 plots), naturally regenerated oaks in pine stands (23 plots) and pure oak plantations (9 plots). The age of the oak stands was 7 to 14 years where they were planted, and 25 to 60 years in the natural regenerations. Biomass growth and nutrition of the oaks was studied by means of foliar analysis, soil analysis, biomass evaluation and regression techniques, considering site variables, meteorological parameters and pine cover as explicative variables.

The vegetation structure of the stands in the forest-transforming areas is still dominated by the species spectrum of the original pure pine stands. As the quality of a site decreases, so the dominance of a few species increases and the diversity decreases. The manipulative effect upon the vegetation of underplanting with oaks is less severe than that of underplanting with beeches. With the progressing development of the ecological system, more demanding deciduous tree types replace the undemanding pine forest vegetation.

On principle, the pine-tree canopy influences the supply of nutritional elements to the under-planted oaks. However, neither in average weather periods nor during droughts could any symptoms of nutrient deficiency or growth-impeding nutritional element disharmonies be detected by the naked eye. Only in the «Summer of the Century», 2003, did the laboratory analysed macro-element leaf-index reveal slight deficiencies of Ca- und S.

The modelling of the above-ground increase in oak biomass growth, differentiated according to site and depending on time and the canopy of pine trees revealed increasing increment losses the greater the canopy cover, which even lead to stagnation in growth as the quality of the site deteriorates.

Key words; sessile oak; Scots pine; forest conversion; site; vegetation; nutrition, growth.

Resumen

Crecimiento y nutrición de *Quercus petraea* plantado bajo cubierta en pinares artificiales de *Pinus sylvestris* en transformación en las tierras bajas del noreste de Alemania

Este estudio presenta resultados de crecimiento y estado nutricional de *Quercus petraea* plantado bajo cubierta de pinares de repoblación como proceso de transformación. Un total de 162 parcelas de 400 a 800 m^2 fueron establecidas en masas plantadas bajo cubierta de pino (130 parcelas), pinares con subpiso de roble de regeneración natural (23 parcelas) y plantaciones puras de roble (9 parcelas). La edad del roble fue de 7 a 14 años donde fue plantado y 25 a 60 años en los regenerados naturales. El crecimiento en biomasa y la nutrición de los robles se estudió mediante análisis foliar, evaluación de la biomasa y técnicas de regresión, considerando variables estacionales, parámetros meteorológicos y la cubierta de pino como variables explicativas.

La estructura de la vegetación de las masas en proceso de transformación todavía está dominada por el espectro de especies del pinar puro original. Al decrecer la calidad de estación se incrementa la dominancia de un conjunto reducido de especies, reduciéndose la diversidad. El efecto sobre la vegetación producido por la plantación bajo cubierta de robles es menor que el producido por plantación de hayas. Es esperable que con la progresión del ecosistema, especies frondosas más exigentes reemplazarán a la vegetación frugal de pinos.

En principio, la cubierta de pinos influye en el suministro de nutrientes al subpiso de roble. Sin embargo, ni en el caso de periodos meteorológicos considerados como normales ni en periodos de sequía se han podido detectar síntomas de deficiencias nutritivas o de desequilibrios nutricionales que condicionen el crecimiento. Únicamente en el verano más seco del siglo, 2003, los análisis de laboratorio detectaron pequeñas deficiencias en Ca y S.

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La modelización del crecimiento de la biomasa arbórea del roble, diferenciado de acuerdo a condiciones estacionales, dependiente del tiempo y de la cubierta del pinar reveló que se producen pérdidas de incremento a medida que la cubierta de pinar es más densa, lo que incluso determina un estancamiento del crecimiento del roble a medida que la calidad de estación es inferior.

Palabras clave: roble albar; pino silvestre; reconversión forestal; ubicación, vegetación; nutrición, crecimiento.

Introduction

At the end of the 20th century, the natural extent of tree species composition in the forest cover of the northeastern German Lowlands was a mere 14% (Hofmann, 1996). A dominance of *Pinus sylvestris* (potential natural share of the forest: 8.0%) extending over more than 70% of the forest area was to the detriment of the natural percentage of *Quercus petraea* (potential natural share: 25.0%; actual share: 1.0%). Because of the high operational risk associated with pine forests, the increasing number of pollutants and the advancing climate change, pure pine tree stands not suited to their sites have been underplanted with sessile oaks since 1990.

Owing to the lack of a scientific basis, the underplanting of oak trees has been the subject of interdisciplinary research (Noack, 2008) based on 162 trial stands in the State of Brandenburg. The most important objectives of this study were to make a comparison of ground vegetation diversity and composition between areas underplanted with oak and in pure pine stands. Furthermore to establish the nutritional status of underplanted oaks and relate this to pine cover, oak age, nutrition level in soils or meteorological conditions. Also to study the biometry, including slenderness, biomass and growth of underplanted oaks and after all to relate this information to pine cover and site parameters and propose a regression model to explain average single tree oak biomass.

Material and methods

Based on 162 trial stands the primary datasets represents the potential area of naturally beech-forests and sessile oak- or sessile oak-mixed-forests in the State of Brandenburg (Fig. 1). The verified site spectrum

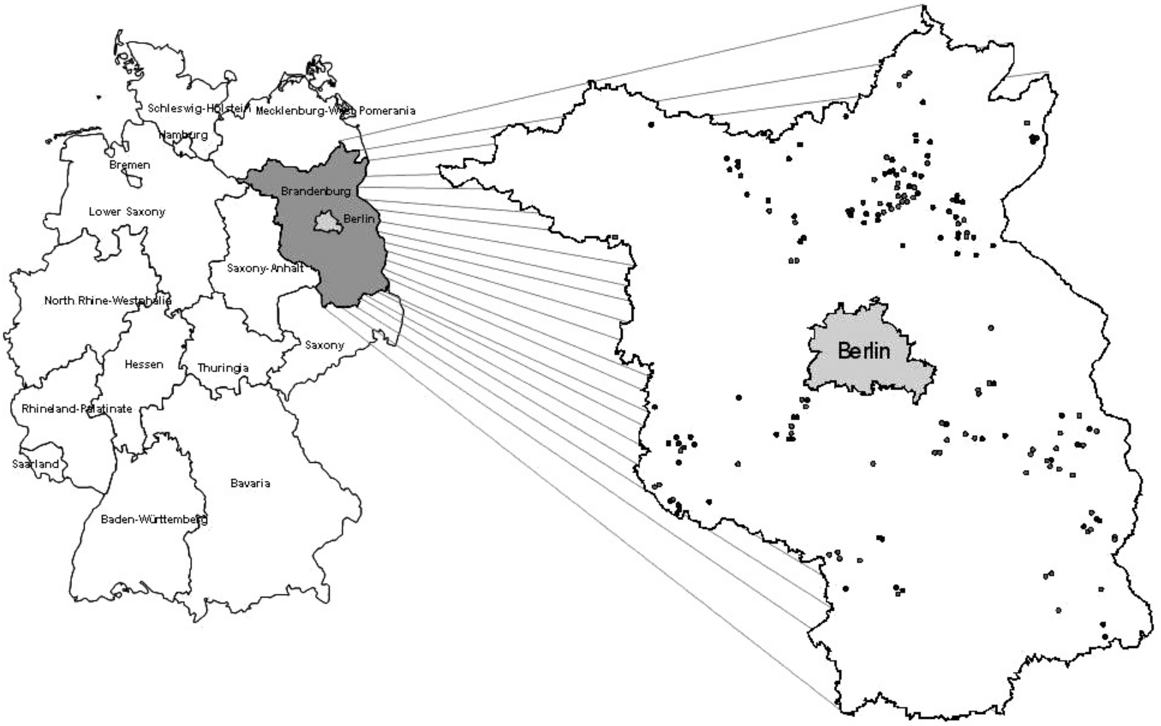


Figure 1. Distribution of the trial stands in Germany in the State of Brandenburg.

follows the naturalistic claim to site of sessile oak in NE Germany. Because of this the sample plots comprises exclusively soils free of ground water with nearly poor to nourishing trophic level. In substance these are sites of clayless to claylike sandy soils and also a low water storage capacity.

