Problems, Approaches, and Results in Restoration of Dutch Calcareous Grassland During the Last 30 Years

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Abstract

This paper is based on research of the restoration of species-rich calcareous grasslands in The Netherlands, over the last 30 years. Chalk grassland is a semi-natural vegetation with a high density of species at a small scale. This type of vegetation was once widespread in Western Europe as common grazing land, mainly for flocks of sheep for which the main function was dung production. In some regions of Central Europe, these grasslands were also used for hay production. The dung was used to maintain arable field production at a reasonable level. In the chalk district in the southernmost part of The Netherlands some 25 sites of this vegetation, varying in area from 0.05–4.5 ha, are still present. Chalk grassland completely lost its significance for modern agricultural production after the wide application of artificial fertilizer following World War II. This grassland has a high conservation value both for plants and animal species, of which a large number of species are exclusively restricted to this biotope. When conservation activities started at a large scale in the early 1960s, three different types of restoration activities could be distinguished: (1) restoration of fertilized sites; (2) restoration of abandoned grasslands; and (3) recreation of chalk grassland on former arable fields. The main aim of the restoration attempt is to create and/or improve sustainable conditions for both plant and animal species characteristic of the chalk grassland ecosystem. In the process of restoration, several phases of different activities can be distinguished: (1) pre-restoration phase, during which information of the land use history is collected and, based on these data, clear restoration goals are established; (2) initial restoration phase, during which effects of former, non-conservational land use has to be undone in order to stimulate germination and establishment of target species originating from soil seed bank and species pool; (3) consolidation phase, including the introduction and continuation of a regular management system for sustainable conservation; and (4) long-term conservation strategy, including measures to prevent disturbance from the outside and genetic erosion and extinction of locally endangered plant populations.

Key words: chalk grassland, conservation management, grazing, mowing, natural resource, productivity, restoration phases, semi-natural vegetation, species diversity, The Netherlands.

Introduction

The most species-rich plant communities in the world at a small scale (<10 m^2) are temperate grassland communities (Peet et al. 1983). These grasslands are often manmade, and their maintenance completely depends on human interference, viz. mowing, grazing or burning. Among the best known and intensively studied examples of such species-rich grasslands are the calcareous grasslands in Western Europe (Scherrer 1925; Tansley 1939; Pottier-Alapetite 1943; Willems 1982, 1990; Ellenberg 1988; van Speybroek 1989; Dutoit 1996). These grasslands originated and were extended under specific conditions after humans cleared the primeval forest over large areas several thousand years ago (Ellenberg 1988). These grasslands were once widespread, especially in the hilly calcareous areas in Western Europe, but are now greatly diminished in extent due to changes in agricultural land use (Keymer & Leach 1990; Willems 1990)

Calcareous grassland was mainly used as common grazing land for sheep and cattle. However, in some areas in Central Europe it was used for haymaking for winter fodder, also (Schleumer 1934; Pottier-Alapetite 1943). There is no historic evidence that the Dutch chalk grasslands, located on the border of their distribution range, were mown regularly (Willems 1987). Apart from episodic removal of foliage, either by grazing or mowing, the calcareous grasslands are also characterized by low soil fertility as a consequence of the absence of intentional fertilization, and by a high species richness, usually exceeding 30–40 phanerogams/m^2 (Willems 1987; Willems & van Nieuwstadt 1996). Records of 54

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species/m^2 are known from the Netherlands (Willems 1987), and 63 phanerogams/m^2 exist in Estonia (Kull & Zobel 1991). The species in the calcareous grassland often include a substantial number which are either rare and/or endangered (Willems 1995).

The southernmost part of The Netherlands, the chalk district of South-Limburg, has an undulating hilly landscape up to more than 300 m above sea level. Many species of Central and Southern Europe reach the northernmost border of their distribution in this chalk district (Meusel et al. 1965; Willems & Ellers 1996). Calcareous grassland is a rare type of vegetation in The Netherlands and its distribution is restricted to a small area in South-Limburg. Some 30 phanerogamic species occur only within this plant community. Some 250 phanerogams and 120 cryptogams are found in this grassland community on an area of about 20 ha. This represents approximately 15 and 25% of the total indigenous Dutch flora, respectively (Willems 1987).

