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Genotype-Species Interactions in Neighbourhoods of Forest Tree Communities

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Abstract

Studies on plant communities of various annual species suggest that there are particular biotic interactions among individuals from different species which could be the basis for long-term species coexistence. In the course of a large survey on species-genetic diversity relationships in several forest tree communities, it was found that statistically significant differences exist among isozyme genotype frequencies of conspecific tree groups, which differ only by species identity of their neighbours. Based on a specific measure, the association of the neighbouring species with the genotypes of the target species or that of the genotypes with the neighbouring species was quantified. Since only AAT and HEK of the five analysed enzyme systems differed in their genotype frequencies among several tree groups of the same target species, a potential involvement of their enzymatic function in the observed differences was discussed. The results of this study demonstrate a fine-scale genetic differentiation within single tree species of forest communities, which may be the result of biotic interactions between the genetic structure of a species

and the species composition of its community. This observation also suggests the importance of intraspecific genetic variation for interspecific adaptation.

Key words: Association, tree species, neighbourhood, isozymes, species-genotype interaction.

Introduction

It has generally been recognized that the adaptive genetic variation of plant species results not only from abiotic selective forces, such as stressful climatic or edaphic conditions, but also from local biotic stressors, such as herbivores, parasites and other pests of plants (for review, see MITTON, 1997). Furthermore, competition during the first ontogenetic stages by conspecific individuals or individuals from other species of related taxa may also be a selective factor shaping the genetic structure of the growing plant population (for reviews, see SILVERTOWN, 1987, chapter 8; KEDDY, 1989). However, in recent years there have been an increasing

number of studies revealing particular interactions between neighbouring individuals from different species in a plant community leading not always to suppression of one or the other individual but also to higher vitality of both individuals in special cases (for reviews, see TURKINGTON and AARSEN, 1984; CALLAWAY, 1995). For example, natural neighbouring plant pairs of the grass *Lolium perenne* and the clover *Trifolium repens* produced higher yield than non-natural neighbours, suggesting the existence of a particular biotic specialization of genotype pairs from the same two species in a single community (AARSEN and TURKINGTON, 1985). This study especially indicated that natural selection may result in more balanced competitive abilities for contested resources and that this may be an important evolutionary mechanism of coexistence in plant communities. Moreover, it was recently postulated that the association of various plant species in a community is characterized by positive interactions among individuals from different species and that competition may, in fact, play only a minor role (CALLAWAY, 1995; GIGON, 1994, 1999).

In order to get better insight into the biochemical, physiological and ecological bases of the processes which lead to the coexistence of individuals in a community, irrespective of taxonomy, it is necessary to investigate the biotic specialization in nature (for review, see TURKINGTON and AARSEN, 1984). Such investigations on various annual plant species have shown, that micro-evolutionary forces, such as reciprocal selection for balanced interaction, determined the formation of neighbourhoods between specific genotypes of different species, however, a specific study on this subject using genetic markers, like DNA or isozyme polymorphisms, has not yet been announced. Therefore, it was particularly interesting to search for such differences in the genetic structure of tree subpopulations when the neighbourhood of their members changed from conspecific individuals to individuals of other tree species. The results which are presented in the following sections are part of a large-scale study on the relationships between genetic diversity and species diversity in various forest tree communities (WEHENKEL et al., 2006). The main question of the present study is: are there effects on the genetic structure of a species by the species with which it interacts? Interaction is here defined by nearest neighbour relations.

Material and Methods

When describing interaction by nearest neighbour relationships, reference individuals must be identified for which nearest neighbours can be determined. Since we are interested in relationships between genetic characteristics of a species and the species affiliation of its nearest neighbours, the reference individuals belong to the genetically scored species. This species will be called the target species in the following sections. Thus, each member of the target species is characterized by two traits, one of which specifies the member's genotype and the other specifies the species affiliation of its nearest neighbour. Given this representation, analyses of interaction can be performed with the help of analyses of association between the two traits.

Individual random sampling of communities does not allow for an analysis of association of genotypes of a target species with the species affiliation of their nearest neighbour. Nearest neighbours in individual random samples cannot reflect the interactions resulting from nearest neighbourhood in the overall community. Sampling of communities is therefore restricted to fully scored plots. This sampling strategy is further enforced by the inclusion of several target species in the same study. Since we are interested in detecting large-scale effects, sample plots were taken from different forest communities. The plant material investigated belongs to three target tree species (maple, beech and spruce) as well as to seven neighbouring tree species (maple, beech, spruce, pine, birch, ash and linden). The trees were differently distributed over four stands (from different communities), of which two are represented by two plots and two by one plot each (see Table 1). The natural regeneration (at the seedling, sapling and young tree stage at age 3–8 years) of the target tree species was fully scored in six plots (mean radius of a plot was 230 cm). The plants were counted, measured (height, distance to the margin and centre of the plot), the genetic characteristics were specified for five enzyme systems, and the species affiliation of the nearest neighbour of each young tree within the plot was determined. If the distance from the nearest neighbour exceeded the distance from the plot circumference, the plant was excluded.

