Variation in performance of beech saplings of 7 European provenances under shade and full light conditions

K. Kramer
A.F.M van Hees
W.W.P. Jans

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ABSTRACT

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The use of beech seedlings from south-east (SE) European and north-west (NW) provenances for underplanting in coniferous forests in NW Europe was investigated by means of experimental shading. The effects of this treatment on survival, morphology, phenology, physiology and growth were analysed by applying an individual plant growth model integrating these aspects. It was concluded that plant performance under full light conditions are representative for shaded conditions, so that selection of good performing provenances can be done in a field situation. It was further concluded that good performing SE-European seedlings can be used in NW-European conditions. The modelling results indicated an interesting trade-of between height growth and biomass increase and different provenances show different strategies. This allows selection of suitable provenances for specific situations, *e.g.* when beech seedlings needs to compete with other plant species in the understory.

Keywords: *Fagus sylvatica*, beech, provenances, underplanting, plant performance, survival, growth, morphology, phenology, physiology, modelling

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Alterra is the amalgamation of the Institute for Forestry and Nature Research (IBN) and the Winand Staring Centre for Integrated Land, Soil and Water Research (SC). The merger took place on 1 January 2000.

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Contents

Preface

In this report the results are presented of the Dutch project *"Genetic variation in growth and survival of beech saplings under shaded and non-shaded conditions"*. This project is part of *the* EU-financed project *"Common beech for forestation and diversification: development of forestation techniques of the genetic variation in reproductive material"* (FAIR3-CT96-1464). The general objectives of the EU-project included:

1) improvement of methods for the procurement of reproductive material,
2) development of efficient forestation methods,
3) study of the genetic variation throughout the beech range distribution by molecular markers,
4) study of the genetic variation as well as the adaptability of beech provenances to be able to select highly qualified and adapted reproductive material for the various sites to be forested.

The research was carried out in the period 1996 – 2000, 12 participants from 8 European countries were involved in this project.

The task of Alterra in this project was to investigate *"Genetic variation in growth and survival of beech saplings under shaded and non-shaded conditions"*. Its specific objectives were:

1) to provide information on genotype variation in phenological, physiological and morphological features of beech,
2) to relate this variation to survival and growth under both shaded and non-shaded conditions,
3) to provide insight in the causes of this survival and growth based on the carbon budget of the saplings,
4) to indicate which provenances are suitable for planting under shaded and non-shaded conditions.

Summary

In northwest and central Europe coniferous forests are being converted into deciduous forests because of economic and ecological reasons. Beech is an important species for this conversion. In the absence of seed trees this conversion into a mixed beech-coniferous forest has to be based on the underplanting with beech. In NW-Europe plant material from selected SE European provenances can be used. These SE-European beech provenances are adapted to a continental climate with severe winters and hot and dry summer, whereas the Atlantic climate has mild winters and relatively cool and humid summers. Furthermore, the selection of these SE-European provenances is based on field trials and performance of provenances is evaluated under full light conditions. Thus the use of plant material of beech for underplanting in coniferous forest in northwest Europe may not be optimal. This may be attributable to genetic differences between provenances in phenological, physiological or morphological features. This study aims to provide suitable beech provenances for underplanting at northwest European conditions, and to identify the characteristics associated with this suitability. This was done by a shading experiment where potted seedlings are grown for several years in shade halls at 90% shade and 50% shade relative to full light conditions, and at full light conditions. We analysed plant performance in terms of survival, growth, phenology, morphology and physiology and analysed the implications of these features for the plants' carbon budget by means of linked leaf photosynthesis - individual plant growth model.

The following questions were addressed: 1) are there geographic differences in response to shading between southeast and northwest European provenance? and 2) do the provenances differ in their response to shading?

The northwest European provenances included Graf von Westfalen, Grasten, Aarnink and Lohmen whereas the southeast-European provenances were Buynovtzi, Postojna Javor and Maramures-Baia. Originally the provenance Ebrach (classified as SE-European) was included in this study. However due to the exceptional high mortality this provenance was excluded from most of the analyses.

The results showed for the first question that there are no systematic differences between the pooled southeast and northwest European provenances for phenological, morphological and physiological features. The best performing provenances were Grasten (NW-Europe), Maramures-Baia (SE-Europe) and Graf von Westfalen (NW-Europe). These provenances had an average mortality and the highest relative growth rates. Thus we concluded that some southeast provenances selected as a seed source for The Netherlands are potentially good candidates in the Atlantic climate.

The second question referred to differences between the provenances in response to the light treatments. The results of the experiments showed that the provenances respond similarly to the light treatments. In all provenances shading reduced seedling

mortality, reduced seedling growth and had a major effect on leaf development (low probability of repeated flushing) and plant morphology (more biomass allocated to the stem and less to the roots). Thus it can be concluded that the evaluation of the performance of seedlings raised under full light conditions is representative for their growth under shaded conditions.

We found a clear functional response for the 90% shade treatment when pooling the results over the provenances. There was an increase in the light use efficiency over the years and a reduction in the photosynthetic capacity such that the actual rate of net photosynthesis was not reduced.

The model on plant growth showed accurately predictions of the total plant biomass for the 90% shade treatment, but was less accurate for the 50% shade and the no shade conditions. As in literature is indicated that the second flush has higher photosynthetic capacity, this result is most likely because our measurements on photosynthetic capacity were done at leaves of the first flush for all treatments, whereas the 50% shade and no shade treatment did have a second flush. Thus the photosynthetic parameter values measured and used in the model may underestimate the average value of the entire canopy of a provenance. The 5-year model analysis on increase in biomass and height indicated a trade-off in these features for plants grown under 90% shade condition, and that different provenances show different strategies. These results can be used for the selection of provenances under specific growing conditions. E.g. Lohmen would be a good choice if seedlings need to compete with herbaceous vegetation. If this is not the case, and it can be assumed that the allocation pattern has a genetic base that is also valid for adult trees, then provenances such as Buynovtzi, Graf von Westfalen or Aarnink with a stronger increase in biomass can be favoured.

1 Introduction

Common beech (*Fagus sylvatica* L.) is an indigenous tree species covering approx. 12 million hectares in Europe. The natural beech forests have been cleared since the Middle ages to gain land for agricultural use. At the same time over-exploitation of the natural forests resulted in the replacement of these forests by heaths and drift sands. Later, these forest-less sites were afforested with fast growing coniferous trees, e.g. Norway spruce in Central Europe and Scots pine in northwest Europe. These production forests are typically even-age monocultures and are not sustainable with respect to both production and ecology. Based on economical and ecological consideration conversion of these coniferous stands into (mixed) broad-leaves stands is one of the major objectives of forestry in northwest Europe. One of the broad-leaves suitable for this conversion is beech. In the absence of beech seed-trees, conversion will take place by underplanting. Several southeast European provenances are currently selected as suitable to be planted under northwest European conditions. However, common practice is to evaluate these provenances under full light conditions. Under shaded conditions, growth and survival of provenances from southeast Europe, adapted to warm and dry summers, may differ from northwest European provenances that are adapted to relatively cool and humid summers. These differences may be attributable to genetic variation in phenological, physiological or morphological features. This study aims to provide suitable beech provenances for underplanting at northwest European conditions, and to identify the characteristics associated with this suitability. This was done by a shading experiment where potted seedlings are grown for three years at different levels of shading. We will focus on plant performance in terms of survival, growth, phenology and morphology and in terms of physiological features and then analyse the implications of these features for the plants' carbon budget my means of a linked leaf photosynthesis - plant growth model.

The general objectives of this study were: 1) to analyse genetic variation in growth, phenology, morphology and physiological of beech; 2) to provide insight in the growth of beech under shaded and non-shaded conditions based on the carbon budget of the saplings; and 3) to indicate which provenances are suitable for planting under shaded conditions.

2 Experimental set-up

Saplings of 4 provenances from southeast Europe and 4 provenances from northwest Europe were obtained from a beech nursery in Grosshansdorf, Germany, where the beech saplings were raised for one year. Table 1 indicates the locations of the sites from which the provenances were obtained.

The experiment started March 1997 on the nursery of the former Institute for Forestry and Nature Research (IBN-DLO), now Alterra, in Wageningen, the Netherlands. One-year-old beech seedlings were planted in 70-litre pots filled with local topsoil of the nursery. This topsoil used can be characterised as a coarse sandy soil with 3 to 4% humus and 10 to 15% loam. Nutrient availability in the upper soil is low for a nursery, but not limiting for the growth of broad-leaf species (pH-KCL 4.1, N-org 3.3 %, P-tot 185-mg P_2O_5 100 g^{-1}, K 7 mg 100 g^{-1}). Saplings were grown for three years (1997-1999) under 3 light conditions: no shade (NSH), 50% shade (50SH) and 90% shade (90SH). Metal constructions covered with shade cloth were build to create the 50SH and 90SH conditions. For each light condition there were 3 plots each containing 4 rows of plants with 3 replicates per row for each provenance (a total of 864 plants). Care was taken that water was not limited at any moment during the growing season. At least once a week all pots were automatically irrigated with 10 litre of water. In periods with high temperature and a prolonged drought irrigation took place twice a week. Pots were placed free from the soil and excessive water could drain freely out of the pots.

Data on phenology, survival, growth and morphology was collected each year of the experiment. A detailed description of the data collection, data processing and data analysis is given in paragraph 3.1. Data on photosynthesis is collected in 1998 and 1999. These data is used in the analysis of sapling growth through modelling of leaf photosynthesis and plant growth. A detailed description of the analysis of photosynthesis and the modelling is given in paragraph 4.1.

Table 1. *Location of the sites of the different provenances, and their reference number*

Provenance	SbNo	Country	Elevation	Longitude	Latitude
Buynovtzi	9104	Bulgaria	800	25°53’	42°56
Graf von Westfalen	9209	Germany-North	375	8°47’	51°31’
Aarnink	9170	The Netherlands	45	6°44’	51°56’
Grasten	9184	Denmark	45	9°35’	54°55’
Postojna Javor	9189	Slovenia	1040	14°21’	45°44’
Maramures-Baia	9229	Romania	800	24°0’	47°33’
Lohmen		Germany-East	-	-	-
Ebrach	9245	Germany-South	406	10°30’	49°51’

3 Analysis of mortality, growth, phenology and morphology

3.1 Material and methods

3.1.1 Mortality

Sapling mortality was assessed every spring and autumn; in spring during the monitoring of flushing and in autumn at the moment of harvest. Data on spring and autumn mortality were lumped into yearly mortality figures.

3.1.2 Biomass and growth

At the beginning of the experiment the diameter at root collar, sapling length and structural biomass (dry matter) of the different plant compartments (roots, stem and branches, including buds) was measured on 15 randomly selected plants per provenances. This data is used to characterise the initial condition of the provenances used in the experiment.

Each year at the beginning of October approximately one-third of saplings was harvested and on these plants again diameter at root collar, sapling length and structural biomass (dry matter) of the different plant compartments (main root, lateral roots, stem, branches and leaves) were measured. To determine plant biomass leaves were dried for 24 hours at 70°C and roots, stems and branches were dried for 48 hours at 90°C. Amongst others collected data is used to calculate the relative growth rate (RGR) per provenance per plot according to the following model:

$$RGR = \frac{\ln\left(B_{T(n)}\right) - \ln\left(B_{T(n=0)}\right)}{T} \qquad Eqn\ 3.1$$

where: RGR is the relative growth rate (g g^{-1}), $B_{T(n)}$ is the total biomass of the sapling harvested in year n (1 to 3), $B_{T(n=0)}$ is the average biomass per provenance measured at the beginning (year 0) of the experiment and T is the year of harvest (1 to 3).

We intended to harvest each year 4 plants per provenance per plot. However due to the high mortality at the beginning of the second year of the experiment only 2 to 4 plants per plot could be harvested in the second and third year.

3.1.3 Leaf development

Flushing was assessed every year. Once a week, starting the second half of April until the second half of June, the flushing stage of all beech plants was classified according to a seven-stage scale (see Table 3.1). In the months June to September of the second

year of the experiment the course of repeated flushing was assessed as well. Every two weeks, three plants per provenance per plot were checked for repeated flushing. This data is used to determine the onset and length of the repeated flushing. These three plants were harvested at the end of the growing season (first half of October). As the leaves of the first and later flushes are easy to distinguish it was possible to separate leaves from the first and later flushes at harvest and to measure the leaf area produced in these flushes. Also in the second year, leaf discoloration has been assessed. Again three plants per provenance per plot were monitored for discoloration with a two weeks interval, starting from the second half of September. Discoloration was assessed with the SPAD-520 meter (Minolta), which measures the relative amount of chlorophyll in the leaves. On each plant discoloration was measured at 5 randomly selected spots on 10 randomly selected leaves. Average SPAD-readings per plant were used as indicator for the discoloration of the whole plant canopy.

Table 3.1*. Description of flushing stage. Source: Institute of Forest Genetics in Grosshansdorf Germany (Liesebach, pers. comm).*

stage	Description
1	Dormant but
2	Buds swollen and elongated
3	Buds begin to burst, first green visible
4	Folded and hairy leaves begin to appear
5	Individually visible folded and hairy leaves
6	Leaves unfolded, still fan-shaped, pale scale present
7	Leaves unfolded, smooth and bright

At the end of September in the second year of the experiment leaves were collected ranging from dark green to yellow to establish a relation between SPAD-readings and chlorophyll content. The following model could describe this relation:

$$Chl = 36.19 \cdot e^{1.0575 \cdot SPAD} \qquad Eqn\ 3.2$$

where: Chl is the absolute chlorophyll content (mg m^{-2}), and SPAD is the relative chlorophyll content as measured with the SPAD 520-meter. This model accounts for 83.6% of the variation in the data.

