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16.1 Introduction, or "Why Do We Need Diversity Experiments with Trees?"

One way to assess the functional significance of biodiversity in forests would be to compare existing stands of contrasting diversity and to study ecosystem functioning and/or the provision of ecosystem goods and services in these stands (see contributions in this book). However, unless site conditions are extremely similar, across-habitat or across-locality comparisons can be misleading, because environmental differences between stands may hide potential within-habitat effects of differences in biodiversity on ecosystem processes in such sample surveys or comparative studies (Lawton et al. 1998; Schmid 2002; Vilá, Chap. 4, this Vol.). Almost all forests, particularly in Europe, have been managed for long time periods, so land-use history will certainly have long-term influences on both biodiversity and ecological processes (Mund and Schulze, Chap. 10, this Vol.). Thus, sample surveys or comparative studies can be used to document correlations between diversity and ecosystem processes, but they cannot be used to establish causality or underlying mechanisms of this relationship (Caspersen and Pacala 2001). Therefore, manipulative experiments, with random allocation of biodiversity treatments to plots while keeping environmental conditions as constant as possible, are needed to complement observational diversity-functioning studies. Such experimental approaches have successfully been applied during the last decade in the study of the interlinkages between biodiversity and ecosystem functioning of grasslands, and of terrestrial and aquatic microcosms (Kinzig et al. 2002; Loreau et al. 2002). In our view, an intriguing challenge will be the adoption of the basic principles and lessons learned from the design and interpretation of these small-scale and short-term experiments to long-lived forest communities.

As life cycles of tree species are in the order of decades or centuries, such experiments have to be planned with a long-term perspective. Such long-last-

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ing studies exceed normal funding periods, but are regularly demanded by scientific advisory bodies (e.g., WBGU 2000). However, experiences from silvicultural investigations show that the maintenance of such long-term experiments is generally possible.

In this chapter, we discuss the setup of long-term biodiversity experiments manipulating tree species diversity. We do not discuss general aspects of the design and interpretation of manipulative biodiversity–ecosystem functioning experiments; these have been discussed in depth elsewhere (e.g., Huston and McBride 2002; Schmid et al. 2002).

16.2 Experimental Approaches

In order to study the relation between tree diversity and ecosystem functioning, a gradient of species number ranging from single-species stands to multispecies mixtures is necessary. Alternatively, other aspects of diversity such as functional diversity or genetic diversity may be manipulated. In principle, such a gradient may be created by two different approaches. First, certain species may be removed from an already established natural or semi-natural multi-species forest stand (so-called "removal experiments"). The inverse case, i.e., "addition experiments", where species are added to an existing monoculture or low diversity stand, may not be feasible in mature stands, but would merit consideration in recently planted afforestations or natural regrowth in gaps or after clear-cut. Removal or addition experiments have some drawbacks (e.g., large disturbance effects, change in density, spatial segregation of species), but can be useful under certain circumstances (Freckleton and Watkinson 2000; Díaz et al. 2003). In the second approach, forest stands differing in tree diversity may be created by new planting, similar to the experiments with herbaceous species (e.g., Hector et al. 1999; Tilman et al. 2001). It may thus be called the "synthetic-community approach" - on which we will focus in this chapter.

16.2.1 Basics: Some Population Biological Rules to Be Considered in Plantation Experiments

There are several aspects specific to plants that should be considered in biodiversity experiments. In particular, plants as modular organisms grow continuously by adding new parts to their "body" and, therefore, individuals can vary greatly in size (Harper 1977; Hallé 1986). Indeed, an individual woody plant can itself be viewed as a population of twigs and branches. In most plantation experiments, stand or community dynamics are entirely due to processes at this within-plant population level: individuals increase or

decrease in size, they may die, but usually there is no new generation establishing itself from seeds. Two basic rules have been observed in such one-generation plantation experiments using single species. The constant-yield law (Kira et al. 1953) states that over a large range of planting densities the size of individuals is adjusted plastically in such a way that the total amount of biomass in the stand remains constant. If planting densities are very high, however, size plasticity cannot absorb all competition pressure and therefore some individuals die. This leads to an ordered process of size-dependent plant death described as the self-thinning rule (Yoda et al. 1963), in which, for each mortality-related reduction in density, the final yield of a stand increases by a greater amount than accounted for by the losses.

The constant-yield law and the self-thinning rule suggest that similar processes may occur in plant stands consisting of a mixture of species. It is therefore important that biodiversity experiments control for potentially confounding effects of density. This is most often done by holding total density constant and, instead of adding individuals of different species to a mixture, substituting a number of individuals of one species with the same number of individuals of another species (so-called substitutive experiments or replacement series, see e.g., de Wit 1960; Harper 1977). This approach assumes a null hypothesis of equivalence of individuals between species. If this assumption is not justified, a group of individuals or a patch of unit size may be used instead, although the term "total density" then loses some of its meaning for mixed stands. Similarly, the term "abundance" in a plant stand may sometimes be better defined in terms of cover or biomass than in terms of number of individuals, especially if these vary in size both between and within species.

16.2.2 The Use of Existing Experiments in Forestry

For a long time, foresters tried to understand the factors influencing the performance of forest stands (in terms of growth, timber yield, nutrient-use efficiency, or stability) using experimental plantations. However, different species have mostly been grown only in monocultures or two-species mixtures. Nevertheless, these experiments have yielded a wealth of information concerning the effects of species mixtures on ecosystem processes (Jones et al., Chap. 6, this Vol.). Because establishing a new forest diversity experiment is an expensive and time-consuming task, and is unlikely to provide many results during the first few years, and because environmental conditions are very variable, it may be appropriate to identify already existing experiments from forestry with similar goals and designs. Such existing experiments may complement the new ones, for example, by allowing comparisons of different stages of stand development at the same time, or by elucidating differences related to soil chemistry. Although forestry plantations were not planned from a biodiversity perspective, and only cover the very low end of the diversity gradient

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(usually one or two species), they may save some tests and treatments in new experiments, yield extra data, and promote cooperation between forestry and ecosystem science.