The five enzyme systems were: aspartate aminotransferases (AAT, E.C. 2.6.1.1), phosphoglucose isomerases

Table 1. – Number of trees characterized by stand, plot and species affiliation and the forest tree communities.

Stand	II	III	IV	IV	V	V	
Plot	1	1	1	2	1	2	Sum
<i>Acer pseudoplatanus</i> L.	190				71	78	339
<i>Betula pendula</i> Roth			26	30			56
<i>Fagus sylvatica</i> L.	36	261			8	45	350
<i>Picea abies</i> L.			70	127			197
<i>Pinus sylvestris</i> L.			14	11			25
<i>Tilia cordata</i> M.	15	79					94
<i>Fraxinus excelsior</i> L.	263				38		301
	504	340	110	168	117	123	1362
forest tree communities	Stellario-Carpinium stachyetosum	Galio odorati-Fagetum luzuletosum	Vaccinio-Piceetum	Vaccinio-Piceetum	Galio odorati-Fagetum luzuletosum	Galio odorati-Fagetum luzuletosum	

(PGI, E.C. 5.1.3.9), hexokinases (HEK, E.C. 2.7.1.1), malate dehydrogenases (MDH, E.C. 1.1.1.37), and isocitrate dehydrogenases (IDH, E.C. 1.1.1.42). In most cases, dormant buds were homogenized with a dithiothreitol-based buffer and these homogenates were separated by means of horizontal starch-gel zone electrophoresis using suitable buffer systems. The electrophoretic procedures used in this study for conifers were described by KONNERT and MAURER (1995) and those used for deciduous tree species were given by MÜLLER-STARCK and STARKE (1993). Some modifications of the staining recipes were adopted from Wendel and WEEDEN (1989).

In order to be able to detect differences among enzyme systems in genotype-species associations for different target species, each enzyme system had to be scored in each target species. Comparisons between species of a genetic trait defined across species, however, have to consider the fact that the determination of allelic states of the trait requires crosses, which can generally be performed only within species. Hence, the genetic trait cannot be compared between species for characteristics that involve allelic states (such as heterozygosity, see GREGORIUS et al., 2003; WEHENKEL et al., 2006). For this reason, the zymograms of our enzyme systems are simply considered as “genetic types” of a well-defined genetic trait without any reference to the (intraspecific) mode of inheritance of that trait. Thus, the numerical designations of isozyme types (such as AAT-1) refer to a particular zymogram (and not an allele).

Analysis of association

The way in which the genotypes of a target species co-occur with particular species in their nearest neighbourhood can be analyzed by considering these two characteristics as two traits of the members of the target species, and by computing measures of association. The standard measures of correlation and regression are, however, not applicable to our study, since it is based on quantitative rather than qualitative traits. For qualitative traits the measures of association developed by GREGORIUS (1998) are particularly suited. Given two traits α and β representing genotype and species affiliation of nearest neighbour, these measures are denoted by $A(\alpha|\beta)$. They can reach two extreme values, complete association of α with β (genotypes with neighbouring species), where $A(\alpha|\beta) = 1$, and complete absence of association of α with β , where $A(\alpha|\beta) = 0$. The wording “ α is associated with β ” can also be read as “ α depends on, is determined by, or is a function of β ”. Analogously to regression coefficients, the measures are basically unsymmetrical in the sense that $A(\alpha|\beta) \neq A(\beta|\alpha)$.

In the special case, where the association of genotypes (α) with species affiliation of nearest neighbour (β) is considered, the measure $A(\alpha|\beta)$ is based on the subdivision of the target species into subpopulations or groups each specified by one neighbouring species. Thus, the population of maples as target species would consist of a group with its own species as nearest neighbour, a group with beech as nearest neighbour and so on. Hence, the genetic structure of the whole population of the target species could be compared with that of several subpopu-

lations (or groups) characterized by different natural neighbourhoods. The average genetic difference of these subpopulations from the remaining members of the target species then quantifies the association $A(\alpha|\beta)$. In $A(\beta|\alpha)$ the roles of genotypes and species are simply reversed such that groups of species are defined by the genotypes of the target species.

Associations of the above kind may be the result of selective effects provoked by neighbouring species on the genetic structure of the target species or vice versa. Selective effects provoked by abiotic environmental conditions are unlikely to produce such associations. Particularly in small collections of individuals, random events may also result in associations. In order to detect non-random effects producing associations, we must consider sufficiently large collections in which independence of association between the genotypes of the target species and their neighbouring species is realized prior to selection. For this purpose plots of sufficient size were scored, in which all initially arriving species and genotypes had the same chance to occur as neighbours. This condition is fulfilled, since the ranges of seed dispersal of the investigated tree species exceed by far the chosen plot size. Since on larger scales equal chances of all associations cannot be guaranteed, random sampling of target tree individuals over the whole stand and determination of the species affiliation of their neighbours was discarded as a sampling strategy.