3.1.4 Morphology

Plant morphology is characterised by the biomass distribution over the different plant compartments, the leaf area ratio (LAR), the specific leaf area (SLA) and chlorophyll content of the leaves. Biomass distribution is expressed as the fraction biomass in each of the plant compartments (roots, stem, branches and leaves). LAR is described as the amount of leaf area per unit plant biomass ($cm^2\ g^{-1}$). SLA is described as the leaf area per unit leaf biomass ($cm^2\ g^{-1}$). Leaf area of the harvested plants has been measured with the LI-310 area meter (LI-COR). Chlorophyll content was assessed at day 263. The relative

amount of chlorophyll was measured with the SPAD-520 meter and the SPAD readings were transformed into absolute chlorophyll values using Eqn 3.2.

3.1.5 Data analysis

In this experiment data on large number of parameters and processes are analysed. In the analysis different statistical tools are used. The experiment was designed for an ANOVA. However the high mortality resulted in an unbalanced design and thus the majority of the data were analysed with the REstricted Maximum Likelihood (REML). In addition logit regression was used for the analysis of the probability that a plant would die and for the analysis of the probability that plant would flush more then once. All statistical analysis were performed with GENSTAT (Genstat 5 committee 1993)

3.2 Results

3.2.1 Mortality

The analysis showed that mortality differed between light conditions and between years and provenances (significant interaction). These combined effects are presented in Figure 3.1.

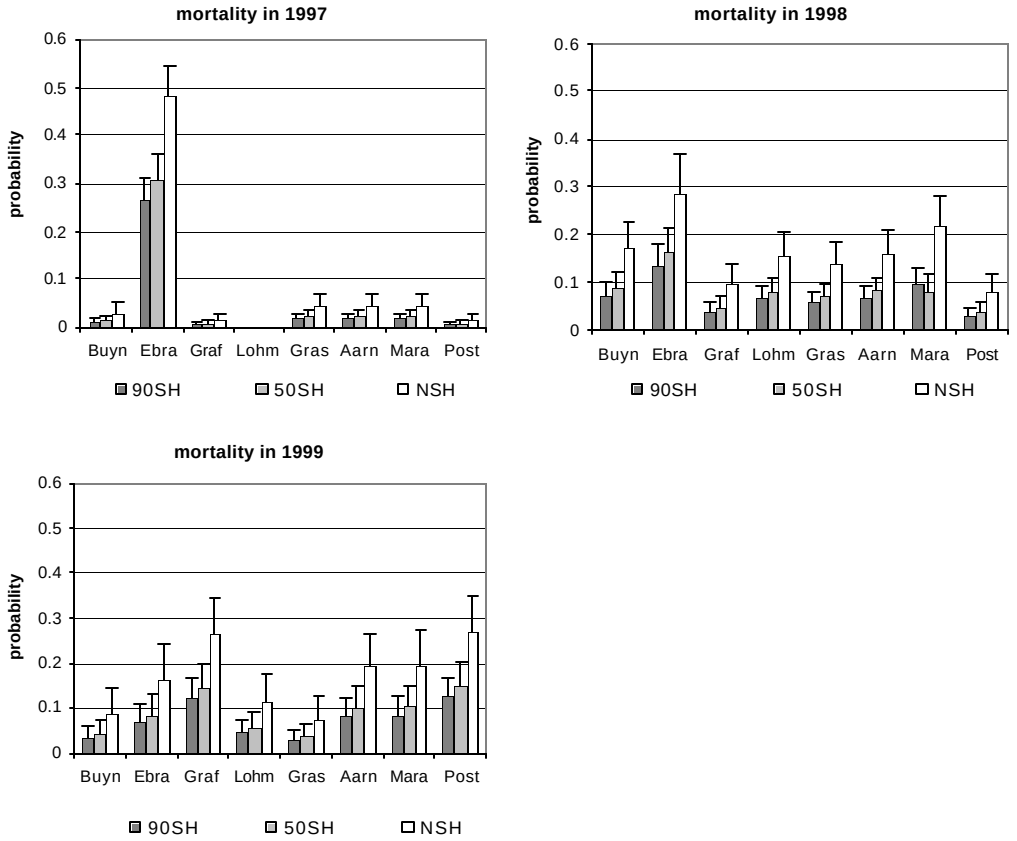

Figure 3.1*. Estimated mortality (P). Estimates are based on the model: logit (P) =* b_0 + b_1 *light* + b_2 *provenance.year*

The largest mortality was found under non-shaded conditions. At no-shade the estimated mortality was twice as high as at 50% shade and 90% shade, with values of 12.0% and 6.6% and 5.5% per year respectively. The highest mortality was found in the second and third year of the experiment. In these two years 10% (1998) and 11% (1999) of the plants died, while in the first year of the experiment mortality was limited to 5%.

The provenance Ebrach had the highest mortality. Pooled over light conditions and years the mortality was 25.3% per year, while for other provinces mortality varied between 4.6% and 8.5%. Due to this exceptionally high mortality the provenance Ebrach is excluded from some of the analyses of leaf development and plant morphology (see further). The variation in mortality between the provenances was not consistent over the three years. In the first year mortality was high for Ebrach with 35.6%. This mortality dropped to 19.4% in the second year and 17.9% in the third year. For all other provenances mortality was low in the first year (between 0% and 2.7%), but high in the second year (between 5.0% and 14.5%) and third year (between 4.7% and 18.0%).

A comparison between provenances from SE-Europe and NW-Europe did not show any significant difference in mortality between these two geographical regions.

The high mortality in the second and third year was primarily due to root damage by Taxus beetle (Otiorhynchus sulcatus (*Fabricius*)). This beetle killed the young beech plants by debarking the stem at the root collar, just below the soil surface. A check of the roots of the dead plants indicated that debarking was the main cause for mortality at 90% shade and 50% shade. At no shade debarking was less evident at dead plants.

3.2.2 Plant biomass and biomass increment

Each year approximately one-third of the plants was harvested at the end of the growing season (half October). Total biomass of the beech plants at each harvest is presented in Figure 3.2. Statistical analysis of the variation in biomass (analysis based on logarithmic transformed biomass) does not reveal any consistent response pattern over the three years.

At first harvest difference between provenances are significant and differences between light treatment are not. The differences in total plant biomass between provenances at the end of the first year must be attributed primarily to the initial variation in biomass at the start of the experiment. Provenance Lohmen had the largest biomass at harvest and the largest initial biomass, provenance Ebrach the smallest biomass at harvest and the smallest initial biomass.

At the end of the second year differences in total biomass between provenances are no longer significant. Plants of the provenance Ebrach are not harvested and the differences between other provenances are to small to be significant. Only an effect of light treatment is evident. In general harvested plants at no-shade have more biomass then at 50% shade, which in turn have more biomass then at 90% shade.

At the end of the third year differences between light levels and provenances are significant. The effect of light is less clear then at the end of the second year. In general differences in plant biomass between 50% shade and no-shade are to small to be significant, while differences of both light levels with 90% shade are. Comparing provenances, the SE-European provenances Maramures-Baia and Buynovtzi now have the largest plant biomass, which suggests that these provenances are growing faster then the other provenances.

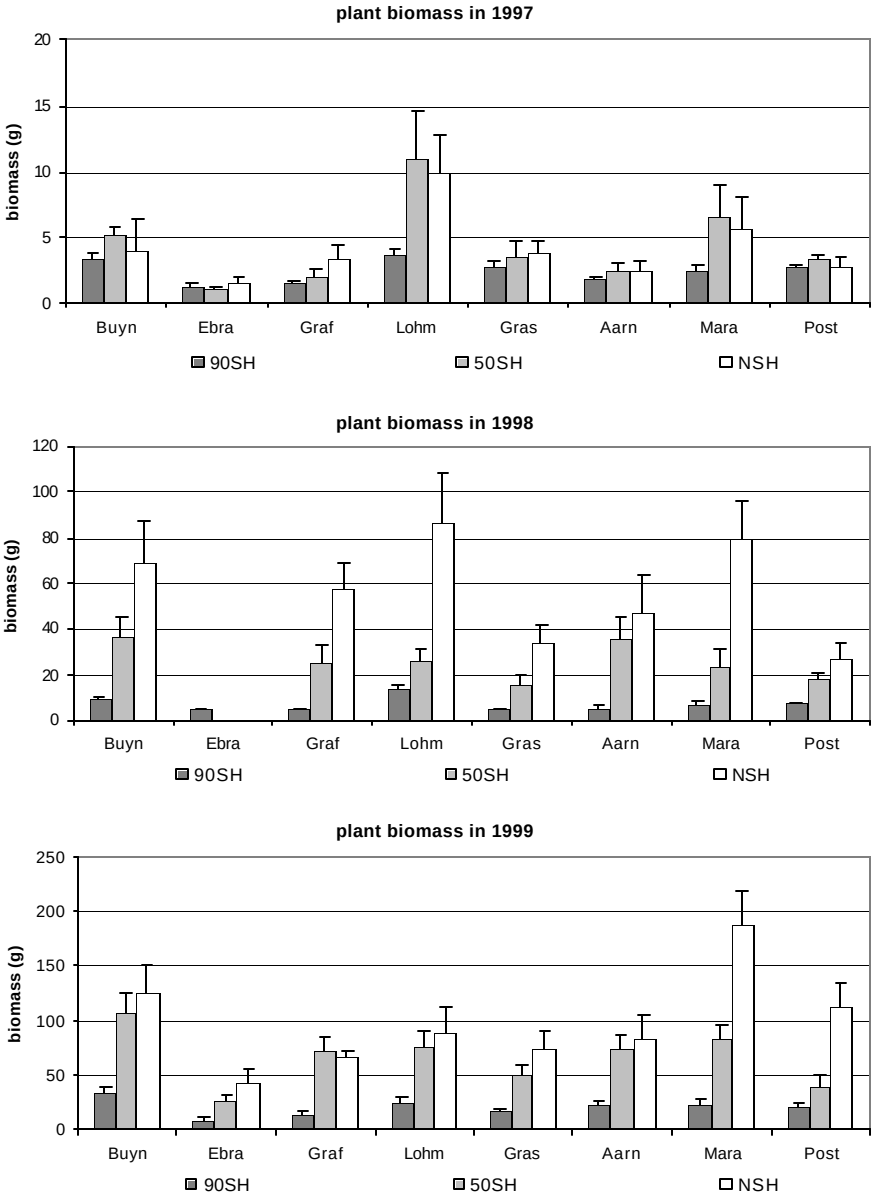

Figure 3.2*. Average plant biomass (g dry matter) and s.e. at three harvest periods.*

Differences in biomass growth are presented in Figure 3.3. The analysis shows that growth rates (RGR) differed between light conditions and provenances and that the interaction between light and provenance is not significant. Shading reduces growth rates. At no-shade growth rate is 1.422 g g^{-1} y^{-1}, at 50% shade growth drops to 1.152 g g^{-1} y^{-1} and at 90% shade the growth rate is 0.748 g g^{-1} y^{-1}. Based on the average growth rates three different groups can be distinghuised: the fast growing provenances Grasten, Maramures-Baia and Graf von Westfalen with a RGR ranging from 1.329 g g^{-1} y^{-1} to 1.256 g g^{-1} y^{-1}, the intermediate growing provenances Buynovitze, Lohmen and Aarnink with a RGR from 1.120 g g^{-1} y^{-1} to 1.096 g g^{-1} y^{-1} and the slow growing provenance Postojna Javor with a RGR of 0.909 g g^{-1} y^{-1}. Although the data on plant biomass suggested that the SE-European provenances had a better growth then the NW-European provenances an additional analysis showed no significant difference between plants from these two geographical regions.

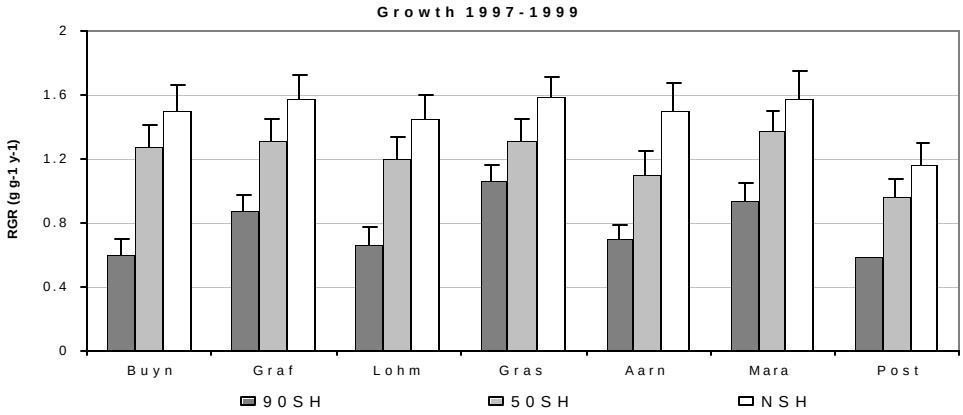

Figure 3.3*. Average biomass increment (RGR in g g^{-1} y^{-1}) and s.e.*

3.2.3 Leaf development

Leaf development has been studied in detail in 1998. The course of leaf development over the year at the experimental light levels has been described by a set of seven parameters (see Figure 3.4). A general overview of the observed leaf development is presented for seven out of eight provenances (Figure 3.5). The provenance Ebrach is not included in the study of leaf development. A first look at the data presented in Figure 3.5 gives the impression that the variation between provenances in leaf development is small. Only differences between light levels are clear. Looking at the parameters used to describe leaf development in more detail, differences between provenances become evident.

