

Impacts of fructification on biomass production and correlated genetic effects in Norway spruce (*Picea abies* [L.] Karst.)

Thomas Seifert · Gerhard Müller-Starck

Received: 25 June 2007 / Revised: 20 March 2008 / Accepted: 9 May 2008
© Springer-Verlag 2008

Abstract For the period 2003–2006, fructification of Norway spruce (*Picea abies* [L.] Karst.) was recorded at the Kranzberg forest site in Southern Germany by employing a crane with access to the canopy of more than 266 trees. For each tree, stem diameter and growth parameters were assessed annually as well as biomass of cones and seeds, number of seeds per cone, and proportions of empty seeds for a total of 371 trees with cone crop. Genotypes at 19 enzyme coding gene loci of 110 trees were included in the study of correlations between morphological and genetic traits. Re-scaling the observed values for a virtual pure Norway spruce stand of 1 ha, cone biomass including winged seeds (oven-dried at 38°C) varied between 706.8 kg/ha in 2006 (average value per tree was 3.6 kg) and values close to zero in 2005. Corresponding values for vegetative biomass increment of the coning trees in 2006 were 9,273.0 kg/ha and 10.8 kg/tree. A significant higher biomass investment was determined for dominant trees in terms of absolute cone mass as well as in terms of cone mass

relative to vegetative biomass and fructification frequency. No trade-off effects in decreased vegetative biomass growth were found in the fructification year, compared to trees that did not grow cones. Although the dominant trees invested proportionally considerable biomass in cones, they showed no significant reduction in vegetative biomass growth. In the following year no decrease in vegetative growth was detected. Based on logistic regressions and homogeneity tests, respectively, significant genetic effect became evident with respect to the gene loci AAP-B and AAT-C concerning fructification probability in the year with maximum generative biomass investment. These and closely related loci also have been found to be indicative for growth and viability, respectively, in other species.

Keywords Vegetative biomass · Generative biomass · Coning · Fructification · Trade-off · Logistic regression · Genotype · Allele · Norway spruce · *Picea abies* · Canopy crane experiment

Communicated by A. Roloff.

This article belongs to the special issue. “Growth and defence of Norway spruce and European beech in pure and mixed stands.”

T. Seifert was formerly Chair of Forest Yield Science, Technische Universität München.

T. Seifert (✉)
Department of Forest and Wood Science,
Faculty of AgriSciences Stellenbosch University,
Private Bag X1, Matieland 7062, South Africa
e-mail: seifert@sun.ac.za

G. Müller-Starck
Section of Forest Genetics, Technische Universität München,
Weihenstephan Center of Life and Food Sciences,
Am Hochanger 13, 85354 Freising, Germany

Introduction

Fructification is the major gateway in the transmission of parental genetic information to the offspring. It is a determinant of the reproductive success of genotypes and of populations and subpopulations, respectively (for survey and functional aspects see e.g. Boshier 2000; Müller-Starck et al. 2005).

The term “fructification” usually refers to the reproductive organs or cones of a plant (Merriam-Webster’s 2003). Following this general definition, in this paper fructification is related to cone and seed production (“coning”) in spite of the fact that conifers, being gymnosperms, do not form cones.

The start of the maturation phase is also an important marker in the life of trees, regarding the allocation of resources. Assimilates which previously have been exclusively reserved for vegetative growth, maintenance, defence and respiration are then also allocated to generative processes.

Masting is a typical phenomenon in forest tree species. Masting means that trees show a characteristic alternating frequency of fructification over the years with the effect that there are years with many fruits or cones and years with less or even none.

Interestingly the trees of one species often synchronise their reproduction over a larger area, which is presumably caused by an interaction of endogenous factors with a climatic stimulus (Selås et al. 2002).

The ecological function of masting has been extensively discussed in literature (cf. Koenig et al. 1994; Herrera et al. 1998; Satake and Iwasa 2000; Koenig and Knops 2000, Kelly and Sork 2002). Some authors attributed masting mainly to exogenous factors like Bûsngen and Mûnch (1929) who established the base of the ‘resource-matching hypothesis’, but more recent studies revealed that the annual fluctuation of reproduction is rated too large to be explained only by environmental factors (cf. Satake and Iwasa 2000). Masting might be interpreted as a strategy to focus resources in order to achieve a better representation of the parental gene pool and to avoid genetic loads such as inbreeding. This hypothesis of improved pollination efficiency was supported by the findings of Smith et al. (1990) and Koenig et al. (1994) amongst others.

The seed dispersal hypothesis states that tree species that rely on seed dispersal by frugivores (cf. Stimm and B s-wald 1994) try to feed their mutualistic animals more consistently than species without frugivore dispersal. This hypothesis was challenged by Koenig et al. (1994). They favoured the ‘predator satiation hypothesis’ instead, and argued that the predominant principle is the minimization of the loss of fruits or seeds to frugivorous animals such as insects, birds, and rodents. The strategy of the tree is simply to deliver as many seeds as possible over a short period of time (*r*-strategy). Even if a large proportion is consumed, there are seeds enough remaining for regeneration. This was supported by the results of Silvertown (1980). The population of seed predators subsequently increases (cf. Schnurr et al. 2002), but it is most likely to collapse before the next masting because the trees will not invest that much again in the subsequent years.

Apart from the frequency of fructification, the amount of biomass invested in fruits or cones is of interest. Fructification is often treated as a third-party trade-off when growth allocation is in the focus of research. Reproduction involves investments in flowers, pollen and fruits or cones. The latter two can be expected to contribute the biggest

proportion of reproductive investments (Rohmeder 1972). For that matter it is evident that there are significant differences in diameter growth in tree species that show a typical sexual dimorphism in flowering and fruit production. Rohmeder (1949) found that predominantly male flowering ash trees (*Fraxinus excelsior* L.) had about 50% more woody biomass than mainly female flowering individuals at an age of 75. The ‘female’ individuals invested in resource intensive fruits.

Analogously, in monoecious trees a trade-off between growth and fructification was described. Von Jazewitsch (1953), based on the results of Schwappach (1895) and her own studies in the Spessart Mountains (Northern Bavaria), observed a significant growth reduction in European beech (*Fagus sylvatica* L.) in years when fructification was above average.

Also for Norway spruce (*Picea abies* [L.] Karst.) a decreased diameter growth in years with abundant fructification is documented. Danilow (1953) observed a reduced year ring width of around 38% in such years compared to years without cone production in spruce stands near St. Petersburg. In the year following the masting, a reduction of year ring width of 20% was still evident. This fits well with the known fact that between two years of fructification there are usually some years of recovery, where the reserves of the trees (mostly starch) are filling up again. Holmsgaard (1955) and Eklund (1957) also describe reduced diameter growth of Norway spruce due to fructification in Scandinavia. Dohrenbusch et al. (2002) detected a minor height growth of trees that had a lot of cones in the same vegetation period.

Most studies about fructification in forest trees, however, are based on qualified estimations of fruit or cone numbers and involved biomass as stated by Rohmeder (1972). The main reason is that problems arise if plausible quantifications of biomass allocation into fruits or cones have to be made. A main problem is the accessibility of fruits or cones in forest trees. Rohmeder (1972) emphasised the need for reliable quantification of data of long-term experimental plots, where each tree is identified. He admitted that this task would be rather time-consuming and would cause problems for all tree species that have seeds that typically do not fall to the ground. However, many studies rely on the counting of fruits or cones that fall down and are usually collected with litterbags according to a defined sampling scenario of a stand. A certain loss cannot be avoided when this method is applied. Another drawback of litterbag sampling is the fact that the fruits or cones cannot be attached to individual trees anymore. Tree climbing methods, which could overcome this disadvantage, are common practice in harvesting cones of conifers, but this method does not ensure that every cone is found and can be accessed or seen. It has to be considered that

tree-climbing causes damage to the trees by breaking twigs and damaging bark and therefore can lead to growth artefacts. Recording of cones at felled trees offers the possibility to access most of the cones at a single-tree level (Siegel 1953; Messer 1958). Only the cones that fall off during the felling cannot be attributed to an individual tree. This destructive sampling is obviously not applicable for records to be taken in successive years at the same trees.

To sum up, despite the big amount of available literature the problems of sampling result in a considerable lack of knowledge about fructification over several years, especially at the single-tree level. This is a definite hurdle when making trade-off calculations as well as to the further investigations on the genetic effects that modify reproduction. A sound knowledge of the allocation pattern in cones and fruits is also prerequisite for allocation modelling with eco-physiological simulation approaches which are usually lacking such information (Rötzer et al. 2008).