From the beginning of the 19th century there was an increasing interest in the characteristic plant species occurring in the chalk grasslands of South-Limburg. These grasslands lost their role in agriculture as common grazing land for the sheep, in the 1930s and late 1940s, after the introduction and widespread application of chemical fertilizers. In the greater part of Western Europe, the dung from the flocks of sheep was completely replaced by artificial fertilizer and the majority of the chalk grassland sites were transformed into highly productive grassland with low diversity by the application of this new invention (Willems 1980*a*; Green 1990; Keymer & Leach 1990; Muller et al. 1998).

Some of the most species-rich sites which included many rare species were set aside as nature reserves already in the 1930s, e.g., Bemelerberg in 1938 (Bobbink & Willems 1993). World War II interrupted modern agricultural developments, and reintroduction of sheep grazing on calcareous grasslands took place to a certain extent, with wool for clothes as the main product. Furthermore plowing of parts of ancient calcareous grasslands took place for growing cereals and potatoes. After World War II the agricultural activities changed completely within a short time span, and most of the semi-natural vegetation lost its economic function. As a consequence, many sites became available for nature conservation bodies. In the late 1950s and early 1960s a number of sites were set aside as nature reserves, often after a period of arable production and/or abandonment (Hennekens et al. 1985; Willems & Bobbink 1990).

Among conservationists the opinion of non-interference in reserved areas was questioned during that time (Bakker 1979; Westhoff 1979). None of the former agricultural management took place on any of the South-Limburg sites after becoming nature reserves. The conservation authorities introduced mowing as a substitute for the former sheep grazing, in order to prevent trees and shrubs from invading the open grasslands (Willems 1983; Willems & Bik 1998).

Nomenclature follows Flora Europaea (Tutin et al. 1964–1980) for scientific names, and Rose (1981) for English names.

The Situation in the Early 1970s

In 1970 a research program on structure and functioning of the calcareous grasslands was started at Utrecht University, The Netherlands, resulting in a number of Ph.D. theses (Willems 1980*b*; Schenkeveld & Verkaar 1984; Bobbink 1989; van Tooren 1989; de Kroon 1990; van Dam 1990; van der Hoeven 1999). In the early 1970s the situation in the South-Limburg chalk district, covering an area of approximately 20 km from east to west and 10 km from south to north, was as follows:

(1) Some 25 sites with remnants of calcareous grassland were left, varying in area from about 0.05 ha (Zure Dries site) (Willems 1995) to about 4.5 ha (Wrakelberg site) (Willems et al. 1993), with a total area of only about 20 ha.
(2) Each different site was characterized by a number of its own species as a result of different soil characteristics, geomorphology, history, local climatic conditions, etc. As a consequence, all sites deserved to be preserved for the future in order to maintain the maximum species diversity of the remaining chalk grasslands in the region.
(3) The sites became more and more isolated, not only by the absence of flocks of sheep moving around as seed distributors, but also by the gradual disappearance of wildlife in the farm land by a large increase of intensive agriculture.
(4) There was a decline in a number of characteristic plant species, especially in some non-managed sites. This was concluded from a comparison of current species with a well-documented phytosociological review of most calcareous grasslands of South-Limburg. This was carried out during the period 1940–1952 when the majority of the sites were still managed in a traditional way (Diemont & van de Ven 1953).

Results of Restoration Attempts

Restoration After Fertilization. As an example of the restoration process of formerly fertilized calcareous grassland, I will refer to the work carried out at a site in the Nature Reserve Gerendal, in the southernmost part of The Netherlands (50°51′ N; 5°54′E). In this area, permanent plots with different experimental management regimes were established in a grassland in 1971, four years after cessation of fertilizer application. At the start of the experiment a number of plant species characteristic of calcareous grassland were still present, although in small populations (Willems 1980*a*). After ten years the plots (2.25 m^2), which were mown yearly in August and from which the hay was removed soon after cutting, showed a significant increase in species numbers, viz. from less than 30 to more than 40 species (Willems 1980*a*). This was the result of strong species flux: weeds and highly productive grasses decreased in abundance or even disappeared completely, whereas local species characteristic of moderately productive calcareous grasslands increased in the plots. The yearly aboveground phytomass showed some fluctuations, but there was no clear trend and amounted to about 300 g/m^2 dry weight (Willems 1983). Approximately 20 years after the start of the experiment, the species number stabilized at a level between 30–40 species per plot, while the aboveground phytomass varied between 200–300 g/m^2 during the same period (Willems & van Nieuwstadt 1996) (Fig. 1).