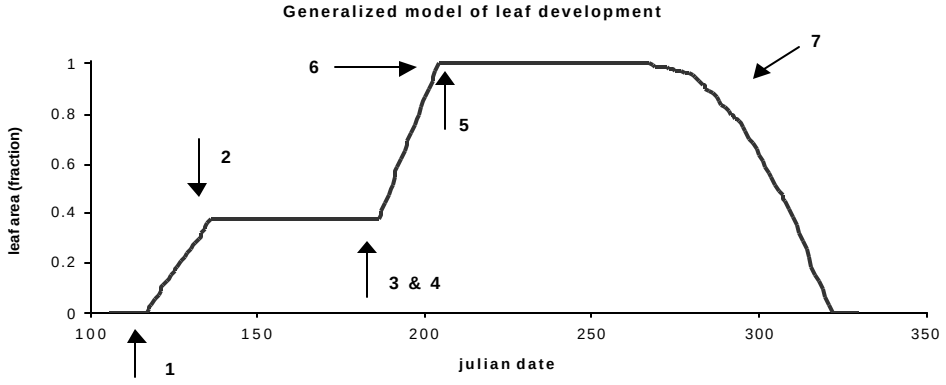

Figure 3.4. *Generalised pattern of leaf area development and parameters studied to describe leaf development. 1 – onset of flushing; 2 – length of first flushing period; 3 – probability of repeated flushing; 4 – start of repeated flushing; 5 – end of repeated flushing; 6 – leaf area produced by repeated flushing; 7 - break down of chlorophyll.*

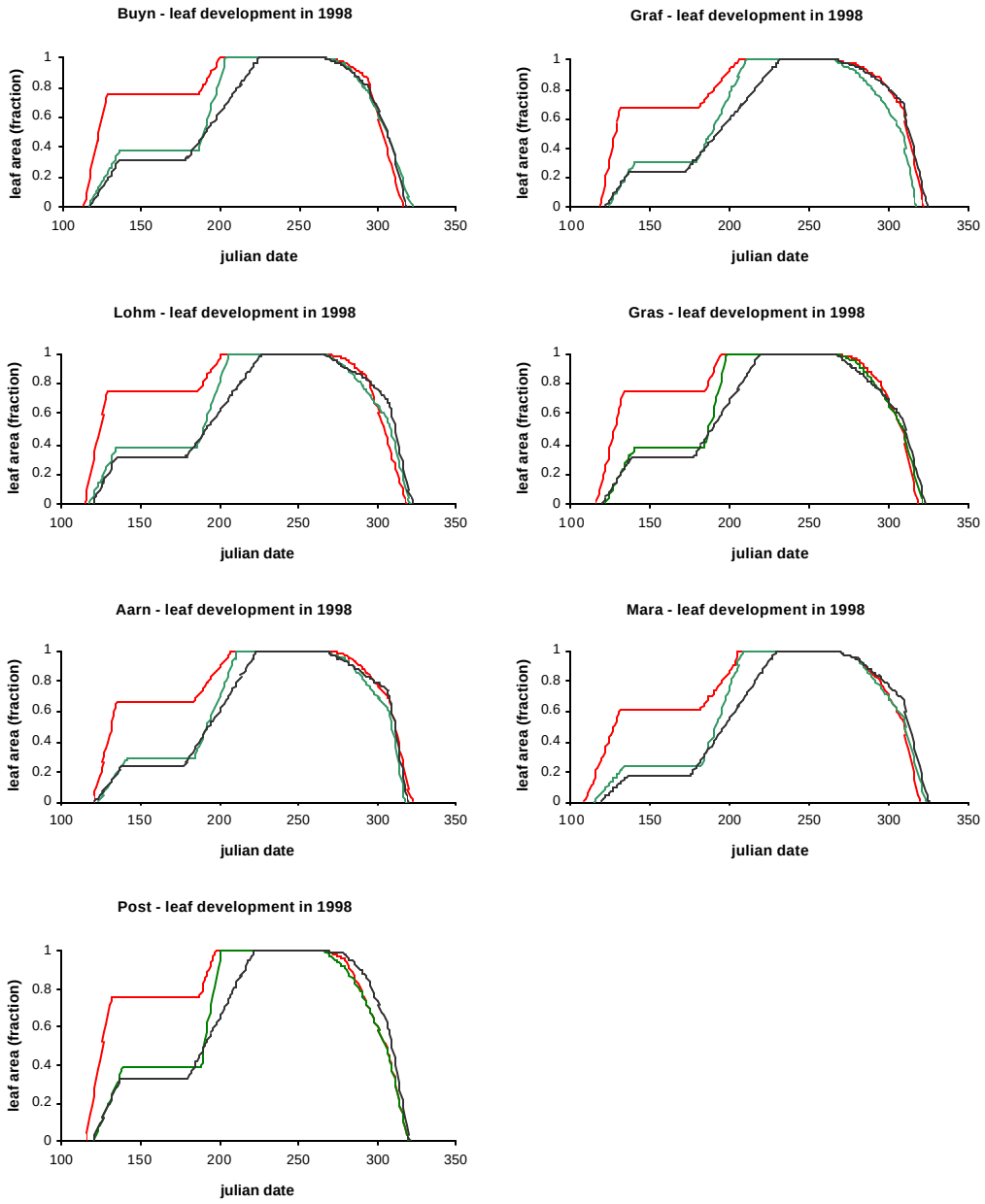

Figure 3.4. *Leaf development of young beech plants in 1998. The red line describes leaf development at 10% shade, the green line at 50% shade and the black line at no shade*

3.2.3.1 Initial flushing

The analysis of initial flushing has been performed in the second (1998) and third (1999) year of the experiment. Figure 3.6 presents the observed variation in the onset of flushing, which is defined as the date on which a plant reaches flushing stage 2 (buds are swollen).

In general, the onset of flushing differs between 1998 and 1999. Although the differences are small (1.5 days). Of more importance is the effect of shading on the onset of flushing, severe shading (90% shade) accelerates flushing with 3.0 days (compared to no-shade) to 3.7 days (compared to 50% shade). This shading effect is similar for all, but the Ebrach provenance. Shading does not accelerate flushing of the Ebrach provenance.

In both years the order of flushing of the provenances is approximately constant (Maramures-Baia > Buynovtzi > Lohmen > Postojnovitz ~ Grasten ~ Ebrach > Graf von Westfalen > Aarnink). This order approximates the SE-NW gradient in the provenances. Two out of three SE-European provenances (Maramures-Baia and Buynovtzi) are the first to flush and two out of four NW-European provenances (Graf von Westfalen and Aarnink) are the last to flush.

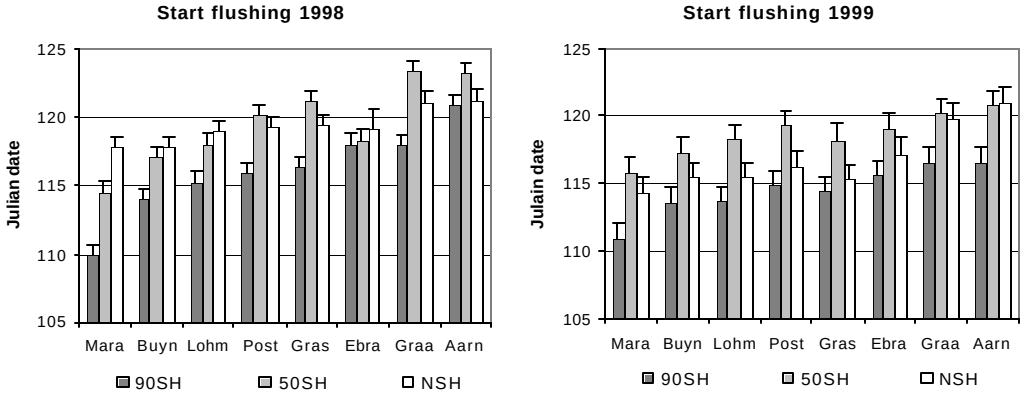

Figure 3.6*. The onset of flushing in different years and at different light levels*

The length of the flushing period (date of flushing stage 7 minus date of flushing stage 2) differs between the years and between the light levels, but was similar for the provenances. The length of the flushing period was 15.6 days in 1998 and 1.5 days shorter in 1999. Severe shading (90% shade) reduced the length of the flushing period with 1.5 days in comparison to intermediate shading (50% shade) and 1.7 days in comparison to no-shade.

3.2.3.2 Repeated flushing

Young beech plants are able to flush more then once. This repeated flushing has been studied in 1998 on seven out of eight provenances. The provenance Ebrach was excluded. Estimated probabilities of repeated flushing are presented in Figure 3.7.

The analysis showed that the probability of repeated flushing is significantly larger in no-shade and 50% shade then in 90% shade. In general 37% of the young beech plants flushed more then once at 90% shade, while at 50% shade and no-shade these

percentages were 82% and 81%. Differences between provenances in probability of flushing are also significant. Only the difference between the provenances Grasten and Postjna (low probability of repeated flushing) and Maramures-Baia (high probability of repeated flushing) are significant.

The onset of repeated flushing does not differ between light levels and provenances. In average repeated flushing starts at day 180. However the length of this flushing period differs between light levels. Flushing continues until day 202 (90% shade), 206 (50% shade) and 227 (no-shade).

Figure 3.7. *Estimated probabilities of repeated flushing of young beech plants in 1998 and standard errors. Fitted model: Logit (p) = b_0 + b_1 light level + b_2 provenance*

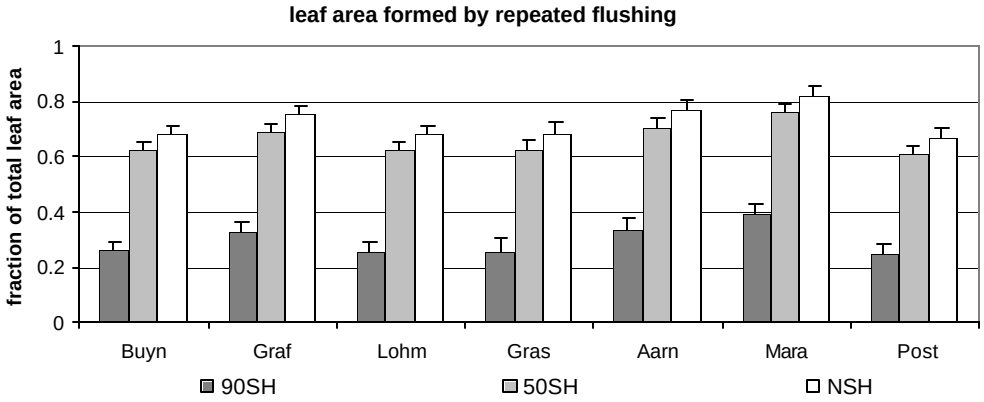

Figure 3.8. *Estimated fraction of the total leaf area produced by repeated flushing.*

Repeated flushing results in an increase of the leaf area of the young beech plants (see Figure 3.8). The magnitude of this increase mainly differs between light conditions; differences between provenances are too small to be significant. Pooled over all provenances repeated flushing accounts for 29.8% of the total leaf area at 90% shade, whereas at 50% shade and no-shade this percentage increase to 66.6% and 72.8% respectively.

3.2.3.3 Chlorophyll breakdown

Differences in rate of chlorophyll breakdown are assessed by comparing the Julian dates on which the chlorophyll content is estimated to be 75% (75-percentile) and 50% (50-percentile) of the chlorophyll content of the first measurement on day 263. The analysis shows that the days on which the 75-percentile and the 50-percentile are reached primarily differ between provenances. The effect of shading is not significant. Chlorophyll breakdown is fast in the provenance Postojna Javor and slow in the provenances Aarnink, Graf von Westfalen and Maramures-Baia with the other provenances holding an intermediate position (see Table 3.2).

***Table 3.2**. Estimated day on which the chlorophyll content has reached 75% or 50% of the late summer value. Estimates are based on linear interpolation between the measured chlorophyll percentages on fixed sampling dates*

Provenance	**75-percentile**		**50-percentile**	
	Average (Julian date)	se	Average (Julian date)	se
Buynovtzi	293.7	1.54	304.3	1.06
Graf von Westfalen	297.0	1.56	308.7	1.08
Lohmen	293.8	1.53	305.8	1.05
Grasten	294.2	1.61	305.7	1.11
Aarnink	297.6	1.60	310.1	1.10
Maramures-Baia	207.9	1.59	307.9	1.09
Postojna Javor	290.2	1.57	300.9	1.08

An additional analysis shows that the rate of chlorophyll breakdown differs between the SE-European and the NW-European provenances. Chlorophyll breakdown is slower in the NW-European provenances, although the difference with the SE-European provenances are small (2.6 days at 75-percentile and 3.6 days at 50-percentile).

3.2.4 Plant morphology

Plant morphology will be analysed by a set of characteristics at the plant level (biomass distribution and leaf area ratio) and at component level (specific leaf area and chlorophyll content).

3.2.4.1 Biomass distribution

Initial analysis of the biomass distribution of the harvested beech seedlings showed that the biomass distribution in the first year differed from the second and third year of the experiment. Especially the fraction biomass in the roots was lower in the first year. This affect has been attributed to the plant shock and the analysis of biomass distribution focussed on the plants harvested in the second and third year. Average biomass of these plants is presented in Figure 3.9.