The sampling strategy suggests a permutation analysis for an assessment of the possibility that the observed associations may have resulted from random assignment of genotypes to the species affiliation of their nearest neighbour. Significance probabilities (p-values) are given in terms of the proportion of permutations for which the association measures exceed the observed value. On this basis, observed association values are to be interpreted as significantly large or significantly small if the pertinent significance probability is small (below 0.05) or high (above 0.95), respectively. In both cases, forces other than random have to be assumed to be involved in the generation of the observed associations. Differences in genotype frequencies between two groups of individuals (defined by the species affiliation of the nearest neighbour) are analyzed in the same manner, where the difference is measured using the index d_0 (GREGORIUS, 1974, see also GREGORIUS, 1998, equation 2a).

Results

In the context of a large-scale survey on species-genetic diversity relationships, the genetic structures of several tree species were determined in each of eight stands as well as in the whole population (WEHENKEL et al., 2006). In four of these stands the nearest neighbours of the three target species maple, beech and spruce were determined and each species was subdivided into different groups characterised by their specific neighbours. The genetic structure of these neighbour-specific tree groups of each target species was again examined (see Material and Methods for details) and these structures were then compared among the tree groups and the

whole population of each target species. The results of these comparisons are presented separately for each of the target tree species and isozyme systems.

Maple was the predominant species in two stands (*Table 1*) and its neighbours consisted of maple, beech and ash. Among the five variable isozyme systems assayed, only AAT and HEK showed remarkable differentiation among the maple groups defined by the species affiliation of the nearest neighbour. In stand V (plot 1) the maple groups differed markedly in multilocus AAT genotypes (zymograms) (*Fig. 1a*). Whereas

AAT-1 and AAT-2 were the most frequent types in the total maple population and the tree group with maple as nearest neighbour (maple-maple group), AAT-2 and AAT-3 were at a higher frequency in the maple-ash tree group. Only AAT-1 was the by far most frequent genotype in the maple-beech tree group. The genetic difference d_0 between the maple-maple and the maple-ash group as well as the difference between the maple-beech and maple-ash group produced significantly large values in the permutation test (with $p = 0.001$ and $p = 0.026$, respectively). In plot 2 of the same stand V some differ-

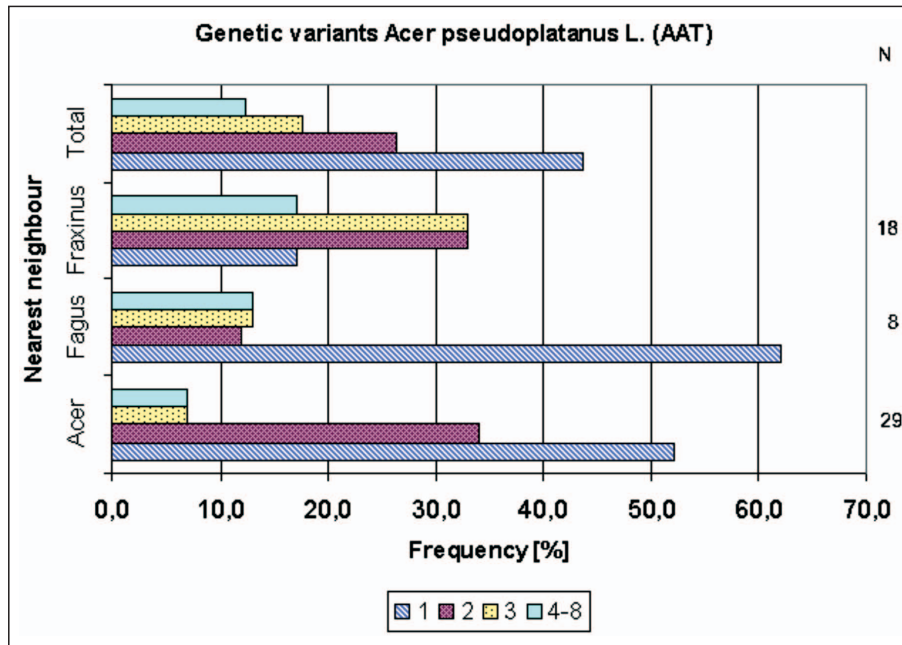


Figure 1a. – Histogram showing the AAT genotype frequencies in three groups of maple as target species: the maple-ash, the maple-beech, the maple-maple group, and the total maple population for comparison (stand V, plot 1) (frequencies of AAT-4 – AAT-8 $\leq 3\%$). The number of individuals in each group is given in the right column.