Suitable tools to find such experiments are databases on the Internet, which can be used to search for different tree species, mixtures, ages, objectives and geographical locations. Examples from Europe include the European Forest Ecosystem Research Network EFERN (http://ifff.boku.ac.at/efern/) and the Nordic Database for Long-Term Forest Experiments NOLT-FOX (http://noltfox.metla.fi/).

16.2.3 A New Generation of Biodiversity Experiments with Trees

Very recently, ecologists have begun to perform manipulative biodiversity experiments with multiple species of trees, similar to those in grasslands or aquatic ecosystems that exceed the range of species grown together in traditional silvicultural experiments. To our knowledge, there are only seven experiments of this type: two in Finland, two in Germany, two in Panama, and one in Borneo (Table 16.1). We do not consider here the experiment by Ewel and colleagues (Berish and Ewel 1988; Ewel et al. 1991), which was not designed to test diversity effects on ecosystem processes, but to explore the possibility of using natural succession as a model for sustainable, low-input agroecosystems for the humid tropics. However, the experiment was analyzed for its diversity effects by Vitousek and Hooper (1993), who pointed out that the results were consistent with an effect of biodiversity on biogeochemistry, but that they did not prove a relationship, mainly because all of the observed dynamics occurred in the transition between maize (planted as monoculture in the first two years) and highly diverse treatments consisting of more than 100 plant species.

16.2.3.1 The Boreal Tree Diversity Experiments in Finland

The Finnish tree species diversity experiment (coordination: Julia Koricheva) was established in spring 1999 on three clear-cut areas (about 1.5–2 ha each) located 20–30 km from each other in the Satakunta area, western Finland (61° N, 22° E). The sites are within the boreal coniferous forest belt, dominated by spruce, Scots pine, and birch. Each experimental area contains 38 plots randomly allocated to 19 treatments which represent monocultures and two-, three- and five-species combinations of five tree species (see Fig. 16.1, Table 16.1). Tree species used in the experiment include the locally dominating and economically important species for Finland (*Pinus sylvestris, Picea abies*, and *Betula pendula*), one nitrogen-fixing species (*Alnus glutinosa*), and one exotic conifer (*Larix sibirica*). Species mixtures are composed in such a



Fig. 16.1. Experimental layout at one of the three sites (Pomarkku) of the Finnish diversity experiment with boreal tree species

way that they represent a gradient from completely coniferous forest (pine, spruce, and larch) through mixed conifer/deciduous stands to deciduous ones (birch and alder). There are two replicates of each species mixture per area (six replicates altogether). Mixed plots contain the same number of saplings of each species; the positions of saplings of each species are randomized within plots.

Another experiment established in the Satakunta area in summer 2000 is aimed at studying the effects of within-species genetic diversity. It consists of an approximately 2-ha clear-cut area which contains 49 plots planted with micropropagated plantlets of eight clones of silver birch (Betula pendula). Plots are randomly allocated to the following treatments: single-clone stands, five different two-clone mixtures, five different four-clone mixtures, and eight-clone mixtures (Table 16.1). Each particular clone combination is replicated two to three times within the experimental area to allow the separation of effects of the number of clones, particular clone identity or mixture, and residual variation among plots of identical clone composition. Birch clones chosen for this experiment are of southern Finnish origin and are known to display different degrees of resistance to herbivores and pathogens. Clone combinations were selected on the basis of clone resistance, e.g., two-clone mixtures include either two susceptible clones, two resistant clones or one susceptible and one resistant clone. This design allows testing of the "associational resistance hypothesis," which predicts that susceptible plants growing in association with genetically or taxonomically diverse plants may gain benefits in terms of reduced herbivore or pathogen attacks (Andow 1991).

Table 16.1.	Main chara	cteristics of ϵ	existi	ng biodiver	sity ex	Table 16.1. Main characteristics of existing biodiversity experiments with trees	1 × 1 × 1 × 1	100		3 8 8
Biome	Country	Planting	No. of sites	Plot size	Total no. of plots	No. Plot size Total Diversity variables of no. sites of plots	Diversity gradients	Replica- tion ^a	Size of species pool	Tree-to- tree planting distance
Boreal	Finland	1999	3	0.04 ha	114	Species richness Number of functional groups	1, 2, 3, 5 Species Deciduous/coni- ferous vs. mixed	s, f, m	5	1.5 m
Boreal	Finland	2000	-	0.04 ha	49	Within-species genetic diversity of <i>Betula pendula</i>	1, 2, 4, 8 Clones	c, cm	8 Clones	2 m
Temperate Germany	Germany	2003/2004	2	1.2 ha 0.6 ha	40 16	Species richness Species richness	1, 2, 4, 6 Species 1, 2, 3, 4 Species	s, m ^b s, m ^b	6 4	2 m ^c 2 m ^c
Temperate Germany	Germany	2003	-	0.2 ha	25	Functional diversity (FD ^d)	Very low, low, high, very high FD	FD	16	2 m, 1 m ^e
Tropical	Panama	2001	Lintelli	0.2 ha	24	Species richness Identity of functional groups	1, 3, 6 Species Pioneer, shade- tolerant, intermediate	s, m ^b	9	3 m
Tropical	Panama	2003	1	0.03 ha	24	Species richness Assemblage identity	6, 9, 18 Species 4 Different assemblages	s, m	28	3 m
Tropical	Borneo	2002/2003	in the second	4.0 ha	124	Species richness Generic diversity (no. of genera) Tree height (short, medium, tall)	1, 4, 16 Species 2 vs. 4 Genera 2 vs. 3 Height classes	s, g, h s, g, h	16 16	10 m, 3 m ^f 10 m, 3 m ^f

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tures. g each level of generic diversity is replicated with different species mixtures. h each level of height diversity is replicated with different Given are the experimental factors that are replicated. s each level of species richness is replicated with different species mixtures, except the highest level. f each level of functional group richness is replicated with different species mixtures. m each particular species mixture (= individual species composition or assemblage) is replicated identically. c each level of clone diversity is replicated with different clone mixtures. cm each particular clone mixture (= individual clone composition) is replicated identically. FD each level of FD is replicated with different species mixspecies mixtures

^b Individual species mixtures are replicated only at the highest diversity level, but not at lower diversity levels