The objective of this study is to contribute to the above-mentioned questions on the impact of reproduction on biomass production at single-tree level. For this reason, reproduction of Norway spruce (*P. abies* [L.] Karst.) was recorded consecutively over four years in a long-term canopy crane experiment in Southern Bavaria. Every individual crown was accessible from the crane. For a subsample of the trees, genotypes were mapped before.

Fructification, stem diameter growth and genotype as tree individual variables were used to help answering the following questions:

1. What amounts of seeds and cones are typically produced by mature Norway spruce trees in a mixed stand at cone, tree and stand level?
2. In what way does the social class of a tree influence biomass investment in cones and seeds and fructification frequency?
3. Is there a trade-off between vegetative and generative growth?
4. Is there a genetic effect on amount and probability of fructification?

Materials and methods

Stand

The studied mixed stand of Norway spruce (*P. abies* [L.] Karst.) and European beech (*F. sylvatica* L.) is located in Southern Bavaria close to Freising, at 11°39'42"E, 48°25'12"N 35 km northeast of Munich at an elevation of 490 m above sea level. Following common silvicultural practice at the time of stand establishment, Norway spruce is strongly assumed to originate from plantation. In this

stand, the canopy crane experiment FRE 813 Plot 1 "Kranzberger Forst" was established in 1994. Since 1998 the experiment is part of the collaborative research centre SBF 607 "Growth and Parasite Defence" (Matyssek et al. 2002) of the Deutsche Forschungsgemeinschaft DFG (for yield related details see Grote and Pretzsch 1998). Data on fructification, tree growth and genotypes were assessed within the SFB 607.

The site is a luvisol originating from loess over tertiary sediments. Annual precipitation is 730–890 mm with a mean temperature during vegetation period of 14.0–15.0°C. The potential natural vegetation was classified as a Galio-odorati-Fagetum (Walentowski et al. 2004). Site class of spruce was determined to be 43 m at age 100 according the yield tables of Assmann and Franz (1963).

Norway spruce and European beech are the dominating species with 36.0 and 13.1 m² basal area and an average tree age of 51 and 61 years, respectively in spring 2003, the first year when fructification was recorded. This conforms to the average maturation age of spruce at 50–60 years provided by Burschel (1987). Other tree species like Pedunculate oak (*Quercus robur* L.), European larch (*Larix decidua* Mill.) and Scots pine (*Pinus sylvestris* L.) do not make a relevant contribution to the basal area of the stand. Further information on stand structure and growth can be retrieved from Pretzsch and Schütze (2005).

The background of the fructification measurements was to investigate third-party trade-off of trees and its effect on growth and defence allocation (Matyssek et al. 2002). An exceptional property of the stand is that a small part of it (20 × 20 m plot) had been artificially fumigated by double ambient ozone for several years (Werner and Fabian 2002; Wipfler et al. 2005). However, for the major part of the stand no elevated ozone effect can be expected. Controlled pollinations of Norway spruce trees inside and outside the fumigation area in 2003 and 2006 did not reveal any statistically significant impacts of elevated ozone concentration on metric traits of cones and seeds (Müller-Starck et al., in preparation). For this reason, the impact of ozone is not explicitly taken into account in this paper.

Sample trees

From 2003 to 2006 the trees in a range of 51.2 m around the crane were inspected for cones from a cabin that was fixed at the crane arm. The sampling area covered 5,858 m². In 2002 the proportion of spruce at the total crown projection area of 7,124 m² was 49%, beech covered 47%, pine 3% and oak 1%. The total basal area of 40 m² in the sampling area was clearly dominated by spruce (61%), followed by beech (35%), and pine (3%) and oak (1%)

The sampling took place in a typical mixed stand. The spruce trees in the sampling area included individuals from

the whole diameter spectrum of the stand. Mean diameter did not significantly differ from the whole stand, so a representative sampling considering diameter classes can be assumed.

Record of diameter growth

Data on diameter growth at breast height (1.3 m) was available for all trees from 1999 to 2006. Diameter data were recorded by permanent girth tapes, which were read in monthly intervals during the vegetation period (cf. Wipfler et al. 2005). The first value after the end of the vegetation period was chosen as a reference diameter to assure that growth had ceased in the corresponding year.

Record of diameter growth, fructification and cone treatment

Litter sampling with plastic bags from 1999 to 2002 indicated that the first fructification in the stand that may account for masting was recorded in 2003. Later, the trees in the population were inspected in yearly intervals whether they had cones or not. The inspections were carried out at the end of October to beginning of November after the cones had ripened and lost their green colour. The total number of cones was determined from the crane. In 2003 and 2006 a sub-sample of 10% of the cones but not more than 30 per tree was harvested and packed in paper bags. After determining the fresh weight the cones were immediately oven-dried at 38°C for at least 48 h until they lost no more weight and they opened. The winged seeds were extracted from the cone, weighed and separated into winglets and seeds. The seeds were then weighed again. The proportion of full and hollow seeds was determined by separation in ethyl alcohol. In 2006 additionally the thousand seed weight was measured for a sub-sample of 40 cones, which was determined as a statistically significant proportion according to the variance of the data gathered in 2003. The procedure of thousand seed weight determination and sub-sampling followed the guidelines of ISTA (1999).

Additionally a sub-sample of 100 cones from 10 trees was used for establishing a drying sequence. The cones were oven-dried and weighed at temperatures of 38°C for 48 h, then dried at 60°C for another 24 h, and finally at 105°C for another 48 h to check whether drying temperature influenced the resulting weight. This procedure was necessary to calculate conversion factors for cones and seeds according to different biomass drying methods and definitions.

Genotyping

For 110 of the inspected trees, multi-locus genotypes were assessed beforehand (Riegel 2001): based on starch gel

electrophoresis (for survey see Konnert and Maurer 1995; Müller-Starck 1998), each individual was genotyped at 19 enzyme coding polymorphic gene loci by using bud samples. Gene loci are the following: AAP-B; AAT-A,-B,-C; ACO-A, GDH-A, IDH-A, LAP-A,-B; MDH-B,-C; MNR-B,-C; NDH-A; 6PGDH-B,-C; PGI-B; PGM-A; SKDH-A. Genetic variation was quantified by means of the observed heterozygosities (H_a ; Gregorius et al. 1986) and the frequencies of genetic types (alleles, genotypes).

Statistical analysis

Classification and strata

Trees were classified according to different types of allocation strategy in fructification and social class of a tree in a stand. This was mainly done to reveal and separate effects of the social status and genetics. Several classification variables were determined for each tree.

First of all the fructification frequency was calculated. The trees were classified in groups that displayed 0, 1, 2, and 3 years of fructification during the four years of observation.

To account for the social status, the trees were assigned to three classes according to their diameter at breast height (1.3 m) in the year 2002. Trees of dbh smaller than 25 cm were attributed to class “dominated”, trees from 25 to 35 cm to class “intermediate” and above 35 cm to class “dominating”. This procedure resulted in 76 individuals in the first, 129 in the second and 58 in the third class. The class thresholds were intentionally chosen in such a way that the biggest amount of trees would be in the intermediate class, in order to increase the probability of finding differences in the extremes. Diameter at breast height was chosen as the most suitable classifier because it had been measured for all trees.

All trees were additionally classified according to the accumulated cone number in the years from 2003 to 2006 and assigned to three equal sized groups. This classification should separate trees with different biomass investments during the study period.

Furthermore the trees were classified according to their cone biomass and the proportional cone biomass investment in relation to vegetative biomass also in groups of equal size.

Testing and regression modelling

The data were characterised by standard descriptive statistics with mean values and standard deviation. Additionally tests were performed to test for significant differences of mean values as well as correlation analysis to check for interrelations between variables. A one-way ANOVA was applied to investigate influence of dbh class

on cone biomass investment and fructification probability. A nonparametric “Tamhane T2” test was added to test the effects of social class because a Levene test revealed inhomogeneous variance that excluded standard t-statistics. The same method was used to validate the significance of differences identified in error bar plots. Cross-table analysis was used in combination with a χ^2 and a gamma test for trade-off comparisons in different years.