The analysis of biomass fractions in different plant compartment showed that in the second and third year of the experiment the biomass distribution is independent of plant size, but differs between provenances and light conditions. In general

differences in biomass distribution are small between the provenances Ebrach, Graf von Westfalen, Lohmen and Grasten. Variation in biomass distribution is observed between the provenances Buynovtzi, Aarnink, Maramures-Baia and Postojna Javor (see Table 3.2). Buynovtzi is characterised by a proportionally large branch biomass and a small leaf and stem biomass. Aarnink has a proportional large leaf and stem biomass and a small root biomass. Maramures-Baia has a proportional large leaf biomass and a small stem biomass. Postojna Javor has a proportional large stem biomass and a small root biomass.

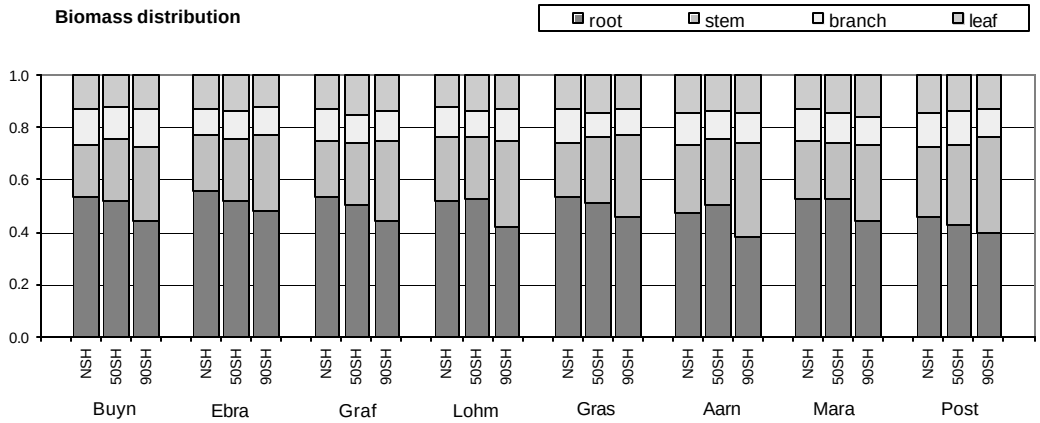

Figure 3.9. Observed biomass distribution of the plants harvested in the second and third year of the experiment

Shading has no effect on the fraction biomass in leaves and branches, but has a strong effect on the relative size of the stem and the roots (see Table 3.3). At 90% shade the young beech plants have proportionally more stem biomass and less root biomass compared to beech plants growing at 50% shade and no-shade.

Table 3.3. *Predicted biomass in different plant compartments per provenance. Predictions are based on the model; fraction plant biomass* = $a + b_1 \cdot provenance + b_2 \cdot light\ levels$, *where the effects of light level are pooled*

	Leaves (*)		Branches (**)		Stem (***)		Roots (***)	
	predicted	se	predicted	se	predicted	se	predicted	se
Buy	0.128	0.0054	0.137	0.0066	0.237	0.0095	0.499	0.0271
Ebra	0.137	0.0072	0.105	0.0078	0.259	0.0131	0.499	0.029
Graf	0.140	0.0054	0.117	0.0066	0.254	0.0094	0.489	0.0271
Lohm	0.130	0.0056	0.112	0.0067	0.270	0.0098	0.489	0.0273
Gras	0.133	0.0054	0.107	0.0067	0.261	0.0094	0.498	0.0271
Aarn	0.145	0.0056	0.112	0.0068	0.292	0.0098	0.451	0.0273
Mara	0.145	0.0057	0.116	0.0068	0.240	0.0101	0.499	0.0274
Post	0.137	0.0054	0.122	0.0066	0.316	0.0094	0.426	0.0271

Table 3.4. *Predicted biomass in different plant compartments at different light levels. Predictions are based on the model; fraction plant biomass = a + $b_1$provenance + $b_2$light levels, where the effects of provenances are pooled.*

	Leaves (ns)		Branches (ns)		Stem (***)		Roots (***)	
	predicted	se	predicted	se	predicted	se	predicted	se
no-shade	0.135	0.0069	0.122	0.005	0.232	0.0112	0.510	0.0112
50% shade	0.139	0.0067	0.111	0.005	0.247	0.0108	0.504	0.0108
90% shade	0.136	0.0067	0.115	0.005	0.319	0.0108	0.430	0.0108

3.2.4.2 Leaf area ratio

LAR (cm^2 leaf area per gram plant dry matter) has been analysed to compare the relative size of the photosynthetic apparatus between provenances and light levels. Again a major difference between the first and the second and third year of the experiment was observed. This difference has been attributed to the effect of the plant shock and thus the data from the LAR data from the first year of the experiment were exclude from further analysis.

There was no significant difference in LAR between the provenances. The LAR of the provenances ranged from 24.71 $cm^2\ g^{-1}$ to 28.44 $cm^2\ g^{-1}$, with an average of 26.41 $cm^2\ g^{-1}$ (se 1.165). Light had a strong impact on the LAR of the beech plants. At full light the average LAR was 18.40 $cm^2\ g^{-1}$ (se 1.075). At 50% shade the LAR increased to an average of 24.28 $cm^2\ g^{-1}$ (se 1.011) and reached at 90% shade an average value of 36.55 $cm^2\ g^{-1}$ (se 1.002). As light didn't have any significant effect on the relative amount of leaf biomass (see Table 3.3), the increase in LAR must be attributed to an increase in the specific leaf area with a decrease in light availability.

3.2.4.3 Specific Leaf Area

Light had a dominant effect on the specific leaf area (SLA) of the harvested beeches (see Figure 3.10). Average SLA at harvest varied from 133.9 $cm^2\ g^{-1}$ (s.e. 7.61) at no-shade and 183.3 $cm^2\ g^{-1}$ (s.e. 7.45) at 50% shade to 296.3 $cm^2\ g^{-1}$ (s.e. 8.58) at 90% shade. Hence the leaf area per unit leaf biomass more then doubled at 90% shade as compared to no-shade. Differences in SLA between provenances were too small to be significant.

As can be seen in Figure 3.10 there is a consistent difference in SLA between the leaves of the first and second flush. The leaves of the second flush have a smaller SLA and thus less leaf area per unit leaf biomass. In general the SLA of the second flush is 17.0% (s.e. 1.1) smaller then the SLA of the first flush. Light and provenance did not have any significant effect on the difference in SLA between both flushes.

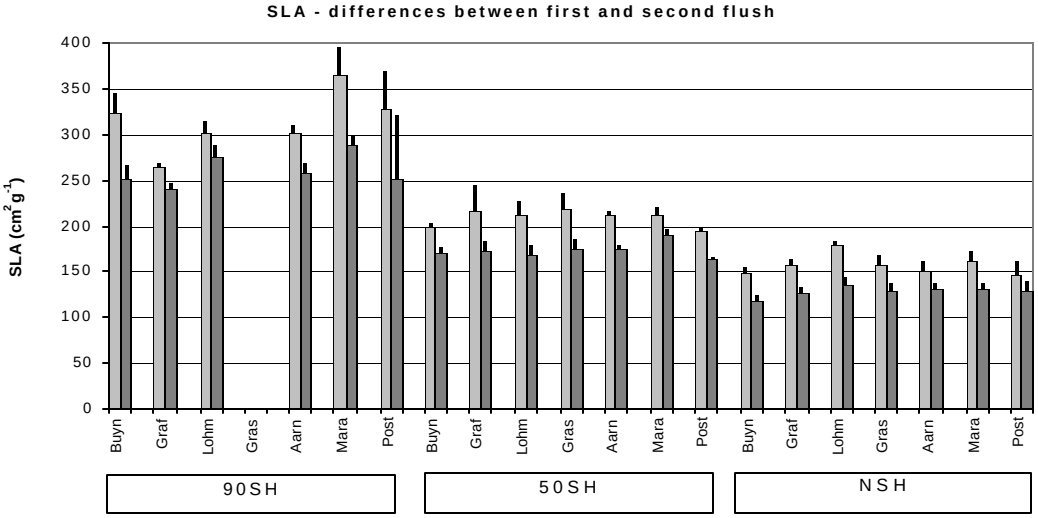

Figure 3.10. SLA of first flush (light bars) and second flush (dark bars) of the harvested plants in the second year of the experiment.

3.2.4.4 Chlorophyll content

The chlorophyll content of the leaves at day 263 is presented in Figure 3.11. The analysis showed that the chlorophyll content differed between light levels. At 90% shade the chlorophyll content of the leaves was significantly larger then at 50% shade and no-shade. The differences between the latter are too small to be significant.

The differences between provenances were also significant. However these differences must be attributed to the high chlorophyll content of the provenances Buynovtzi and Maramures-Baia. With the light levels pooled these provenances have a chlorophyll content of 294.7 and 284.7 mg m^{-2}, whereas in the other provenances the chlorophyll content ranges from 234.6 tot 255.4 mg m^{-2}.

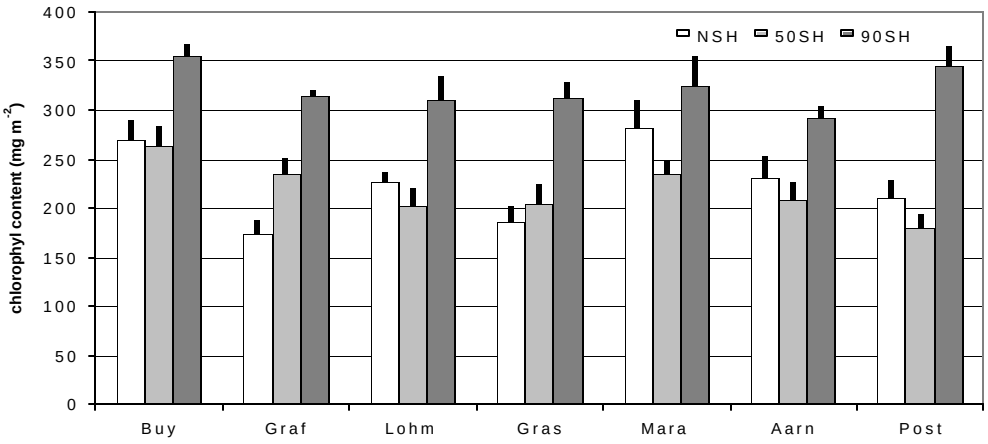

Figure 3.11. Average chlorophyll content of the leaves at day 263 in the second year of the experiment.

3.3 Discussion and conclusions

The outcome of beech provenance trails in NW-Europe indicates that a number of SE-European provenances are suitable for planting under NW-European conditions (pers. comm. S. de Vries - Alterra). In these trails the performance of the provenances are evaluated under field (full light) conditions. Selected provenances can be used for the underplanting of coniferous forests and thus for planting under shaded conditions. In this experiment the effect of shading on the mortality, growth, phenology and morphology of a limited number of SE and NW-European provenances is studied.

We did not find any evidence that the mortality differed between SE and NW European provenances. However mortality did differ between provenances and light conditions.

The provenance Ebrach (classified as a SE-European provenance) had a very high mortality and as a consequence this provenance had to be excluded from some of the analyses. The same plant material of the provenance Ebrach has been used in a nursery experiment in Germany and some provenance trails in NW Europe. In all cases the mortality for the provenance Ebrach was exceptionally high, which leads to the conclusion that the plant material used was of low quality.

In this experiment a repeated attack (year 2 and 3) by the Taxus beetle resulted is a high mortality. An attack by Taxus beetle is not common in nurseries and forests. This beetle primarily occurs in potted plants (pers. comm. L. Moraal – Alterra) and we used potted plants in this experiment. The attack by the Taxus beetle reduced the number of plants we could use for analyses but, as all provenances were approximately equally affected, the attack did not have a major impact on the outcome of the experiment.

In the experiment mortality was the highest under non-shaded conditions and the severity of the attack by Taxus beetle was the lowest at non-shaded conditions. Thus the high mortality at full light could not be attributed the effect of the beetle. We did not find any clear cause for this high mortality under full light conditions. The high mortality might be indicative for the preference of young beech plants to grow under shade conditions and confirms its classification as a shade tolerant species (Ellenberg 1988).

In this study we found large difference in growth within the SE and NW-provenances. Fast growing provenances were Maramures–Baia (SE) and Graf von Westphalen (NW); slow growing were Ebrach (SE) and Postojna Javor (NW). This response pattern indicates that there are large differences in beech growth within geographical regions.

Plant growth differed between provenances and light conditions. However there was no evidence that some provenances proportionally were more reduced by shading then others. This indicates that a good growing provenance under non-shaded conditions is also a good growing provenance under shaded conditions. This result

seems to contradict the findings of Larsen and Buch (1995), who found that the growth of provenances from NW-Germany were less reduced by shading then the provenances from Italy. However Larsen and Buch started their experiment with seeds and harvested their plants after one growing season. This is a very short period and as the authors did not present any data on the seed weight it is not clear if the observed effects might be due to provenance specific variation in seed weights. Tognetti et al (1998) studied the acclimation of two-year old shade-grown seedlings from two provenances to changing light conditions. In their experiment the provenance responded, in terms of biomass accumulation as well as morphological characteristics, similar to the changing light condition. This result confirms the finding in this study that the difference between provenance in magnitude of response to shading is too small to be significant.

The analysis of different components of leaf development gave no evidence for a difference in response of the provenances to shading. This leads to the conclusion that with respect to leaf development the provenances are equally acclimated to shading.

Light had an effect on the onset of flushing and on the length of the first flushing period, but not on the rate of breakdown of chlorophyll content. At 90SH the leaf area is a few days longer photosynthetic active then at 50SH and NSH. At the same time light had a strong effect on the total leaf area. At 50SH and NSH repeated flushing was common, leading to a larger leaf area for the beech plants growing under these light conditions.