 $^\circ$ Distance between rows: 2 m; distance within row, depending on species (1.0, 1.5, or 2.0 m)

^d Based on FD approach by Petchey and Gaston (2002)

Distance between rows: 2 m; distance within rows: 1 m
 f Distance between rows: 10 m; distance within rows: 3 m

16.2.3.2 BIOTREE: BIOdiversity and Ecosystem Processes in Experimental TREE Stands

In Germany, two experiments with temperate tree species have been planned since 2000, and have now been established in close cooperation between the Max Planck Institute for Biogeochemistry and the State Forest Research Institution of Thuringia (coordination: Michael Scherer-Lorenzen and Ernst-Detlef Schulze). The planting of a total of 250,000 trees was started in spring 2003, covering a total area of approximately 80 ha, located at three sites (51° N, 11° E) with different geology (one acidic and two calcareous sites, see Table 16.1, Fig. 16.2). The natural vegetation would be beech-dominated forests with oak, the latter being in higher abundances at the drier calcareous site. Prior to planting, the sites were in agricultural use until the mid-twentieth century and then converted into mown and grazed grasslands.

Two different approaches have been used to establish a gradient in tree diversity. First, varying the number of tree species (BIOTREE-SPECIES), and



Fig. 16.2. Experimental layout at one of the three sites (Mehrstedt, calcareous) of the German diversity experiment BIOTREE with temperate tree species. Ecosystem C fluxes will be measured by eddy covariance over the plantation

second, varying the functional diversity within four-species mixtures (BIOTREE-FD). Within BIOTREE-SPECIES, all possible species combinations at four diversity levels (one, two, three, four species at the acidic site, and one, two, four, six species at the calcareous site, respectively) are grown, which enables the following hypotheses to be tested: (1) that random species loss matters for ecosystem functioning, (2) that particular species affect ecosystem functioning, and (3) that there is a minimum set of complementary species that is sufficient to explain diversity effects (Spaèkova and Lepš 2001; Loreau et al. 2002; Schmid et al. 2002). Similar to the Panama experiment, the diversity levels are replicated with different species mixtures, while replications of the specific mixture are only done at the highest diversity level. Besides the manipulation of tree species richness, the impact of silvicultural management and the addition of rare species are considered, using a splitplot design with three treatments: unmanaged ("U"), managed according to prevalent silvicultural practices ("M"), and managed with additional species ("M+"; Fig. 16.3). The comparison between unmanaged and managed subplots will help to solve the debate about whether diversity effects might be obscured by silvicultural practice (Mund and Schulze, Chap. 10, this Vol.). The inclusion of subplot "M+" allows the testing of the additional hypothesis that the deletion of subdominant or rare species is irrelevant for ecosystem functioning (Walker et al. 1999). Species have been planted in a random checkerboard pattern of 64 m² patches for each species (Fig. 16.3), thus minimizing



Fig. 16.3. Within-plot design of the BIOTREE-SPECIES experiment in Germany, shown for a four-species mixture as an example. Different *gray scales* represent different species, different *letters* represent different subdominant species. Each single patch has an area of 8×8 m and was planted in rows with 2 m row-to-row distance. *M*+ Managed with addition of subdominant species, *M* managed, *U* unmanaged

species loss due to interspecific competition at an early stage of establishment. This should also prevent dominance of species with particular traits (at least during the first decades until species start to regenerate), which reduces the possibility that "selection effects" (sensu Loreau and Hector 2001) may occur.

In contrast to BIOTREE-SPECIES, the diversity gradient in the BIOTREE-FD experiment has not been established by manipulating the number of species, but by mixing species with different functional attributes. Based on the "FD"-approach by Petchey and Gaston (2002), the functional diversity (FD) of all 1,820 possible four-species mixtures from a pool of 16 tree species was calculated. The trait matrix contained nine criteria for which data for all species were available. The criteria selected represent attributes which are indicative for complementary resource use and nutrient cycling, the two main functions of interest of this experiment. Six mixtures were randomly selected out of four groups, representing "very low" (i.e., a mixture of functionally very similar species), "low", "high", and "very high" (i.e., a mixture of functionally very different species) functional diversity (Table 16.1).

16.2.3.3 The Forest Biodiversity Experiments of Panama

The Forest Biodiversity Experiment of Panama (coordination: Catherine Potvin) was specifically designed to test how increases in tree species richness might affect the cycling and storing of carbon (C). The native tropical semi-deciduous lowland forest at the experimental site 55 km north of Panama City (9° N, 79° W) was logged in 1952/1953. The area was used for agriculture for 2 years and then converted into pasture by seeding grasses.

An area of 9 ha was planted with six native tree species: two pioneer (Luehea seemanii and Cordia alliodora), two light-intermediate (Anacardium excelsum and Hura crepitans), and two shade-tolerant species (Cedrela odorata and Tabebuia rosea). Functional groups were classified based on relative growth rates (9.1 and 7.0 %; 5.9 and 4.9 %; 2.3 and 3.4 %, respectively) and on frequency of encounter in gaps or closed forests of the 50-ha permanent plot of Barro Colorado Island (BCI). Twenty-four diversity plots were established with either one, three, or six species (Fig. 16.4, Table 16.1). The design allows testing for the effect of species richness without confounding it with species identity. It also controls the effect of certain functional groups, but the number of functional groups is not varied. Thus, using the monoculture plots, one can test for a functional-group effect but cannot test the relation between functional diversity and ecosystem functioning. The basic analysis of the variance (ANOVA) model compares six monocultures, six triplets and six sixspecies plots. In this model, the type of replication differs among diversity levels, i.e., the triplets differ in species composition while the six-species plots do not (Table 16.1). This might potentially lead to violation of the homogeneity-

Fig, 16.4. Experimental layout of the main plantation in the Forest Biodiversity Experiment of Panama with tropi-F F Pasture cal tree species. Ecosystem C fluxes will be measured by eddy covariance over A D the plantation and over an adjacent pasture. The letters represents different C C species grown in monoculture Е D 1 species В 3 species

6 species

Eddy-towers

E

A

В

45m

of-variance assumption. If needed, corrections, e.g., those developed by Dutilleul and Potvin (1995) in the context of genotype-by-environment analysis, will be applied.

