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INFLUENCE OF GENETIC STRUCTURES AND SILVICULTURAL TREATMENTS IN A BEECH STAND (*FAGUS SYLVATICA*) ON THE POPULATION DYNAMICS OF BEECH SCALE (*CRYPTOCOCCUS FAGISUGA*)

Vincenz Gora[1], Romy Starke[2], Martin Ziehe[2], Jürgen König[1], Gerhard Müller-Starck[2] & Jörg Lunderstädt[1]

1) Institut für Forstzoologie der Universität Göttingen, Büsgenweg 3, D–37077 Göttingen, Germany
2) Abteilung für Forstgenetik und Forstpflanzenzüchtung der Universität Göttingen, Büsgenweg 2, D–37077 Göttingen, Germany

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ABSTRACT

The dynamic of beech scale infestation of a mature beech stand was investigated over a period of 5 years. In the gap-bordering areas an increase of the trees with medium infestation and at the same time a decrease of the uninfested beech trees has been observed. In contrast to this, beech trees in the uninfluenced reference areas (closed stand) exhibited an increase of slightly infested trees and a decrease for every other infestation status.

The identification of isoenzyme genotypes of beech trees representing different degrees of scale infestation revealed significant differences of the allele frequencies at the enzyme gene loci *Mdh–B* and *Idh–A*. A comparison among pairs consisting of an uninfested and a closely neighboured infested tree delivered an even more pronounced contrast if *Idh–A* is combined with *Per–B*. The degree of heterozygosity determined over 11 gene loci was clearly higher with infested than with uninfested trees.

The effects on the ecosystematic linkage between beech and beech scale are discussed.

Key words: *Cryptococcus fagisuga* Lind., *Fagus sylvatica* L., infestation, enzyme gene loci, heterozygosity

INTRODUCTION

Cryptococcus fagisuga Lind., being a monophagous insect, shows a close link with *Fagus sylvatica* L.. The insect is endemic in beech stands from the pole wood stage onwards (RECCIUS 1990). It is regarded as the triggering factor for infection with *Nectria* (LONSDALE 1980) and beech bark disease (BRAUN 1977). In mature forests left in their natural state the insect is considered to play an important role in initiating the succession of beech forests (KÖNIG 1992).

Resistance of beech trees against beech scale is based on physiological reactions within the plant's secondary metabolism and depends on time and age class (LUNDERSTÄDT & EISENWIENER 1989; KÖNIG 1992). Secondary plant compounds in interplay with primary metabolites, determine nutrient quality for the beech scale and are thus the basis for the beech trees' susceptibility. The type, time and extent of these metabolites' production sttack and by beechscaleare modified largely by site conditions (RECCIUS 1990) and by forest management (LUNDERSTÄDT & V. WERDER 1993). Temporal as well as spatial cyclical fluctuations in the beech scale population density therefore reflect the fluctuations in the resistance reactions of the plant to the phytophages (LUNDERSTÄDT & EISENWIENER 1989).

For many tree species, plant genotype has been reported to affect herbivore and insect abundance (EDMUNDS & ALSTAD 1978; SERVICE 1984; STRAUSS 1990; QUIRING & BUTTERWORTH 1994). With *Fagus sylvatica*, beech scale attacks were found to differ between clones (WAINHOUSE & DEEBLE 1980; WAINHOUSE & HOWELL 1983). However, the present state of knowledge of attack patterns and dynamics does not suggest a simple genetic control of the susceptibility of beech to attack. In the following investigation, genetic structures of various enzyme gene loci are applied to characterize not or less infested trees in their genetic information at some specific enzyme gene loci.

MATERIAL AND METHODS

Area under investigation

Investigations were carried out in a 146-year old naturally regenerated pure beech stand in the forest