The size of the sample plots varied from 400 m^2 to 800 m^2 in dependent of the shaping of pine cover and oak plantation.

For the examination and evaluation of the growth of covered sessile oaks in pure pine stands it was measured 12.692 heights and root collar diameters (measuring point 10 cm above the top humus layer) of sessile oaks in underplanted pine stands (130 plots), naturally regenerated oaks in pine stands (23 plots) and pure oak plantations (9 plots) as of the key date 01.01.2003.

The average age of the pine tree conversion stands examined was 114 years, their canopy cover 21%-93%. The examined oaks were in the age range from 7-14 years (underplanted and pure oak plantations) o.r. 25-60 years (naturally regenerated oaks).

The measurements of heights and diameters of oaks were distributed by random selection all over each sample area. On the basis of an iterative sample planning for standard errors of heights and diameters the minimum number of measurements was fixed by 80.

The modelling of the above-ground biomass is based upon the determination of the dry matter content of 99 sessile oaks. Drying occurred by 103°C to the mass constance.

The volume-correct top humus layers and mineral samples (0-40 cm) from 75 sample plots have been chemically and physically analysed in the laboratory by the methods in Table 1.

For the nutritional analyses oak-leaf composite samples were taken in August 2002 and August 2003 from approximately 20 dominating and healthy oaks from each sample plot. These samples were dehydrated by a temperature of 80°C and crushed with titanium-blade-mill. Afterwards the leaf-flours were analyzed under Kjeldahl-disintegration method in a elementary analyzer (N) o.r. by nitric acid pressure disintegration method with following atom emission spectroscopy with ICP-animation (rest of macro- and micronutrients).

The determining of abundance of ground vegetation based on estimation of percent dot area in the period from July to August 2002 and its organization according to the system of Braun-Blanquet. For the description of the specific site-indicator of the vegetation species serves the sociological-ecologically species groups with its decadic indicators of trophic and moisture soil-level according to Passarge and Hofmann (1964) o.r. Hofmann (2002).

The quantification of diversity and dominance of ground vegetation species based on:

— Shannon-Index (Shannon and Weaver, 1976):

$$H' = -\sum_{i=1}^{N} p_i \cdot \ln p_i$$

(with N… total number of species and p_i… share of abundance i refered to total abundance).

— Eveness (Mühlenberg, 1993):

$$E = \frac{H'}{H_{Max}} \cdot 100$$

(with $H_{Max} = \ln N$ and N… total number of species).

— McNaughton-Index (McNaughton, 1968):

Table 1. Soil indicators and methods for analysis

Indicator	Methode
pH (H_2O, KCl)	Extraction with H_2O o.r. KCl, potentiometric analysis
C	Wet oxydation with $K_2Cr_2O_7$ / H_2SO_4, volumetric analysis
N	Kjeldahl-disintegration method, flow-injection-analysis FIA
Soluble macro- and micronutrients	
K, Ca, Mg, S, Na, Al, Fe, Mn, Zn	Extraktion with NH_4Cl, plasma-spektrometer ICP
P	Extraktion with ALE-solution, flow-injection-analysis FIA
Total content of macro- and micro-elements	
P, K, Ca, Mg	HF- disintegration, plasma-spektrometer ICP
Exchange acidity (total-, H- and Al-acidity)	Extraktion with KCl-solution, volumetric analysis
Kation-exchange acidity	Process according to Kappen-Adrian
Grain size analysis for depth stage 20-30 and 30-40 cm	Strainer- and sediment analysis

$$D = \frac{\left(A_{Max_1} + A_{Max_2}\right)}{A_{Gesamt}}$$

(with A_{Max1}… abundance of species with the maximum abundance, A_{Max2}… abundance of species with the second-biggest abundance, A_{Gesamt}… total abundance).

The raw meteorological precipitation and temperature data from 84 main- and 285 precipitation measuring stations in the period from 1990-2003 were provided by the Deutscher Wetterdienst (German Meteorological Service-DWD) and the Potsdam-Institute for Climate Impact Research (PIK) interpolated them to the geographical sample plot sites.

For the nutrition analysis in the years 2002 and 2003, the field precipitation (N) from 01. April to 31. August was reduced by the interception losses caused by the pine canopy with the aid of the model developed by Jenssen (2002). The growth analysis, on the other hand, used the annual interception losses according to Jenssen (1996, 1997) on the basis of the annual precipitation totals between 1990 and 2002. For the average stand temperatures (T) the DWD-field values were taken by Lützke (1984) and Flemming (1994) as a makeshift solution.

Results and discussion

Diversity and dominance of the under-planted ground vegetation

The Shannon-Diversity Index (Fig. 2) which drops as the quality of the site deteriorates from mould to raw humus makes it clear that number of species decreases and the unequal distribution of the relative abundance of individual species increases.

The relatively high Evenness-average values reveal a dominance of several species for all types of ecosystems. This phenomenon is somewhat more pronounced in the better sites (mould, duffy mould) than in «trophically weaker» areas (duff). The McNaughton-Index, which increases as the quality of humus decreases, confirms that the dominance of a few species tends to be greater at poorer sites than at better ones, and that the diversity also decreases. Evidence of this is also provided by the significantly falling species' numbers for the site-specific ecosystem types from mould through duffy mould to duff.

The degree of coverage of the shrub-and herb layer on the one hand and the moss layer on the other develop