The results of BIODEPTH and other grassland experiments suggested that the diversity-by-function relationship might be asymptotic (e.g., Hector et al. 1999; Tilman et al. 2001). Thus, the main experiment in Panama was set up with plots of one, three and six species. We hypothesized that these three levels of species richness would be within the linear portion of the diversityecosystem functioning relationship. This design however leaves two questions unanswered: (1) is the high diversity treatment relevant to the natural level of tree diversity in the forest? (2) What is the importance of community composition at high diversity? Another experiment was therefore set up in July 2003 in which high-diversity plots, comparable to the diversity of natural forests, were established (Table 16.1). The aim of this second experiment was to study the asymptotic portion of the diversity vs. functioning relationship. In addition, the plantation specifically accounts for environmental heterogeneity by embedding replicated blocks in the landscape. Eight different blocks, containing three plots of 36 saplings, were planted on either steep slopes or flatter landscape. The blocks correspond to four different species assemblages, each replicated on steep and flat landscapes. The idea of multiple experiments at one site could be a practical way to address more than one question while remaining in budget.

The Panama Forest Biodiversity Experiment provides preliminary data allowing examination of the adequacy of the experimental approach. Six months after planting, basal diameter, representing secondary growth (Kohyama and Hotta 1990), was measured for each individual planted seedling. Two different nested ANOVAs were used to test for the effect of (1) species richness and (2) species identity on seedlings' diameter. In both ANOVAs, plots were nested under the main effect of interest (six plots per level for species richness and two plots per level for species identity). Accordingly, the mean square (MS) for plots was used as the MS error for either species richness or species identity. The ANOVAs indicated that species identity exerted a significant effect on mean diameter ($F_{4,5}$ =7.05, P<0.05), and that the effect of species richness was nearly, but not quite, statistically significant ($F_{2,15}$ =2.53, P<0.08). The six species differed significantly from each other, the largest one being *Tabebuia rosea* (13.7±5.2 cm), while the smallest was *Luehea seemanii* (6.9±3.8 cm). Although the difference was not statistically significant, seedlings tended to be smallest in the monoculture plots and largest in the triplets (9.6±5.1 cm for monocultures and 13.5±8.5 cm for triplets).

Several authors suggested that productivity may increase with diversity because of trait complementarity among species (e.g., Hector et al. 1999; Tilman et al. 2001). The observation that seedlings planted in the monoculture tended to be the smallest supports that hypothesis. We anticipate that, with time, the effect of species richness on seedling growth and plot productivity will become stronger and clearer as saplings begin to compete for light and nutrients.

16.2.3.4 The Sabah Tropical Forest Biodiversity Experiment, Malaysian Borneo

The southeast Asian dipterocarp forests are some of the most diverse on earth, and are also the most productive tropical forests in terms of timber yield. Because large areas have been lost through logging, replanting schemes have been developed that aim to provide future logging timber, and to offset industrial C emissions. These plantations generally consist of monocultures or mixtures much lower in species diversity than natural forests. However, the availability of seedlings from a wide variety of species means that replanting could also be conducted at levels closer to natural diversity. The aim of the Sabah Forest Biodiversity Experiment (Sabah is the eastern state of Malaysian Borneo) is to compare community and ecosystem processes in replanted plots of low and high tree diversity (Holden 2003). The experiment (coordination: Andy Hector and Charles Godfray) is a collaboration between the NERC Centre for Population Biology at Imperial College, The Royal Society's research station in Danum Valley, Sabah, and the Innoprise Corporation (carbon offset, timber replanting, and forestry).

The native dipterocarp forest at the site (5° N, 118° W) had been logged in the early 1990s and then left unmanaged until replanting started in



Fig. 16.5. Experimental layout of the Sabah Forest Biodiversity Experiment with tropical tree species

2002/2003. The total area of the experiment is approximately 500 ha (Fig. 16.5). Sixteen species were available for the experiment and these are being grown alone and all together to provide the two possible extremes of diversity along with a number of intermediate four-species mixtures (total of 96 plots, see Table 16.1). The 16 four-species treatments are a factorial design that separates the effects of generic diversity (2 vs. 4) from canopy thickness (combinations of short, medium, plus tall species versus less varied combinations of only tall plus medium or short plus medium). In addition, 12 plots were left as uncut and unplanted controls. A further 16 plots were planted with the 16-species mixture, but will receive reduced climber cutting once the trees are established – to address this usual management option. Finally, in the center of each plot, two replicate seedlings of each of the species were planted to compare levels of herbivory and mortality of the 16 dipterocarps in the different background communities provided by the experimental plots.

16.3 Methodological and Design Considerations

There are numerous difficulties in designing, executing, and interpreting manipulative diversity experiments (Lamont 1995; Huston 1997; Allison 1999; Huston and McBride 2002; Mikola et al. 2002; Schmid et al. 2002), and different designs may yield different answers to the same research question. Obviously, there cannot be one single optimal design for an experiment to analyze

the relation between tree species diversity and ecosystem functioning, and/or the provision of goods and services. Even if the aim of the study is defined in such a broad way, the functions or response variables of interest may be quite distinct, requiring different designs. For instance, if the aim of the project is more applied (e.g., to provide recommendations for forest management strategies), the design should be based more closely on current forestry practices. In contrast, if the main interest is on the effects of species numbers the inclusion of certain mixtures that would never be planted by foresters because they are of no economic value becomes more important, as done in the BIOTREE experiment, for example. Additionally, logistic constraints and limitations of resources very often prevent the adoption of an appropriate design so that pragmatic compromises have to be chosen. Below we discuss some factors which may affect the experimental design of forest diversity experiments.

16.3.1 Environmental Heterogeneity

In order to exclude confounding influences of environmental variables, abiotic factors within the field site should be as homogeneous as possible. For example, small variations in soil conditions can have large effects on growth of trees (Oliver and Larson 1996), which introduces the possibility that soil heterogeneity can act as a "hidden treatment" (Huston and McBride 2002). On the other hand, one important effect of biodiversity may be to allow efficient exploitation of a heterogeneous habitat. Because environmental heterogeneity is presumably the rule rather than the exception in forest ecosystems, and because it will frequently be in large part due to the big areas required for replicated experiments, tree diversity experiments may be well suited for testing this potential biodiversity effect.