Logistic regression was applied for binary response variables like fructification ‘yes’ or ‘no’ in a defined year. In logistic regression different factors or interval scaled covariates are used to predict the probability of the response. Also the genotypes (dummy coded) were tested on their effect on the response variable. Logistic regression proved its suitability for revealing genetic effects in several cases (e.g. Henshall and Goddard 1999; Lerman et al. 1999) although examples of its application seem to be rare in forest related fields (Cortesi et al. 2001). For further reading on logistic regression please refer to Hosmer and Lemeshow (2000) or Norušis (2005). In this study logistic regression was applied to test genetic effects on fructification probability. The response variable was the dichotomous information about the incidence of coning of a tree in a certain year. All gene-loci were separately dummy coded (sequential numbers) and checked for significant influence in a first forward stepwise logistic regression respective their likelihood-ratio. The gene-loci with a significant contribution were selected and recoded to explore effects at the allele level. The codes were attributed according to the observed p-values in the first logistic regression in order to reveal homozygote and heterozygote allele combinations. The recoded gene-loci were used as predictors in a second forward stepwise logistic regression to predict fructification probability. Stem diameter increment from the preceding year was additionally added as a predictor to avoid artefacts based on different growth years. Hosmer–Lemeshow tests and Nagelkerke’s R^2 were used to evaluate the total model.

All analysis except for the quantification of genetic parameters was performed with the statistical software package SPSS 14.0. Further statistical analysis of genetic effects was done by utilising the computer software package GSED (Gillet 2004).

Scaling from cone to tree and from tree to stand

The results of biomass and seed analysis were aggregated at the levels of cone, individual tree and stand. Between each level, different scaling steps were necessary to derive complete values from samples.

Cone numbers per tree were fully recorded individually for each tree in every year as described above. Therefore it was used to scale up from cone to tree level. To receive a

full set of cone and seed parameters for each individual tree, the number of cones was multiplied with the adequate tree specific cone biomass or seed variables of the sampled cones. Average cone parameters of all trees in a year were used when no specific cone variables were available for a tree. In 2004 only a non-representative amount of cones from 11 trees was analysed. For this reason mean values of all sampled cone parameters from 2003 and 2006 were used for scaling of the data in 2004.

The fact that the cone recording took place in a mixed stand required a rescaling of the spruce part of the stand to a virtual pure spruce forest of 1 ha in size. Consequently the trees in the sampling area (search radius of the crane) were summed. The proportion of crown projection area of spruce was determined (49.1%) based on tree dimensions of 2002. Missing crown radii were estimated by the functions developed for the growth simulator SILVA (Pretzsch et al. 2002). Finally, the values of the spruce proportion of the stand were rescaled based on the proportion of spruce in crown projection area. This ensured a plausible scaling, because Norway spruce and the admixed species show distinct differences in crown size and space sequestration (Pretzsch and Schütze 2005). A conventional proportional scaling according to tree number or basal area would have led to misinterpretations of the results. The resulting values were converted to a hectare base to provide values comparable to published results.

To compare biomass investment in reproduction and vegetative elements it was necessary to calculate biomass and biomass increment of the stem, the branch and the needles. Data on tree biomass were derived from a data set originally compiled by Wirth et al. (2004) based on results of several other authors. For our purpose, trees were only selected for modelling when all biomass compartments were available for the same individuals to avoid a bias induced by unbalanced data. Additional original biomass data from the experimental station “Kranzberger Forst” were added (cf. Grote and Reiter 2004). Allometric models for each compartment were parameterised based on the compiled data set of 263 trees with a wide diameter and age spectrum (Eq. 1).

$$\ln \text{BM} = a + b \cdot \ln(\text{dbh}) + c \cdot \ln(h) \quad (1)$$

Estimated response variables were needle, branch and stem dry mass (kg). Diameter at breast height (cm) and tree height (m) were used as predictor variables. Diameter at breast height was available from permanent girth tape measurements for each year of the study. Tree height was measured for all trees in 2002. Tree heights for 2003–2006 were calculated based on the assumption that the height–diameter ratio of 2002 can be attributed to these years. This can be done, because height–diameter ratios are known to react only slowly over time.

Table 1 Biomass and seed properties of Norway spruce determined at individual cone level

Values per cone	2003	2004	2006
N trees tested for cone traits	55	11	111
Fresh cone mass including seeds and wings (g)	48.4 (SD 21.2)	26.7 (SD 4.9)	44.8 (SD 9.2)
Cone biomass ^a including seeds and wings (g)	28.8 (SD 10.0)	20.4 (SD 4.3)	38.7 (SD 8.0)
Seed biomass ^a with wings (g)	2.7 (SD 1.0)	0.4 (SD 0.2)	2.2 (SD 0.5)
N seeds per cone	95.8 (SD 90.6)	39.3 (SD 28.6)	225.4 (SD 56.5)
Proportion of empty seeds [%]	24.9 (SD 12.3)	57.5 (SD 20.9)	39.3 (SD 7.7)

^a Oven-dried at 38°C

Results

Amount of seeds and cones

At the cone level a high variation in cone biomass was detected between individuals and between the years as well (Table 1). The seed biomass per cone was also highly variable.

At tree level, the fructification patterns varied significantly between the years regarding the number of trees that fructified and the amount of cones per tree (Table 2).

From a total of 266 trees under survey, 57 trees (21%) had cones in 2003, 194 (73%) in 2004 and 120 (45%) in the year 2006. In 2005, fructification of Norway spruce trees was not observed within “Kranzberger Forst”. That a few single cones remained undiscovered during aerial inspection at crown level by means of a crane supported cage cannot be excluded. The lack of fructification in 2005 is confirmed by annual observations of the flowering intensity of tree species compiled by Schneck (2005): within the provenance area 84,027 (“Alpenvorland”) to which Kranzberg belongs, 2005 was the only year without flowering in Norway spruce (minimum grade of “1.0”). Starting in 1992, the average grading in Germany for Norway spruce is 2.2 with a minimum value of 1.31 in 1994 and a maximum value of 3.45 in 1998. Within

84,027, the 2005 value of 1.0 is uniquely low during the observed time span 1992–2006.

During the observation period an average cone number of 76 (SD = 124) per tree was observed.

At stand level, oven-dried cone biomass ranged from 470 to 700 kg for a 1 ha stand which was virtually recalculated for pure spruce (Table 3). The resulting seed biomass was 25–62 kg/ha.

The amount of seeds is listed at cone, tree and stand level in Tables 1, 2 and 3. Values per hectare were found to amount to between 1.3 and 4.3 million. The results prove that neither the number of coning trees nor the number of cones per hectare provide satisfying predictors for seed density estimations at stand level, because seed numbers per cone and full seed proportions are highly variable between different years and between individuals.

The influence of dbh class on biomass investment in cones and seeds and fructification frequency

The social class of a tree, classified according to its dbh had a significant effect on its cumulative investment in cone biomass during the observation period (Fig. 1). The relationships regarding cone number were just analogue. In both cases, trees of a more dominant social class invested much more biomass in cones and seeds in absolute terms.

Table 2 Biomass and seed properties of Norway spruce determined at individual tree level

Values per tree	2003	2004	2006
N sampled tree population	266	266	266
Amount of trees with cones	57 (21%)	194 (73%)	120 (45%)
N cones per tree	122.7 (SD 157.0)	18.3 (SD 22.3)	43.5 (SD 47.8)
Cone biomass ^a per tree including winged seeds (kg)	3.6 (SD 4.9)	0.7 ^b (SD 0.8)	1.7 (SD 1.7)
Seed biomass ^a per tree including winglets (g)	322.1 (SD 442.8)	37.6 ^b (49.9)	96.3 (SD 108.4)
N seeds per tree	6,747 (SD 12,788)	3,062 ^b (SD 3,960)	10,073 (SD 11,475)
N full seeds per tree	4,777 (SD 8,009)	1,889 ^b (SD 2,461)	6,153 (SD 7,271)

^a Oven-dried at 38°C

^b For scaling at tree level mean cone and seed values of 2003 and 2006 were used for 2004 in absence of representative data for 2004 (crop traits for only 11 trees available)

Table 3 Biomass and seed properties of Norway spruce determined at stand level. The proportional species specific crown projection area of spruce at the total sampled area was used to rescale results for a virtual pure spruce stand of 1 ha

Values per hectare pure spruce	2003	2004	2006
Spruce trees per ha	924	924	924
Trees with cones per ha	194 (21%)	674 (73%)	416 (45%)
N Cones per ha	23,805	12,342	18,085
Cone biomass ^a per ha with winged seeds (kg)	698.4	472.1 ^c	706.8
Seed biomass ^a with winglets per ha (kg)	62.5	25.4 ^c	39.9
Seed density ^b (full seeds only) N/ha ²	1,309,001	2,065,086	4,187,757

^a Oven-dried at 38°C

^b Under the assumption that seeds input and output are equal

^c For scaling at tree level mean cone and seed values of 2003 and 2006 were used for 2004 in absence of representative data for 2004 (crop traits for only 11 trees)

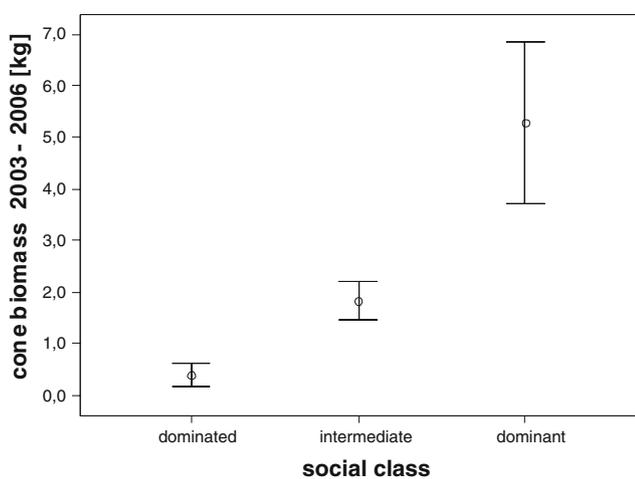


Fig 1 Cumulative cone biomass investment in 4 years of the different social tree classes in comparison. The whiskers illustrate the 95% confidence intervals of the mean value

The significant differences between the social classes based on the error bar plots were confirmed by one-way ANOVA in combination with a nonparametric Tamhane T2 test.