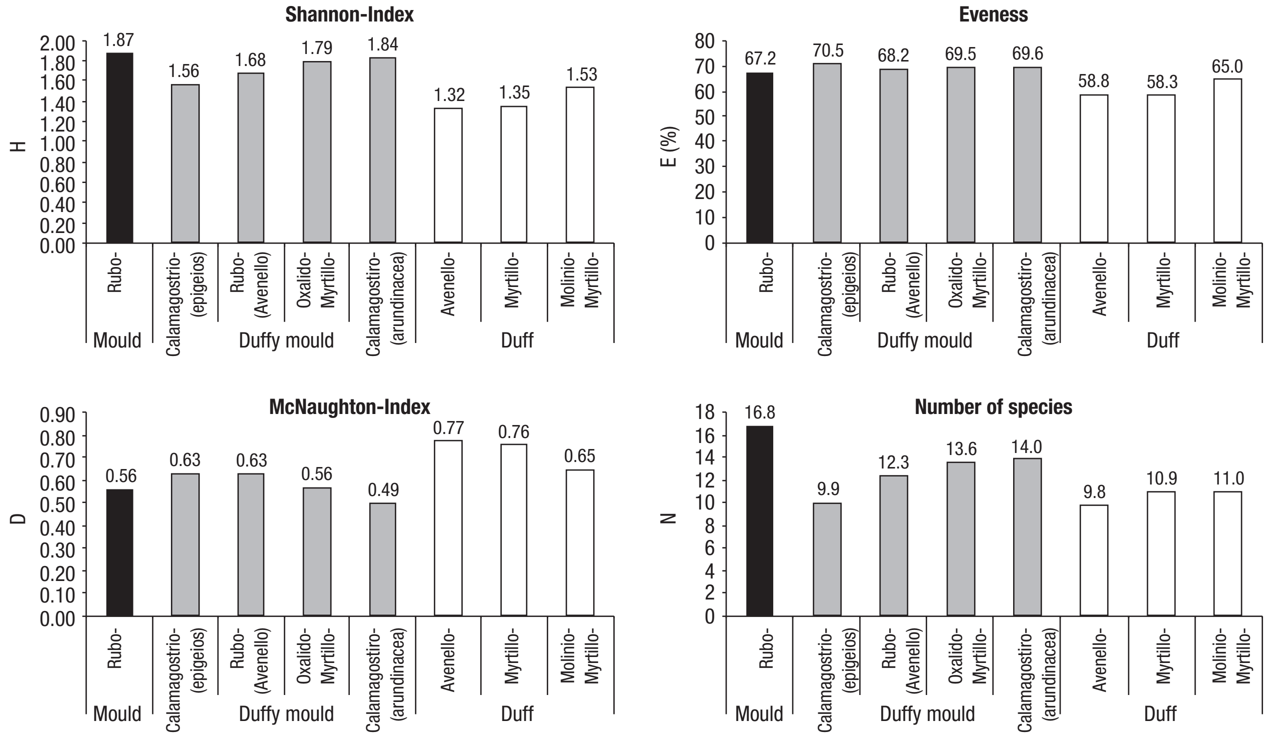


Figure 2. Shannon-Index (H´), Evenness (E), McNaughton-Index (D) and species' number (N) of the vegetation of the sample plots (showing only species of the shrub, herb and moss layer, not counting trees and woody types of shrub); arithmetical averages, stratified according to pine forest ecosystem types as per Hofmann (2001).

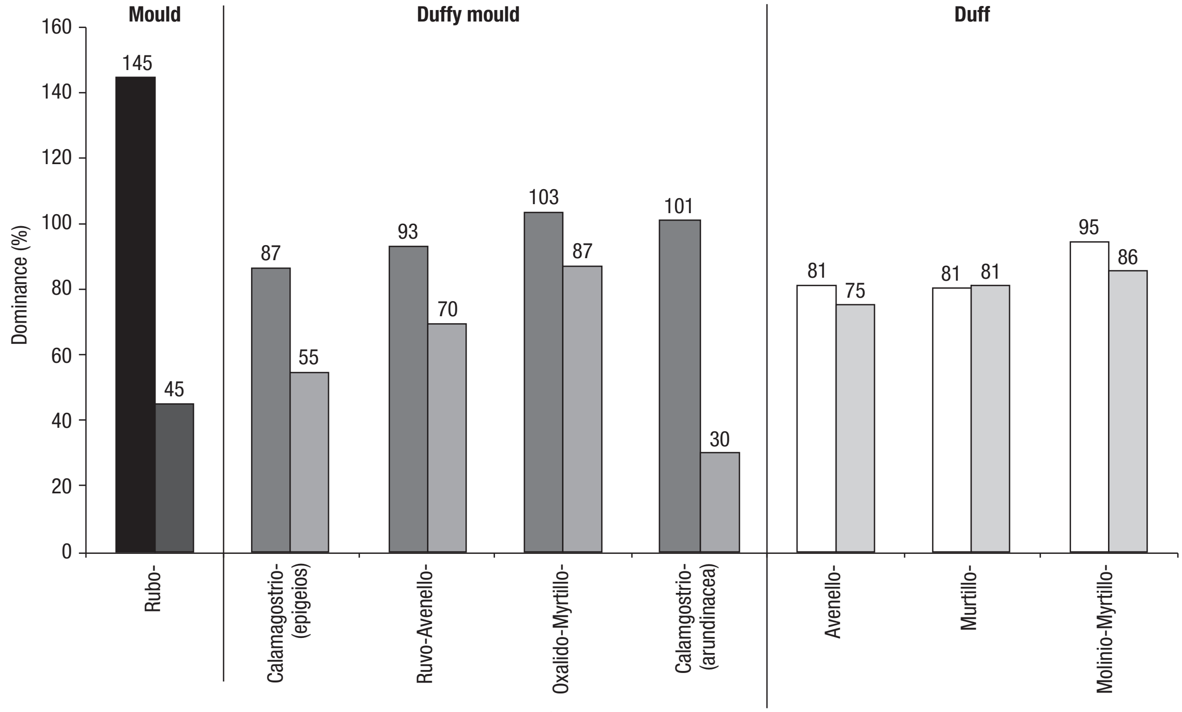


Figure 3. Average degrees of coverage of the herb and moss layers (shaded) on the sample areas stratified according to pine forest ecosystem types as per Hofmann (2001) (without tree- and woody shrub types).

in diametrically opposed directions depending on the site (Fig. 3). Whereas the covering ratio of the shrubs and herbs sinks along with the declining site quality from mould through duffy mould to duff, the moss covering increases in the same direction.

In contrast to the site-dependency of diversity and dominance, a differentiating effect of the pine canopy upon the vegetation within the ecosystem types examined could only be established in a very few isolated cases (cf. Noack, 2008). This independence of the named indicators from the percentage cover of the pine canopy is probably due to the uniform shadowy effect of the closed oak layer in the understorey.

Figure 4 quantifies the average numbers of species in «ecological fairways» in the consecutive phases of development within the ecosystems «pine forest», «pine forest with underplanted sessile oaks» and «oak forest or wood» on the basis of vegetation descriptions contrasted in non-genuine time series (cf. Noack, 2008).

According to this and agreeing with Zerbe (2002) and Zerbe and Kreyer (2007), the underplanting effects an increase in diversity in the transition between the humus forms duffy mould and mould, *i.e.* in mesotrophic and nutrient-rich trophic areas. This results from a comprehensive exchange of species. Plant types typical for pine forests forfeit their abundance or are eliminated completely; more demanding deciduous forest types replace them to an increasing extent. In the less nutrient-rich sites of the duff pine forests and the oak forest communities that follow them in the ecological succession, the species numbers and spectrums remain almost unchanged.

The analysis thus reveals that the stands in the forest transformation areas had indeed still been dominated by the characteristic community of species of the original pure pine stands, but that the underplanting of oaks had already effected a change in vegetation. This progresses less severely than in the case of the underplanting of beeches, however, which leads to a temporary darkening of the ground vegetation. Wavy hairgrass and sand-reed layers favoured by air-borne calcium- and nitrogen depositions but which are ecologically harmful are, however, noticeably restrained in their unfolding, which is positive for the settling of more ecologically beneficial types of plant. Particularly in mesotrophic and nutrient-rich trophic areas more demanding types of deciduous forest accompany or replace the original, less demanding pine forest vegetation as the development of the ecosystem progresses. The efficiency of this species dynamism reflecting the