Obviously, environmental heterogeneity can be dealt with *a posteriori* and measured environmental properties can be used as covariates in the analyses. Another possibility is to account for it at the planning stage by blocking. Randomized block and Latin square designs have been shown to be an efficient means of controlling and accounting for environmental heterogeneity or gradients (Potvin 2001). However, because simple randomization of treatments in space may not be sufficient to "equal out" this heterogeneity, without the number of replicates becoming prohibitively large, the spatial arrangement of plots in forest diversity experiments should be considered carefully. Furthermore, any analysis of data obtained from these experiments should include a "geographical" model, in which spatial information and neighbor-relationships between plots are included as additional explanatory variables (see, e.g., Ford and Renshaw 1984; Kempton and Lockwood 1984; Schmid et al. 2002).

The Panama forest diversity experiment provides an example of the possible importance of the environment on seedling growth. Over the whole land-

scape, topography, drainage, facing, height and density, and diversity of herbaceous vegetation were scored on an ordinal scale. Additionally, soil color was rated, based on Munsell soil color chart classifications (Munsell Colour 1990). To provide an adequate scale for measuring these micro-environmental characteristics, each diversity plot was divided into four sub-plots. Redundancy analysis (RDA) indicates that 86.3 % of the species-environment variance in height can be explained by the first canonical axis (F=17.154, P<0.001). RDA for diameter similarly shows that 82.4 % of the variance is explained by the first canonical axis (F=15.499, P<0.001). The environmental characteristics that correlate most strongly with the first canonical axis for both variables are topography and density of herbaceous vegetation. The inter-set correlations (topography, density) are -0.4241 and +0.3385 for height and -0.3811 and +0.3292 for diameter. The biplots for diameter (Fig. 16.6) and height reveal an almost identical distribution of species, suggesting that in the first year, primary and secondary growth responded in the



Fig. 16.6. Redundancy analysis (RDA) biplots for the species-environment variance in diameter with species scores positioned with regard to the first two canonical axes. Species abbreviations are as follows: (*Ls*) Luehea seemanii, (*Ca*) Cordia alliodora, (*Ae*) Anacardium excelsum, (*Hc*) Hura crepitans, (*Co*) Cedrela odorata, and (*Tr*) Tabebuia rosea

same way to environmental characteristics. They also reveal that all six species grow taller on the top of a hill than in depressions. Growth also has a positive correlation with areas of dense herbaceous vegetation. Herbaceous vegetation in contrast appeared to correlate mainly to soil color (inter-set correlation with first axis -0.4694) and litter accumulation (inter-set correlation with second canonical axis 0.4685). The cumulative percentage variance of species–environment relation explained by the two first canonical axes was 89.6%.

These results suggest that in theory plots could have been established as blocks positioned differently in the landscape (hilltop, slope, depression). In practice, however, this was not possible because a sloped terrain offers unequal surface area of the three topographies, preventing the establishment of an equal number of plots for each topography.

Within-site heterogeneity is not the only factor to be considered. Variability of environmental conditions across larger areas must be included too. For instance, the outcome of species interactions critically depends on soil fertility. A nitrogen-fixing species in a mixture usually improves growth of other tree species on poor soils but may result in increased competition on rich ones (Binkley 1992). Therefore, it is important for the experiment to be replicated at several sites differing in geology, soil type or climate, as done in the Finnish and German experiments. Interestingly, within the BIODEPTH project it was shown for grasslands that, besides strong differences in environmental conditions – a general diversity – productivity relationship could be detected across eight sites (Hector et al. 1999).

16.3.2 Unit of Diversity

The term biodiversity encompasses several levels of biological variability, from genes to species and ecosystems (Heywood and Watson 1995). It is therefore necessary to define the term for the purpose of the study. For manipulative experiments with trees, one has to decide whether genotypes, species or some sort of functional type (groups of species with contrasting effects on ecosystem functioning) should be the basic unit of diversity. Most of the previous and existing forest experiments manipulated tree species richness. There is growing consensus, however, that any biodiversity effects on ecosystem functioning will arise from phenotypic variation between species, i.e., from their functional traits or from species' interactions (Loreau 2000), and even within species, i.e., from their age and stage classes or ecotypes (Schmid et al. 2002). Effects of species (or phenotypic variants within species) will thus be related to the size of their functional differences (Petchey and Gaston 2002), and the use of functional types instead of, or in addition to, species might be appropriate for many studies (Díaz and Cabido 2001; Hooper et al. 2002). However, grouping always reflects functional differences of a par-

ticular kind, and if several functional dimensions are combined, one often arrives at as many groups as there are species or phenotypic variants (Körner 1993; Smith et al. 1997; Wirth, Chap. 15, this Vol.).

In addition, because of the large plot sizes required for forest experiments, manipulations of both species number and functional diversity may not be feasible in a single experiment (but see examples in Table 16.1). Nevertheless, functional characteristics of individual species have to be considered when choosing the species for an experiment because they may affect the outcome of species interactions in mixtures. For instance, complementarity in resource use is more likely to be observed in mixtures of species that are using resources in different ways (e.g., between deciduous and evergreen species or between deep- and shallow-rooted species) than among species with similar requirements. Certain functional characteristics of tree species may even put constraints on the experimental design. For instance, it might be impossible to grow monocultures of late successional species on a clear-cut area because the species may only establish under a canopy of pioneers. Similarly, some species mixtures are unlikely to be maintained without human interference in the form of thinning, trimming, etc.

While functional characteristics of most native boreal and temperate species are well known, and the outcomes of interactions between these species may be to some extent predictable, ecological consequences of an introduction of an exotic tree species are more difficult to foresee (Engelmark et al. 2001; Peterken 2001). Therefore, some of the new forest diversity experiments include exotic tree species such as Siberian larch in Finland and Douglas fir in Germany, making it possible to assess interactions between native and introduced tree species.