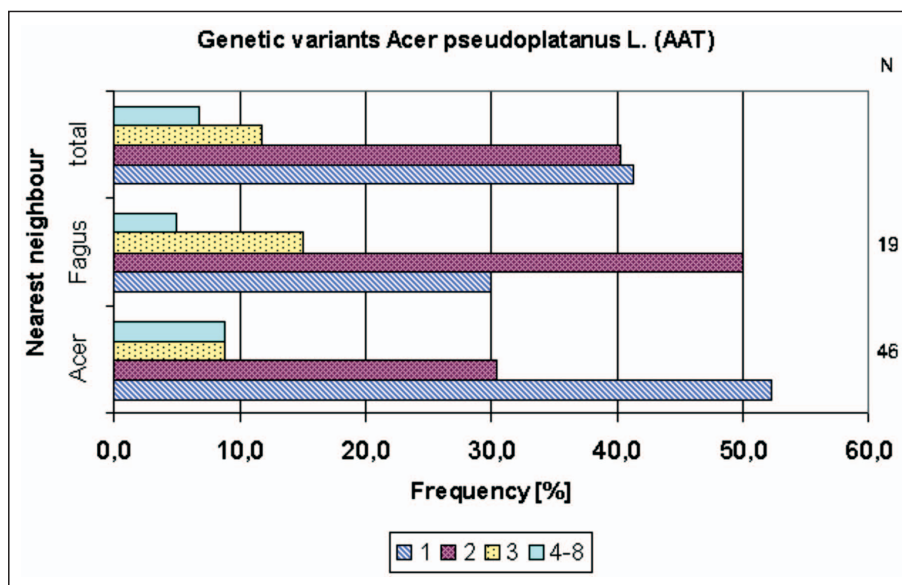


Figure 1b. – Histogram showing the AAT genotype frequencies in two groups of maple as target species: the maple-maple, the maple-beech group, and the total maple population for comparison (stand V, plot 2) (frequencies of AAT-4 – AAT-8 $\leq 3\%$). The number of individuals in each group is given in the right column.

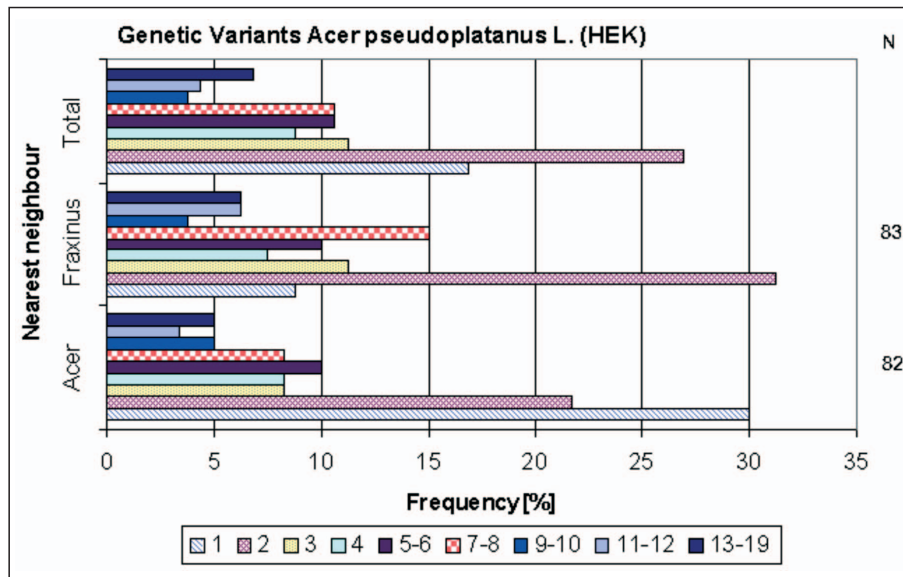


Figure 2. – Histogram showing the HEK genotype frequencies in two groups of maple as target species: the maple-ash, the maple-maple group, and the total maple population for comparison (stand II), frequencies of two or more rare HEK genotypes were pooled in five cases. The number of individuals in each group is given in the right column.