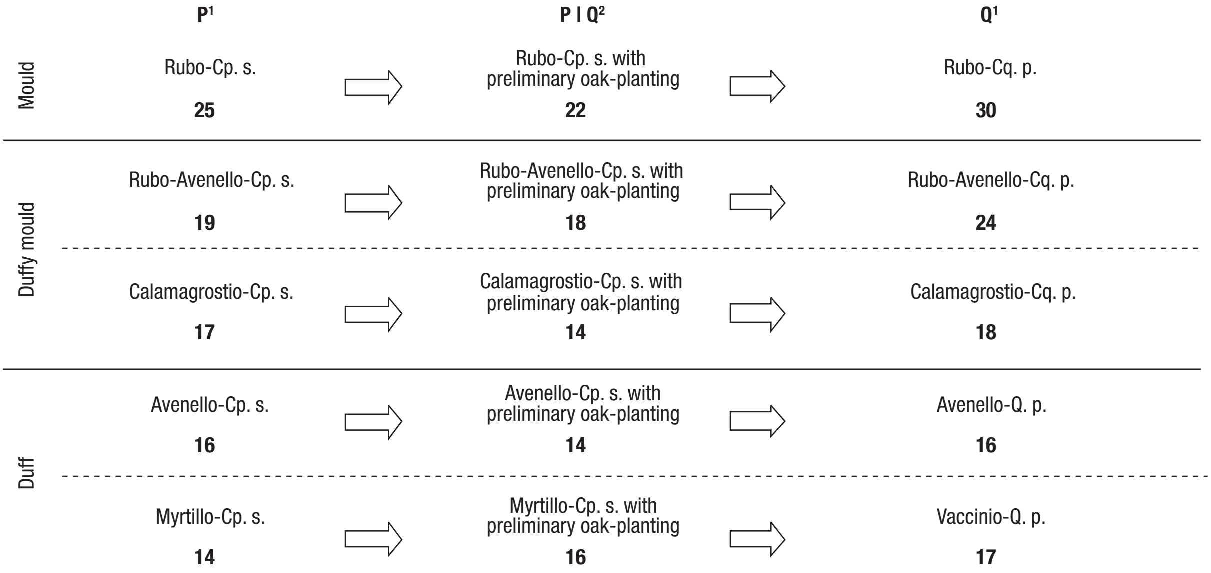


Figure 4. Overall species numbers for the successive development phases in ecosystems during forest conversion with the aid of the sessile oak (P… pine forest, P | Q… pine forest with underplanted sessile oaks, Q…sessile oak forest or wood); data basis for the non-genuine time series [1] Hofmann (2008), [2] my own surveys; arithmetical average values, all recordings over an average forest area of 600 m^2 were taken after 1990. Cp.s.: *Cultopinetum sylvestris.* Cq.p.: *Cultoquercetum petraeae.* Q.p.: *Querecetum petraeae.*

regeneration process of a site subsides as the quality of that site deteriorates, however. The number of species remains relatively unchanged in nutrient-poor sites.

Understorey oak nutrition

According to Table 2, the pine canopy influenced significantly oak nutrition with nitrogen, calcium, magnesium, sulphur, sodium, iron, aluminium and manganese in the year 2002. Increasing canopy covering resulted in this case in an enrichment effect for the oak leaf indices, whereby extreme cases of supernutrition were not encountered.

Parallel to this, the stand atmospheric conditions also exert a significant influence upon the supply of calcium, sulphur, iron, aluminium and manganese. The positive correlations established in each case mean that, under constant temperature conditions, heightened canopy throughfalls, *e.g.* as a result of reduced pine canopies, lead to increasing foliage.

The significance tests of the influence exerted by the nutritional elements present in the soil evidence the central importance of the nutritional power of the soil for the nourishment of the oak. With the exception of magnesium, it has been statistically proven that the soil supplies of all main nutritional elements influence the corresponding leaf indices. Due to positive interaction directions, richer endowment of the solum resulted in better nutritional states.

In 2002, the age of the oaks only had a negative correlation upon the supply of Al- and Zn.

Whilst a significant dependency of the Al- and Zn-leaf indices upon the age of the oak had been revealed in the year 2002 alone, this relationship was confirmed in 2003 only for aluminium with an unchanged direction of effect. In addition, the N- and S contents of the oak leaves are now in a significantly positive relationship to the age of the oak.

Under the extreme weather conditions of the year 2003, the pine canopy only significantly influenced the N- und S-nourishment according to sound statistics, whereby the leaf indices of both macro-elements correlated in a significantly positive manner with the percentage of the pine canopy. The average nutritional state of both elements nevertheless remained within the optimal range even where the canopy attained levels of 80-90%. It was, however, a little below the level of the previous year.

A weather effect, as in the previous year, could also be established in 2003 for the Ca-, S- and Mn-nourishment. Whereas the Al- and Fe-leaf indices, in contrast to 2002, were now independent of the stand weather conditions, the influence on the N- and Zn-leaf contents proved significant. The leaf indices of all five elements correlated positively with the N / T – quotients, which

Table 2. Significant correlations between nutritional element contents of leaf of underplanted sessile oaks in the years 2002 and 2003 and: age of the oak, percentage of the pine canopy, stand atmospheric conditions during the nutritious vegetation period (N / T – Quotient, 01.4-31.8) and nutritional element-soil supply (top layer of humus and 40 cm mineral soil)

	N	**P**	**K**	**Ca**	**Mg**	**S**	**Na**	**Zn**	**Fe**	**Al**	**Mn**
2002											
Age								+ –0.228		+ + –0.322	
Canopy	+ + + 0.446			+ + 0.308	+ + + 0.505	+ + 0.372	+ + 0.335		+ 0.353	+ + + 0.419	+ 0.278
N / T				+ + 0.384		+ 0.297			+ 0.205	+ + 0.315	+ + 0.315
Nutrient	+ + + 0.550	+ + + 0.711	+ + + 0.531	+ 0.216		+ –0.261					+ + + 0.770
2003											
Age	+ 0.212					+ + 0.331				+ –0.212	
Canopy	+ + 0.382					+ 0.289					
N / T	+ + + 0.399			+ 0.301		+ + 0.349		+ 0.298			+ 0.199
Nutrient	+ + + 0.447	+ + + 0.710	+ 0.262		+ 0.276		+ –0.234		+ 0.297		+ + + 0.706

is why a higher rate of precipitation, also as a result of a diminished canopy, brought about increased concentrations of the nutritional elements in the leaves.

The enormous importance of the soil trophic level on the nutritional state was also revealed in the year of drought, 2003. As in 2002, the leaf indices were significantly influenced by the soil supplies of N, P, K, and Mn. The previous year's significance for Ca and S was not confirmed, however. To make up for that, the relationships for the elements Mg, Na and Fe have now been statistically secured. The leaf indices and soil supplies of N-, P-, K-, Mg-, Fe- and Mn were correlated positively thereby, those of Na on the other hand negatively.

The nutritional state in the years examined, 2002 and 2003, is described by the foliage-index frequency distributions depicted in the Figures 5 and 6.

According to these, in the growth-friendly weather period in 2002, the under-planted cultures were essentially ideally provided with all major nutritional elements. Regarding the trace elements the supply state revealed itself to be somewhat more heterogeneous. The very low Na-supply and the very high Zn- and Al-leaf concentrations should be highlighted (Fig. 5).

In the «Summer of the Century» that then followed in 2003, on the other hand, only the supply of N and Mg was ideal. Whereas the P- and K-leaf contents now revealed a slight surplus, the Ca- and S-indices were deficient. The Na-, Fe- and Cu-nourishment was indeed extremely low, and the supply of Zn, Mn and Al on the other hand luxurious (Fig. 6).

The very strongly pronounced weather differences between the two observation years only led to a significantly lower supply of elements in the year 2003 in the case of the macro-elements N and Ca. The average N-supply could still be considered optimal, whereas that of Ca sank to the deficient level.

The reactions for all micro-elements with the exception of Al were clearer. As a result of the long-lasting drought of 2003 the Na-indices were significantly higher, but still lay mainly in the region of supply level 2. On the other hand the leaf concentrations of Zn-, Fe-, Mn-, B- and Cu fell considerably,-whereby only the Cu-concentrations fell to the very low values of supply level 1.

