Why do we need permanent plots in the study of long-term vegetation dynamics?

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Abstract. This paper presents a survey of vegetation studies on permanent plots, with an emphasis on the long-term character of these studies. It makes remarks on the external and internal causes of succession, pays attention to the pathways of succession, links up permanent plots studies and chronosequences, discusses internal causes and mechanisms of succession, and finally mentions the significance of long-term vegetation dynamics for nature conservation.

Keywords: Chronosequence; Mechanism; Nature conservation; Pathway; Succession.

Long-term vegetation dynamics

The meeting on long-term permanent plot studies in Groningen is just one in a series of conferences on long-term vegetation dynamics. Recently, two other meetings on vegetation dynamics have been reported, namely; 'Spatial processes in plant communities' (Krahulec et al. 1990) and 'Mechanisms and processes in vegetation dynamics' (Agnew et al. 1993). Several papers dealt with ideas on mechanisms of directional changes in species composition governed by either abiotic influences or species interactions (competition) (e.g. van Rijnberk & During 1990), or characteristics of dominant plant species affecting abiotic conditions (e.g. Rode 1993).

According to Pickett et al. (1987) we can distinguish between pathways, causes and mechanisms of vegetation change in order to describe, explain or predict aspects of succession: (1) a pathway is the temporal pattern of vegetation change; (2) a cause is an agent, circumstance or action responsible for successional patterns; (3) a mechanism is an interaction that contributes to successional change. Permanent plots can, of course, indicate pathways of succession, but may also generate hypotheses on mechanisms and causes.

It needs a great deal of discipline to maintain a series of permanent plots and analyse them yearly over a period long enough to answer relevant questions on succession. This raises the question: how long do 'long-term observations' have to last? Since this term appears in the new name of the Working Group, this is an obvious question. However, as yet we do not have an adequate answer. The same holds for the size of the permanent plots: we do not know what the optimal size is. It depends on the hypotheses to be tested, the vegetation type involved and financial and technical constraints as to the maximal duration of the research. During the Groningen meeting a minimal period of 10 yr was accepted as a criterion for long-term qualification of a project.

The series of permanent plots in the Park Grass Experiment at Rothamsted started in 1856 (Johnston 1991; Silvertown et al. 1994) and most probably holds the world record. However, this and other long-term series include many time gaps which can easily arise in such a long series (see also van den Bergh 1979; Collins 1995). Despite the problems attached to this type of work many researchers study permanent plots. Westhoff (1969) mentioned a number of ca. 500 permanent plots which were recorded 'regularly' in the Netherlands in the 1960s. Since a recent inventory is lacking, one may wonder how many permanent plots have disappeared or been established since the early 1970s. An inventory by Schmidt (1974) included ca. 800 permanent plots, which were unevenly spread over several (only European) countries. In addition, Schmidt (1974) and Londo (1978) provided a methodological manual for the study of vegetation succession by means of the permanent plot method.

External and internal causes of succession

Apart from the interesting question of what happens during succession, the questions 'why' (causes) and 'how' (mechanisms) this is happening, are important from a fundamental scientific point of view. With respect to causes of succession, it seems useful to distinguish between immediate causes and long-term causes. Some permanent plots were established for monitoring vegetation changes in time in relation to various abiotic conditions (e.g. inundation, Roozen & Westhoff 1985), or fluctuations in abiotic conditions (e.g. groundwater level, van der Laan 1979, 1985). Many permanent plot observations were started in order to study the effect of external causes, such as the application of fertilizers (Willems 1980; Silvertown et al. 1994), the application of different grazing regimes in interaction with different habitat conditions (Welch & Scott 1995; O'Connor & Roux 1995), the exclusion of herbivores (Watt 1957; Rosén 1982; Andresen et al. 1990), the start of restoration management (Oomes & Mooi 1981; Schmidt 1985; Willems 1983, 1985; Dierschke 1985; Schreiber & Schiefer 1985; Bakker 1989), the result of excluding marine influences due to building coastal protection works such as dikes (Westhoff & Sýkora 1979; Beeftink 1987; Olff et al. 1993), the commencement of groundwater extraction in wetlands (Grootjans et al. 1996) or the simulation of air pollution (Tamm & Popovic 1995; Falkengren-Grerup 1995). These external causes often give rise to different internal causes of succession (mediated by the local community itself), such as organic matter accumulation in the soil, gradual soil impoverishment or soil acidification. Such internal causes may affect community composition by different mechanisms, such as altering local colonization or extinction rates (competition). Furthermore, the internal causes are again affected themselves by community composition, e.g. by differential effects of dominant species on soil factors and nutrient cycling (Miles 1987; Bobbink & Willems 1987; Bobbink et al. 1988; Berendse & Jonasson 1992).