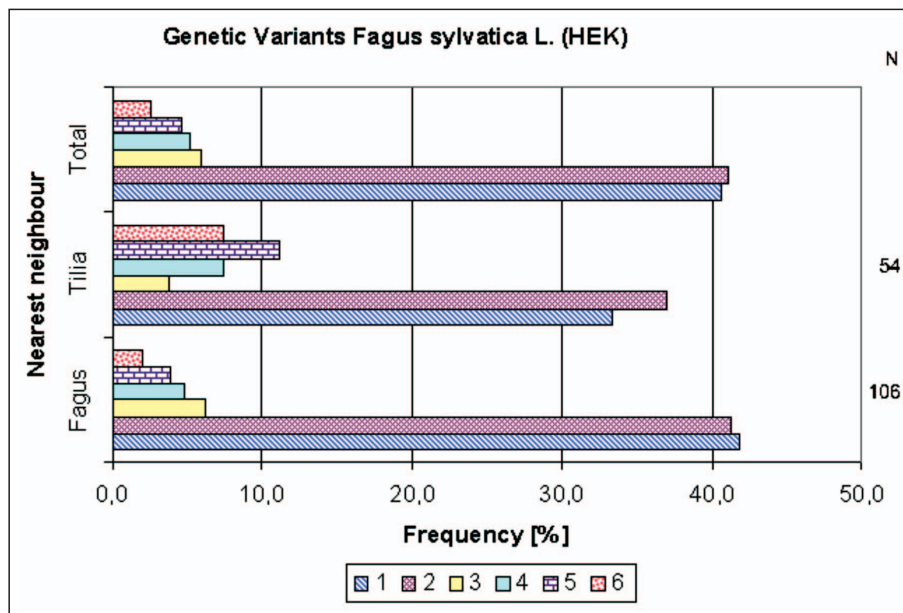


Figure 3. – Histogram showing the HEK genotype frequencies in two groups of beech as target species: the beech-linden, the beech-beech group, and the total beech population for comparison (stand III). The number of individuals in each group is given in the right column.

ences in the AAT genotype structure could only be observed between the maple-maple and the maple-beech tree groups (Fig. 1b). AAT-1 appeared as the most frequent type in the maple-maple group, but AAT-2 predominated in the maple-beech tree group. The respective values in the permutation test ($p = 0.075$ and $p = 0.081$) indicated non-random relationships between tree groups and neighbours near significance.

In stand II the maple-maple and the maple-ash tree groups differed in frequencies of the HEK patterns, which comprised nine genotypes (very rare genotypes

were pooled, e.g. HEK-9/10, HEK-13/19) (Fig. 2). The most frequent genotype HEK-1 in the maple-maple group (30%) occurred with 17% in the whole population but reached only 9% in the maple-ash group. On the other hand, HEK-2 (32%) and HEK-7/8 (15%) appeared to be the most frequent genotypes in the maple-ash tree group (Fig. 2). The d_0 difference between the maple-maple and the maple-ash tree groups is significantly large in the permutation test ($p = 0.041$). Some differences in the HEK patterns could also be established between the beech groups in stand III (Fig. 3). HEK-1

and HEK-2 were the most frequent genotypes in all three collections, however, the tree groups beech-beech and beech-linden showed some differences in the less common HEK types, although these differences were not significant.

Although the allelic composition underlying the isozyme patterns (phenotypes) observed in the members of a tree species could not be identified in this study, differences in these patterns among conspecific individuals must be attributed to at least one allelic substitution at one enzyme locus. Of course, such differences can also be based on allelic changes at several gene loci, if the isozyme patterns under study are encoded by two or more loci, as is the case for AAT in all conifers (see MEJNARTOWICZ and BERGMANN, 2003). Therefore, it is reasonable to conclude that the differences in the frequency of isozyme patterns, referred to as genotype differences, among the tree groups of one species are allelic differences, which may reflect at least differences in allele frequencies.

Associations

Associations were computed only for the isozyme systems HEK and AAT, which showed in several cases strong deviations from independent association with species affiliation of neighbouring trees. The following order of tables of associations does not conform to the above order of the figures on frequency comparisons, since now we had to combine the results of each of the two isozyme systems.

In the first case, the association of the HEK genotypes of maple as target species with its neighbouring species in stand II showed only a small value (*Table 2a*) compared to the reciprocal index A, the association of neighbouring species with the HEK genotypes of maple (*Table 2b*). The value of the latter association ($A = 0.282$) was by far greater than that of the former association ($A = 0.163$). It is further interesting to note that both neighbouring species, maple and ash, were to the same degree associated with HEK genotypes of maple. Based on the clear difference between the two types of association, it is suggested that the HEK genotypes of maple affected the species composition in their neighbourhood to a higher degree than species in the neighbourhood of maple determined their genotypic composition.

In the *Tables 3a* and *3b* the values of association between the HEK genotypes of beech and their neighbouring species beech and linden of stand III are listed. Again the association of the HEK genotypes with their neighbouring species showed a lower degree ($A = 0.084$) than the reciprocal association of adjacent species ($A = 0.146$ for beech and linden) with the HEK genotypes of beech. This supports the above conclusion about the dominating effect of HEK genotypes on their association with neighbouring species for completely different target and neighbouring species.

In correspondence to the AAT genotype comparisons among the different maple tree groups in each of two plots of stand V, the degree of association between maple genotypes and neighbours was also measured in

Table 2a. – Observed association values for A(Acer-HEK-Genotypes | Species) in stand II, p-value, and upper and lower 0.05 quantiles.

Species → Acer-Genotypes	Acer-Genotypes	p-value	upper 0.05 quantile	lower 0.05 quantile
Species	0.163	0.031	0.157	0.074

Table 2b. – Observed association values A (Species | Acer-HEK-Genotypes) for individual species (Acer and Fraxinus) with Acer genotypes as well as overall species with Acer genotypes in stand II. The p-value and the 0.05 quantiles are given only for the overall association of species with Acer-genotypes.