Table 1a Survey of enzyme systems used for investigation of buds

Enzyme system	EC–code	Gene locus	Buffer
Aconitase	4.2.1.3	*Aco–A(*), –B(*)*	3
Diaphorase	1.6.99.–	*Dia–A*	4, 3
Glutamate oxaloacetate transaminase	2.6.1.1.	*Got–A(*), –B*	2
Isocitrate dehydrogenase	1.1.1.42	*Idh–A*	4, 5
Leucine aminopeptidase	3.4.11.1	*Lap–A*	1
Malate dehydrogenase	1.1.1.37	*Mdh–A, –B, –C*	4, 5
NADH-dehydrogenase	1.6.99.3	*Ndh–A(*)*	4, 5
Peroxidase	1.11.1.7	*Per–B*	2
Phosphoenolpyruvate carboxylase	4.1.1.31	*Pepca–A(*)*	4, 5
6-Phosphogluconate dehydrogenase	1.1.1.44	*6Pgdh–A*	3, 4
Phospohoglucose isomerase	5.3.1.9	*Pgi–B*	1
Phosphoglucomutase	5.4.2.2	*Pgm–A*	4
Shikimate dehydrogenase	1.1.1.25	*Skdh–A*	4, 5
(*) = only pair method			

Table 1b Survey of electrophoretic methods used for investigation of buds

No.	Electrode buffer / pH	Gel buffer / pH
1	0.05 M LiOH – 0.19 M boric acid / 8.1	0.05 M Tris – 0.01 M citric acid / 8.1 (with 10 % of electrode buffer)
2	0.06 M NaOH – 0.03 M boric acid / 8.0	0.07 M Tris – 0.02 M HCl / 8.7
3	0.14 M Tris – 0.04 M citric acid / 7.8	Diluted electrode buffer (2.5 : 1)
4	0.14 M Tris – 0.04 M citric acid / 7.0	Diluted electrode buffer (2.5 : 1)
5	0.14 M Tris – 0.04 M citric acid / 7.0	0.04 M Tris, 0.001 M EDTA and 0.05 M histidine HCl / 5.7

district Neuhaus (Lower Saxony, northern Germany) at 500 m above sea level. The stand is situated on acid light podzol brown earth developed from loess material overlying weathered sand stone. It belongs to the plant community of the *Luzulo–Fagetum typicum* and has not been subjected to forest management since 1960. An average annual precipitation of 1050 mm and an annual mean temperature of 6.5 °C indicate that the climate is of sub-oceanic mountain character (ELLENBERG *et al.* 1986).

In 1989 liming was carried out in one part of the stand (3 t ha^{-1}) and the lime was worked into the top soil. Two gaps, 30 m in diameter, were felled in 1989 in both the limed and the unlimed areas.

Test trees

In 1989, 344 test trees bordering on the four gaps and 75 trees on two uninfluenced reference areas with closed leaf canopy were selected and permanently marked on the basis of their spatial distribution. From the total of the 419 beech trees, 211 trees chosen at random were assessed regarding their genetic characteristics. In 1989, a further 100 trees were selected for pair method analysis (50 pairs) whereby each pair consisted of one unattacked tree and one tree severely attacked by beech scale. The mean distance between the trees in each pair was 3.6 m. If only small-scale site differences between the trees were responsible for the phenotype differences, then apart from random effects, genetic structures of the attacked beeches should be identical to those of the unattacked ones. Significant differences at gene loci therefore point to differences in the genetic susceptibility to attack (for more information about the pair method see GREGORIUS 1989).

Attack by beech scale

Colonization density of the beech trees by beech scale was determined only once for those trees included with the pair method when they were selected in July 1989. The test trees bordering on the gaps and in the reference areas were examined for beech scale attack every month from August 1989 to October 1993 during the vegetation period. Beech scale density was recorded using a 5 point scale (from 1 = very sporadically dispensed wax wool points indicating the scale colonies up to 5 = wax wool points covering large areas of bark) (RHUMBLER 1931; BRAUN 1977). The infestation status of the beech trees, measured as annual mean value of the monthly observed beech scale density, was devided into 4 classes (no or very slight infestation: < 0.2, slight infestation: <1.0, medium infestation:<= 2.0, severe infestation: > 2.0).

Genetic investigations

Multiple locus genetic structures were established over 11 enzyme gene loci for 211 randomly selected beech trees. For a different sample of 50 selected pairs of trees, multiple locus structures were determined for 17 enzyme gene loci. Enzyme systems and gene loci are listed in table 1.

Bud tissues were investigated by means of horizontal starch gel electrophoresis. Crude material was homogenized in a 0.08 M Tris–1.0 N HCl buffer pH 7.3 with the addition of Titriplex II, Mercaptoethanol, DTT and soluble PVP before electrophoretical investigations. For further information about the extraction method and buffer formulations see MÜLLER–STARCK (1985, 1989).