Experiments manipulating genetic diversity within tree species have been rare, probably because within-species variation in functional characteristics, which may affect ecosystem functioning, is considered to be less than between-species differences. Yet, genetic diversity is the basis of all biodiversity, because it provides raw material for the adaptation, evolution and survival of species and individuals, especially under changing environment and disease conditions. Forest management practices, including tree improvement, can significantly affect the genetic variability of forest plantations (Gomory 1992; Rajora 1999). Several recent studies in Europe suggest that reduction in genetic diversity predisposes forests to an environmentallyrelated decline in health and productivity (Bergmann et al. 1990; Oleksyn et al. 1994; Raddi et al. 1994; Müller-Starck, Chap. 5, this Vol.) and to attacks by pests and pathogens (McCracken and Dawson 1998). Thus, genetic diversity is the foundation for forest sustainability and ecosystem stability. An experiment recently started in Finland (see Sect. 16.2.3, Table 16.1) specifically addresses the importance of within-species genetic variation in stand susceptibility to herbivores and pathogens by manipulating the number of silver birch clones per plot. In the BIOTREE experiment in Germany, the effects of high versus reduced genetic variation will be addressed by adding subplots at the one-species level planted with single clones or individuals derived from the same parent tree.

16.3.3 Diversity Gradient and Creation of Mixtures

The decision on the appropriate diversity gradient depends very much on the general aim of the study. If feasible, the gradient should range from single species stands to a certain maximum diversity mixture that could mimic either the diversity of natural or managed forest, or multi-species plantations of practical relevance.

Including monocultures of all species allows the comparison of the performance of mixtures vs. pure stands and the separation of selection versus complementarity effects. However, as discussed by Schmid et al. (2002), there are alternatives available to test for selection effects. In addition, having all monocultures or low-diversity mixtures of a restricted species pool also has some drawbacks, such as the restriction of random sampling of different species combinations at high diversity levels or the variance reduction effect (Huston 1997; Schmid et al. 2002). This implies the use of different communities at high diversity levels or repeating an entire design with several species pools.

From a practical point of view, one should ask what the "appropriate" background diversity level is in highly diverse systems. In the grassland BIODEPTH experiment, for example, the various sites used best estimates of natural "background" diversity as their reference point for determining the highest diversity level (Hector et al. 1999, 2002). In Panama, the 50-ha permanent forest plot on the island of Barro Colorado (BCI), near the tree diversity experiment, contains 177 tree species with diameter at breast height (dbh) larger than 20 cm. At a smaller scale in the forest, however, diversity is reduced (Palmer et al. 2000) because of the clustered distribution of species (Thorington et al. 1991). Thus we suggest that the appropriate background level of diversity to establish high diversity plots should be obtained from forest plots of equal size as the reforestation ones. In Panama, for example, preliminary work on BCI shows that, on average, a forest plot of 45×45 m has 19 different tree species of dbh >20 cm.

However, practical difficulties will complicate the design of tree diversity experiments in species-rich regions. First, most of the species are rare and therefore obtaining seeds is seldom possible except for those of the most common species. Once seeds have been obtained, and in contrast with the wellestablished forestry practices of northern countries such as Finland and Germany, germination protocols have to be developed. Even if seedlings are successfully germinated, establishment in the field is far from guaranteed. In Panama, the PRORENA project, which develops reforestation protocols for

native trees, has been able to establish reforestation plots successfully with 40 species (www.prorena.org). We therefore believe that the maximum species number available for planting high tree-diversity plots will be limited by the existing knowledge in tropical forestry practices.

If the species pool is small (as in the experiments in Finland and Germany), a complete design with the planting of all possible species mixtures may be feasible (e.g., a pool of six species and one-, two-, four- and six-species mixtures: 37 possible combinations), which minimizes problems associated with the use of random-selection experiments (Huston and McBride 2002; Schmid et al. 2002; Schmid and Pfisterer 2003). With large species pools, as in the tropical systems, either a random selection of mixtures or a specific extinction or planting scenario may be used to create the gradient of diversity.

As an alternative, one could combine both approaches as in the Panamaexperiment, planting a complete design with a small number of species plus some high-species-diversity plots (see Sect. 16.2.3.3; Table 16.1).

16.3.4 Plot Size

The appropriate size of the plots certainly will very much depend on the aim of the study. For example, if one is mainly interested in decomposition rates and effects on soil quality, plots smaller than 1 ha would probably be sufficient. However, if one wants to know how forest diversity affects diversity of birds, mammals, insects, etc., or if silvicultural management is to be performed, larger plots are required. In most cases, one will face a trade-off between size and number of plots due to the available field size. In attempting to solve this dilemma, the main factors influencing the ecosystem processes and characteristics of interest should be kept in mind. For instance, the influence of neighboring stands on soil chemistry of a target plot due to litter input can easily reach distances of several tens of meters (Rothe and Binkley 2001). This is dependent on the neighboring species (e.g., litter of broad-leaved species may be blown farther than needle litter), the main wind direction, and the presence of a closed forest edge that acts as a windbreaker. Thus, a checkerboard design with plots of say 20×20 m might even be too small to study effects on decomposition and soil chemistry.

The optimal plot would be large enough for a typical interior forest microclimate to develop, which for most forest types will certainly be larger than 1 ha, as edge zones with altered physical conditions may be up to two to three tree heights (e.g., Chen et al. 1995). Principles of conservation biology suggest that patches of 10 or even 100 ha may contain no true interior forest habitat. Because such large areas are never likely to be available for a replicated experiment, and would also exceed any reasonable level of financial and labor resources, one has to go for a pragmatic selection of plot sizes. As a rule of thumb we would recommend the use of double the height of the final tree height as side length of a plot, corresponding to a size of 0.5–1.0 ha, while recognizing that this size is still difficult to obtain and to manage. Given a replication of 20–40 plots, the whole experimental area would then be a size that also allows for the development of a typical forest microclimate.