Acer-Genotypes → Species	Acer	Fraxinus	Species	p-value	upper 0.05 quantile	lower 0.05 quantile
Acer-Genotypes	0.282	0.282	0.282	0.041	0.277	0.133

Table 3a. – Observed association values for A(Fagus-HEK-Genotypes | Species) in stand III, p-value, and upper and lower 0.05 quantiles.

Species → Fagus-Genotypes	Fagus-Genotypes	p-value	upper 0.05 quantile	lower 0.05 quantile
Species	0.084	0.347	0.138	0.031

Table 3b. – Observed association values A (Species | Fagus-HEK-Genotypes) for individual species (Fagus and Tilia) with Fagus genotypes as well as overall species with Fagus genotypes in stand III, p-values, and 0.05 quantiles are given only for the overall association of species with Fagus-genotypes.

Fagus-Genotypes → Species	Fagus	Tilia	Species	p-value	upper 0.05 quantile	lower 0.05 quantile
Fagus-Genotypes	0.146	0.146	0.146	0.291	0.213	0.055

Table 4a. – Observed association values for A (Acer-AAT-Genotypes | Species) in stand V, p-value, and upper and lower 0.05 quantiles.

Species → Acer-Genotypes	Acer-Genotypes	p-value	upper 0.05 quantile	lower 0.05 quantile
Species	0.303	0.024	0.252	0.085

Table 4b. – Observed association values A(Species | Acer-AAT-Genotypes) for individual species (Acer, Fagus, and Fraxinus) with Acer genotypes as well as overall species with Acer genotypes in stand V, plot 1, p-values, and 0.05 quantiles are given only for the overall association of species with Acer-genotypes.

Acer-Genotypes → Species	Acer	Fagus	Fraxinus	Species	p-value	upper 0.05 quantile	lower 0.05 quantile
Acer-Genotypes	0.316	0.324	0.455	0.362	0.028	0.292	0.106

Table 4c. – Observed association values for A (Acer-AAT-Genotypes | Species) in stand V, p-value, and upper and lower 0.05 quantiles.

Species → Acer-Genotypes	Acer-Genotypes	p-value	upper 0.05 quantile	lower 0.05 quantile
Species	0.196	0.075	0.203	0.035

Table 4d. – Observed association values A (Species | Acer-AAT-Genotypes) for individual species (Acer and Fagus) with Acer genotypes as well as overall species with Acer genotypes in stand V, plot 2, p-values, and 0.05 quantiles are given only for the overall association of species with Acer-genotypes.

Acer-Genotypes → Species	Acer	Fagus	Species	p-value	upper 0.05 quantile	lower 0.05 quantile
Acer-Genotypes	0.309	0.309	0.309	0.081	0.333	0.054

each plot separately (*Tables 4a–d*). The association of the AAT genotypes of maple with their neighbouring species in plot 1 revealed a similar index value ($A = 0.303$) (*Table 4a*) as the association of the neighbouring species maple ($A = 0.316$) and beech ($A = 0.324$) with the AAT genotypes of the target species maple (*Table 4b*). Only the association of the neighbour ash with the maple AAT genotypes showed a somewhat higher value ($A = 0.455$). The small p-values indicated significance in all cases. In plot 2 of stand V the association of maple AAT genotypes with their neighbouring species (maple, beech) yielded only a value of $A = 0.196$ (*Table 4c*), whereas the association of the neighbours maple and

beech with the AAT genotypes of maple revealed by far higher index values (in both cases $A = 0.309$) (*Table 4d*). Although the p-values only approached the significance level, it can be suggested that the AAT genotypes of maple affected the species composition in their neighbourhood to a higher degree than vice-versa.

The association values between the AAT genotypes of the target species spruce and its neighbouring species spruce, birch and pine were relatively small in plot 1 of stand IV (*Tables 5a, 5b*). Since the p-values indicated no significance, it can be assumed that there was only a random neighbourhood between the different species

Table 5a. – Observed association values for A (Picea-AAT-Genotypes | Species) in stand IV, plot 1, p-value, and upper and lower 0.05 quantiles.

Species → Picea-Genotypes	Picea-Genotypes	p-value	upper 0.05 quantile	lower 0.05 quantile
Species	0.102	0.529	0.206	0.050

Table 5b. – Observed association values A (Species | Picea-AAT-Genotypes) for individual species (Picea, Betula, and Pinus) with Picea genotypes as well as overall species with Picea genotypes in stand IV, plot 1, p-values, and 0.05 quantiles are given only for the overall association of species with Picea-genotypes.