Permanent plot observations are not only important because they enable the description of the effect of external causes, but also because of the possibility of generating hypotheses on internal causes and mechanisms of species replacement during vegetation succession. These can only be unravelled on the basis of knowledge of the exact sequence of species in a successional sere and of the relevant ecosystem processes. In the actual field situation hypotheses on internal causes and mechanisms of succession can be tested if we can find multiple sites which represent well-defined phases or stages of succession, i.e. chronosequences (e.g. During & Willems 1984; Tilman 1987; Olff et al. 1993; Bakker & Olff 1995).

Pathways of succession

Pathways of succession at the level of plant communities can be derived from repeated vegetation mapping (Londo 1974; van der Maarel 1975; van Dorp et al. 1985; van der Maarel et al. 1985; Bakker 1989). The succession derived from subsequent vegetation maps from 1956, 1963 and 1968 indicated that only a small proportion of the total number of succession lines could be detected with the aid of permanent plots. Positioning of permanent plots in transects perpendicular to abiotic gradients will give detailed information on changes in vegetation patterns and individual species in small areas. The best method for the investigation of succession proved to be a combination of a restricted number of permanent plots and successive vegetation mapping (Londo 1974). A comparison between data from 80 permanent plots and repeated vegetation mapping revealed that permanent plots did not render the information on the relationship between pattern and succession derived from mapping. The minimum number of permanent plots of 4 m^2 needed for estimation of the probability of the most frequently occurring transitions would have been 248; hence, for the purpose of quantitative estimation of vegetation changes in a dynamic habitat an annual mapping according to a 'rough' typology seems preferable (van den Berg et al. 1985).

One may argue that any study of vegetation dynamics at the species level is impossible without permanent plots. A pathway of a certain succession is defined as the directional change in plant species composition, characterised by a certain speed and a direction. With respect to the speed of succession, we can distinguish between the incident rate (in a given year) and the overall rate (net result) over a certain period. The annual rate of succession can be calculated as the percentage dissimilarity between consecutive years (Londo 1978; Bornkamm 1981; Olff & Bakker 1991) or as the Euclidian distance between subsequent years in an ordination (Myster & Pickett 1994). The overall rate of succession (or net rate) up to a specific year can be calculated as the percent dissimilarity (or Euclidian distance) between that year and the first year of observation (Olff & Bakker 1991). The overall rate of succession can be further analysed by calculating the number of species gained and the number of species lost over a specific time span (e.g. Rydin & Borgegård 1988a; Oomes 1992; Tilman 1993). The rate of successional convergency or divergency in species composition can be analysed by comparing the beta diversities in different years (Christensen & Peet 1984; Rydin & Borgegård 1988b). However, in order to gain insight into the direction of change in community composition other methods are required:

1. Deduction of cluster transitions of communities (e.g. van Noordwijk-Puijk et al. 1979; Roozen & Westhoff 1985; Bakker 1989), obtained from cluster analysis;

2. Results of an ordination (e.g. Detrended Correspondence Analysis) can be represented in a biplot of sample and species scores (Jongman et al. 1987; Cramer & Hytteborn 1987; Rydin & Borgegård 1988b), where in the sample plot subsequent years can be connected by arrows, and a comparison with the species plot provides the direction in terms of species composition;

3. Non-linear regression analysis of individual species abundances against time provides a description in terms of individual species dynamics, also offering the opportunity to distinguish between trends and fluctuations on an individual-species level (Huisman et al. 1993; Olff et al. 1993);

4. The average abundance of groups of functionally equivalent species (e.g. life forms or growth forms) can be plotted against time (Willems 1985; Olff et al. 1993);

5. The change in relative abundance of different syntaxonomic elements can be plotted against time (van der Maarel 1975; Westhoff & S□kora 1979).

Permanent plots and chronosequences

Experimental work on chronosequences greatly enhances our knowledge on mechanisms of succession. Pickett (1989) concludes, from a review, that although chronosequences or 'space-for-time substitutes' may be useful for qualitative purposes and for hypothesis generation, they are unreliable for a deeper understanding of successional change because site history is so often important. The implicit assumption of 'similar environments' of different ages (i.e. same soil conditions, microclimate, availability of propagules) may not be valid (Miles 1987; Glenn-Lewin & van der Maarel 1992).