Taking into account the nutritional element ratios for leaf mineral contents for the limiting of harmonious nutrition ranges according to Bergmann (1993) and

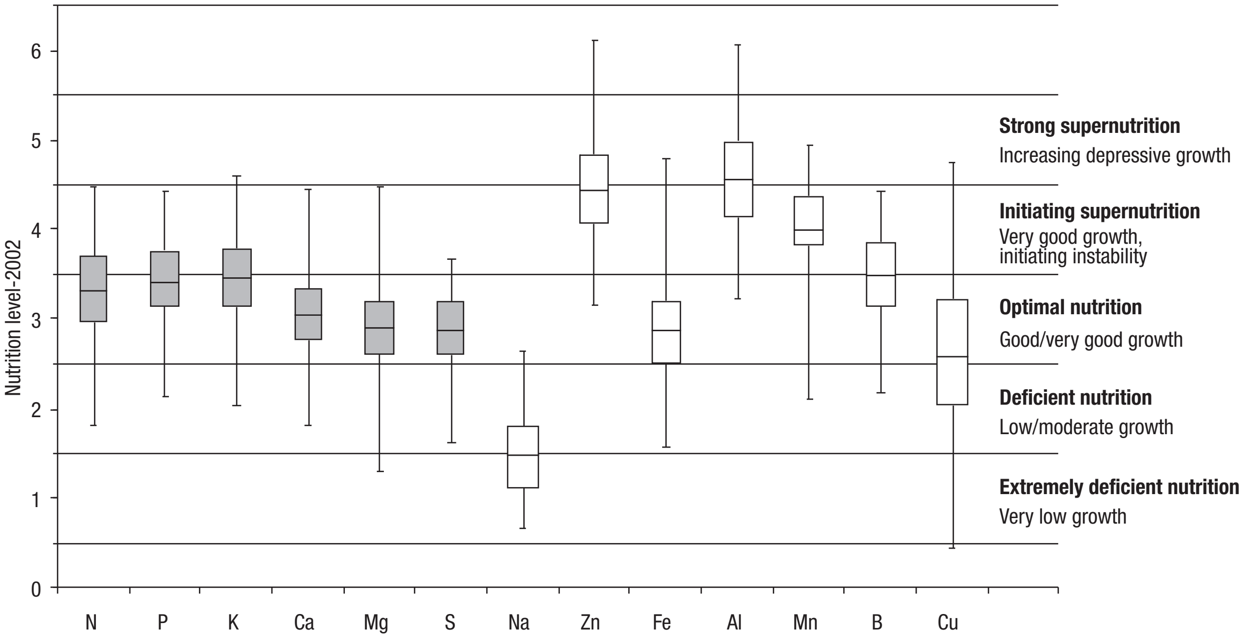


Figure 5. Distributions of nutrition levels for the empirical main nutritional element- and trace element- leaf indices of underplanted sessile oaks in the year 2002.

Heinsdorf (1999), the ratios in Table 3 exclusively characterised balanced nutritional conditions. Thereby, only the Mg-ratio reveal a significant dependency upon the pine canopy.

The weather differences of the years 2002 and 2003 also influenced the leaf index relations according to Heinsdorf (1999) for sessile oaks optimally supplied with N (2.07 ≤ N% ≤ 2.56) (Fig. 7). With the exception of the frequency distributions of the N : P-, P : K- and K : Mg- quotients all element quotient frequencies are significantly different. Whereby the N : K-, N : Mg-, P : Mg-, Ca : Mg - ratios in the drought year of 2003

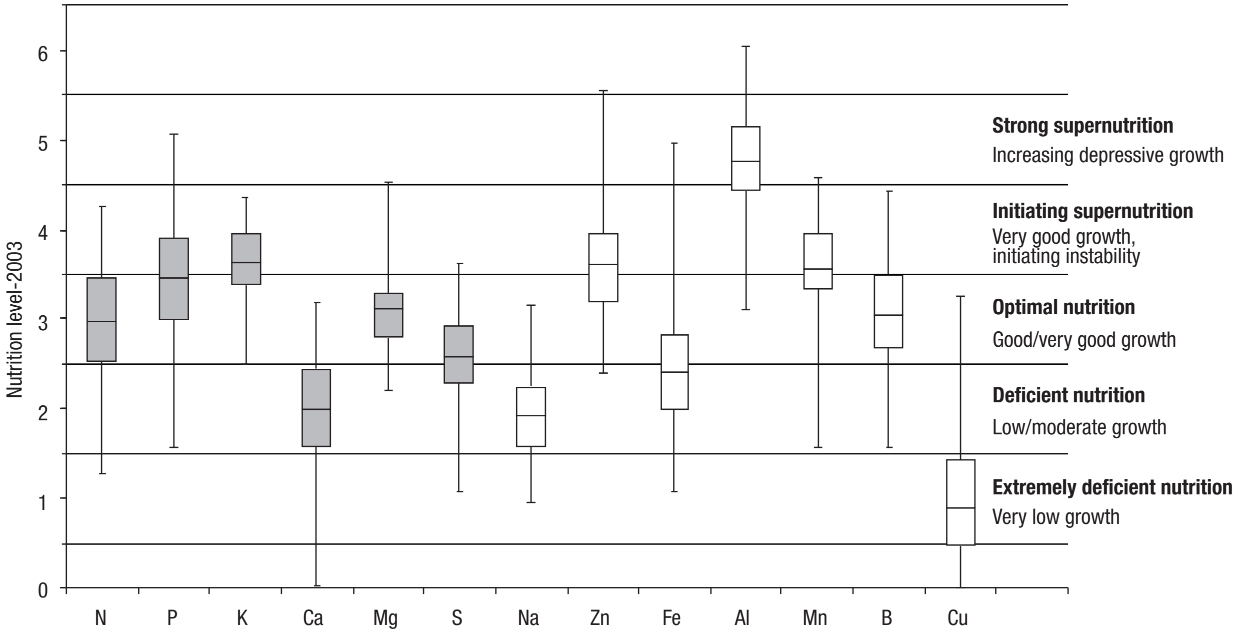


Figure 6. Distributions of nutrition levels for the empirical main nutritional element- and trace element- leaf indices of underplanted sessile oaks in the year 2003.

Table 3. Sessile oaks leaf index relations for the main nutritional elements N, P, K, Ca and Mg in the year 2002 stratified according to the percentage classes of pine canopies CP < 0% (CP_1), 50% ≤ CP ≤ 7 % (CP_2) and CP > 70% (CP_3); arithmetical average values with ANOVA-significance levels

<table>
<tr><th></th><th colspan="3">P</th><th colspan="3">K</th><th colspan="3">Ca</th><th colspan="3">Mg</th></tr>
<tr><th></th><th>CP_1</th><th>CP_2</th><th>CP_3</th><th>CP_1</th><th>CP_2</th><th>CP_3</th><th>CP_1</th><th>CP_2</th><th>CP_3</th><th>CP_1</th><th>CP_2</th><th>CP_3</th></tr>
<tr><td rowspan="3">N</td><td colspan="3">–</td><td colspan="3">–</td><td colspan="3">–</td><td colspan="3">+ +</td></tr>
<tr><td colspan="3">– –</td><td colspan="3">– –</td><td colspan="3">– –</td><td colspan="3">– +</td></tr>
<tr><td colspan="3">12.52 ↔ 12.88 ↔ 13.41</td><td colspan="3">3.385 ↔ 3.613 ↔ 3.657</td><td colspan="3">3.526 ↔ 3.876 ↔ 3.904</td><td colspan="3">18.15 ↔ 17.47 ↔ 15.32</td></tr>
<tr><td rowspan="3">P</td><td colspan="3"></td><td colspan="3">–</td><td colspan="3">–</td><td colspan="3">+ +</td></tr>
<tr><td colspan="3"></td><td colspan="3">– –</td><td colspan="3">– –</td><td colspan="3">– +</td></tr>
<tr><td colspan="3"></td><td colspan="3">0.275 ↔ 0.288 ↔ 0.282</td><td colspan="3">0.290 ↔ 0.310 ↔ 0.297</td><td colspan="3">1.486 ↔ 1.401 ↔ 1.175</td></tr>
<tr><td rowspan="3">K</td><td colspan="3"></td><td colspan="3"></td><td colspan="3">–</td><td colspan="3">+ +</td></tr>
<tr><td colspan="3"></td><td colspan="3"></td><td colspan="3">– –</td><td colspan="3">– –</td></tr>
<tr><td colspan="3"></td><td colspan="3"></td><td colspan="3">1.071 ↔ 1.097 ↔ 1.082</td><td colspan="3">5.651 ↔ 5.097 ↔ 4.375</td></tr>
<tr><td rowspan="3">Ca</td><td colspan="3"></td><td colspan="3"></td><td colspan="3"></td><td colspan="3">+ + +</td></tr>
<tr><td colspan="3"></td><td colspan="3"></td><td colspan="3">– –</td><td colspan="3">– –</td></tr>
<tr><td colspan="3"></td><td colspan="3"></td><td colspan="3"></td><td colspan="3">5.288 ↔ 4.628 ↔ 4.069</td></tr>
</table>

were significantly narrower in 2002 and the N : Ca-, P : Ca-, K : Ca- ratios wider.