The genetic control of the applied enzyme systems had been verified by studying offspring from controlled crossings (see MÜLLER–STARCK & STARKE 1993).

RESULTS

Infestation of test trees

The test trees in the areas bordering on the gaps showed an uniform increase of the mean population density of beech scale. It deviated from that of the reference areas. In the region of the limed areas bordering on the gaps, the number of not or very slightly infested trees decreased continuously from 1989 to 1993 (–66%) while the number of trees with medium infestation strongly increased (+218%). The number of slightly infested and severely infested trees remained more or less constant. A decrease of the number of uninfested trees (–59%) was also observed in the unlimed areas bordering on the gaps, as well as an increase of the number of trees with a medium degree of infestation (+177%). In contrast to this, the test trees in the reference areas showed a reduction in the infestation classes "not or very slightly infested" (–36%) and "medium infestation" (–60%) while the number of trees with slight infestation increased (+127%) (Fig.1). No or very slight infestation was observed only on 40 trees during the entire period of investigation. 24 of the trees, belonged to the random sample of trees that were examined genetically.

Genetic analyses

Contingency table tests for the comparison of genotypical structures of uninfested and infested trees were applied for all gene loci. Statistically significant correlations between the susceptibility of beech to infestation by beech scale and their genotypical information were observed for the gene locus *Idh–A*, for *Idh–A* in combination with *Per–B* and for *Mdh–B*.

Genetic comparison between pairs of trees (pair method)

Clear differences between infested and not or only very slightly infested trees were established for relative frequencies of two–locus genotypes of the gene loci *Idh–A* and *Per–B*. The homozygous genotype *Idh–*A_3A_3 combined with the homozygotes *Per–*B_4B_4 or *Per–*B_5B_5 was found nearly 3 times as often among the uninfested trees as among the infested (Fig. 2). Three quarters of the 28 trees with these two–locus genotypes proved uninfested. Among the remaining 72 trees with different genotypical structures, only slightly more than a third was uninfested.

Test trees in the areas bordering on the gaps and in the reference areas

A significantly (*) high frequency of the genotype A_3A_3 at the *Idh–A* gene locus was found among not or very slightly infested trees (Fig. 3). The correlation between genotype and susceptibility to infestation was revealed even more clearly by a comparison of the 12 completely uninfested trees with the 30 most severely infested beeches. While 10 of the 12 uninfested trees exhibited the alleles A_3A_3 at *Idh–A* gene locus less than half of the severely infested beech trees did so.

Significant differences (*) in the genetic structure of infested and uninfested beech trees became also obvious at gene locus *Mdh–B*. However, for the present considerations it proved appropriate to designate both fast migrating alleles B_1 and B_2 as B_2 and both slowly migrating allele variants B_3 and B_4 as B_3. The genotypes containing a fast moving allele (B_2) occurred nearly twice as often among the uninfested or very slightly infested trees as compared to the infested trees (Fig. 4). In particular, the presence of two fast moving alleles at the *Mdh–B* gene locus appears to indicate a considerable resistance of beech trees to attack by beech scale.