16.3.5 Within-Plot Design: Spatial Arrangements

In most grassland biodiversity-functioning experiments that adopted the "synthetic community approach", plant mixtures were sown in bare soil. As a result of sowing, the spatial distribution of species within a plot initially is more or less homogeneous (random at the smallest scales - at least at initial sowing), and the identity of neighbors cannot be controlled. Nevertheless, the spatial pattern of mixed-species stands can influence community variables such as biomass in experiments with herbaceous species (Harper 1977; Schmid and Harper 1985; Stoll and Prati 2001). In particular, regular arrangements may lead to more rapid suppression of competitively inferior species by superior ones than random arrangements, and even more so than clumped ones. This is because regular arrangements maximize the frequency of interspecific neighbor relationships. Because trees are usually planted, it is possible to choose a spatial distribution of species and of individuals within a plot that yields a particular frequency (number of neighbors) and intensity (distance to neighbors) of neighbor relationships. This enables a plant-to-plant view in adopting techniques for neighborhood analyses (see e.g. Stoll et al. 1994).

In principle, within a plot, individuals could be arranged at random, in a regular manner, or in clumped patches (Fig. 16.7, upper part). For practical reasons, one would mostly adopt a regular planting scheme, which also mimics silvicultural practice for even-aged afforestations. Within such a pattern, the spatial distribution of different species may also be at random (as in the experiments in Finland and Borneo), in regular intervals (as in the Panama experiment), or in clumps (as in the BIOTREE experiment, Fig. 16.7, lower part). However, random placement of large numbers of seedlings may generate a wide range of spatial patterns within the plots. Finally, within a planting scheme in rows, the tree-to-tree distance between all neighbors could either be the same (hexagonal planting), or it could differ (quadratic planting, as shown in Fig. 16.7). The former is preferable for studying species interactions (Kelty and Cameron 1995; Gibson et al. 1999), whereas the latter is commonly used in silviculture.

The decision as to whether to plant in an aggregated pattern or not mainly depends on the expected duration of the experiment. Clumping is an effective way to prevent species loss due to interspecific competition at an early stage of the experiment, and to ensure the maintenance of the initial diversity gradient over long time intervals in terms both of species numbers and area occu-



Fig. 16.7: Spatial distribution of individual trees within a plot. For manipulative diversity experiments adopting the "synthetic community approach," individuals will mainly be planted in a regular pattern (*upper part, center*). Within such a regular pattern, the distribution of different species can follow random, regular, or aggregated patterns (*lower part*), as shown for a two-species mixture here

pied by species. In contrast, if the expected duration of the experiment is short, a random or even a regular planting of each species might be preferable because this allow early interspecific interactions. However, strong competitors may outcompete inferior species, thus leading to changes in species composition. Such "species takeover" is surely less probable in tree than in grassland experiments, although fast-growing, clonal species like aspen or alder in boreal sites, for instance, may quickly outcompete neighboring species unless management interventions such as weeding or thinning are adopted (see Sect. 16.3.6).

In summary, we expect that the spatial distribution of species within a plot strongly affects ecosystem processes through alteration of competitive interactions (Pacala and Deutschman 1995; Stoll and Prati 2001). It would thus also be of interest for the outcome of the diversity-functioning relationship to test

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this assumption experimentally by comparing different spatial planting schemes.

16.3.6 Management Options

It is important to consider the maintenance strategy when designing largescale experiments with trees. Usually, some sort of management has to be applied to ensure the establishment and maintenance of the communities. However, should the experiment mimic current silvicultural practices, or should management interventions be restricted to a minimal level? In most cases, site-specific trade-offs between requirements of science and of practice will have to be solved in pragmatic ways. Some examples should illustrate this:

- Weeding: If the experiment is to mimic natural forests, one should not weed. On the other hand, if the aim is to examine effects of a particular species loss on ecosystem functioning, the presence of this species as a weed on plots where it should not occur may spoil the whole experiment.
- Mowing: If the aim is to study successional dynamics after planting, it
 would be inappropriate to mow the understory. However, initial mowing
 will usually be necessary to reduce competition by grasses or herbs and to
 ensure successful tree establishment. Decisions concerning mowing could
 also have unforeseen side effects: in the Panama experiment, for instance,
 unmown plots were quickly infested by venomous snakes.
- Fencing: The need for this will relate to the density of mammalian herbivores in the experimental area. If it is so high that without fencing the experiment (or some parts of it) would be eliminated within a short time, one certainly should fence. On the other hand, if a very promising tree mixture (in terms of productivity, ecosystem processes, biodiversity maintenance, etc.) is identified in a fenced experiment, it may turn out that this mixture would not exist without a fence because it is much more susceptible to herbivores than other mixtures.
- Fertilization, fumigation: Given the financial investment needed to establish such experiments, tree survivorship should be maximized, at least in the first years. Thus, initial fertilization after planting must be carefully considered, as well as spot treatments with insecticides (in the tropics) or rodenticides (in temperate or boreal zones) if needed. However, since such treatments may also affect ecological processes at a later stage, they must be applied at an absolute minimum.
- Replacement: Judging whether tree mortality at an early stage should be regarded as a "valid" biodiversity effect (e.g., herbivores could be more attracted to high-diversity mixtures, see Jactel et al., Chap. 12, this Vol.), or as a danger for the success of the whole experiment might sometimes be difficult. Again, pragmatic choices depending on the site-specific situation will be necessary.

- Thinning: Requirement for this will depend on the duration of the experiment and on the initial planting density. If the planting density is high, seedlings will start to interact sooner, which might provide some results earlier. However, one probably needs to thin at some stage, otherwise alien thinning might eliminate some tree species in the mixtures. If thinning is planned, then the spatial arrangement within a plot should allow for that. On the other hand, natural thinning processes may reveal important species interactions, and only unmanaged plots can be used to determine the carrying capacity (in terms of total biomass for example) of the communities.
- Trimming: Plantation managers would usually trim to favor height growth or stemwood quality. However, if the experiment is considered as a model system for C-sink plantations, for instance, then any losses of C by management interventions should be avoided.

Because tree diversity experiments are more likely to mimic situations of managed forests or even plantations than natural, undisturbed forests, some sort of management will certainly have to be applied. The specific management options will first and foremost be dictated by the aim of each experiment. We believe that management strategies will often have to take into account both the risk of losing the experiment and the cost of the various options. In the context of dichotomous management strategies, we suggest the possibility of establishing split-plot experiments with managed and unmanaged subplots. Split-plot designs are indeed amenable to all the above questions (e.g., to fence or not, to fertilize or not, to thin or not – the latter is done in BIOTREE, for instance) and their analysis is well known (Winer 1971; Potvin 2001). The advantage of using them is to allow testing of additional experimental factors, while the disadvantage is a reduction in plot size as each main plot would be subdivided into subplots.