However, many researchers cannot rely on long-term observations on species replacements and it is difficult to check if chronosequences really reflect succession. In this context we need to be aware that spatial zonation frequently does not always represent a chronosequence (see e.g. Roozen & Westhoff 1985; Cramer & Hytteborn 1987; Zobel & Kont 1992; de Leeuw et al. 1993). Once a chronosequence has been established it can be used to measure parameters which are usually not recorded during succession. Examples are biomass (above and below-ground) of individual plant species and other relevant traits of individual plant species e.g. tissue concentration, plant height, vertical light extinction profiles, soil characteristics (e.g. availability of nutrients and water, organic matter and carbon con-

tents), stress factors (e.g. salinity, waterlogging, pH), herbivore and pathogen densities, decomposition dynamics of organic matter, genetic changes in plant populations, emergence of seedlings from the seed bank and colonisation dynamics from outside. Also, in the case of a chronosequence one can eliminate 'climatic noise', e.g. measurements of production or mineralisation in different years in a successional series can vary from year to year as a result of dry or wet growing seasons.

By measuring the aforementioned parameters in chronosequences, hypotheses derived from permanent plots can be tested. Permanent plot data enable verification of predictions from experimental studies (Herben 1996). We think that data derived from permanent plots and chronosequences can be complementary. A parallel can be found for permanent plots and experiments in order to test hypotheses derived from permanent plots (see further Herben 1996).

Hypotheses of causes and mechanisms of change in ecological systems can be formulated at various ecological levels (see O'Neill et al. 1986). Hypotheses of the nature of changes in ecosystem properties can be generated from permanent plot observations by careful investigation of 'what the plant species tell us'. For example: indicator values *sensu* Ellenberg et al. (1991) with respect to the nutrient status of the soil (Bakker 1989). In this case, the number of species indicative of nutrient-poor conditions increased in permanent plots after cessation of fertilizer application; not suddenly, but gradually over a period of 20 yr. On the basis of this information it was hypothesized that a pool of high-quality organic matter was slowly disappearing, leading to a gradual decrease in N-mineralization rates. This was then confirmed by *in situ* measurement of N-mineralization rates in a chronosequence, which was validated using permanent plot information (Olff et al. 1994b). Long-term studies have also provided valuable data about the dependence of forest community succession, after clearcutting, on the dynamics of the soil nutrient pool (Bormann & Likens 1979; Reiners 1992) or about the pollution-induced changes in biogeochemical processes and resulting changes in vegetation structure and composition (Tamm & Popovic 1995; Falkengren-Grerup 1995).

In the above-mentioned examples the allogenic causes of vegetation succession seem obvious. Before continuing on the community level (at which succession is mostly described) it should be stressed that it is often not worthwhile to distinguish between allogenic causes and autogenic mechanisms at the level of the vegetation, because the continuous interaction (feedback mechanism) between vegetation and soil renders the two processes indistinguishable. This is particularly the case in wetlands, where vegetation succession is incorporated into eco-

system succession to such an extent that it is advisable to make a choice for the 'ecosystem' as the entity of study (van Andel et al. 1993). This implies the sequential measurement of at least part of the aforementioned list of parameters in chronosequences together with a description of vegetation in permanent plots.

Internal causes and mechanisms of succession

Various methods for using permanent plot information in order to generate hypotheses on the nature of changes exist, especially at the community level. For example, we may take the ongoing discussion about the relationships between productivity, stability and diversity of ecological communities. Based on studies of permanent plots in species-rich calcareous grassland, it was shown that the optimum above-ground phytomass for species density in Grime's corridor model (Al-Mufti et al. 1977) may vary depending on the plant community involved (During & Willems 1984). Furthermore, the latter study revealed that the response surface model of Huston (1979) could be interpreted in terms of mowing and grazing impact on the frequency of population reduction on one axis in the model. On the second axis, representing the rate of displacement, the relative position of the fertilized and unfertilized permanent plots could be indicated. Consequently a slight alteration was suggested in the shape of Huston's response surface shape to a more 'table-mountain' form (Huston 1979; During & Willems 1984).