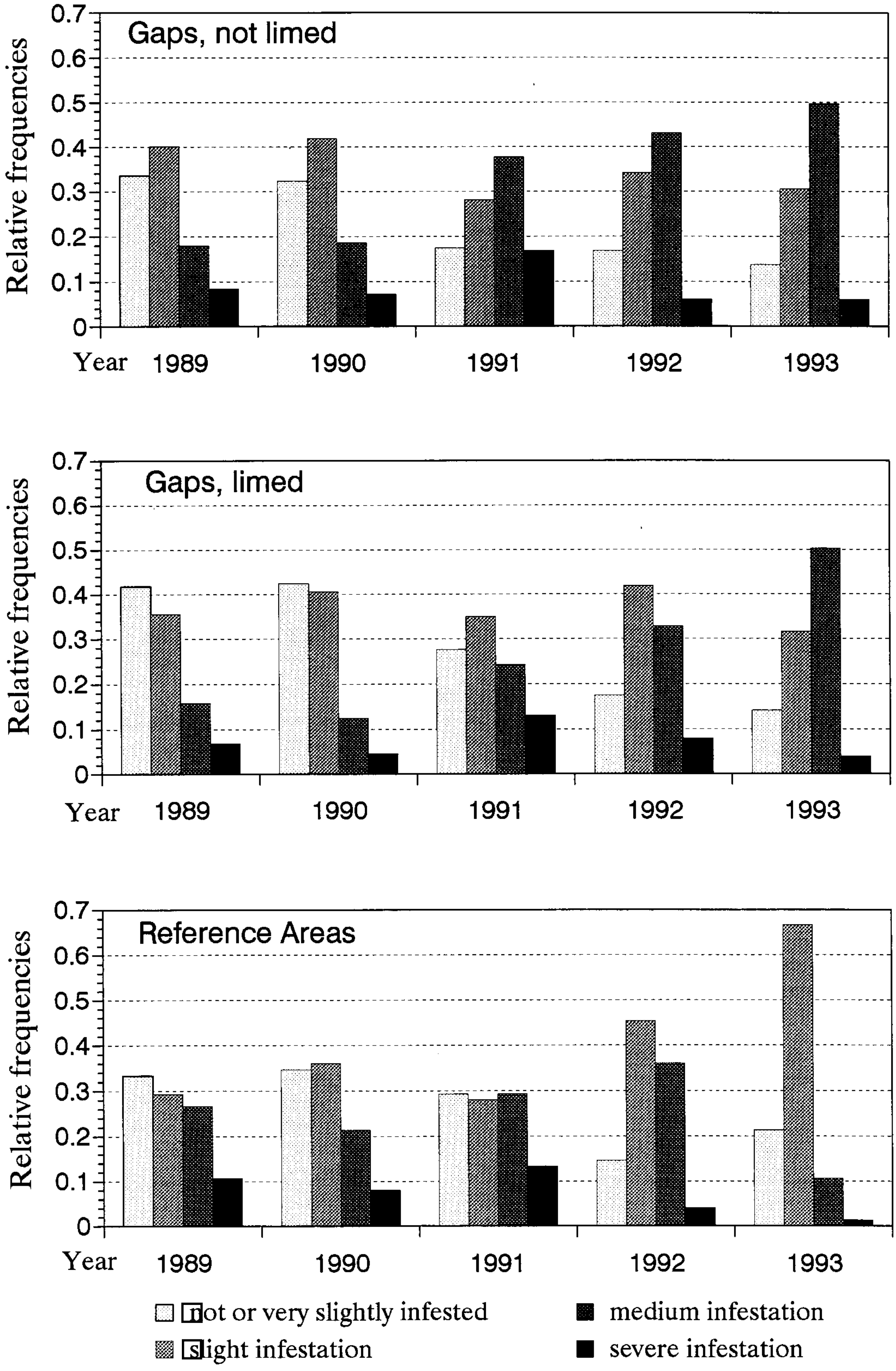

Figure 1 Dynamics of beech scale infestation of mature beech trees (N = 419) for three differently treated partial areas of a pure beech stand during the years 1989 - 1993