16.4 Response Variables

The general aim of forest diversity experiments is to examine the relationship between forest diversity and ecosystem functioning and/or the provision of goods and services. Optimally, the experimental design should enable responses in terms of different ecosystem processes and properties to be examined. The following list of key response variables is quite ambitious but would allow comparisons across different experiments:

- Tree mortality
- Tree growth and stand productivity (timber production)
- Canopy architecture (leaf area index, crown stratification)
- Phenology

- Carbon sequestration (in plants and soil)
- Nutrient retention in plants and soil (N, P, cations)
- Nutrient loss to groundwater (leaching)
- Decomposition, mineralization
- Soil respiration
- Microclimate, including soil temperature and water content
- Associated diversity (plants, above- and belowground arthropods, nematodes, earthworms, birds)
- Stand stability (resistance, resilience, and invariability)

Yet, depending on the specific interests and fields of expertise of the research team establishing the experiment, some response variables may have priority over others. Different research aims may put different constraints on the experimental design; and the design, in turn, has important consequences for the sampling procedures. For instance, plots with a clumped arrangement of species require a sampling that allows merging the properties of the many small, single-species patches at the whole-plot level. In Table 16.2, we attempt to analyze which features of experimental design are likely to be influenced by different response variables. Several generalizations emerge:

- 1. Variables that involve responses of individual trees (e.g., tree survival, growth, and canopy architecture) or a sum of individual tree responses (e.g., stand productivity) seem to be affected mainly by design features which concern tree distribution within plots (spatial arrangement, density, and proportion of each species in a mixture).
- 2. Response variables that are measured at the stand level and that are the products of stand functioning as a whole (e.g., nutrient retention, decomposition, hydrology- and microclimate-associated diversity) may be largely dependent on plot size and environmental heterogeneity. It is better, therefore, if experiments aimed at measuring the above variables are planted on the largest possible plots, and replicated on different soil types.
- 3. If response variables of interest involve dynamic properties of ecosystems (Schläpfer and Schmid 1999), such as resistance to invasions and frequency and severity of attacks by forest pests and pathogens, the duration of the experiment is crucial because it has to allow the above events to take place.

16.5 Major Caveats

Experiments using the "synthetic community approach" to study diversity effects on ecosystem functioning clearly have several general limitations (Huston and McBride 2002). In those with trees, additional restrictions have to be kept in mind. The most obvious ones are:

Key response variables	Design features which are likely to influ- ence the outcome of the experiment
Tree mortality/survival	Spatial arrangement of trees within plots
	Planting density and proportion of each species in a mixture
	Presence/absence of herbivores (e.g., fencing)
Tree growth and stand productivity	Spatial arrangement of trees within plots
	Planting density and proportion of each species in a mixture
Canopy architecture	Spatial arrangement of trees within plots
	Planting density and proportion of each species in a mixture
Carbon sequestration	Stand management (trimming, thinning)
Nutrient retention and loss to groundwater	Plot size (microclimate)
	Proportion of each species in a mixture
Decomposition and mineralization rates	Plot size (litter input from adjacent plots, microclimate)
	Proportion of each species in a mixture
Soil respiration	Plot size (microclimate)
	Proportion of each species in a mixture
Microclimate	Plot size
Associated biodiversity	plot size (depending on size and mobil- ity of the organisms)
Stability	Duration of the experiment

Table 16.2. Experimental design factors that can influence measured processes and properties of tree experiments in addition to the effects of abiotic factors

- It is an even-aged plantation and not a naturally established forest. Many multi-species forests established from natural seedling invasion and regeneration contain trees of several age classes. Differences in age also influence stand structure, which is another important factor of forest bio-diversity (Franklin et al. 2002). However, there are also numerous examples for natural even-aged and homogeneous forests, e.g., after stand-replacing fires in the boreal zone.
- Large field sites are needed. Depending on the number of replicate communities and the chosen plot size, the field sites may extend over large areas. For example, the experiments described here use single field sites

ranging from <2 ha (Finland), 9 ha (Panama), 50 ha (Germany), up to 500 ha (Borneo). This also restricts the options for an "optimal" location (in terms of environmental heterogeneity, infrastructure, accessibility, etc.). Communications with the state forestry administration or commercial forestry companies may help to find and get access to such large areas.

• High costs for establishment and maintenance. Due to the large field size needed, leasing costs for land may be substantial and regular research-funding institutions will presumably not be in a position to pay them. Unorthodox alliances may help to solve this problem. In the Borneo experiment, the planting of such a large area was possible, for example, by linking the infrastructure of a commercial carbon offset project with the biodiversity experiment. In Germany, loss of forest area due to the recent construction of a new highway has to be offset by afforestation, which will be achieved by the proposed experiment. Researchers could take advantage of similar legislation that may exist in other countries. Together with the increasing demand for afforestation in implementing the Kyoto Protocol (Schulze et al. 2002), such large-scale experiments might then be feasible.

16.6 Outlook

Existing manipulative tree biodiversity experiments demonstrate that such large-scale and long-term projects are feasible and furthermore indicate biodiversity effects even at a very early stage, contrary to most expectations. Of course, experiments using the "synthetic community approach", though promising, represent only one way to study biodiversity effects on ecosystem functioning and/or the provision of ecosystem goods and services. There are many possibilities for integration and comparison with complementary approaches, such as removal experiments and observational studies. Indeed, such integrated perspectives are needed in order to assemble the general picture about diversity-functioning relationships in forests.

We would thus like to encourage researchers to explore the possibilities to set up similar experiments that could be complementary to those presented here with respect to experimental design, size, species pool, or biome. The inclusion of manipulations of genetic diversity within species would be particularly important. A global network of tree diversity experiments would indeed be a fascinating opportunity to improve our understanding of ecosystem functioning, closing the gap between ecosystem process studies and population and biodiversity studies.

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