Regarding fructification frequency, the histogram plot (Fig. 2) and a Spearman’s correlation coefficient of $r = 0.653$ indicate a significant positive correlation between frequency of reproduction and dbh-class. It is obvious from Fig. 2 that the lion’s share of the dominated trees (70%) had no fructification during the observation period. The biggest proportion of the dominating and intermediate trees coned two (around 60 and 40%) or three times (20 and 10%). It has to be mentioned, that for a noteworthy proportion of dominating and intermediate trees no fructification was observed.

The results of the ANOVA in combination with a Tamhane T2 test proved the significant positive effect of social class on the fructification frequency of the trees throughout the 4 years of observation. Dominant trees had a significantly higher frequency of reproduction than

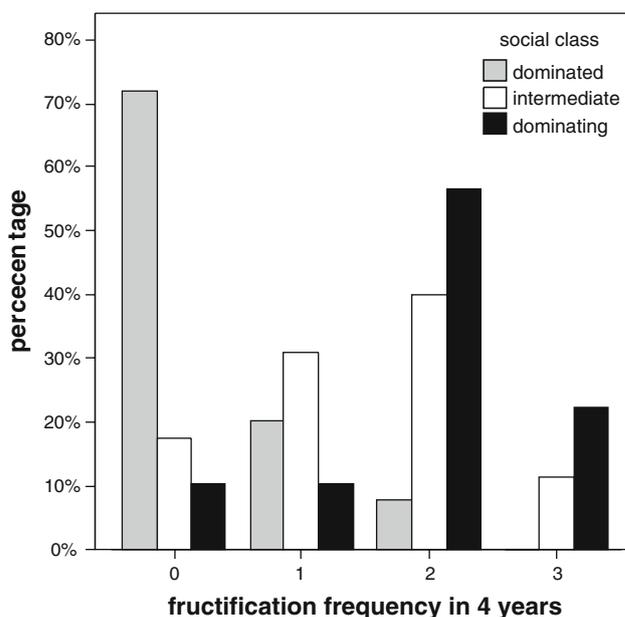


Fig 2 Fructification frequency of different social tree classes in the 4 years observation period

co-dominant trees, and the latter showed a higher reproduction frequency than dominated ones.

The trade-off between vegetative and generative growth

The mean annual diameter increment at breast height showed a significant drop in 2003 without recovering to the level of the preceding years afterwards (Fig. 3). Assuming a start of masting with the same date, this growth pattern could serve as a first indicator for a trade-off of vegetative and generative growth.

The influence of the exceptionally dry year of 2003, however, is included in the plant response and therefore a real trade-off can only be calculated based on biomass investment. For this reason the biomass of vegetative and

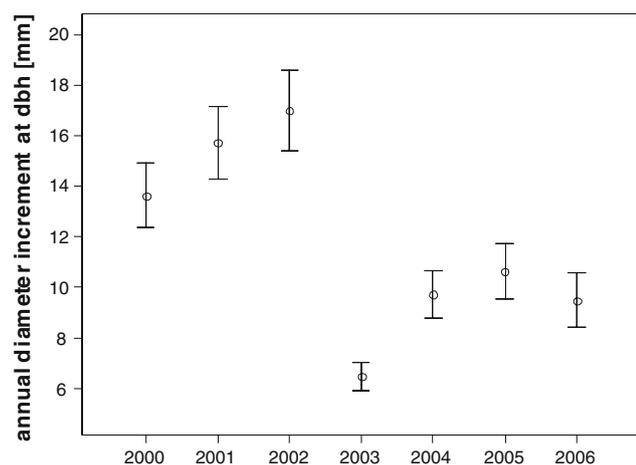


Fig. 3 Annual diameter growth of the sample trees during observation period 2003–2006 and the 3 years before. Masting began most probably in the exceptionally dry year 2003. The *whiskers* illustrate the 95% confidence intervals of the mean value

generative parts has to follow the same definition of drying conditions etc. The results obtained from the drying sequence enabled the conversion of cone and seed biomasses, which are typically dried at 38°C, into values oven-dried at 105°C, the common standard for wood biomass determination.

By drying, the weight of the total cones including winged seeds was reduced to 84% (dried at 38°C), 80% (dried at 60°C) and 78% (dried at 105°C) in proportion to fresh weight.

The models for tree biomass estimation showed high degrees of determination as expected for allometric models. Model parameters and statistics of the allometric models for Norway spruce tree biomass are summarised in Table 4.

Based on these allometric functions and the yearly tree dimensions the vegetative biomass increment was calculated for comparison with the cone biomass. A first step was the comparison of trees that had cones with trees without cones. There were significant differences between

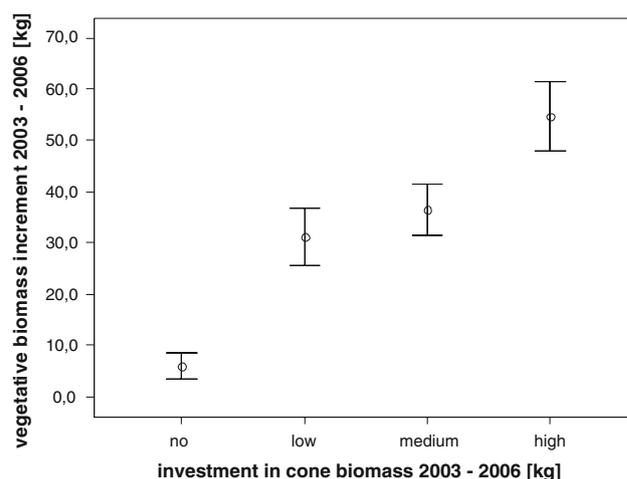


Fig. 4 Cumulative biomass increment in the observation period of trees which had no, low, medium or high cumulative investments in cones. The *whiskers* illustrate the 95% confidence intervals of the mean value

these groups revealed in the error bar plot and by ANOVA. The trees that had grown cones from 2003 to 2006 showed a significant higher vegetative growth than the trees that had not grown cones. A more differentiated classification of the coning trees into three equally sized classes of trees that had a low, medium or high cumulative biomass investment in cones during the observation period revealed significant differences between these classes (Fig. 4). These results were also validated by a Tamhane T2 test and a one-way ANOVA.