Intuitively, one may consider that diverse systems will be more stable in terms of floristic constancy and less susceptible to external influences, plagues; etc. (e.g. compare a tropical rain forest with an agricultural crop monoculture). However, this has been contradicted on the basis of the analysis of imaginary food webs (May 1973). The only opportunity to check these predictions in real ecological communities is the use of long-term permanent plot observations, i.e. to see whether more diverse communities are indeed more stable. Tilman & Downing (1994) concluded, after 12 years of observations on plots in old fields, that more diverse communities are more stable because plots with a higher species richness showed less temporal total biomass variation. They analysed the stability of the abundance of C3 versus C4 species as the 'response variable' for which the 'effect' of diversity was checked. A similar approach was followed by Dodd et al. (1995) for the Rothamsted plots, where the variability of biomass productivity was analysed in relation to species richness. They concluded that biomass variability tended to be lower in more diverse vegetation. These field observations from permanent plots need further experimental

testing and causal analysis, where species diversity is experimentally manipulated and the consequences thereof for ecosystem functioning investigated (see e.g. Naeem et al. 1994).

Once succession is established, the investigation which traits characterize plant species occurring in various successional stages may help in the formulation of hypotheses on the mechanisms of species replacement. Information which can be deduced from permanent plot analyses involves changes in maximum height and growth form with respect to light attenuation (Bobbink 1991; Olff et al. 1993; Willems et al. 1993), germination characteristics with respect to the possibility of seedling establishment (Olff et al. 1994a; Sykes et al. 1994) or seed size with respect to the possibility of persistency in the soil seed bank (Thompson et al. 1993). Once a regression between time and species abundance has been established, one may replace 'time' by a more causal variable (e.g. the cumulative nutrient balance of the system) and see if the regression improves (Bakker & Olff 1995).

Another application of permanent plot studies has been the investigation of small-scale dynamics in plant communities, and the inference of hypotheses on underlying mechanisms such as competition (e.g. Herben et al. 1993). In these studies, one seeks for 'replacement rules' (species B is always locally replaced by species A) which might be further investigated by growth and competition experiments. However, such data should be treated with caution. For instance, a gross process may be an increase of a species A and a decrease of species B. A more detailed analysis, through fine-scale replacement graphs, may show that species A increases at the cost of another species, C, which in its turn increases at the cost of species B. This effect, however, cannot be found without recording the fine-scale spatial pattern (Herben 1996).

Apart from providing an understanding of the mechanism of vegetation change, permanent plots may also help us to improve our understanding of an even more fundamental question: the mechanism of species coexistence. Stable coexistence is, in principle, a long-term phenomenon, and it is evidently not enough to address this problem with the help of only short-term studies carried out in only one part of the world. One of the most popular explanations of species coexistence has been the hypothesis that niche differentiation and environmental heterogeneity promote species coexistence without competitive exclusion (Whittaker & Levin 1977; Tilman 1982, 1986). Many species can coexist because each species is a superior competitor at a certain combination of environmental resources and no one species will achieve superior competitive ability over all different microsites. Though there have been difficulties in

demonstrating the real niche differentiation (Hubbell & Foster 1986; Mahdi et al. 1989) or the correlation between habitat microheterogeneity and species richness (Tilman 1993), the new theory has been developed mainly on the basis of permanent plot studies.

In many investigations the structure of plant communities is viewed as a photograph at just one moment in time and further analysis is made on the basis of this 'photograph' only. However, in nature, populations are shifting in time through microsites like clouds in the sky (Grubb 1984). The 8-yr observation of the plots in limestone grassland made it possible to formulate the so-called 'carousel model' which suggests that in a homogeneous community many (if not all) species can reach virtually all microsites (van der Maarel & Sykes 1993; Sykes et al. 1994). The speed of the carousel seems to be non-uniform, but depends on the externally and internally induced rhythms of generative and vegetative reproduction (Zobel et al. 1994). These results also question the usefulness of the niche concept, and the explanation of coexistence through niche differentiation. Observations of permanent plots over many years and calculation of the cumulative species richness also enables a more general approach to minimum area: instead, one can speak about the minimum time necessary to obtain the occurrence of the majority of species in a small plot (van der Maarel & Sykes 1993; van der Maarel 1993).

The validity of the niche differentiation hypothesis and the existence of the 'carousel model' in plant communities is connected with another general question - which is the role of biotic interactions in structuring plant communities. The failure to show the clear role of niche differentiation as a way for plants to avoid competition has led to an approach giving less significance to biotic interactions - a 'species pool' hypothesis. This hypothesis argues that at least the level of species richness (but not local abundances, and thus not diversity) is determined by the local and regional availability of species (Taylor et al. 1990; Zobel 1992; Eriksson 1993; Pärtel et al. 1996). On a local scale, it can be a matter of a trade-off between dispersal followed by colonization and competition (Tilman 1994; Willems & van Nieuwstad 1996), but on a regional scale, the availability of species is a result of biogeographic and evolutionary processes (Ricklefs 1987; Ricklefs & Schluter 1993; Cornell & Lawton 1992; Zobel 1992).