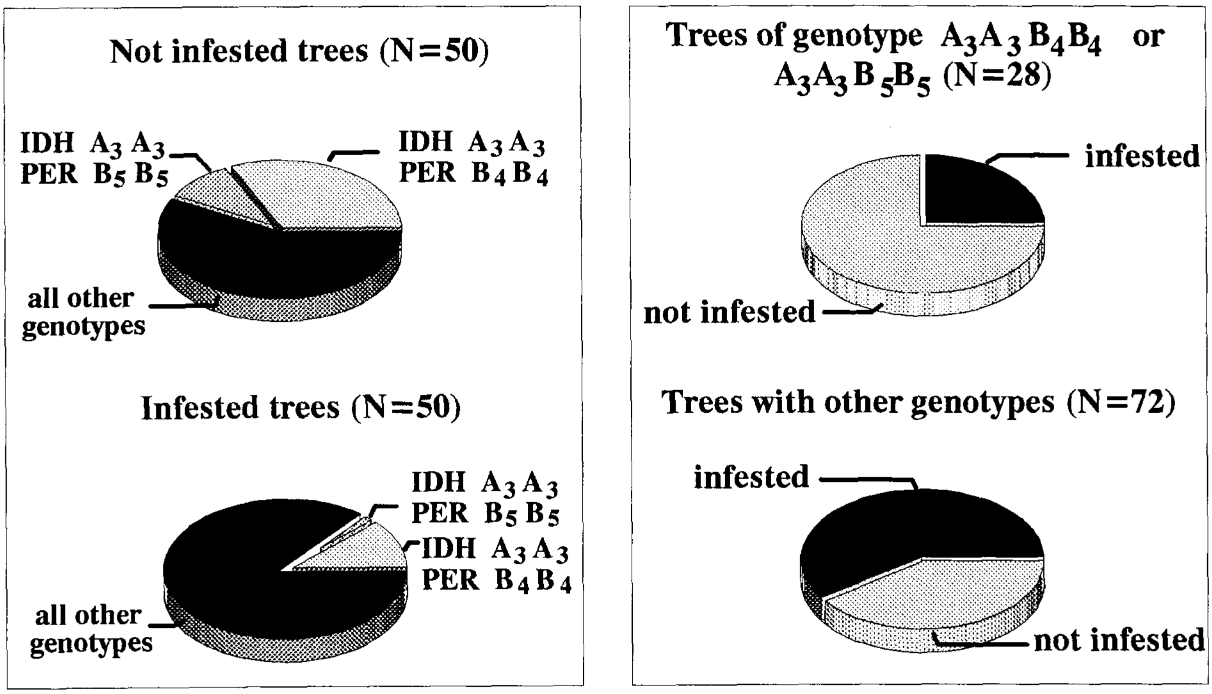

Figure 2 Genotypical structure of uninfested and beech scale infested mature beech trees at the gene locus combination *Idh-A* and *Per-B*

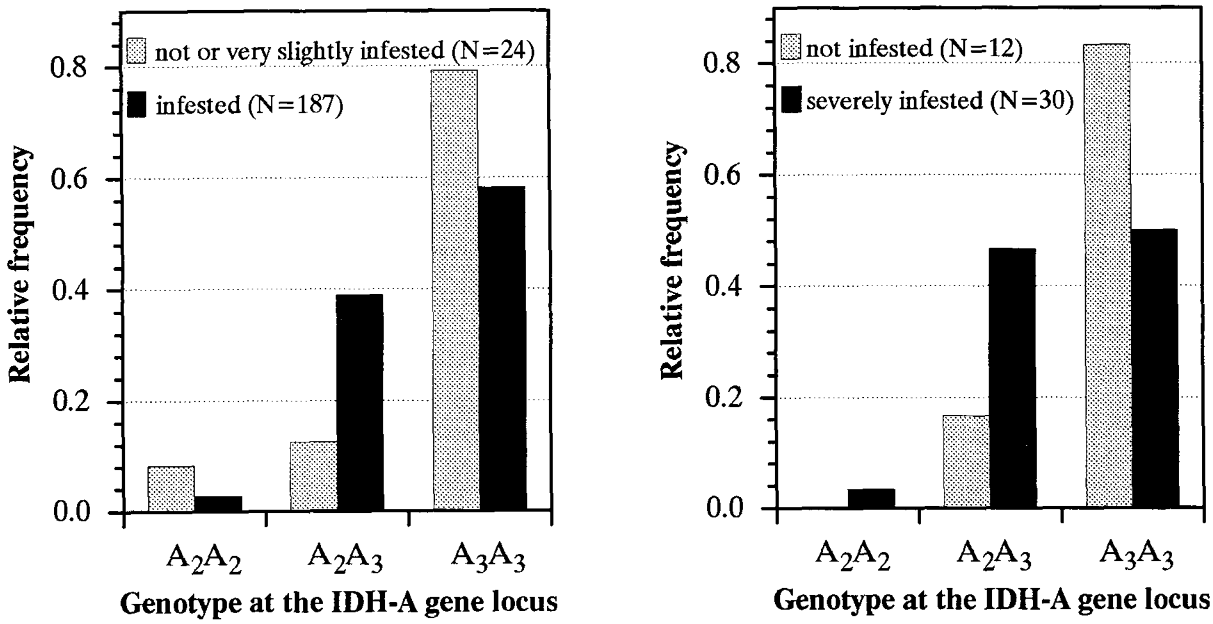

Figure 3 Relative frequencies of the genotypes at the *Idh-A* gene locus of mature beech trees. Left: trees from the gaps and the reference areas divided into two groups: (1) uninfested and very slightly infested beech trees (infestation density as annual mean values < 0.2; (2) beech trees infested by beech scale (infestation density as annual mean values > 0.2 up to 3.4). Right: Subcollectives of infested and severely infested beech trees