A linear regression was used to describe the interrelation between the sum of the invested cone biomass and the sum of the vegetative biomass increment of all coning trees during the 4 years of observation (2003–2006). A natural logarithmic transformation was used for both variables to account for the highly nonlinear nature of the relationship (Eq. 2).

$$\ln(\text{vegetative biomass increment}) = 3.4910 + 0.2141 \cdot \ln(\text{biomass cones}) \quad (2)$$

Table 4 Parameters and statistics for the allometric models to determine vegetative biomass (oven-dry at 105°C) of the sample trees

Response	Parameter	Non standardised coefficients	Standard deviation	Standardised coefficients	<i>T</i>	Significance
Needle biomass $R^2 = 0.880$	a	−2.4632	0.1386		−17.770	0.000
	b	2.7573	0.1264	1.3915	21.823	0.000
	c	−1.1194	0.1438	−0.4964	−7.786	0.000
Branch biomass $R^2 = 0.904$	a	−3.2779	0.1441		−22.742	0.000
	b	2.9321	0.1314	1.2743	22.317	0.000
	c	−0.9186	0.1495	−0.3508	−6.144	0.000
Stem biomass $R^2 = 0.988$	a	−3.6004	0.0599		−60.143	0.000
	b	1.7341	0.0546	0.6491	31.780	0.000
	c	1.0886	0.0621	0.3581	17.532	0.000

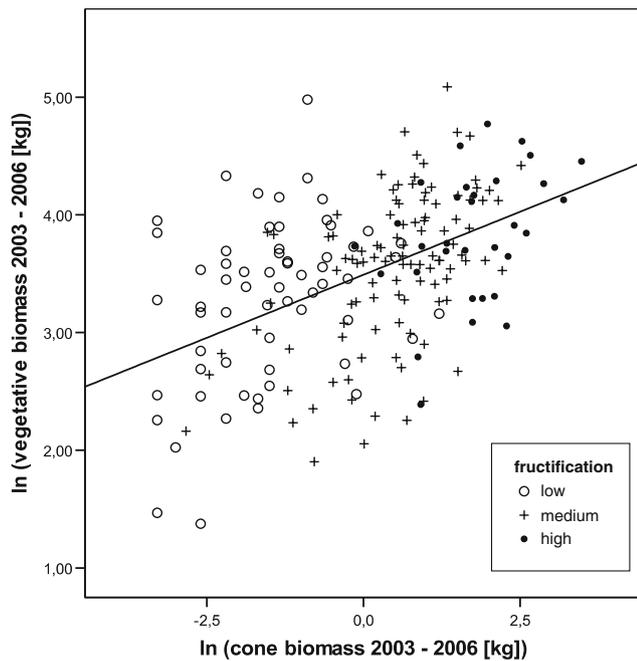


Fig. 5 Cumulative vegetative biomass in the observation period per cumulated cone mass. Trees with low, medium and high fructification rate during this period are indicated

The regression proved the significant positive correlation of cone formation and vegetative biomass. The degree of determination was 0.23. Trees with a high vegetative biomass increment also had a higher investment in cone biomass (Fig. 5).

To check for trade-offs, the proportion of cone biomass to vegetative biomass investment was tested for the individual years. This was to exclude size effects of the trees. The data set was split according to the dbh class to test for possible effects of the social class (Fig. 6).

The proportions of cone biomass to vegetative biomass revealed significant differences between the years within one dbh class. In 2003 the intermediate and dominant trees invested much bigger proportions of cone biomass than in the other years. The differences of 2004 and 2006 were also significant for these social groups. No differences were found between the years for the dominated trees.

To check for a trade-off between the consecutive years 2003 and 2004 a cross tabulation analysis with Chi² and gamma tests revealed apparent differences in cone biomass proportions compared to expected values (Table 5)

The empirical values of cell occupation N in 2004 show apparent differences from the expected numbers. If we compare the trees that had a low fructification in 2003, the table shows that no tree with low fructification proportion achieved a high proportion in 2004. However 56.3 trees were able to have a medium fructification rate. In contrast, most of the trees with a high proportional investment in

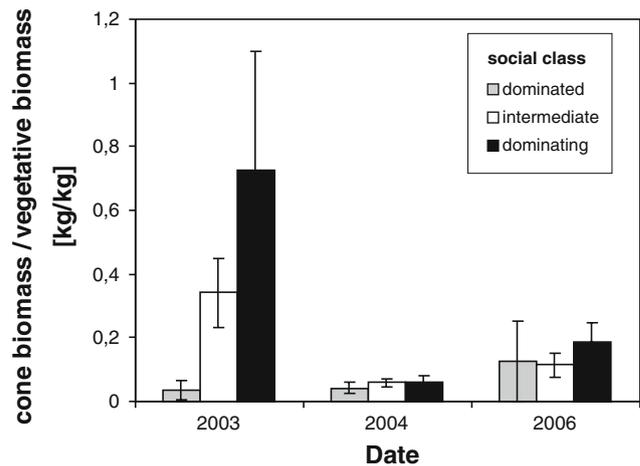


Fig. 6 Influence of social tree class on proportional biomass investment in cones in comparison with vegetative biomass over 3 years of fructification

cones in 2003 again showed a high fructification in 2004 (40.0%) whilst 35.0% had a medium and 25.0% a low fructification in 2004. Only a small change of the proportions was detected. A similar pattern was found when absolute cone biomass was used instead of proportional biomass investment.

No significant decrease in vegetative growth was detected in 2004 if dominant trees with high investment in cone biomass were compared to trees without or with only low investment. No ‘delayed’ trade-off was evident in the consecutive year of fructification. The proportion of cone investment did not change and the vegetative growth was not significantly reduced.

The results prove that the pattern of trade-off expressed as the ratio of investment in fructification to vegetative biomass varies strongly between the years and between different social classes of trees.

Genetic impacts on fructification

Statistically significant genetic effects were evident with respect to the fructification probability of Norway spruce in case of alleles at the gene locus AAT-C (AAT = aspartate aminotransferase, E.C. 2.6.1.1). For results see Table 6.

These effects refer to the vegetation period with maximum generative biomass per hectare (2003) and the stem diameter increment in the preceding growth period as a covariate. The allele information was coded as follows: 1 designates homozygotes for non-affecting alleles ($N = 17$), two heterozygotes ($N = 55$) and three homozygotes for affecting alleles ($N = 31$).

Without covariates the effect was persistent. A non-significant Hosmer–Lemeshow test indicated that the model fit was reasonable; though the genetic effect was not strong (Nagelkerke’s R^2 was 0.16).

Table 5 Cross-tabulation table of biomass proportions (cone biomass per vegetative biomass) invested in 2003 (columns) and 2004 (rows). Given are the measured numbers of 2004 in total (N) and percentage of 2003, the expected numbers and the residuals (measured minus expected)

		Proportional biomass investment [cone biomass per vegetative biomass (kg/kg)]				
		2004				
2003			Low	Medium	High	<i>Total</i>
			Low	N	7	
		Expected N	4.8	6.6	4.5	16
		Percentage of 2003	43.8	56.3	0.0	100
		Residuals	2.2	2.4	-4.5	
	Medium	N	4	6	7	17
		Expected N	5.1	7.1	4.8	17
		Percentage of 2003	23.5	35.3	41.2	100
		Residuals	-1.1	-1.1	2.2	
	High	N	5	7	8	20
		Expected N	6.0	8.3	5.7	20
		Percentage of 2003	25.0	35.0	40.0	100
		Residuals	-1.0	-1.3	2.3	
	<i>Total</i>	N	16	22	15	53
		Expected N	16.0	22.0	15.0	53
		Percentage of 2003	30.2	41.5	28.3	100

Table 6 Regression parameters of the logistic model. AATC denotes for the parameter correlated with the genetic effect of this gene loci, id is the annual diameter increment over bark of the preceding year 2002

Variable	Regression coefficients	Standard deviation	Wald	df	Significance	Exp (B)
AAT-C	0.95615412	0.44398982	4.6377760	1	0.0312755	2.6016715
id 2002	2.18723369	1.00919817	4.6971828	1	0.0302121	8.9105296
Constant	-4.52159065	1.23365239	13.4337379	1	0.0002471	0.0108717

Table 7 Test of homogeneity of genetic types at the gene locus AAP-B among those 12 dominant and intermediate trees which never produced cones (2003–2006) and those 26 trees which regularly participated in fructification

Genetic types	Sample without fructification	Sample with max fructification	0 -value	Level of significance (G -value)	X^2 -value	Level of signif. (X^2 -value)
Alleles	24	52	7.377	0.01 (6.635)	4.712	0.05 (3.841)
Genotypes	12	26	7.017	0.05 (5.991)	4.677 ns	>0.05

Altogether 82.3% of the fructification or non-fructification events were predicted correctly.

All parameters and also the total model were significant at the 0.05 confidence level. A similar genetic effect, however, was not observed in the years 2004 and 2006.

Other genetic effects were evident only at a significance level of 0.1. These were omitted from further consideration.

In the study of genetic impact on the amount of cones per tree, the applied gene loci did not reveal statistically significant allelic or genotypic effects. In contrast, if dominant and intermediate trees that never participated in fructification during 2003–2006 were compared with those regularly displaying fructification (2003, 2004, 2006), homogeneity tests (GSED, Gillet 2004) revealed statistically significant

deviations at the gene locus AAP-B (AAP = alanine aminopeptidase, E.C. 3.4.11.2) for both, alleles and genotypes (see Table 7). The study of 2-locus combinations with the involvement of AAP-B did not result in the verification of statistically significant deviations.