However, the role of biotic interactions is more essential when different trophic levels are considered at the same time. Long-term observations and experiments show the significant effect of herbivores on the structure of plant communities (see the reviews of Crawley 1983; Huntly 1991; Brown 1994; Sinclair & Arcese 1995). Traditionally, the role of domestic animals and large

mammals has been considered (e.g. Prins & van der Jeugd 1993). However, even a quite subtle change in the composition of the herbivorous insect community can result in drastic changes in a successional plant community (Brown & Gange 1989). Similarly, a reduction in the level of root arbuscular mycorrhizal colonization can result in changes in plant community composition (Gange et al. 1990, 1993) and the interaction between the effects of insects and fungi on plants is also possible (Gange & Brown 1992). This provides a new factor in the explanation of the mechanism of plant succession since, for example, there can be a lack of spores of mycorrhizal fungi in certain successional ecosystems (Allen 1991) which will certainly result in a different structure of that successional community. The similar role of pathogenic organisms has been stressed recently (van der Putten et al. 1993; Dobson & Crawley 1994).

In this respect, the need for *long-term* studies, including both observational and experimental investigations, should be strongly stressed (see also Pickett 1991). Even when a well-designed manipulative field experiment has been established, without long-term observations the results obtained may be insufficient or even misleading. (Tilman 1989; Inouye & Tilman 1995) provided examples where the more frequently used (i.e. 3-5 yr) period of observations and manipulations has not been long enough to catch the main trends in vegetation change. Relatively longer periods of observations are needed when the community under investigation is rich in species. Tilman (1989) found also that among the papers published in *Ecology*, only 7 % used material from experiments which lasted for five or more field seasons. This percentage was higher for observational studies, but this was mainly due to the use of chronosequences or paleoecological reconstructions. Interestingly, Tilman found that the authors of the long-term studies were all well-known ecologists. This result clearly indicates one of the major shortcomings in current vegetation science and ecology in general - the conduction of field studies of sufficient duration is (and probably will remain) the privilege of a few (financially) well-established scientists, while the majority of projects will conclude field work far too early because of a lack of financing. This is in spite of the need for long-lasting monitoring projects in this era in which both local and global changes are actual and important political issues.

Nature conservation interest

Many permanent plot observations are carried out in order to record whether envisaged changes in plant communities really take place. Monitoring the effects of nature management practices will prove to be more

important the longer the series of permanent plot observations lasts. Monitoring is becoming an important topic with respect to environmental policy e.g. drainage or eutrophication, whereas the authorities tend to establish many new monitoring programmes without taking advantage of already existing permanent plot observations.

The relevance of the existing permanent plot observations is (1) separating trends and fluctuations; (2) the possibility to extrapolate beyond the time range of available observations (now often 20 - 40 years); (3) to improve extrapolation to other sites (which have of course their own characteristics); (4) to predict vegetation change at future combinations of environmental factors which have not occurred so far (scenario analyses); (5) to test ecological models which are often based on assumptions not derived from solid field studies.

Nature preservation aims at a sustainable survival of complete ecosystems with high conservational value, e.g. high species diversity including rare and/or endangered species (Margules & Usher 1981). Long-term monitoring, by using permanent plots, will clearly reveal that the applied management is in accordance with the conservation goals. Since long-term plot research is the most appropriate method to distinguish between trends and fluctuations, this method should generally be used in the evaluation of vegetation development. This method can clearly indicate undesirable developments caused by external influences which are often beyond the control of Nature Conservancy Authorities, e.g. global warming and atmospheric pollution. Changes in species composition, indicative of such developments, always start at a small scale, either as a change in vegetational structure or in population characteristics of vulnerable species. Therefore, a combination of monitoring both the vegetation and the population dynamics of (some) target species in the same permanent plot should be stimulated in future research.

Insight into the underlying mechanisms in the functioning of ecosytems is the best guarantee for long-term survival of these ecosytems. This knowledge of the ecosystem allows a flexibility in necessary management practices for preservation. To obtain this knowledge on vegetation succession, long-term permanent plot monitoring is an appropriate research tool.

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