Part of the experimental site in Gerendal was mown twice a year, in late spring and summer, from 1970–73, and from that time onward grazed by sheep at a low stocking rate, viz. 2 sheep/ha in the period April–October. Mowing was applied to enforce the reduction of the nutrient content of the soil during the first 3 years of restoration. A 7-year period of sheep grazing followed this mowing regime, resulting in a higher species density compared to the part of the grassland with only mowing treatment, especially in a higher number of low-growing rosette species (Willems 1983; Mitchley & Willems 1995).

Restoration attempts on this former fertilized grassland resulted not only in increased evenness and abundance of species of local origin, already present when the restoration started, but also in establishment of new characteristic chalk grassland species from neighboring

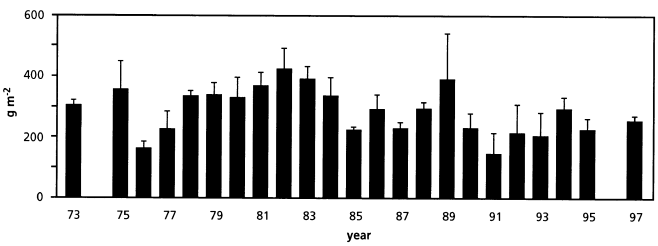

Figure 1. Aboveground phytomass (dry weight) at peak standing crop (August) of chalk grassland in the Gerendal nature reserve (South-Limburg, The Netherlands) during the period 1973–1997. The yearly fluctuations in productivity are determined by yearly changing weather conditions. No trend in decreasing phytomass can be seen during a 6–30 year period after the last intentional fertilization took place.

sites. After a 5–10 year period, a number of orchid species established spontaneously, e.g., *Listera ovata* (Common twayblade), *Orchis militaris* (Military orchid), *Gymnadenia conopsea* (Fragrant orchid) and *Aceras anthropophorum* (Man orchid), likely originating from two chalk grassland sites at a distance of approximately 300 m from the one under restoration. Other wind-dispersed species such as *Tragopogon pratensis* (Goat's beard), *Crepis biennis* (Rough hawk's beard), *Senecio jacobaea* (Common Ragwort) and *Clematis vitalba* (Traveler's joy) settled at the site in the same period. For species with non-airborne seeds it took many more years to cover this distance, viz. *Gentianella germanica* (Chiltern gentian) a species which arrived 25 years after the start of the experiment, probably by seed transport by wild mammals, probably Badgers (*Meles meles* L.). A network of their tracks clearly connected all three chalk grassland sites. Within the project on the ecology of short-lived species in chalk grassland (Schenkeveld & Verkaar 1984), it was proved in a small-scale controlled sowing experiment that the biannual *G. germanica* was able to germinate at the site under restoration, already in the early 1970s. The resulting seedlings were all removed before they reached the flowering phase.

The contribution of the soil seed bank to the process of restoration was rather limited and mainly consisted of a number of weedy species, originating from seeds in the deeper soil layers, and which disappeared after a number of years (Willems 1983, 1995; Bekker et al. 1998).

Restoration After Abandonment. After the loss of their importance for modern agricultural practices, the greater part of the calcareous grasslands in Western Europe were either intentionally transferred into high productive grassland or left abandoned (Willems 1982, 1990; Keymer & Leach 1990; Dierschke & Engels 1991; Muller et al. 1998). After abandonment, natural succession resulted first in a dramatic change in floristic composition, since one or a few tall grass species gained dominance in aboveground phytomass and, moreover, overtopped most of the accompanying subordinate species, most of them disappeared as a result of competition for light (Mitchley & Grubb 1986; Mitchley & Willems 1995). In The Netherlands the tall grass *Brachypodium pinnatum* (Tor grass) is the "aggressive invader" (Bobbink & Willems 1987), whereas this role can also be played by another tall-growing grass, e.g., *Bromus erectus* (Upright brome) in Belgium (Verbeke & Lejeune 1998), England (Wells 1974; Willems 1978) and Germany (Dierschke & Engels 1991).