Discussion

Evaluation of the methods

The method of cone harvesting from a crane proved to be very successful in this study. It allowed for a consecutive inspection and sampling of the same trees and additionally

facilitated genotyping. The possibility of an accurate diameter measurement by girth tapes for the same individuals allowed for a combination of these variables to check trade-off effects without destructive sampling of the stem. For this reason the “Kranzberger Forst” canopy crane experiment offered a unique chance for recording the fructification. Of course this cannot be proposed as a standard procedure, because of the high costs for the installations.

The unusually small sample size of 11 trees tested for cone traits in 2004 implies a weakness in our study, but this uncertainty was limited by applying scaling approaches with inclusion of 166 trees from 2003 and 2006 (see Table 2). Further limitations arise from the fact that only a very small fraction of gene loci is known for Norway spruce. The selected sub-sample of enzyme coding gene loci appears small but includes expressed genes that were proven to be indicative for growth and viability, respectively, in other species (for survey see Geburek 2000).

However, our results refer to a time series on fructification of Norway spruce over 4 years where coning and diameter growth were measured annually in parallel. It avoids weaknesses following cone number estimations in defined relative levels by using data of exact counts for cones, and mathematical functions for scaling.

Biomass investment and seed numbers

The results of this study provide an overview of the biomass investment in cones and seeds by Norway spruce grown in a mixed stand at cone, tree and stand level. The mean fresh weight of a cone including seeds yielded very similar results to the published data of other authors. Siegel (1953) found fresh weights ranging from 24 to 48 g, while Ernst (1930) provided mean fresh weights in a range of 18–27 g. The latter also determined a mean oven-dried cone weight of 16.2–42.1 g without specifying drying conditions, which hampers a true comparison. Nonetheless, the magnitude of his values is similar to ours. Ernst (1930) found a mean seed weight of 0.87–0.95 g per cone, which is a little bit lower than our results for 2004 and 2006, but lies within the variation range.

Considering the total amount of biomass invested in cones and seeds per hectare our findings match the published results of other authors quite well. Messer (1958) found 247 trees with cones per hectare, which is just in the middle of our findings.

Siegel’s (1953) results yielded mean seed biomass values from 91.9 to 277.0 kg/ha on base of cone biomass values per hectare that amounted from 621 to 4,758 kg. Interestingly, he calculated a maximum seed biomass more than four times higher than our maximum values, whilst his cone biomass values exceed our maximum by a factor of

almost seven. Messer (1958) calculated a cone and seed biomass of 258.5 and 108.3 kg/ha, respectively. While his cone biomass per hectare value is clearly less than our findings, his seed biomass values seem to be very high in comparison. This implies that either seed numbers or seed weight per cone should significantly differ between the two studies. Indeed Messer (1958) found a big influence of pollination in the preceding years on the proportion of full seeds and hence cone weight. This variability of cone weight between different years was confirmed by our studies.

Siegel’s (1953) statement of a negative correlation between cone number and cone weight between different years can be reproduced based on our results as well. In 2003 we had the highest mean cone weights and the highest numbers of cones per tree, but the lowest proportion of trees with cones in the stand. In comparison in 2004 we had the highest proportion of trees with cones, but the lowest average cone weight and cone numbers per tree.

This is most likely a consequence of an interaction between climatic signals and pollination in preceding years, which induce cone formation, and the status of reserve pools and actual assimilation, which determine the cone growth in the year of cone formation. The unexpected low cone weight and seed number per cone in 2004 could be also, at least partially, affected by the comparably small sample subset of trees in that year ($N = 11$).

The amount of seeds that could potentially form regeneration is an ecologically important variable and also affects regeneration planning in silviculture. Germination rates are known to be constantly high for Norway spruce. Rohmeder (1972) provided a proportion of 95% of germinating seeds. For this reason the amount of full seeds is a good indicator for regeneration potential.

At cone level Siegel (1953) provided mean seed numbers of 158–239 which compares well to our findings in 2006 but exceeds our seed numbers in 2003 and 2004 clearly. In contrast Ernst’s (1930) results suggest an average of 119–157 seeds per cone, which is comparable to our measurements in 2003 and 2004.

At stand level the seed numbers per hectare from other authors were much higher than our values. The results of Messer (1958) indicated a density of full seeds of 16.64 million per hectare, which exceeds our maximum findings by a factor of 3.8. Also Siegel (1953) determined a seed density between 6.86 and 19.75 million full seeds per ha originating from 37,270 to 187,620 cones. These cone numbers exceed our findings tremendously. Our comparably lower seed numbers of max. 4.2 million full seeds were formed by 18,000 cones (cf. Table 3).

To sum up, we received results comparable to those from other authors working at cone level regarding biomass and seed numbers. An inherent lack of publications

regarding the individual tree level became obvious, which would contribute a lot for a true comparison of scaled values. Our results contribute to filling this missing link. At stand level our values were much lower than the published data of other authors. The clearly lower cone numbers in our studies may be a consequence of the younger trees in our study compared to the samples of the other authors. Tree age and size may influence hormonal status, which is known to affect fructification (Matschke 1992; Kozłowski and Pallardy 1997), and also affects the size of reserve pools. In addition to the differences in ontogenetic phase of the trees in comparison to published data, the virtual rescaling from a mixed stand to a pure stand can be a cause for deviation in results. There is not yet enough known about differences in allocation of resources to generative elements between pure and mixed stands for a detailed comparison (Pretzsch and Schütze 2008).

Influence of the social class

Dependence of the biomass investment in cones and fructification frequency on the social class of trees is important for the study of the impacts of silvicultural treatments. We were able to show that dominant and co-dominant trees produce the majority of cones in the stand. The positive correlation of cone mass and dbh is evidence that biomass investment in fructification is increasing with social status and decreasing competition from other trees.

The results suggest that social class is also a good predictor for fructification frequency. Even if our study remains exemplary for the chosen site, tree age, and time frame, we were able to show that trees of higher social classes had a higher probability to grow cones than dominated trees.

Our findings match well with the published results of other authors. Also Ernst (1930), Siegel (1953), Messer (1958), and Dohrenbusch et al. (2002) stated that dominant spruce trees had more cones than dominated trees. Interestingly, Messer (1958) found a higher biomass of the single cones at dominated trees in this context. This seems to be an allocation effect like the biomass variation of cones between different years (see above).

Trade-off

The highest investments in cones were found in 2003, both in terms of absolute cone biomass as well as in proportions. The social class had a significant influence. Dominant trees allocated significantly higher proportions of biomass to cones. This may serve as an indicator for a strong involvement of reserve carbon in the process of cone growth. Trees with more living biomass have a bigger reserve pool, which enables them to grow more cones—

also with unfavourable conditions. A possible explanation for the fact that dominant trees showed not only a higher absolute biomass investment but also a higher proportion of cone biomass to vegetative biomass may be found with a closer examination of the reserve pool. In contrast to herbaceous plants and shrubs, which are known to allocate assimilates mainly from current photosynthesis to fruits and seeds (Addicott and Lyon 1973; Krabel and Eschrich 1991), trees are able to mobilise reserves which originate from former years. A possible hypothesis to check—ideally with stable isotope methods—would be: The proportion of surplus carbon in bigger trees is higher. Their reserve pools are filled up and if cone growth is once induced, the sink strength of the cones is rather high, so that the reserves are depleted. In unfavourable years (such as 2003) the pools are not filled up by running assimilation. For that reason reserve carbon, which is usually reallocated partly for vegetative growth, is then used for cone growth. This would mean a definite trade-off as vegetative growth decreases.

The correct determination of vegetative biomass of standing trees is a challenge when carrying out trade-off studies in general. We used allometric equations to estimate the vegetative biomass and derived growth rates by subtraction of the yearly estimations of total tree biomass. Of course this is only an approximation. The method is based on static functions that cover mean conditions of standing tree biomass in an adequate number of stands, some of which may have been sampled. This suggests that the database for allometric equations contains an unknown number of coning trees. The allometric models cannot account for changes in biomass partitioning induced by fructification. Possible interrelations of needle or leaf density and fructification remain hidden (Innes 1994). Also structural changes of wood cannot be accounted for by allometric models. Chalupka et al. (1977) stated that a reduced year ring width in years of strong fructification was accompanied by a reduced density of the wood in that year. This is atypical for Norway spruce as this species usually features a characteristic strictly negative correlation of year ring width and wood density (Olesen 1976). Therefore smaller year ring widths should have led to higher wood density. This may hint that even more assimilates were invested in cones than indicated by the loss of volume growth. Despite the described allometric models, there is no real alternative for determining the total aboveground vegetative biomass for standing trees without felling. So the applied models provide at least a reasonable range and enable comparison on a common base of dry biomass. Future research will have to quantify true nutrient and energy consumption for vegetative and generative biomass growth for a precise comparison. At this stage the analysis of sapwood area may be used in the future to link

above and below ground biomass and help for distinguishing dead from living biomass (Nikolova et al. 2008).