Picea-Genotypes → Species	Picea	Betula	Pinus	Species	p-value	upper 0.05 quantile	lower 0.05 quantile
Picea-Genotypes	0.167	0.164	0.264	0.171	0.242	0.316	0.061

Table 5c. – Observed association values for A (Picea-AAT-Genotypes | Species) in stand IV, plot 2, p-value, and upper and lower 0.05 quantiles.

Species → Picea-Genotypes	Picea-Genotypes	p-value	upper 0.05 quantile	lower 0.05 quantile
Species	0.036	0.571	0.102	0.023

Table 5d. – Observed association values A (Species | Picea-AAT-Genotypes) for individual species (Picea, Betula, and Pinus) with Picea genotypes as well as overall species with Picea genotypes in stand IV, plot 2, p-values, and 0.05 quantiles are given only for the overall association of species with Picea-genotypes.

Picea-Genotypes → Species	Picea	Betula	Pinus	Species	p-value	upper 0.05 quantile	lower 0.05 quantile
Picea-Genotypes	0.315	0.367	0.201	0.312	0.590	0.459	0.043

without any particular relationship. Although the index values of association between the same species were higher in plot 2 of stand IV (*Tables 5c, 5d*), the respective p-values again indicated no significant level. One reason for the inability to detect significant associations may be the low number of birch and pine individuals in these plots, which have led to only a little chance of yielding tree pairs.

Discussion

The long-term existence of plant communities composed of numerous species from different taxa would not be possible if strong competition, i.e. the total inhibition of individuals of one species by individuals of another species, would play a major role during the lifetime of the component species in a community. Rather the alternation between time-limited competition and positive interaction among members of different species will be the prerequisite for long-term coexistence (see GIGON, 1999). Some studies showed that particular genotypes (clones) from two plant species reveal positive interactions leading to continuing coexistence of such neighbouring plant pairs (AARSEN and TURKINGTON, 1985). These and other results (see BOOTH and GRIME, 2003) suggest that the development of such particular species coexistence requires at first some selection when individuals of different species met in the same location (or niche). This selection or interspecific competition then leads to stable neighbourhoods, if suitable partners (genotypes) evolve during the germination and first ontogenetic stages in the plant community. These genotypes may ecophysiologically interact in the sense that both will have benefits during their existence under stressful abiotic conditions (GIGON, 1999). Furthermore, it is concluded that the repeated interaction between individuals of two or more species in a plant community will lead to a co-evolution of such interacting species or competitors (TURKINGTON, 1989).

Although such plant-plant interactions involving specific genotype pairs might be expected to produce fine-scale genetic structures within the respective plant population, there have been no known attempts to search for and document such structures in forest tree species. In most cases the genetic structure (and variation) of

tree populations was determined by analysing many randomly sampled and widely-spaced individuals (for review and references, see BERG and HAMRICK, 1997). In a few studies on several tree species within the same stand, the genetic structure and diversity were assessed for each species separately without any attempt to relate these data to potential species interaction or coexistence (e.g. SHEA, 1990). In contrast to these traditional genetic surveys, the results of our study suggest that there is a local-scale genetic differentiation within single tree populations in several forest tree communities. This conclusion is based on genetic differences among tree groups of a species which are characterized by their particular neighbourhood with other tree species in a community.

The question now arises as to whether the different genotypes of the respective target species dictate the type of species (e.g. by selective competition) in their nearest neighbourhood or whether a species tolerates only particular genotypes of another (target) species as its local neighbours. A method to be used for answering these questions is the measurement of association between the genotypes of a target species and their neighbouring species. Based on the data computed for such associations in four forest stands, it could be shown that the HEK genotypes of maple as well as the HEK genotypes of beech determine their neighbouring species to a higher degree than vice-versa. In contrast to the HEK genotypes, the relationships between the AAT genotypes of maple and their neighbouring species are not as evident. Here the neighbourhood of particular species, as, for instance, ash adjacent to maple genotypes, may be responsible for the greater influence of these genotypes on their neighbours (*Table 4b*).

Besides the competition between individuals possibly due to different levels of height or rooting systems, the physiological function of the involved enzymes may also be important for specific biotic interactions between genotypes of the target species and individuals (genotypes) of particular neighbouring species. Since only AAT and HEK among five enzyme systems appeared to be involved in such interactions, it will be meaningful to briefly recapitulate their metabolic function in plants and to suggest their potential contribution to the mechanisms of competition or positive interaction. The other

three non-responsive enzyme systems seem to have no direct biochemical or physiological relationships to edaphic factors and, hence, were not involved in biotic interactions. AAT catalyses the reversible transamination between the amino acid aspartate and the keto acid ketoglutarate and this function is involved in different steps of both nitrogen and carbon metabolism (IRELAND and JOY, 1985). Therefore, it is conceivable that different neighbours of a target species like maple provide different nitrogen types or quantities in the common soil (by the aid of their mycorrhiza) available for the roots of the target species and that such different nitrogen types are optimally metabolized by different AAT variants. This would explain the influence of AAT genotypes of the target species maple on particular neighbouring species like beech or ash.