Oak biometry

The density functions of the theoretical normal distributions for the empirical stem number frequencies on slenderness ratio classes for sessile oaks under canopies of varying thicknesses as in Figure 8 show a regular displacement in the larger end of the characteristic range as a result of a thicker canopy. According to this, the pine canopy has a detrimental effect upon the mechanical stability of underplanted sessile oaks. Under increasing canopy cover considerably less favourable h / d – relationships are developed which result in an increased susceptibility to pressure loads (cloudbursts, wind, snow).

In the height range up to 500 cm the above-ground tree mass M of underplanted sessile oaks can be reliably quantified by applying the estimator in Table 4 with the aid of the variable plant height h, root collar diameter $d_{0,10}$ and mid-plant diameter $d_{h/2}$. The test statistics presented here demonstrate the above averagely high forecasting quality of the construed regression function. In addition, closest possible biomass estimates for the oak compartments shaft, branch and leaf are made available (cf. Noack, 2008).

For the purpose of creating a model of the above-ground biomass growth of underplanted sessile oaks dependent upon time, site and pine canopy, the canopy indicator CI revealed itself to be the most suitable regressor of the 16 tested pine canopy features as a simple quotient made up of canopy percentage (%) and average position of crown height (m) (pine canopy indicator CI) (cf. Noack, 2008). Moreover, it is extremely practicable.

The three-dimensional response surfaces illustrated in Figure 9 for the description of the biomass development M (g) depending on the age of the oak A (a) and pine canopy indicator CI by whole-number variations

Table 4. Equation and fitting information for the biomass model

$$M(g) = 0.1078414283 \cdot \overset{+++}{h(cm)^{0.4178689801}} \cdot \overset{+++}{d_{0.10}\,(mm)^{1.57424182475}} \cdot \overset{+++}{d_{h/2}\,(mm)^{0.2441630223}}$$

Adjusted coefficient of determination B^*	0.9421
Standard error $s_{y,x}$	220.70
Relative mean residue MF_e %	1.50
Relative absolute mean residue MF_a %	13.70

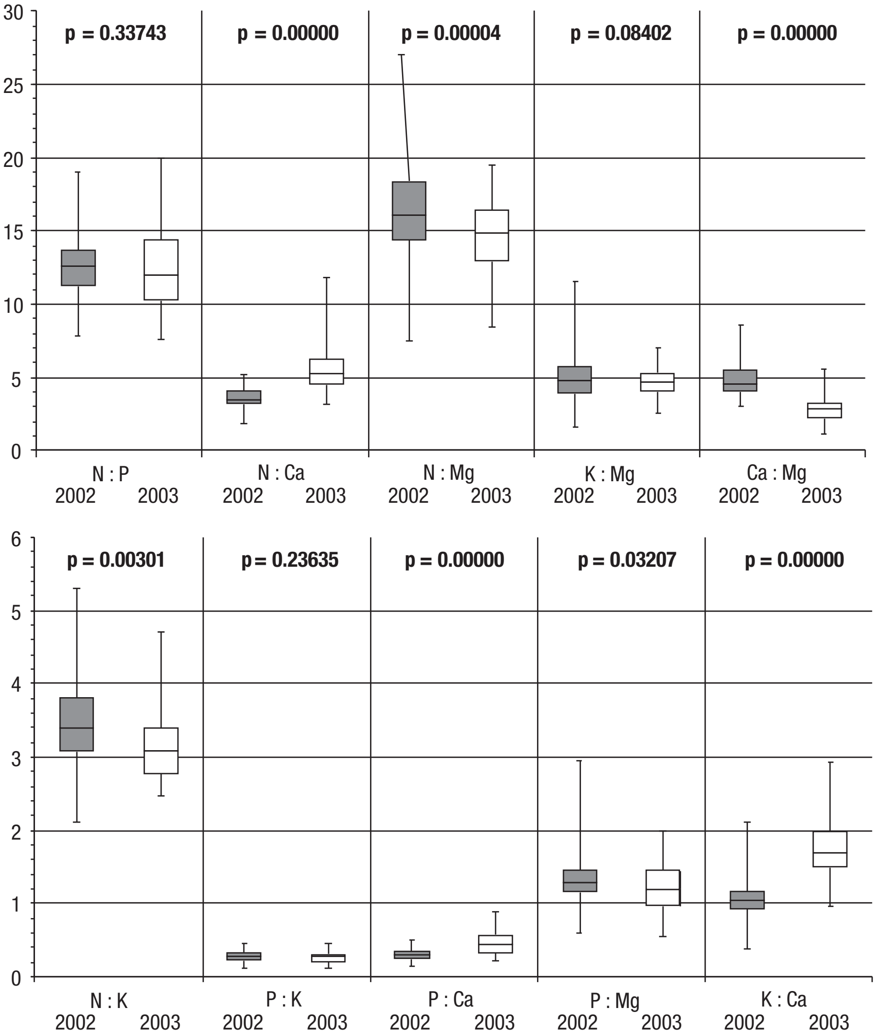


Figure 7. Leaf index relation-frequency distributions of the main nutritional elements N, P, K, Ca, Mg in the years 2002 and 2003 for sessile oaks optimally supplied with N (N-nutritional level III according to Heinsdorf 1999); Box-and-Whisker-Plots und p-values of the ANOVA-averages comparison.

of the C : N-ratios in the topsoil as a parameter for the quality of the site, are derived from the multiple power function found.

The mass response surfaces differentiated according to C : N-ratios thereby differ considerably in their levels and rates of increase. As a consequence of increasing site or humus quality, *i.e.* decreasing C : N-ratio, the biomass output of the underplanted oaks went up continuously. At the same time, the ability of the oaks to react to a decreased pine canopy by producing more biomass improved considerably.

The tree-mass lines of efficiency of 14-year-old underplanted sessile oaks illustrated in Figure 10, serve to underline this growth regularity.

A striking feature is the enormous, site-dependant differences in the tree mass quantity of underplanted sessile oaks when the canopy remains constant. Moreover, the lines of identical growth rate increases also make clear the site-specific ability of the oaks to react to a reduced pine canopy by producing more mass. The example depicted here shows that, in order to achieve a pre-defined tree mass growth rate of 1,000 g, the pine canopy requires a very different type of treatment depending on the site. According to this, pine stands with a C : N-ratio of 28 (duffy mould) must be 34% more strongly opened up than pine stands with a C/N-ratio of 16 (mully mould). The reason is a higher ability to tolerate shadow on the part of the light demanding

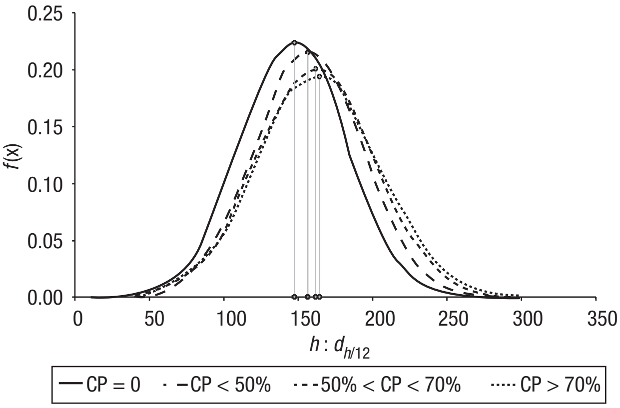


Figure 8. Density functions of the normal distribution for the description of the stem number frequency of underplanted sessile oaks on h : d$_{h/2}$ – classes with arithmetical average values as maximal ordinates; according to pine canopy percentage (CP) classes.

tree type sessile oak as the site becomes increasingly favourable.