Pathogenic factors may also influence fructification in the stand. For example red rot, typically caused by *Heterobasidion spec.* is known to occur in the sampled stand. Relevant proportions of assimilates are allocated for defence against pathogens (Bendz-Hellgren and Stenlid 1997; Seifert 2007). Thus, one could argue that a trade-off into defence may essentially reduce available assimilates for reproduction. In contrast to that, Siegel (1953) found that trees subjected to severe stem decay had even more cones than healthy trees, while he found no difference of trees with moderately and slightly decayed stems compared to healthy trees. This may reflect the so-called “Angstfruktifikation”, where trees shift their resource allocation pattern towards generative growth in times when a sudden decline is probable.

One further effect to consider is the exceptionally dry and hot year of 2003. Climatic effects were not explicitly taken into account by this study. Our results suggest that taking a closer look at the influences of precipitation and temperature would be interesting, because there were significant differences regarding the proportional allocation in cones in 2003 compared to the other years, that may have been caused by the different climatic conditions. However, fructification is a highly complex process influenced by various factors that could not all be considered in this study, such as temperature, mineral and water availability. These may have significantly influenced our results as well as the tree vigour, which is reflected by the diameter growth of the trees.

Genetic effects

Coding and expression of traits such as formation of female gametes and cones in response to complex environmental conditions can be expected to be under multi-locus genetic control and to follow complex regulation schemes.

The regression analyses revealed genetic effects with respect to genetic types, alleles, and genotypes. These effects were statistically significant only with respect to the fructification probability following field observation in the year with maximum cone crop per area (2003). Two gene loci are addressed, AAP-B and AAT-C. These gene loci or others, which are coding for these enzyme systems, were proven to have an indicative potential for biomass production or response to viability selection, respectively, in various forest tree species.

In case of the AAT system, this potential was verified with respect to diameter growth in a 47-year-old provenance trial of Scots pine (*P. sylvestris* L.) by Blumenröther et al. (2001). In this study, heterozygosity at the AAT-A

gene corresponded with a remarkable reduction of diameter growth as compared to the corresponding homozygotes. Such a specific effect is not evident with respect to the fructification probability in Norway spruce.

Loci that are coding for amino peptidases (AP) were proven to be indicative for viability selection following various a-biotic stresses (examples concerning leucine amino peptidases (LAP, E.C. 3.4.11.1) see Ziehe et al. 1999; Müller-Starck et al. 2005).

The present results suggest that both, the AAT and the AAP system might be marginally involved in the coding of generative processes or benefit from hitchhiking effects following non-random recombination events with respect to unknown coding gene loci.

Our findings reveal further evidence for a relationship between the observed gene loci and generative growth. The inclusion of additional gene loci that represent other parts of the Norway spruce genome is necessary to attain better insights into the complex genetic coding for vegetative and generative biomass. Finally, expression of traits appears to be strongly influenced by environmental conditions.

Conclusion

Our results may contribute to the verification of continuous impacts of fructification events on biomass production, because not many data are available on a time series basis. Quantitative results on fructification by spruce trees that have recently gained maturity are rare and even more seldom for trees in mixed stands. This lack of knowledge is an inherent problem to the efforts of modelling allocation (Rötzer et al. 2008) or quantifying the effects of mixture on competition (Pretzsch and Schütze 2008) and has thus to be filled.

Our results confirmed a strong influence of the social position of the tree upon its absolute and relative investments in cone biomass. Dominating trees always invested more. A trade-off in terms of reduced diameter growth in the year of fructification or the following year was not found. Distinct patterns of proportional investment in cone biomass compared to vegetative biomass were identified. Two significant genetic effects also were revealed, which correlated with the fructification probability in 2003.

We are aware that the results may distinctly differ in older trees where masting behaviour is found to be more regular. It would be very valuable to have a longer time series than four years in order to test whether the observed patterns are singular events or will repeat in the future. The reaction in the exceptionally dry year 2003 provided especially interesting results calling for further research with longer time series.

Acknowledgments This research was accomplished within the framework of the collaborative research centre SFB 607 “Growth and Parasite Defence”, funded by the German Research Foundation (DFG). The authors also want to thank Holger Paetsch for his diligent determination of cone and seed parameters, Eliane Esser for her kind assistance with the GSED analyses, Jochen Dieler for supporting data analysis as well as Philip Wipfler and Gerhard Schütze for thorough recording of tree diameter increment over all the years and Hans-Peter Dietrich and Stefan Seifert for helpful discussion. At last we gratefully acknowledge the two anonymous reviewers’ helpful comments on the text and want to express our gratitude to Mr. Iain Barbary for language revision.

References

- Addicott FT, Lyon JL (1973) Physiological ecology of abscission. In: Kozłowski TT (ed) Shedding of plant parts. Academic Press, New York, pp 85–124
- Assmann E, Franz F (1963) Vorläufige Fichten-Ertragstafel für Bayern – Mittleres Ertragsniveau. In: Bayerisches Staatsministerium für Ernährung Landwirtschaft und Forsten [Hrsg.] (1990): Hilfstafeln für die Forsteinrichtung, pp 52–63
- Bendz-Hellgren M, Stenlid J (1997) Decreased volume growth of *Picea abies* in response to *Heterobasidion annosum* infection. *Can J For Res* 27:1519–1524
- Blumenröther M, Bachmann M, Müller-Starck G (2001) Genetic characters and diameter growth of provenances of Scots pine (*Pinus sylvestris* L.). *Silvae Genet* 5–6:212–222
- Boshier D (2000) Mating systems. In: Young A, Boshier D, Boyle T (eds) Forest conservation genetics, principles and practice. CSIRO Australia, pp 63–79
- Burschel P (1987) Grundriß des Waldbaus. Parey, p 352
- Büsgen M, Münch E (1929) The structure of life of forest trees. Wiley, New York, p 436
- Chalupka W, Giertych M, Królikowski Z (1977) Relation between specific gravity of wood in Norway spruce (*Picea abies* (L.) Karst.), some growth parameters and cone yield. *Arboretum Kornickie* 22:205–212
- Cortesi P, McCulloch CE, Song H, Lin H, Milgroom MG (2001) Genetic control of horizontal virus transmission in the chestnut blight fungus, *Cryphonectria parasitica*. *Genetics* 159:107–118
- Daniłow D (1953) Einfluß der Samenerzeugung auf die Struktur der Jahrringe. *Botanitscheskij Journal. German Summary Allgemeine Forstzeitschrift* 8:454–455 (cited from Rohmeder 1967)
- Dohrenbusch A, Jaehne S, Bredemeier M, Lamersdorf N (2002) Growth and fructification of a Norway spruce (*Picea abies* L. Karst.) forest ecosystem under changed nutrient and water input. *Ann For Sci* 59:359–368
- Ernst F (1930) Der Samenertrag von Fichtenbeständen im Jahre 1929/30. *Forstwissenschaftliches Centralblatt* 52:503–512
- Eklund B (1957) Om granens årsring variationer inom meleta Norrland och deras sam band med klimatet. *Medd Stat Skogsforskningsinst* 47:1–63
- Geburek T (2000) Effects of environmental pollution on the genetics of forest trees. In: Young A, Boshier D, Boyle T (eds) Forest conservation genetics. Principles and Practice. CSIRO, Australia, pp 135–157
- Gillet, E. (2004): GSED (“Genetic Structures from Electrophoresis Data”) software for assessing genetic variation. <http://www.uni-forst.gwdg.de/forst/fg/software.htm#GSED>
- Gregorius HR, Krauhausen J, Müller-Starck G (1986) Spatial and temporal genetic differentiation among the seed in a stand of *Fagus sylvatica* L. *Heredity* 57:255–262
- Grote R, Pretzsch H (1998) Die Fichten-Buchen-Mischbestände des Sonderforschungsbereiches “Wachstum oder Parasitenabwehr?” im Kranzberger Forst. *Forstwissenschaftliches Centralblatt* 117:241–257
- Grote R, Reiter I (2004) Competition-dependent modelling of foliage biomass in forest stands. *Trees* 18:596–607
- Henshall JM, Goddard ME (1999) Multiple-trait mapping of quantitative trait loci after selective genotyping using logistic regression. *Genetics* 151:885–894
- Herrera C M, Jordano P, Guitian J, Traveset (1998) Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *Am Nat* 152(4):576–594
- Holmsgaard E (1955) Tree-ring analysis of danish forest trees. *Det forstige Forsogsvæsen i Danmark* 22:1–246
- Hosmer DW, Lemeshow S (2000) Applied Logistic Regression. Wiley Series in Probability and Statistics. Wiley & Sons, 392 pp
- Innes JL (1994) The occurrence of flowering and fruiting on individual trees over 3 years and their effects on subsequent crown condition. *Trees* 8:139–150
- ISTA (1999) International Seed Testing Association. In: Internationale Vorschriften für die Saatgutprüfung, Zürich, Switzerland, 337 pp
- Von Jazewitsch W (1953) Jahrringchronologie der Spessart-Buchen. *Forstwissenschaftliches Centralblatt* 72:234–247
- Kelly D, Sork VL (2002) Mast seeding in perennial plants: why, how, where? *Annu Rev Ecol Syst* 33:427–47
- Koenig WD, Mumme RL, Carmen WJ, Stanback MT (1994) Acorn production by oaks in Central Coastal California: variation within and among years. *Ecology* 75:99–109
- Koenig WD, Knops JMH (2000) Patterns of annual seed production by northern hemisphere trees: a global perspective. *Am Nat* 155(1):59–69
- Konnert M, Maurer W (1995) Isozymic Investigations on Norway Spruce (*Picea abies* (L.) Karst.) and European Silver Fir (*Abies alba* Mill.): A practical guide to separation methods and zymogram evaluation. German federal-state working group “Conservation of Forest Gene Resources”, 79 pp
- Kozłowski TT, Pallardy SG (1997) Growth control in woody plants. Academic Press, San Diego, pp 166–194
- Krabel D, Eschrich W (1991) Influence of phloem transport on flower abscission in *Hibiscus rosasinensis*. *Trees* (1990) 4:128–135
- Lerman C, Audrain J, Main D, Boyd NR, Caporaso NE, Bowman ED, Lockshin B, Shields PG (1999) Evidence suggesting the role of specific genetic factors in cigarette smoking. *Health Psychol* 18(1):14–20
- Matschke J (1992) Blütenbildung, Fruktifikation und Vegetative Vermehrung. In: Lyr H, Fiedler HJ, Tranquillini W (eds) Physiologie und Ökologie der Gehölze. Fischer Jena, pp 497–538
- Matyssek R, Schnyder H, Elstner E-F, Munch J-C, Pretzsch H, Sandermann H (2002) Growth and parasite defence in plants; the balance between resource sequestration and retention: in lieu of a guest editorial. *Plant Biol* 4(2):133–136
- Merriam-Webster’s (2003) Collegiate dictionary, 11th edn, p 1622
- Müller-Starck G (1998) Isozymes. In: Karp A, Isaac PG, Ingram DS (eds) Molecular tools for screening biodiversity: plants and animals. Chapman and Hall, London, pp 75–81
- Müller-Starck G, Ziehe M, Schubert R (2005) Genetic diversity parameters associated with viability selection, reproductive efficiency and growth in forest tree species. In: Scherer-Lorenzen M, Körner Ch, Schulze E-D (eds) Forest diversity and function. ecological studies, vol 176. Springer, Heidelberg, pp 87–108
- Messer H (1958) Das Fruchten der Waldbäume als Grundlage der Forstsamengewinnung. J.D. Sauerländers Verlag, Frankfurt am Main pp 108