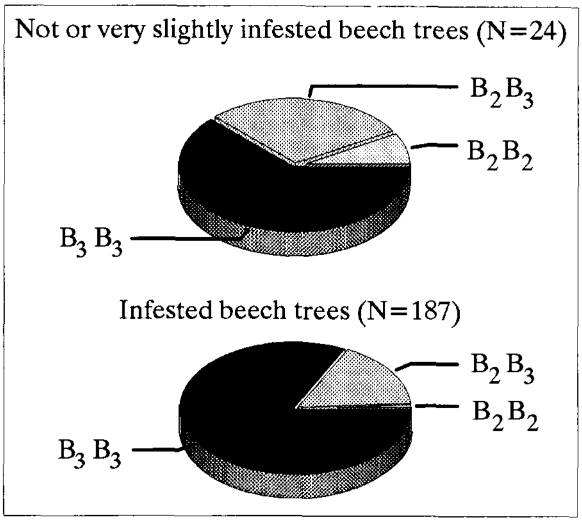

Figure 4 Genotypical structure of mature beech trees from the gap and reference areas at the gene locus *Mdh-B*. Uninfested and very slightly infested trees (infestation density as annual mean values < 0.2) compared with infested beech trees (infestation density as annual mean values > 0.2 up to 3.4). Fast migrating allele variants B_1 and B_2 pooled to B_2, slowly migrating allele variants B_3 and B_4 pooled to B_3

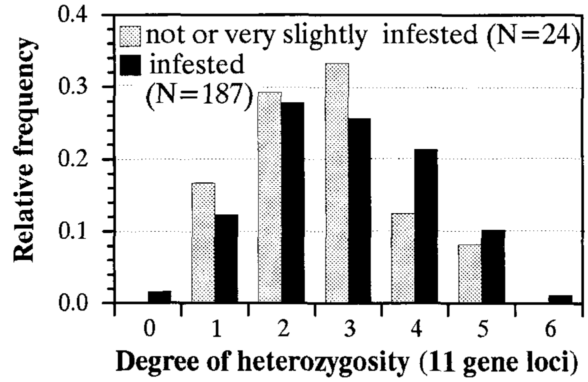

Figure 5 Relative frequencies of the degree of heterozygosityof mature beech trees from the gap and the reference areas determined over 11 gene loci. Uninfested and very slightly infested trees (infestation density as annual mean values < 0.2) compared with infested beech trees (infestation density as annual mean values > 0.2 up to 3.4)

The degree of heterozygosity, defined as the number of gene loci proving heterozygosity, was determined over the 11 gene loci examined for this sample. The observed degree of heterozygosity varied between 0 and 6. The infested beech trees exhibited a clearly higher heterozygosity as compared to the uninfested trees. Moreover, the distribution of the degree of heterozygosity shows a clear shift towards higher numbers of heterozygous gene loci for the individual trees among the infested beech trees (Fig. 5).

DISCUSSION

Beech – beech scale as a system

Cutting gaps in the dense, unmanaged mature forests resulted in a distinct change of stand climate and light conditions. Beech scale populations reacted with great sensitivity to these changes in environmental conditions; during the investigation period the beech scale population density showed a clear increase on the gap bordering areas. A similar increase of attack after thinning and freeing of *Abies alba* was found for *Dreyfusia nordmannianae* (KITZBERGER & FÜHRER 1993).

The performance of arthropods living on bark of forest trees can strongly be influenced by the microclimate (NICOLAI 1986). So scale population around the gaps might be raised because of more favourable temperatures and humidity regimes on the bark surface improving the insects' development. However, we here observed high wax wool wash off on the wind exposed gap bordering trees in cases of heavy rainfall.