The term "aggressive invader" is widely used to characterize the expanding behavior of these tall grasses after changes in environmental conditions, suggesting these are alien species, originating from outside the chalk grassland ecosystem. However, both *B. pinnatum* and *B. erectus* were widespread and phytosociological constant species in chalk grassland communities far before management problems started. Although these species can be characterized as aggressive, they are part of the community, rather than invaders from outside.

Increasing dominance of *B. pinnatum*, reaching up to 90% of the aboveground phytomass, resulted in a dramatic decrease of species diversity and species number of the characteristic chalk grassland species within a time span of 10–15 years (Bobbink & Willems 1987). This grassy stage in natural succession was gradually taken over by shrub species (i.e., *Crataegus monogyna* [Hawthorn], *Prunus avium* [Wild cherry], *Rosa spp.*) 15–20 years after abandonment, depending on the soil conditions, slope exposure, etc. (Willems & Bik 1998) and later on (>35 years) by tree species (Dzwonko & Loster 1998).

Only a few examples of this succession series occurred In South-Limburg, since most of the former chalk grassland sites were either transformed to highly productive grassland or set aside as nature reserves. Therefore an experiment was started at the Gerendal site, where a 3 × 6 m plot was fenced and left unmanaged from 1970 onward. The vegetation was recorded in detail at irregular intervals (i.e., not yearly) in order to minimize disturbance as much as possible. Abandonment of the plot resulted in an increase in cover of *B. pinnatum* up to 80% after 10 years, and a decrease in species diversity by 40% and a loss in species number of 20% compared to the situation at the beginning of the experiment (Willems 1980*a*). The process of succession continued and resulted in a coverage of *B. pinnatum* of almost 100% and a decrease in diversity index till less than 10%, and a species number of about 30% after 17 years. The species number decreased in the following years to only 7 species, viz. less than 15% of the original number (Willems & Bik 1998) (Fig. 2).

In September 1990 the shrubs, mainly *C. monogyna* (coverage approximately 60%), were cleared and the *B. pinnatum* dominated vegetation mown and removed, including standing dead and litter layer. This small-scale restoration experiment lasted 7 years, and included the study of the role of the soil seed bank and the seed rain. The immediate increase in species number after shrub clearance and mowing of the herbs was mainly the result of seed rain from the surrounding vegetation, rather than originating from the soil seed bank. The seed bank was strongly reduced in the permanent plot during the period of abandonment, in comparison with the seed number present outside the plot. During the period of restoration (1990–1997), the number of seeds in the soil of the permanent plot increased, especially in the upper soil layer, demonstrating the slow process of building up a consistent seed bank reflecting the actual vegetation (Willems & Huijsmans 1994; Willems 1995).