The onset of flushing and rate of chlorophyll breakdown also differs between provenances. A comparison of the date of flushing and the date on which 50-percentile chlorophyll has been reached indicates that the provenance Maramures-Baia is approximately 5 days longer photosynthetically active then other provenances. However date on first flushing and chlorophyll breakdown have been collected on different plants thus the exact length of the photosynthetic active period can not be assessed.

With respect to the plant morphology the provenance responded similar to shading and the provenance specific variation in morphological characteristics was of minor importance. The effect of shading on plant morphology was large; shading promoted the biomass allocation to the stem at the expense of the roots, shading increased the specific leaf area, which resulted in an increase in the leaf area ratio, and the shading increased the chlorophyll content of the leaves. These are all common acclimations to shading (Tognetti et al, 1998; Larsen and Buch, 1995; Van Hees, 1995).

This experiment leads to the following conclusions:
The provenances studied differed in their survival, growth, phenology and morphology. However the differences between SE and NW-European provenances were not consistent enough to exclude provenances on the basis of their geographical origin only.

Shading had a large effect on survival, growth, phenology and morphology. However all provenance responded similarly to the shading. Thus provenances selected on the basis of their good performance under full light conditions will also have a good performance under shaded conditions (up to 90% shading).

4 Analysis of physiology and modelling growth of beech saplings

4.1 Material and methods

4.1.1 Gas exchange measurements

Gas exchange measurements were done using the CIRAS-1 portable infrared gas analysis system with an automatic temperature and light control leaf cuvette. In September 1998 light response curves and CO_2 response curves were made on three randomly chosen saplings per provenance and light condition. Light response curves were made at a temperature of 25 ^oC and a CO_2 concentration of 1000 ppm. The CO_2 response curves were made at 20^oC and PAR=1000 $\mu mol\ m^{-2}\ s^{-1}$. In July and September 1999, gas exchange measurements were done at ambient conditions on 3 saplings per provenance of the NSH and 90SH light conditions only. The measurements were done every 2 hours, starting before sunrise until after 12 am.
Based on the photosynthesis to light, and photosynthesis to CO_2 curves obtained in the 1998 measurements, the parameters of a leaf photosynthesis model (see below) were estimated. The 1999 measurements at ambient conditions for both the no shade and 90% shade served to test the leaf photosynthesis model to independent data

4.1.2 Leaf photosynthesis model

The rate of net photosynthesis (A_n), stomatal conductance (g_s) and internal CO_2 concentration (c_i) are interdependent (Baldocchi 1994, Eqn. 1-3) This set of equations was solved using an iterative procedure instead of using the analytical approach of Baldocchi (Falge et al. 1996, 1997). The photosynthesis model was developed by Farquhar and co-workers (Farquhar & Von Caemmerer 1982), in which the net rate of photosynthesis is limited either by carboxylation- (Eqn. 4) or RuBP-regeneration (Eqn. 5). The RuBP-regeneration limited rate of photosynthesis also depends on the rate of oxygenation (Eqn 6) due to competition between CO_2 and O_2 of the active sites of Rubisco. The CO_2 compensation point in the absence of dark (mitochondrial) respiration (Eqn. 7) determines the carboxylation rate of photosynthesis. The maximum electron transport rate at a given light level, but optimal temperature is presented by Eqn 8. The temperature dependencies of the parameters are described following Farquhar & Wong (1984) for the parameters K_C, K_O, R_d, and t (Eqn 9) and were calculated based on Johnson *et al.* (1942) for J_{max} and V_{Cmax} (Eqn. 10).

Table 2 presents the variables used in the photosynthesis model. The parameters presented in Table 3 are assumed to be the same for all provenances (Harvey & Tenhunen 1991). The parameter values indicated in Table 4 were estimated by means of non-linear estimation using the statistical package GENSTAT (Genstat Committee, 1993).

$$A_n = \min\left(V_C, V_J\right) - R_d \qquad Eqn.1$$

$$c_i = c_a - \frac{A_n}{g_s} \qquad Eqn.2$$

$$g_s = g_{s,\min} + C_g \cdot \frac{A_g}{c_i} \cdot f_g\left(h\right) \qquad Eqn.3$$

$$V_C = \frac{V_{Cmax} \cdot c_i}{c_i + K_C \cdot \left(1 + O_2 / K_O\right)} \cdot \left(1 - \Gamma^* / c_i\right) \qquad Eqn.4$$

$$V_J = V_c \cdot \left(1 - 0.5 \cdot V_o\right) \cdot \frac{V_{J\,max}}{V_c + V_o} \qquad Eqn.5$$

$$V_O = \frac{V_c \cdot O_2}{t \cdot c_i} \qquad Eqn.6$$

$$\Gamma^* = \frac{0.5 \cdot O_2}{t} \qquad Eqn.7$$

$$V_{Jmax} = \frac{a \cdot I}{\sqrt{1 + \left(\frac{a \cdot I}{J_{max}}\right)^2}} \qquad Eqn.8$$

$$P\left(T\right) = P\left(298\right) \cdot \exp\left(\frac{H_a \cdot \left(T \cdot K - 298\right)}{R \cdot T \cdot K \cdot 273}\right),\ P = K_C, K_O, R_d, t \qquad Eqn.9$$

$$P\left(T\right) = P\left(298\right) \cdot \frac{\exp\left(\frac{H_a \cdot \left(T \cdot K - 298\right)}{R \cdot T \cdot K \cdot 298}\right)}{\left(1 + \exp\left(\frac{\Delta S \cdot T \cdot K - H_d}{R \cdot T \cdot K}\right)\right) \cdot \left(1 + \exp\left(\frac{\Delta S \cdot 298 - H_d}{R \cdot 298}\right)\right)},\ P = J_{\max}, V_{cmax}$$

$$Eqn.10$$

Table 2. *Description of variables and their units*

Variable	Unit	Explanation
A_n	μmol m^{-2} s^{-1}	rate of net photosynthesis
A_g	μmol m^{-2} s^{-1}	rate of gross photosynthesis
V_C	μmol m^{-2} s^{-1}	rate of carboxylation
V_O	μmol m^{-2} s^{-1}	rate of oxygenation
V_J	μmol m^{-2} s^{-1}	electron transport rate
c_i		internal CO_2 concentration
g_s	μmol m^{-2} s^{-1}	stomatal conductance
Γ^*		CO_2 compensation point in the absence of dark respiration
I		absorbed radiation
T	K	temperature

Table 3. *Values for the parameters at 298 K that are kept the same for all beech provenances*

Parameter	Value	Unit	Description
τ	2339.53	-	
- Ha	-28990	J mol^{-1}	
K_c	404	μL L^{-1}	Michaelis-Menten coefficients for CO_2
- Ha	59500	J mol^{-1}	
K_o	248	mL L^{-1}	Michelis-Menten coefficients for O_2
- Ha	35900	J mol^{-1}	
R_d			dark respiration
- Ha	43460	J mol^{-1}	
J_{max}			maximum electron transport rate
- ΔS	710	J mol^{-1} K^{-1}	
- Ha	33485	J mol^{-1}	
- Hd	220000	J mol^{-1}	
V_{cmax}			RuP_2-saturated rate of carboxylation
- ΔS	656	J mol^{-1} K^{-1}	
- Ha	35068	J mol^{-1}	
- Hd	213000	J mol^{-1}	
g_{smin}	1	μmol m^{-2} s^{-1}	minimum stomatal conductance
g_{sax}	250	μmol m^{-2} s^{-1}	maximum stomatal conductance
C_g	12	-	
O_2	21	ppm	O_2 concentration
c_a	350	Ppm	ambient CO_2 concentration

Table 4. *Parameters that are estimated per provenance*

Parameter	Unit	Description
α	-	initial light use efficiency
R_d	μmol m^{-2} s^{-1}	dark respiration
J_{max}	μmol m^{-2} s^{-1}	maximum electron transport rate
V_{cmax}	μmol m^{-2} s^{-1}	RuP_2-saturated rate of carboxylation

4.1.3 Growth model FORGRO

The leaf photosynthesis model described above was coupled to a simple model of light interception by a single plant. Is assumed that the interception of light is directly proportional to the leaf area of an individual tree. For the first years of growth this is a reasonable assumption because of the low leaf area index (LAI < 0.5) self-shading is negligible. The allocation of assimilates at the individual level is distributed over the different plants components such that the observed ratio's between plant components are met. For height growth a linear growth was assumed, based on the first years of measurements. The model FORGRO (Mohren 1987, Kramer 1996a,b, Kramer et al. 2001) was adjusted to incorporate these features of individual plants. The soil water balance incorporated in FORGRO was switched off in this study, as there was no water stress during the growth of the saplings.

4.1.4 Model-evaluation

Wallach & Goffinet (1987, 1989) conclude that the evaluation of a model should not be based on R^2 values alone, but also on the analysis of mean squared errors (MSE) $MSE = \sum \left(y_o - y_p \right)^2 \Big/ N$. Where y_o and y_p are the observed and predicted values of the dependent variable, and N is the total number of observations. The use of MSE makes it possible to discriminate between systematic (MSE_s) and unsystematic error (MSE_u). If predicted values are linearly regressed on observed values, let the equation of the regression line be: $\hat{y} = a + by_o$. In case of a perfect model fit it would be: $a = 0;\ b = 1;\ y_p = \hat{y}$. In case of an unsystematic error, the modelled points would be scattered around the regression line, while a systematic error would result in values of the parameters that are different from those above. The systematic and unsystematic error can thus be quantified as $MSE_s = \sum \left(\hat{y} - y_o \right)^2 \Big/ N$, and $MSE_u = \sum \left(\hat{y} - y_p \right)^2 \Big/ N$, respectively. In case of a perfect model fit both $MSE_s = 0$ and $MSE_u = 0$. Note that $MSE = MSE_s + MSE_u$.

R^2 can represent the goodness-of fit of the model based either on the data on which the model parameters are estimated, or on the goodness-of-fit of independent data. The first approach will be referred to as the *internal goodness-of-fit,* whereas the second approach as *external goodness-of-fit.* A sound testing of a model can only be done based on the external R^2.

For the analysis of the results of the leaf photosynthesis model the R^2, and the systematic and unsystematic error will be tabulated. For the results of the growth model these statistics will be presented on the graphical presentation of the results.

4.2 Results

The following analyses were performed: 1) the analysis in differences between provenances and light treatments for 4 leaf photosynthetic parameters, and an evaluation of the goodness-of fit of leaf photosynthesis model based on these parameters. 2) more general analyses to identify systematic differences between south-east European and north-west European provenances, and between shade and full light treatments is presented, and 3) an analysis on the implications of differences in parameter values between provenances or light treatment using the growth model FORGRO.

4.2.1 Leaf photosynthesis parameters

Fig. 4.1 shows the results of the photosynthesis parameters that were estimated based on the measurement series of 1998 (see also Table 3). The results indicate that there is a large variability in the initial light use efficiency, a. There were no significant differences found neither between provenances nor between light levels. Hence for the modelling (see below) the overall average value of a was used. For the maximum electron transport rate, *Jmax*, the general trend for all provenances is that the value in 90% shade is lower compared to both the 50% shade and the no-shade treatment. For dark respiration, *Rd*, for all provenances except Postojna Javor, the 90% shade values is the lowest. For 4 provenances to 50% shade value is the highest over the three treatments, although this is usually not significantly different from the no-shade treatment. For the maximum rate of carboxylation, *Vcmax*, there appears to be no clear pattern between treatments and provenances.

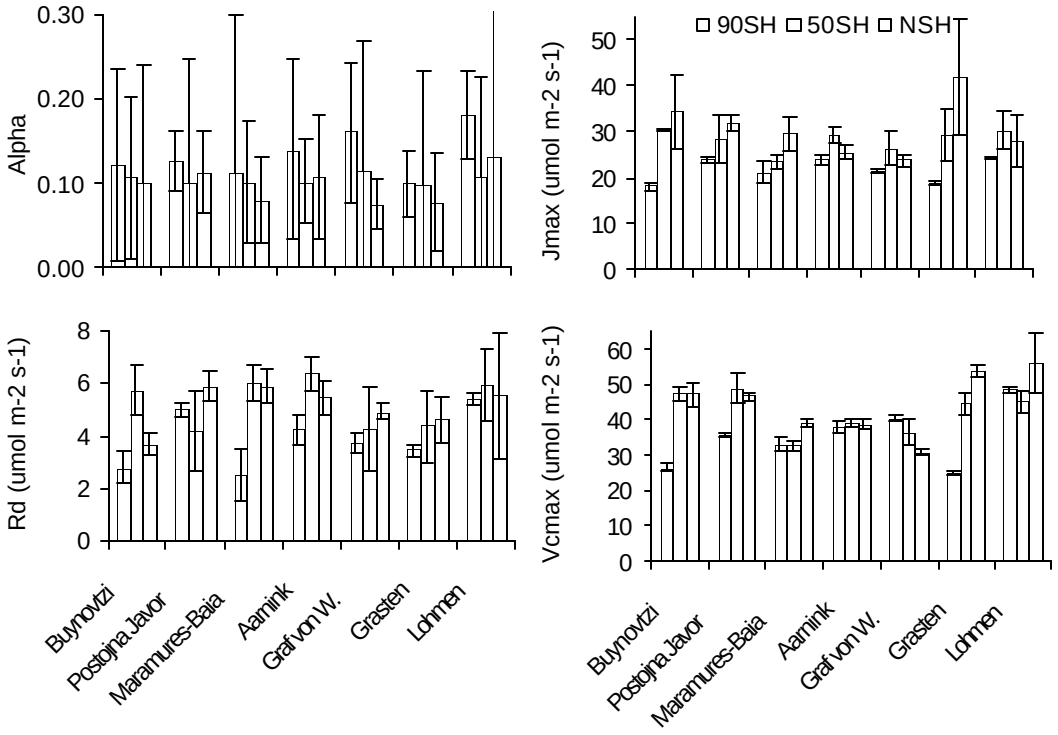

Figure 4.1. *Values of* α, Jmax, Rd *and* Vcmax *(see Table 3) for the different provenances under no shade (NSH), 50% shade (50SH) and 90% shade (90SH) conditions*

The provenances Buynovtzi, Postojna Javor and Maramures-Baia are the south-east European provenances, whereas Aarnink, Graf von Westfalen, Grasten en Lohmen originate from the north-west of Europe. There are no systematic differences found, neither in photosynthetic characteristics nor in the response to shade between the two groups.