Cutting of gaps as well as thinning leads to an improvement in light conditions and a reduction in competition from neighbouring trees for those trees remaining at the edge of the gaps. Beech trees have a high crown plasticity even at an advanced age and can utilize the freeing of their crowns for growth increase (KRAMER 1988). Improved growth conditions trigger a temporary shift in the metabolism and raise the susceptibility for beech scale. Vigorous trees, with large diameter consistently show the most severe scale infestation (WAINHOUSE & DEEBLE 1980, LUNDERSTÄDT & VON WERDER 1993). After thinning younger beech stands, the population density of beech scale and the ratios of soluble carbohydrates to compounds of the secondary metabolism (procyanidins) increased (KÖNIG 1986, HOLZHAUER 1987). Procyanidins and their ratios to protein amino acids and sugars are important as antibodies of the beech trees against beech scale (LUNDERSTÄDT & EISENWIENER 1989, BORGEL 1991). These changes in the physiology of the beech trees cause an improvement in nutrient quality for the beech scales which are favourable for the establishment of higher insect population densities.

The observation that trees released from competition are more susceptible to beech scale seems to be in conflict with the tree stress hypotheses, since many trees show higher insect attack when exposed to different environmental stress factors influencing the plant's metabolism (WHITE 1974, 1984). For a short period beech trees may tolerate higher degrees of scale infestation in order to take advantage of the scale infestation in order to take advantage of the temporarily improved growth conditions thus achieving and maintaining an advantage in competition with neighbouring trees.

Genetic structures of beech trees and the population dynamics of beech scale

The high assimilation and storage capacity of beech trees in conjunction with vigorous growth are considered to be the cause for the heightened susceptibility of the dominant and co-dominant trees to severe infestation by beech scale. Particularly these vigorous, well-growing stand components relatively tolerant to stress conditions proved to be above average heterozygous at some observed enzyme gene loci (MÜLLER-STARCK & ZIEHE 1991, ZIEHE & MÜLLER-STARCK 1991). The observation of the present investigation that infested trees exhibit a higher heterozygosity than uninfested trees is in agreement with this. Damage to vigorous, dominant trees by severe beech scale infestation could therefore on one hand explain the high stand dynamics of beech forests which is indicated by changes of the social positions of trees including advanced age classes. On the other hand, an advantage of genes or heterozygosity promoting vitality in the absence of infestation may be compensated or even overcompensated after the trees are affected. Since finally only the genetic contributions to the next generation are of evolutionary significance, this effect complicates direct evolutionary conclusion.

An observed lower susceptibility of specific beech genotypes to infestation by beech scale can be interpreted as an at least temporally effective evolutionary advantage of the plant. Those trees which remained uninfested or became only slightly infested over the observation period of five years may be able to produce a particularly long-lasting immunization or to repel infestation by the insect at an early stage. In the present paper, significant correlations between genotype and intensity of attack have been established only for enzymes of the plant's central metabolism in the sphere of the citric acid cycle. The gene locus detected for the enzyme shikimate dehydrogenase, which acts in the shikimic acid pathway on the way to the synthesis of procyanidins, here shows up only as a minorpolymorphism which excludes further conclusions. Physiological links between the beech genotype and the resistance to the scale can be suspected to originate from a possible improvement of the substance/energy metabolism ratios in the plant cells or from a direct influence on the nutrition and its assimilation by the scale.

WAINHOUSE and HOWELL (1983) observed 20 year old beech trees descending from three different clones over a period of two years and observed resistance to infestation by beech scale only for trees of one particular clone. Here again specific genetic information of the trees seems to protect against attack of the insect.

The facts that these studies are based on relatively short observation periods, restrict of course the general validity of conclusions. Climatic and site conditions of the present investigations as well as age of the beech trees had an influence on the susceptibility to beech scale attack. Extreme weather conditions can substantially increase the beeches' susceptibility. Other populations with initially the same genetic structures may undergo different viability selection pressures which can also affect the genetic structures at those loci controlling resistance to beech scale (MÜLLER-STARCK 1993). Hence the resistance property of a plant population, as also of an individual, is subject to strong modifications by the environment (STRAUSS 1990, QUIRING & BUTTERWORTH 1994). Besides, adaptation of beech scale is possible with a generation time of a 150th of a tree generation. Trees enable the balance between beech and phytophages populations to be maintained by transmitting advantageous genes to the next generation. The insect responds utilizing "ecological windows" in growth phases of the beech trees and coevolutionary development. Consequently the impact on susceptibility of particular genetic structures observed for a beech stand should not be considered as being constant.

On the other hand, relatively uncommon gene combinations proved advantageous against the scale. Hence, in the long run, the preservation of genetic variation appears to be a crucial prerequisite for the occurrence of resistant trees and thus also for the maintenance of ecological stability.

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