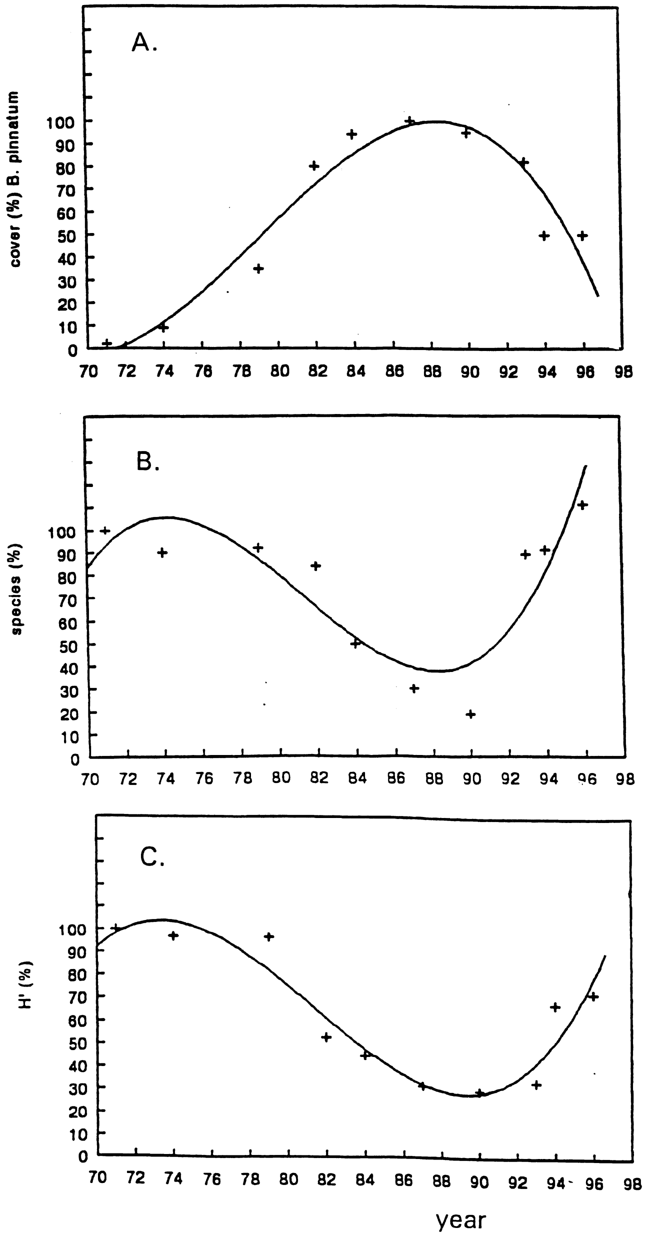

Figure 2. Degradation and restoration of species diversity in relation to increasing dominance of a competitive grass species (*Brachypodium pinnatum*) in a small-scale experiment at Gerendal (South-Limburg, The Netherlands). The plot was intentionally abandoned during the period 1970–1990, whereas clearing of the shrub and mowing of the herb layer as initial restoration measures began in 1990. The regular management during the period 1990–1997 was yearly mowing in autumn and removal of the hay. (A) Percent coverage of *Brachypodium pinnatum*; (B) relative species number; and (C) relative Shannon index of diversity (H'). The fitted curve is a third order polynomial.

The process of restoring species density in the experimental plot was significantly faster than 25 years earlier (Willems & Bik 1998). This was the result of increased seed rain as a consequence of higher species density surrounding the plot, and the appropriate vegetation structure for germination and establishment of the species, due to the applied yearly mowing management (Oomes & Mooi 1981; Willems 1983; Hakes 1988).

Occasionally, the soil seed bank plays a role in the restoration of species richness for species with long-lived seed storage in the soil, as demonstrated at the nature reserve Bemelerberg (Bobbink & Willems 1993). Mowing of an abandoned, and therefore *B. pinnatum*-dominated chalk grassland, resulted in a marked increase of a number of short-lived species with a persistent soil seed bank, both characteristic (*Carlina vulgaris* [Carline thistle], *Linum cathartic*um [Fairy flax], *Arenaria serpyllifolia* [Thyme-leaved sandwort]) and non-characteristic chalk grassland species (*Daucus carota* [Wild carrot], *Centaureum erythraea* [Common centaury]). Frequent mowing during several years resulted in only partial restoration of the original species density. Restoration of a more complete species assortment at this site was hampered by the absence of nearby seed sources of characteristic chalk grassland species (Bobbink & Willems 1991).

Increased abundance of *B. pinnatum,* however, occurred in the mid-1980s even in managed nature reserves as a consequence of increased nitrogen input by atmospheric deposition, which amounted to 50 kg ha^{-1} yr^{-1} in the area (Bobbink & Willems 1987; Bobbink et al. 1988; van Dam 1990).

Ecophysiological investigations on *B. pinnatum* revealed that this species was able to monopolize the extra nitrogen supply resulting from atmospheric deposition by fast uptake and subsequent storage in the extended rhizome system, whose biomass sometimes exceeded the aboveground peak standing crop of this species (Bobbink et al. 1988). Moreover, the growth form was modified into a highly competitive form after increased N supply. The P/N ratio was lowered in the plant tissue, a tremendous advantage compared to the other species in this system where phosphate is the limiting factor as a consequence of the high pH in the soil (Bobbink 1991; Willems et al. 1993; Ryser et al. 1997). Field experiments, carried out to develop a management strategy to control the expansion of this species, showed that mowing in the first half of August was effective. This was the period before reallocation of the nutrients into the underground storage organs and, moreover, the underground shoots were in a dormant stage at that time. A few years of mowing in August suppressed the dominance of *B. pinnatum,* and this potential aggressive species was no longer a threat to the species-rich chalk grassland vegetation (Bobbink 1989).