Tables 5, 6 and 7 presents the results for the statistical tests on differences between the provenances and light treatments for the parameters V_{cmax}, J_{max}, and R_d. In these tables, similar letters in the last column indicate that there are no significant differences found between the treatment no shade, 50% shade or 90% shade. The letters are presented in that order. Similar letters in the columns of the treatment indicate that there are no significant differences found between the provenances within this treatment.

Table 5 shows that for V_{cmax} there are no significant differences between no-shade and 50% shade for 4 provenances (Buynovtzi, Aarnink, Grasten, Postojna Javor). Also there are no significant differences between 50% shade and 90% shade for Graf von Westfalen, Maramures-Baia and Lohmen. For Aarnink and Grasten there are no significant differences found in V_{cmax} between any of the light treatments. Thus, for the other 5 provenances the 90% shade values are significantly different from either no shade or 50% shade.

There appear to be no clear groups of provenances with similar responses to the light treatments: provenances that are similar within *e.g.* the no shade treatment are significantly different in either the 50% shade or 90% shade treatments.

Table 5. *Estimates of V_{cmax} (mmol m^{-2} s^{-1}) per treatment (within a treatment: same letter means no significant difference)*

Treatment / *Provenance*	NSH	50SH	90SH	
Buynovtzi	46.95 a	47.09 a	26.28 a	aab
Graf von Westfalen	30.56	36.31 bc	40.46 b	abb
Aarnink	38.38 b	38.99 b	37.73 bc	aaa
Grasten	53.69 c	44.39 a	24.77 a	aaa
Postojna Javor	46.44 a	48.70 a	35.84 cd	aab
Maramures-Baia	38.93 b	32.54 c	32.76 d	abb
Lohmen	56.10 c	45.14 a	48.55	abb

Table 6. *Estimates of J_{max} (mmol m^{-2} s^{-1}) per treatment (within a treatment: same letter means no significant difference)*

Treatment / *Provenance*	NSH	50SH	90SH	
Buynovtzi	34.34 ad	30.26 a	18.11 a	aab
Graf von Westfalen	23.74 b	26.15 ab	21.40 b	aab/abb
Aarnink	25.51 bc	29.24 a	23.93 bc	aab/abb
Grasten	41.87 ad	29.24 a	18.75 a	abc
Postojna Javor	32.03 a	28.40 ab	23.70 c	aba/abb
Maramures-Baia	29.49 ac	23.39 b	21.21 abd	abb
Lohmen	27.82 ab	30.41 a	24.24 cd	aba/abb

Table 6 presents the similar the results of the same analysis for J_{max}. There are no significant differences in J_{max} found between no shade and 50% shade for Buynovtzi, Graf von Westfalen, and Aarnink, and significant differences between the both no shade and 50% shade and the 90% shade treatment. For the other provenances the differences between the treatments are difficult to interpret. Similar to the results of Vcmax, there are no clear groups of similar provenances within a treatment, that are also similar for other treatments.

Table 7 presents the results of the statistical analysis for Rd. There are no significant differences found between the treatments for all provenances. Significant differences between provenances are only found for the 90% shade treatment.

Table 7. *Estimates of R_d (mmol m^{-2} s^{-1}) per treatment (within a treatment: same letter means no significant difference)*

Treatment / *Provenance*	NSH	50SH	90SH	
Buynovtzi	3.68 a	5.75 a	2.79 a	
Graf von Westfalen	4.92 a	4.27 a	3.73 ab	aaa
Aarnink	5.44 a	6.37 a	4.22 ab	aaa
Grasten	4.60 a	4.37 a	3.44 a	aaa
Postojna Javor	5.88 a	4.19 a	5.01 b	aaa
Maramures-Baia	5.88 a	6.04 a	2.48 a	aab
Lohmen	5.50 a	5.92 a	5.39 b	aaa

Table 8 presents the goodness-of fit statistics of the leaf photosynthesis model. The above-presented parameters are applied in this model. The high internal R^2 for all provenances indicate that the fit of the model to the data on which it is calibrated is very good for all provenances. Also the external R^2 is rather high for all provenances, and in all cases better for the 90% shade light treatment than the no-shade treatment. Also the rather high systematic mean square error for the no-shade treatment indicates that the model performs worse for the no-shade than the shade treatment. When plotting the model output with the data (figures not shown), then the model systematically underestimates high photosynthetic rates, but predicts correctly low photosynthetic rates. Under shade conditions, the model correctly predicts the observations over the entire observation range.

Table 8. *Internal R_i^2 (1988) and external R_e^2 (1999), and systematic (MSEs) and unsystematic mean square error (MSEu) for the 1999 data*

Provenance	Treatment	R_i^2	R_e^2	MSE_s	MSE_u
Buynovtzi	NSH	0.87	0.75	3.725	0.512
	50SH	0.93			
	90SH	0.92	0.88	0.582	1.298
Graf von Westfalen	NSH	0.99	0.74	1.792	6.310
	50SH	0.80			
	90SH	0.98	0.85	1.438	1.165
Aarnink	NSH	0.95	0.83	1.615	3.716
	50SH	0.97			
	90SH	0.95	0.93	0.521	2.400
Grasten	NSH	0.96	0.78	5.849	0.960
	50SH	0.89			
	90SH	0.98	0.89	0.478	2.214
Postojna Javor	NSH	0.98	0.73	5.236	0.533
	50SH	0.85			
	90SH	0.99	0.97	0.162	4.608
Maramures-Baia	NSH	0.96	0.78	2.414	3.893
	50SH	0.93			
	90SH	0.88	0.97	0.469	1.128
Lohmen	NSH	0.77	0.79	3.749	0.545
	50SH	0.88			
	90SH	1.00	0.85	1.321	4.818

4.2.2 South-east vs. north-west European provenances, light vs. shade

Fig. 4.2 presents the time evolution of the 4 photosynthetic parameters if all the results are averaged over all provenances for both the no shade and 50% shade treatment. The error bars indicate the standard error due to the light treatment on the mean value over the provenances. The results indicate that there are no systematic differences between south-east European and north-west European provenances for these parameters.

Fig. 4.3 presents the time evolution of the 4 photosynthetic parameters if all the results are average over all provenances for the no shade and the 90% shade light treatment. The error bars indicate the standard errors due to the average differences between the provenances. The results indicate that the initial light use efficiency, α, increased in time under the heavy shaded conditions, but not under the no-shade situation. Furthermore, α is consistently higher under shade than in full light. Also for Vcmax there is a clear trend in time and effect by the light treatment. Vcmax significantly decreases in time in the shaded situation, and is consistently lower under the shaded condition compared to the full light. Nevertheless, also under the no-shade situation Vcmax decrease in time, although less then in the shaded treatment. For Jmax and Rd no such outspoken trends in either time or treatment were found.

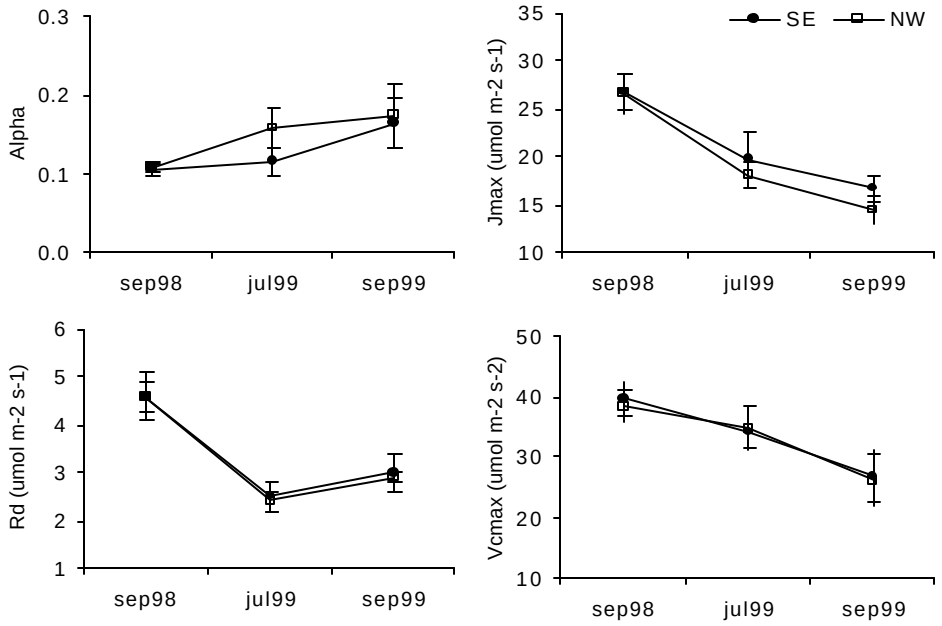

Figure 4.2. *Time evolution of* a*, Jmax, Rd and Vcmax (see Table 3 for their explanation) when all results of the south-east (SE) and the north-west (NW) European provenances are pooled*

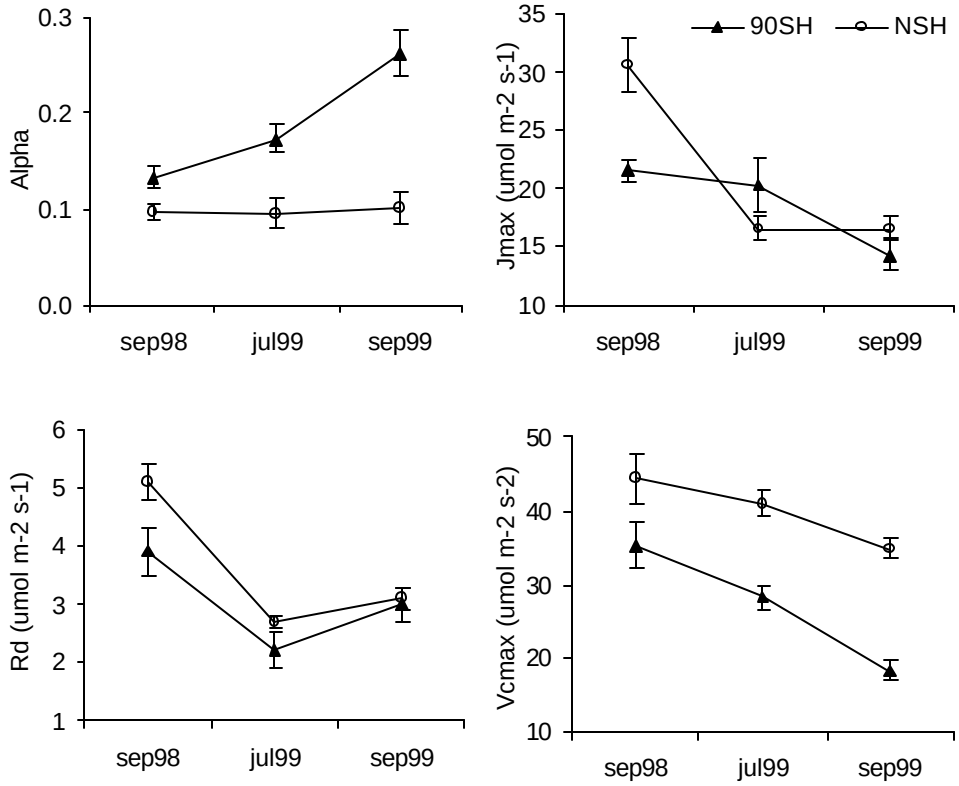

Figure 4.3. *Time evolution of* a*, Jmax, Rd and Vcmax (see Table 3 for their explanation) when all results of the no-shade and the 90% shade treatments are pooled*

Fig. 4.4 presents the net photosynthesis to light response curves if the September average values over all provenances for 1998 and 1999 are taken of both α and Vcmax for the 90% shade and no shade situation. For both Rd and Jmax the overall average values are taken (see Table 9). For these graphs the simulated temperature is set at 25°C, relative humidity at 90% and ambient atmospheric CO2 concentration at 350 ppm.

It can be seen that the increasing value of α for the 90% shade leads to a steeper curve and hence a more efficient photosynthesis at low light levels. The decrease in Vcmax results in a strong decrease of the maximum rate of net photosynthesis. For the no shade situation, the value of α is unaltered between 1998 and 1999, whereas the decrease of Vcmax results in a lower maximum rate of net photosynthesis. Fig. 4.4 also presents the observed distribution of incoming radiation during the growing season. This makes clear that in the 90% shade the available radiation is insufficient to saturate photosynthesis most of the time. Thus the reduction in Vcmax hardly affect the actual rate of net photosynthesis under the prevailing conditions. However, for the no shade situation the available radiation does lead to light saturated photosynthesis most of the time. Thus the reduction in Vcmax between 1998 and 1999 is predicted to reduce the rate of net photosynthesis under the prevailing abiotic conditions.