The critical canopy percentage CP$_{\text{crit}}$. (%) of the pine overstorey quantifies as a threshold value that canopy percentage which, should it be fallen short of as a result of silvicultural actions, would trigger off a site-specific acceleration of the growth in biomass (Fig. 11).

As an argument value of the peak $SP_i(x_{SP_i}; y_{SP_i})$ of the parabola branch defined by the formula:

$$x_0 \equiv CP_{MIN} = 20 \;\le\; CP(\%) \;\le\; x_0 + H \equiv CP_{MAX} = 90$$

typical for light-demanding trees, SP_i defines the average and therefore characteristic increase in the curve $\bar{m}_i = \tan \alpha$ between the points P_0 and P_H.

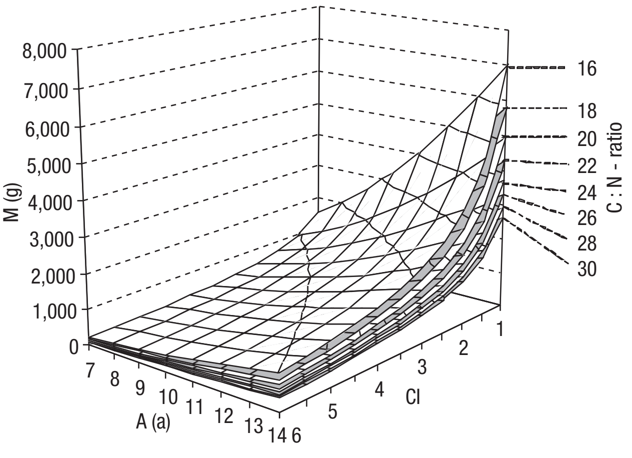


Figure 9. Tree mass M [g] of underplanted sessile oaks under a pine canopy dependant upon the age of the plant A (a), pine canopy indicator CI and C : N-ratio in the upper body of the soil (humus layer and mineral soils to a depth of 40 cm).

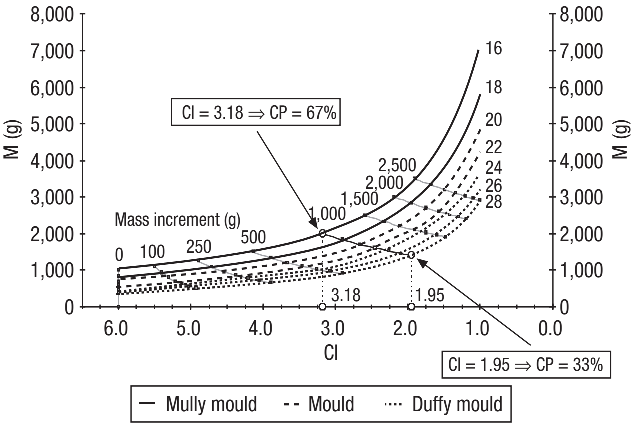


Figure 10. Tree mass M (g) showing the increases in mass growth rates of 14-year-old sessile oaks under-neath pine canopies dependent on the pine canopy indicator CI and the C : N-ratio in the upper body of the soil (Humus layer and miner soil to a depth of 40 cm).

The precisely localised threshold value CP_{krit} thus separates two rates of increase determined by the pine canopy:

1. A «start-up or stagnation phase» of oak biomass growth in the abscissae segment $x_0 + H \ge x_i \ge x_{SP_i}$, in which the empirical curve increases are on principle lower than the average increase in the function. Here, the thick pine canopy considerably impairs the growth of the covered sessile oaks, so that the mass increase rates of the oaks are merely below average.
2. An «upturn or exponential phase» of the biomass growth in the abscissae segment $x_{SP_i} \ge x_i \ge x_0$. In this range the empirical increases exceed the average value $\bar{m}_i$, which is why this range of the pine canopy enables above-average increases in oak mass growth and thus higher-performing underplanting cultures.

Table 5 makes it clear that the critical canopy percentages differentiated by site are, as far as the models are concerned, identical, but that the level of growth M that sets in thereby differs considerably. In particular, in the weaker site range it is therefore logical to exploit the increases in biomass growth that only occur more strongly in the upturn phase. The maximum

Table 5. Critical pine canopy percentages CP$_{\text{crit.}}$ for the acceleration of the growth of underplanted ses-sile oaks with average tree-masses M when CP$_{\text{crit}}$ is achieved

Humus form	CP$_{\text{crit.}}$ (%)	M (g)
C : N = 16 (mully mould)	42	3,320
C : N = 22 (mould)	42	1,814
C : N = 28 (duffy mould)	42	1,081

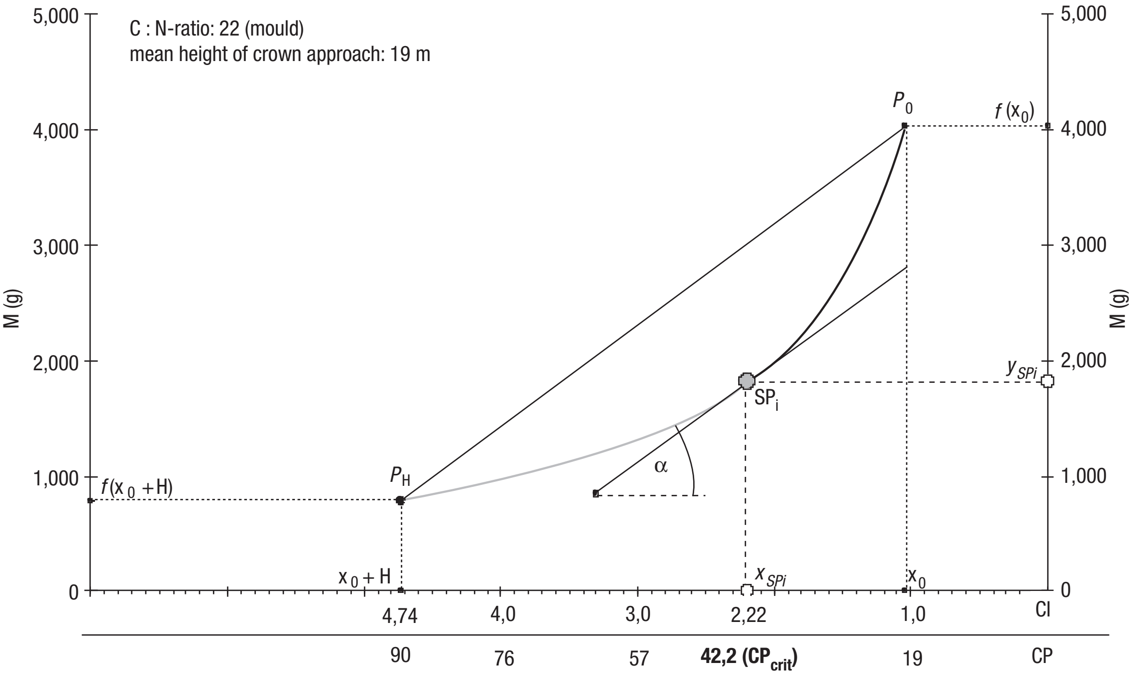


Figure 11. Derivation of the critical canopy percentage $CP_{crit.}$ with the aid of the peak SP_i of the parab-ola describing the tree-mass development of 14-year-old sessile oaks dependent upon the C : N-ratio and from the pine canopy [canopy indicator (CI), canopy percentage (CP)].

possible exhaustion of the, in this range, only relatively low performance capability of the underplanted cultures, thus requires on principle less dense canopies than in sites rich in nutrients where a pre-defined tree-mass also grows under considerably thicker pine canopies.