- Nikolova P, Blaschke H, Matyssek R, Pretzsch H, Seifert T (2008) Combined application of computer tomography and light microscopy for analysis of conductive xylem area in roots of Norway spruce and European beech. *Eur J Forest Res*. doi: [10.1007/s10342-008-0215-9](https://doi.org/10.1007/s10342-008-0215-9)
- Norušis M J (2005) SPSS 14.0 advanced statistical procedures companion. Prentice-Hall, Englewood Cliffs, p 366
- Olesen PO (1976) The interrelation between basic density and ringwidth of Norway spruce. Sammenhængen mellem rumtæthed og årringsbredde hos gran. *Det forstige Forsøgsvæsen i Danmark* 34:340–359
- Pretzsch H, Schütze G (2005) Crown allometry and Growing Space Efficiency of Norway Spruce (*Picea abies* [L.] Karst.) and European Beech (*Fagus sylvatica* L.) in Pure and Mixed Stands. *Plant Biol* 6:628–639
- Pretzsch H, Schütze G (2008) Transgressive overyielding in mixed compared with pure stands of Norway spruce and European beech in Central Europe: evidence on stand level and explanation on individual tree level. *Eur J Forest Res*. doi: [10.1007/s10342-008-0215-9](https://doi.org/10.1007/s10342-008-0215-9)
- Pretzsch H, Biber P, Dursky J (2002) The single tree-based stand simulator SILVA: construction, application and evaluation. *For Ecol Manag* 162:3–21
- Riegel R (2001) Entwicklung molekulargenetischer Marker bei der Fichte und deren Anwendung für genetische Erhebungen in umweltbelasteten Populationen. Dissertation Science Center Weihenstephan, Technische Universität München, pp 99, I–V
- Rohmeder E (1949) Der geschlechtliche Dimorphismus als pflanzenzüchterisches Problem, dargestellt an der Wuchsleistung männlicher und weiblicher Eschen. *Forstwissenschaftliches Centralblatt* 68:680–691
- Rohmeder E (1967) Beziehungen zwischen Frucht- und Samenerzeugung und Holzerzeugung der Waldbäume. *Allgemeine Forstzeitung* 22:33–39
- Rohmeder E (1972) Das Saatgut in der Forstwirtschaft, Parey, pp 273
- Rötzer T, Seifert T, Pretzsch H (2008) Modelling above and below ground carbon dynamics in a mixed beech and spruce stand influenced by climate. *Eur J For Res*. doi: [10.1007/s10342-008-0213-y](https://doi.org/10.1007/s10342-008-0213-y)
- Satake A, Iwasa Y (2000) Pollen coupling of forest trees: forming synchronized and periodic reproduction out of chaos. *J Theor Biol* 203:63–84
- Schneck D (2005) Das Blühen der Waldbäume 2005. *AFZ-Der Wald* 16:836–837
- Schnurr JL, Ostfeld RS, Canham CD (2002) Direct and indirect effects of masting on rodent populations and tree seed survival. *Oikos* 96:402–410
- Schwappach A (1895) Die Samenproduktion der wichtigsten Waldbholzarten in Preußen. *Zeitschrift für Forst- und Jagdwesen* 27:147–174
- Seifert T (2007) Simulating the extent of decay caused by *Heterobasidion annosum* s. l. in stems of Norway spruce. *For Ecol Manage*. 248:95–106
- Selås V, Piovesan G, Adams JM, Bernabei M (2002) Climatic factors controlling reproduction and growth of Norway spruce in southern Norway. *Can J For Res* 32:217–225
- Siegel H (1953) Untersuchungen über den Samenertrag der Fichte im Herbst 1951. *Forstwissenschaftliches Centralblatt* 72:369–379
- Silvertown JW (1980) The evolutionary ecology of mast seeding in trees. *Biol J Linn Soc* 14:235–250
- Smith CC, Hamrick JL, Kramer CL (1990) The advantage of mast years for wind pollination. *Am Nat* 136:154–166
- Stimm B, Böswald K (1994) Die Häher im Visier. Zur Ökologie und waldbaulichen Bedeutung der Samenausbreitung durch Vögel. *Forstw Cbl* 113:204–223
- Walentowski H, Ewald J, Fischer A, Kölling CH, Türk W (2004) *Handbuch der natürlichen Waldgesellschaften Bayerns*. Freising, Geobotanica, p 441
- Werner H, Fabian P (2002) Free-air fumigation of mature trees: a novel system for controlled ozone enrichment in grown-up beech and spruce canopies. *Environ Sci Pollut Res* 9:117–121
- Wipfler P, Seifert T, Heerdt C, Werner H, Pretzsch H (2005) Growth of adult Norway spruce (*Picea abies* [L.] Karst) and European beech (*Fagus sylvatica* L.) under free-air ozone fumigation. *Plant Biol* 7:611–618
- Wirth C, Schumacher J, Schulze E-D (2004) Generic biomass functions for Norway spruce in central Europe—a meta-analysis approach towards prediction and uncertainty estimation. *Tree Phys* 24:121–139
- Ziehe M, Hattemer HH, Müller-Starck R, Müller-Starck G (1999) Genetic structures as indicators for adaptation and adaptational potentials. In: Mátyás C (ed) *Forest genetics and sustainability*, vol 63. Kluwer, Dordrecht, pp 75–89