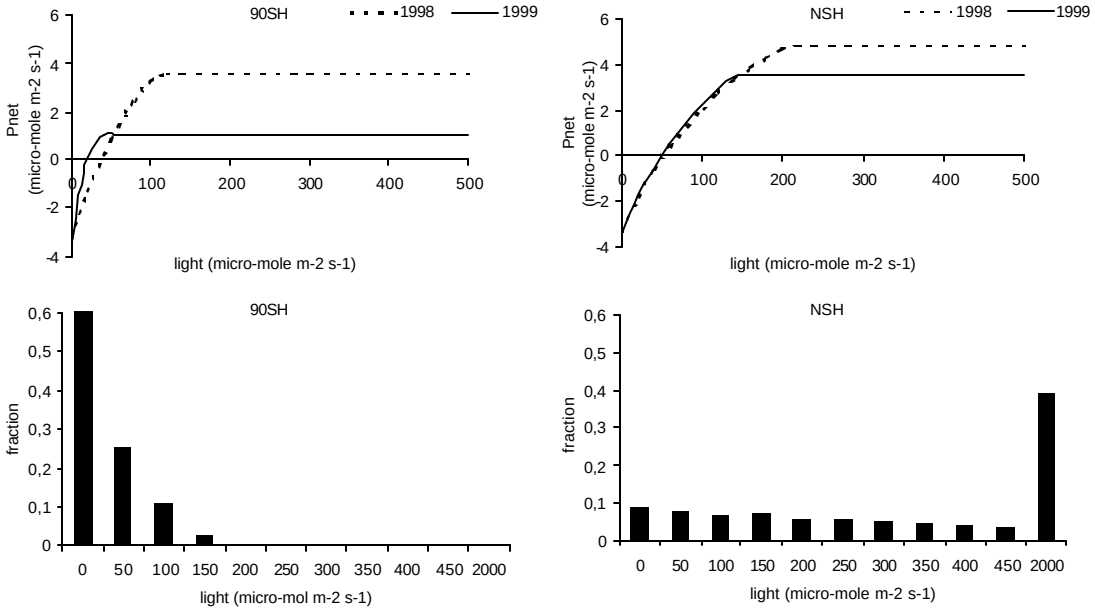

Figure 4.4. *Upper panels: net photosynthesis to light response curves based on the parameter values presented in Table 9 both for 90% shade (90SH) and for no shade (NSH). Lower panels: distribution of incoming radiation during the growing season both for 90% shade and for no shade.*

Table 9. *Parameters averaged over provenances*

Parameter	90% shade		No shade	
	Sept '98	Sept '99	Sept '98	Sept '99
α	0.134	0.262	0.098	0.102
R_d	3.33	3.33	3.33	3.33
J_{max}	20.0	20.0	20.0	20.0
V_{cmax}	35.2	18.3	44.4	34.8

4.2.3 Growth model

Figs. 4.5 and 4.6 present the results of the observed (x-axes) versus the modelled (y-axes) total plant biomass in g dm, per light level (Fig. 4.5) and per provenance (Fig. 4.6). If the model were a perfect representation of reality then all points will be on the line $y = x$. The line $y = a \cdot x$ to is plotted to indicate deviancies of the ideal line, thus, a indicates the systematic error of the growth model. Furthermore, the R^2 value of the data and the plotted line is presented. This R^2 thus indicates the unsystematic error through the independent, external, data.

Fig. 4.5 shows that the systematic error of the growth model increases from the 90% shade to the no shade treatment. Moreover, the unsystematic R^2 decreases from 90SH to NSH. Thus, only the parameter values of the 90% shade give acceptable predictions of total plant growth over the entire growing season.

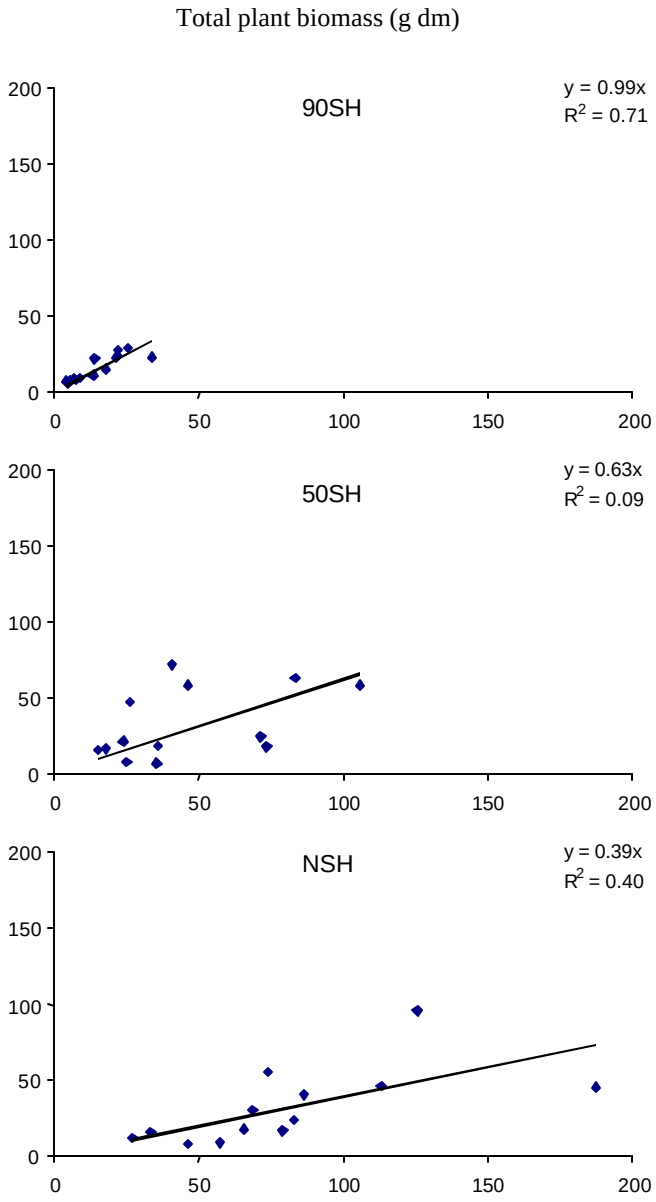

Figure 4.5. *Modelled (y-axis, g dm) versus observed (x-axes, g dm) total plant biomass (g dry matter) for 90% shade (90SH), 50% shade (50SH) and no shade (NSH) for all provenances*

Fig. 4.6 presents the observed vs. model results of the total plant biomass for each of the provenances separately, for all light levels. For most provenances there is a systematic error due to an underestimation of the high values, i.e. the 50% shade and no shade treatment. Whilst for the low values, 90% shade, the parameter values of the model do appear to total plant biomass. Note that the negative R^2 values indicate that the line $y = a \cdot x$ with a zero intercept is not a correct representation through the data points (the residual square error exceeds the explained square error).

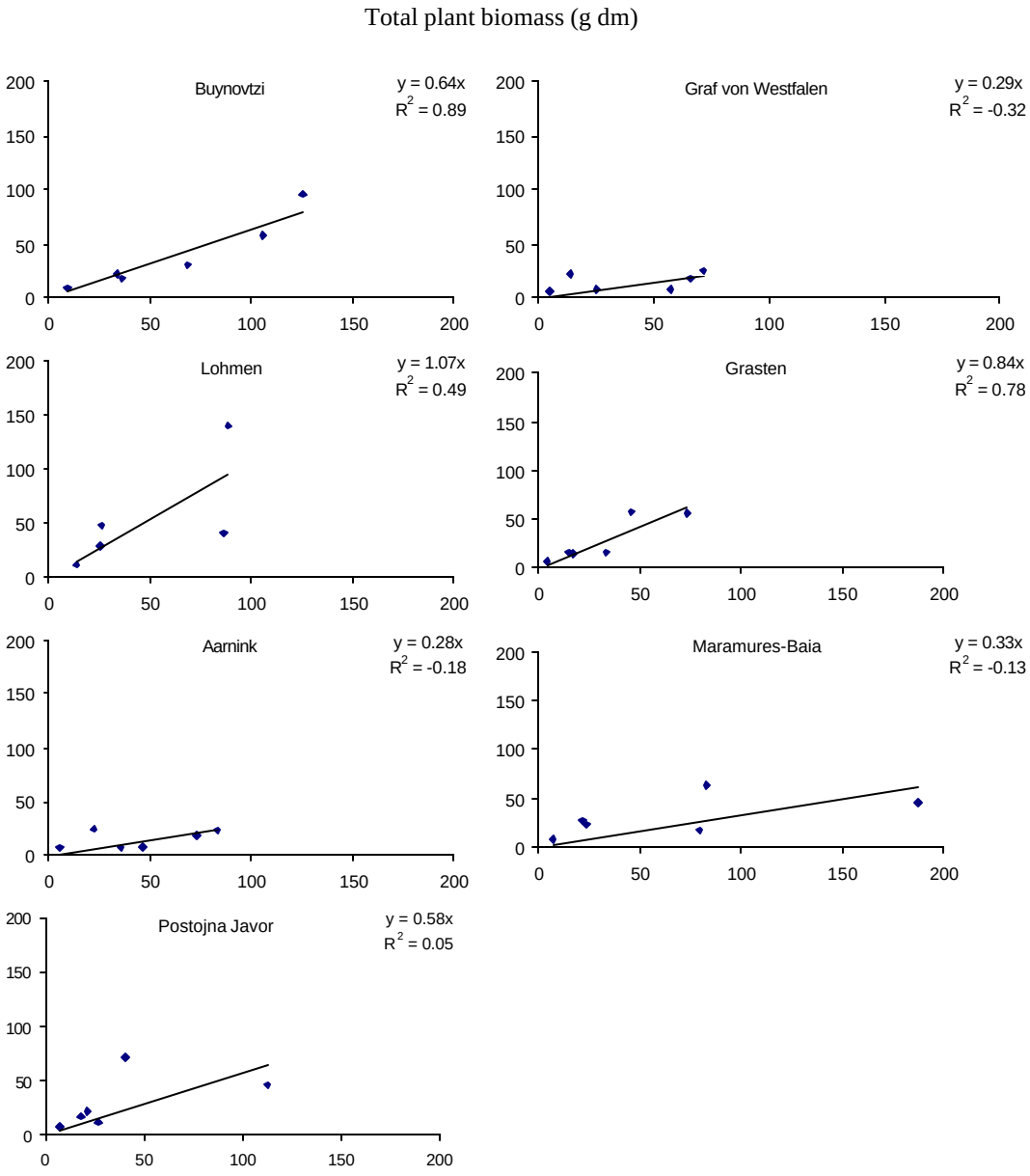

Figure 4.6. *Modelled (y-axis) versus observed (x-axis) total plant biomass (g dry matter) per provenance over all light levels*

Fig. 4.7 presents how total plant weight and root weight depends on the available foliage, both for the observed data and predicted by the growth model. The allocation parameters were estimated based on the biomass data of 1998 and 1999, and input to the growth model. Hence, no independent test of the model output was possible. Fig. 4.6 shows that the simulated results yield a larger amount of roots per unit foliage weight than observed, leading to less foliage and thus less total plant growth. The modelled results therefore show a curvilinear relationship between total plant biomass and foliage biomass, where as in the data this relationship it linear. This effect is the strongest for the high light levels, i.e. 50% shade and no shade.

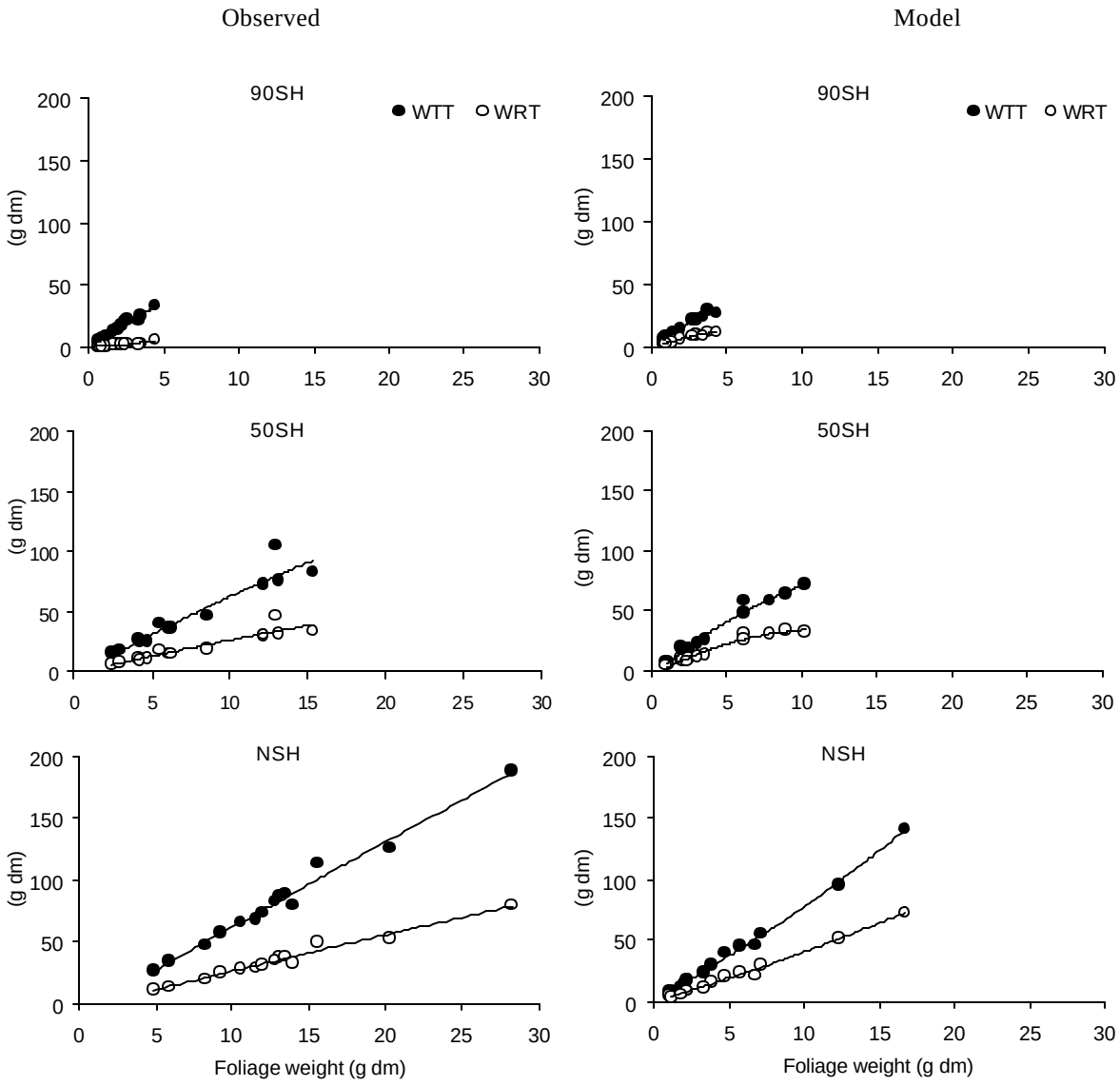

Figure 4.7. *Observed and model results of the amount of both total plant weight (WTT) and root weight (WRT) per unit foliage weight, for the light levels 90% shade (90SH), 50% shade (50SH) and no shade (NSH).*