The relationship between leaf mass and dendro-mass illustrated in Figure 12 dependent on site and pine canopy prove that the relative percentage of leaf mass within the above-ground tree-mass significantly increases as the canopy also increases. According to this underplanted sessile oaks beneath closed pine canopies assimilate less efficiently than do those under light canopies. Additionally, the efficiency of the dendro-mass synthesis is also dependent on the site. The relationships between leaf mass and dendro-mass specific to the types of humus differ in quality. The mass percentage of assimilating leaf organs on the tree as whole sinks as the quality of the site increases, although at the same time the absolute production of dendro-mass increases.

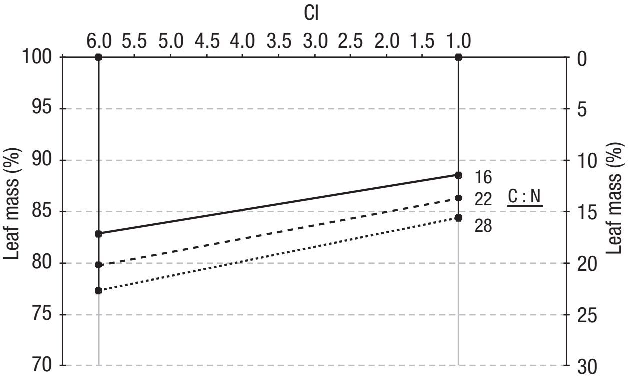
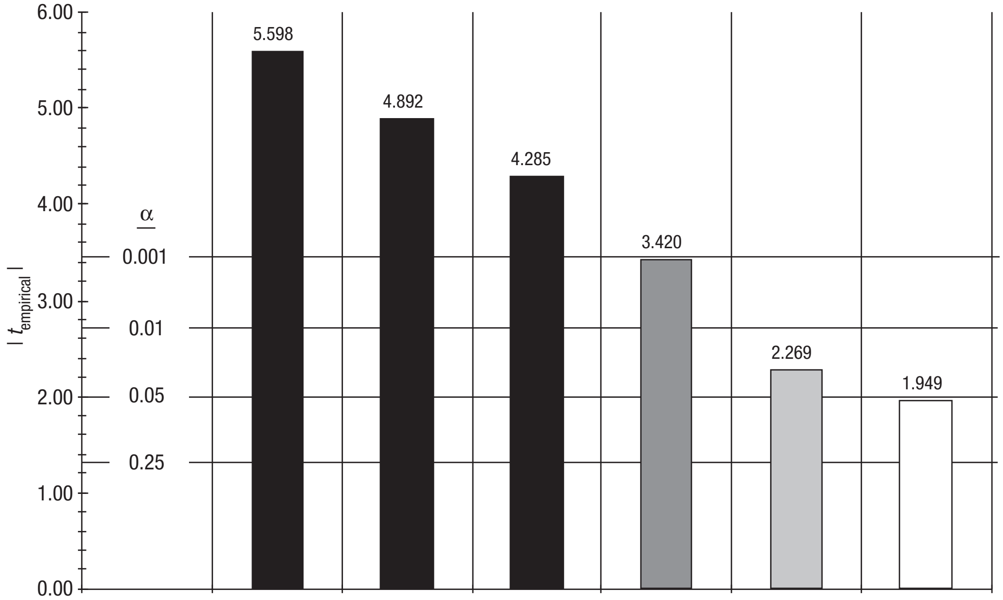


Figure 12. Relative shares of dendro- and leaf masses (%) of the tree-mass of underplanted sessile oaks dependent upon the pine canopy indicator CI; according to C : N- ratios

When raising high-performance and efficiently producing underplanted cultures, care should therefore be taken that underplanted sessile oaks assimilate all the more efficiently the less dense the canopy cover and the better the quality of humus.

Cause-effect analysis of oak growth

The complex dependencies of the growth of underplanted sessile oaks upon the pine canopy and the site were inspected on the basis of a total of 46 forest growth science, soil science, nutritional science and meteorological influences. The average above-ground individual



Ecological factor complexes and character variables		Factor F3	Factor F6	Factor F1	Factor F5	Factor F2	Factor F4
1 Soil acidity	Fe-soil bulk			0.650			
	pH_{H20}			0.542			
2 Nutrients	Mg-soil bulk			0.505		0.620	
	C : N-ratio			0.731			
	Ca-total soil bulk			0.905			
	N-soil bulk					0.928	
	S-value						*0.877*
	V-value						0.935
	N-*leaf level*					0.558	
	Mg-*leaf level*				0.576		
3 Soil sorption	K-soil bulk				0.614		
	Clay				0.750		
	Mn-soil bulk			0.509			
	Mg-total soil bulk			0.771			
	K-total soil bulk			*0.874*			
	Al-soil bulk				0.702		
	T-value					*0.910*	
4 Pine-canopy	Crown admission(ca)	0.717	0.672				
	CI	*0.852*					
	N : T-ratio	0.949					
	Oak age		0.957				

Figure 13. Empirical t-values for the coefficients (bi) of the linear multiple regression between the tree-mass M (Y) of underplanted sessile oaks and the extracted factors F_j with factor-specific charged patterns of their «most highly charged leading variables» (normal type), «> 85%-marking variables» (in italics) as well as other marking variables (grey).

tree mass M (g) of the underplanted cultures analysed in each case served thereby as the dependent target variable.

After correlative and factual ecological dimensional reduction, the 21 most influential growth rate characteristics have been classified in four ecological factor complexes according to their functionality within the ecological system. By means of an analysis of the main components there followed a bundling of the characteristics and the extraction of 6 factors, the effectiveness of which upon the rate of tree-mass growth of underplanted sessile oaks was evaluated using the empirical t-values for its linear partial regressions to the individual tree mass of the sessile oaks (cf. Fig. 13).

Together with the factor-defining charged patterns of the leading and marking variables, it is made clear that the two factors defining the ecological complex of factors «(4) pine canopy», F3 and F6, have the strongest influence upon the growth of tree mass.

This is subscribed to by the «mixed factor» F1, which is characterised by variables from the ecological complex of factors «(2) nutrients» and «(3) soil sorption». It is followed by factor F5 with a leading variable of factor complex «(3) soil sorption». Fifth place is occupied by the «mixed factor» F2, whose distribution of marking variables is identical with that of factor F1.

To sum up, it may be stated that the growth of underplanted sessile oaks is clearly dominated by the complex ecological effect of the pine canopy, *i.e.* by a silvicultural regulative.

The nutrient and soil sorption relationships join the fray as growth-restricting features. A successful underplanting of oaks in the extensively trophic weak and low in precipitation Northeast German Lowlands therefore presupposes a minimum of soil nutritional power and sorptive fine soil components. These are capable of combating the precipitation deficits that regularly occur in the region and cause trophic supply bottlenecks in favour of oak growth and to further or uphold the water-bound metabolic processes.

On the other hand, the soil acidity relationships in the area researched were of less significance for the growth of the oaks under the canopy.

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