HEK represents the initial step in the oxidative phosphorylation of hexoses and is regarded as a regulatory enzyme controlling the flux into the glycolytic pathway (KRUGER, 1990). Stress factors in the soil and/or rhizosphere of plants can negatively affect this enzyme probably leading to differently functioning HEK variants which may regulate differently this most important pathway in the early ontogenetic stages of plants (seedlings) (see BERGMANN and MEJNARTOWICZ, 2001). Therefore, different HEK genotypes may possess different competitive abilities that govern the coexistence with neighbouring trees from only a few other species, so that these species are preferentially associated with particular HEK genotypes of maple or beech (Tables 2 and 3). On the other hand, it cannot be ruled out that genes or gene complexes closely linked to the AAT and HEK loci play major roles in the biotic interactions between the genotypes of the target species scored and the genotypes of the neighbouring species not scored in this study. In order to uncover such specific interactions, it will be necessary to investigate the genotype compositions of both individuals of such particular tree pairs frequently occurring in forest communities which are composed of various tree species.

Although we may only speculate about the causes of such biotic interactions, they clearly indicate that the occurrence of different tree species in a forest community is by far more than the mere addition of the single tree species. Rather, the association among different species appears to be a very complex network of co-adapted genotype groups across species, in the sense that intraspecific genetic variation lays the basis for interspecific adaptation. Moreover, it is argued that the maintenance of the intraspecific genetic diversity may, at least partly, result from the differential genotypic response to competition with other species (Vavrek 1998). On the other hand, it was found that a decrease in species diversity was lower in communities with higher within population genetic diversity (BOOTH and GRIME, 2003). Based on this result, it was suggested that the interaction between particular genotypes of different species in local neighbourhoods may be an essential mechanism for the composition of plant communities. Therefore, the present results may be considered as an explicit contribution to the emerging research field of community genetics (ANTONOVICS, 1992, 2003).

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Results of an International Provenance Trial of *Cordia alliodora* in São Paulo, Brazil at Five and 23 Years of Age

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Abstract

Cordia alliodora (Ruiz & Pav.) Oken (Boraginaceae) is a tropical timber tree of great economic value that occurs in Latin America and through most of the Caribbean. Genetic variation in growth, form and survival of eight Central America provenances – five from a dry zone and three from a wet zone – were studied five and 23 years after establishment in the state of São Paulo, Brazil. Significant differences between dry and wet zone provenances were detected for diameter at breast height (d.b.h.), stem form and survival and between provenances within these zones for height, d.b.h., volume and survival. Provenances from the dry zone had higher growth rates than those from the wet zone. Genetic correlations among ages for these traits were positive but not significant, while ranking of provenances based on growth and survival changed significantly from five to 23 years of age, indicating that measuring traits at five years of age may not be a good predictor of the same traits at 23 years of age. Genetic correlations on growth traits measured at the same age were large and significant, suggesting substantial gains could be made through indirect trait selection. At 23 years of age the La Fortuna provenance performed best for all traits, while Nueva Guinea performed worst for growth traits and survival and Tres Piedras for stem form. The species' poor growth compared to that of other

tropical tree species at the same experimental site suggests that *C. alliodora* is not the best silvicultural option for the Luiz Antonio region.

Key words: Tropical tree species, genetic structure, genetic correlations, tree improvement.

Introduction

Cordia alliodora (Ruiz & Pav.) Oken (Boraginaceae) is a well known timber tree in tropical zones of Latin America and most of the Caribbean (BOSHIER and MESÉN, 1987). It is a medium to large-sized, hermaphroditic, insect-pollinated, outcrossing tree with a widespread distribution from northern Mexico (25° N) through Central and South America as far south as Bolivia, southern Brazil, and northern Argentina (25° S) (CHASE *et al.*, 1995; BOSHIER *et al.*, 1995; BOSHIER and LAMB, 1997). Its precise range in southern South America is uncertain due to taxonomic confusion with the closely related *C. trichotoma* (Vell.) Arrab. Ex Steud. (GIBBS and TARODA, 1983). It is also found on most of the Caribbean Islands from Cuba to Trinidad but is probably not native to Jamaica (CHASE *et al.*, 1995). *C. alliodora* occurs under a wide variety of ecological conditions varying from very wet (as much as 6,000 mm rainfall per year) to seasonally dry (as low as 800 mm per year), and from sea level to as high as 1,400 m in Central America and 2,000 m at lower latitudes in Colombia (GREAVES and McCARTER, 1990). In lowland areas of moderate to high rainfall, trees can reach over 40 m in height and over 80 cm in diameter at breast height. In contrast, in dry regions trees are generally small (10–15 m in height) and of poor form (GREAVES and McCARTER, 1990; CHASE *et al.*, 1995). In general, the provenances

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