Based on the results presented in Table 8 and Fig.'s 4.5, 4.6 and 4.7 we concluded that the parameter values of the 90% shade treatment can be used to assess future growth of the saplings based on the growth model FORGRO. Whereas the photosynthetic parameter values estimated on the September data for the 50% shade and no shade situation are probably an underestimation of the values during the growing season. Also the pattern of allocation for the 90% shade treatment appears to be better represented by the growth model than for the both the 50% shade and no shade treatments (see Discussion).

Fig. 4.8 shows that there are clear differences in growth between the provenances when simulated under 90% shade. Grasten has the lowest biomass in all cases, whereas Graf von Westfalen, Aarnink and Buynovtzi (virtually the same stem weight in Fig. 4.8) show the highest biomass. Lohmen, Maramures-Baia and Postojna Javor show intermediate biomass.

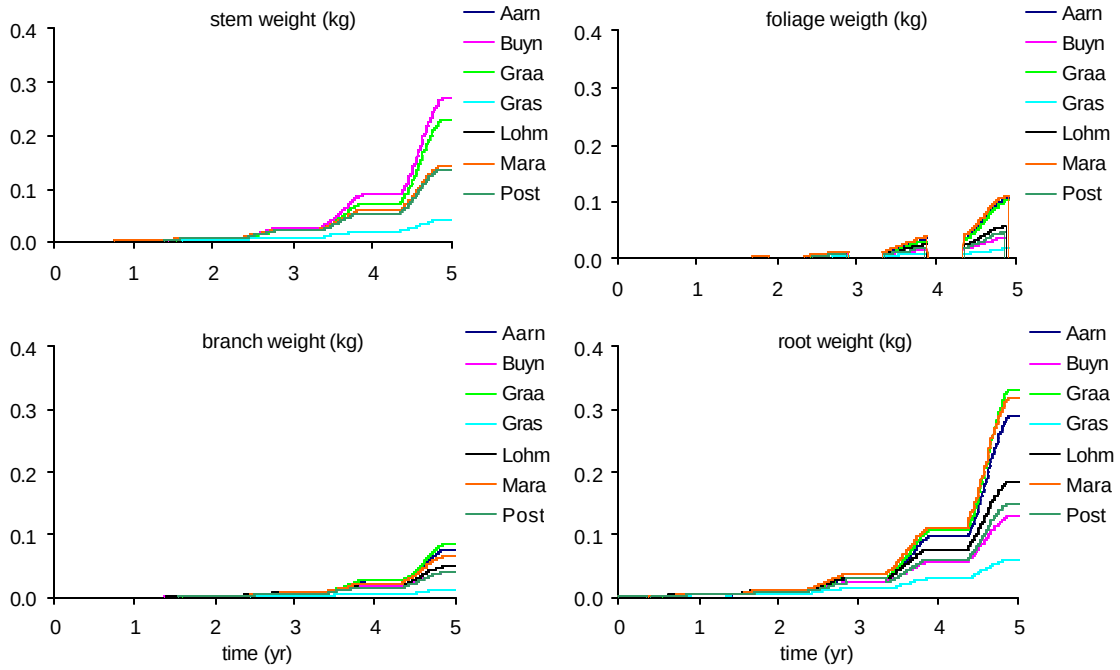

Figure 4.8. *Biomass of the difference plant components for each of the provenances predicted by FORGRO based on parameter values obtained from the 90% shade treatment*

Fig. 4.9 shows that there are also clear differences in height development between the provenances. Lohmen shows the best height growth of all provenances; Grasten, Postojna Javor, Aarnink and Graf von Westfalen (behind the other curves) show a similar, low height increase; Maramures-Baia and Buynovtzi form the intermediate group.

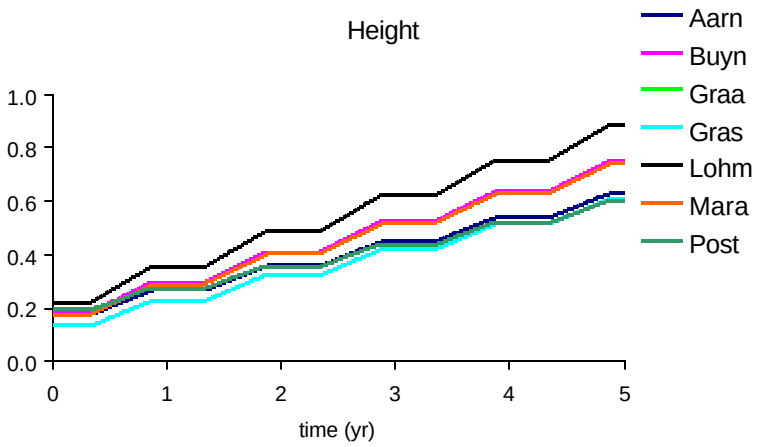

Figure 4.9. *Height development for each of the provenances predicted by FORGRO based on parameter values obtained from the 90% shade treatment*

Based on Figs 4.8 and 4.9 a trade-off between the increase in total plant biomass and height growth can be expected. Fig. 4.10 presents this relationship. There appear to be 3 height-groups (from low to high): 1) Aarnink, Graf von Westfalen, Postojna Javor, Grasten; 2) Buynovtzi, Maramures Baia, and 3) Lohmen. Similarly, there are appear to be 3 'total plant weight'-groups (from low to high): 1) Grasten, 2) Postojna Javor, Maramures Baia, Lohmen, and 3) Graf von Westfalen, Aarnink, Buynovtzi.

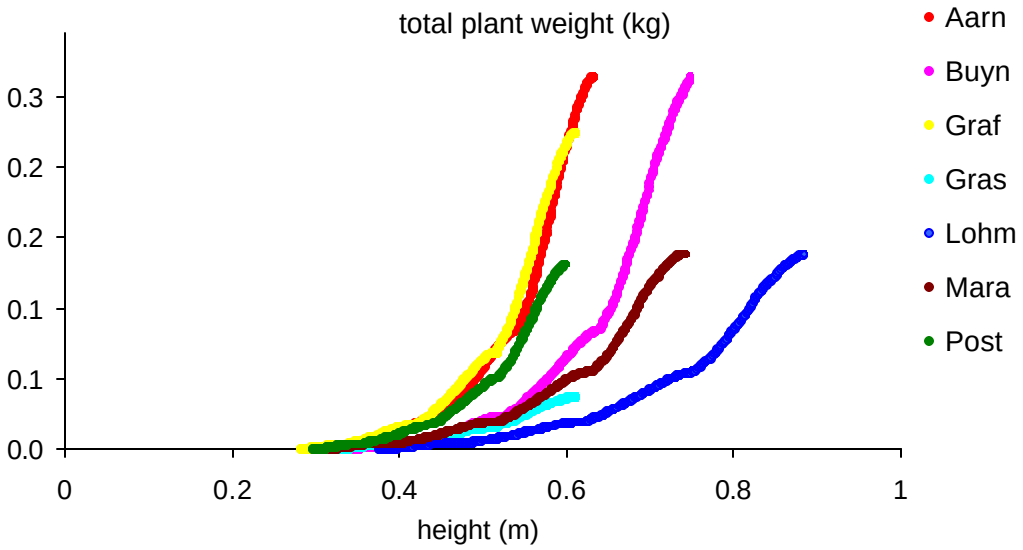

Figure 4.10. *Simulated total plant weight vs. height over a 5-year simulation period for the 90% shade treatment*

4.3 Discussion and conclusions on physiology and modelling growth

In large parts of Europe coniferous are converted into deciduous forests because of economic and ecological reasons. Beech is an important species for this conversion. In the absence of seed sources, beechnuts are in many cases collected in south-east of Europe and raised and planted in north-west Europe. The south-east European beech provenances may be adapted to a continental climate with severe winters and hot and dry summer, whereas the Atlantic climate has mild winters and relatively cool and humid summers. Furthermore, the seedlings are usually raised in a field under full light conditions and the surviving and best performing seedlings are planted under shaded and more moist conditions in the coniferous forest. Thus the selection of plant material of beech for underplanting in coniferous forest in north-west Europe may not be optimal both because the provenances are adapted to a different climate and because the plant performance is not representative for the actual growth conditions. In the following the results of the physiological aspects of the experiment and the implications for growth as simulated by the growth model will be discussed.

The first question considered the differences between the south-east and north-west European provenances. For this analysis the provenances were pooled in a north-west and south-east group. Based on the parameter values for the leaf photosynthesis model the experimental results did not show clear differences between south-east and north-west European provenances (Fig. 4.2)

The second question referred to if there are differences between the provenances in their response to the light treatments. The results of the experiments showed that the provenances respond similarly to the light treatments (Fig. 4.1, Tables 4.5, 4.6, 4.7). Thus it can be concluded that the performance of seedlings raised under full light conditions is representative for their growth under shaded conditions for the features studied.

When using average parameters values over the provenances there was a functional response found for the 90% shade treatment by increasing α and reducing Vcmax. The higher α increases the light use efficiency at low light levels, whereas a reduction of Vcmax under the prevailing conditions does not reduce the rate of net photosynthesis (Fig. 4.3, 4.4 90SH). However, also for the no shade treatment there was a reduction in Vcmax (Fig. 4.3 NSH). Under the prevailing conditions, this will reduce the rate of net photosynthesis (Fig. 4.4, NSH). An explanation could be that the estimated values of Vcmax underestimate the average values in the canopy of the sapling because of the following reason. We decided that the leaf to be measured should be of the same age for all light treatments to avoid difference that are due to senescence. Thus originating from the first flush in spring. However, the saplings in 50% shade and no shade a second flush occurred in the end of June, which was not the case for the 90% shade treatment. This may have lead to a change in photosynthetic characteristics between the first and second growth flush. Also visually the foliage of the 90% shade hall was much darker green and vital than that of the first flush of the 50% shade and no shade. This explanation is in accordance

with the findings of Epron et al (1995) who found that the second growth flush showed a higher photosynthetic capacity per unit chlorophyll than leaves of the first growth flush. They conclude that the their results strongly suggest that the leaves of the second growth flush are better adapted to high light conditions than those of the first growth flush.

The model showed accurately predictions of the total plant biomass for the 90% shade treatment, but was less accurate for the 50% shade and the no shade conditions (Fig. 4.5 and 4.6). This is also most likely caused by the fact that the photosynthetic parameter values measured and used in the model underestimated the average value of the canopy of a provenance (see above). The simulated allocation pattern closely follows the observed pattern (Fig. 4.7). However this is due to the fact that the allocation coefficients used in the model are not estimated on independent data. The 5-year model analysis on increase in biomass (Fig. 4.8) and height (Fig 4.9) indicated a trade-off in these features for plants grown under 90% shade condition. Fig 4.10 shows that the different provenances show different strategies also based on the 90% shade conditions.

These results can be used for the selection of provenances under specific growing conditions. Lohmen would be a good choice if seedlings need to compete with herbaceous vegetation because of its rapid height growth. Provenances such as Buynovtzi, Graf von Westfalen or Aarnink with a more rapid increase in plant biomass can be favoured if the seedlings do not need to compete with herbaceous vegetation.

5 General conclusions

We found no systematic difference between pooled groups of provenances from SE and NW-Europe. In the experiment we had good and bad performing provenances from both climatic regions. Thus we concluded that SE-European might provide good provenances for NW-European conditions.

Shading reduced growth and affected phenology and plant morphology. However the magnitude of response was similar for the provenances studied. Based on this response we concluded that the performance of a provenance under full light conditions is indicative for the plant performance under shaded conditions.

In general we only found good agreement between the measured data and the modelled data under at 90% shade. At full light and 50% shade plant biomass we did not find sufficient agreement between the measured data and the modelled data. Focussing on the modelled performance at 90% shaded conditions we found difference in strategies between provenances. The provenance Lohmen gives priority to height growth whereas and the provenances Buynovtzi, Graf von Westfalen and Aarnink give the priority to increase in biomass. Grasten appears to perform poorly both in height and biomass development, but may have beneficial properties under conditions that are not evaluated in this study.

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