Regeneration on Abandoned Arable Fields. Modern agricultural development after World War II has had an unexpected advantage for nature conservation because some areas of marginal agricultural value were abandoned. These areas often had been only temporary fields for food supply during the war. Due to their abiotic conditions, such areas were often of high potential value for the restoration of wildlife. One of those sites in South-Limburg was Wrakelberg, a south-facing slope with a shallow soil on weathered Senonian chalk (Rendzina soil type). The last arable fields were abandoned in 1961. The study of succession took place by repeated vegetation mapping in the period 1968–1985 (Willems & Bobbink 1990). The research revealed that species-rich chalk grassland (<25 species/m^2) vegetation (*Mesobromion erecti*, Class Mesobrometea; Braun-Blanquet vegetation type), the potential grassland for the greater part of this area, covered some 60% of the area 12 years after crop production ceased. The remaining part was occupied by species-rich grassland with high conservation value, too, the *Arrhenatheretum elatioris* vegetation type (Class Molinio – Arrhenatheretea), which was restricted to the lower part of the slope with deeper and more fertile soil conditions. During the period of restoration the management of the area consisted of mowing in autumn and removal of the hay.

The fast colonization of the species-rich grassland, including a number of rare and threatened plant species, was undoubtedly caused by the adjacent seed sources in the upper part of the slope which had never been plowed (Willems & Bobbink 1990), and which functioned as a local species pool (Pärtel et al. 1996; Willems & Bik 1998; Zobel et al. 1998).

At a distance of only 3 km from the Wrakelberg site, a number of arable fields, called Wylre Fields, were abandoned between 1955 and 1963 and set aside as a conservation area at the same time (Hennekens et al. 1985). Based on the edaphic and management conditions, a similar vegetation development toward a Mesobromion community as happened at Wrakelberg was expected. However, more than 30 years after agricultural practices ceased, the species-rich grass/herb community at the Wylre Fields is not yet a typical Mesobromion vegetation, but a community characteristic of an intermediate stage in the succession from arable weed community toward a chalk grassland. This plant community, the so-called Dauco–Melilotion (Class Arthemisietea vulgaris), is dominated by species like *Daucus carota*, *Melilotus officinalis* (Ribbed melilot), *M. alba* (White melilot), *Artemisia vulgaris* (Mugwort) and *Origanum vulgare* (Marjoram) (Schamineé et al. 1996). At Wylre Fields the vegetation succession toward a chalk grassland clearly is not as fast as observed at Wrakelberg, very likely due to a lack of adjacent seed sources of characteristic species. Besides, it might be assumed that the greater part of the Wrakelberg was arable land for a relatively short period, probably for only about 10 years, whereas the Wylre Fields were already in agricultural use before the beginning of the twentieth century, as could be reconstructed from old topographic maps. This means that in contrast to the situation at Wrakelberg, no diaspores of grassland communities survived in the soil of the Wylre Fields, taking into account the survival time of persistent seeds in the deeper soil layers (Willems 1988, 1995; Poschlod 1993; Thompson et al. 1993; Dutoit & Alard 1995; Milberg 1995; Bekker et al. 1998).

Conclusion

Several phases can be distinguished in the restoration attempts for species-rich chalk grasslands in The Netherlands:

Pre-Restoration Stage

This stage includes an inventory study concerning the presence of plant populations in the underground diaspore bank and in the actual vegetation. A study of the possible presence of remnants of former vegetation adjacent to or near the restoration site may provide information on potential external seed sources. Based on this information, realistic restoration goals can be defined and appropriate management measures can be developed. Knowledge of the recent land use history may contribute to a successful restoration approach, also. If descriptions of the former floristic composition of the vegetation are available, restoration goals can be defined appropriately.

Initial Restoration Stage

During this stage of the restoration process, optimal conditions have to be created for the expansion of the remaining populations of the target species. Moreover, creating the right germination conditions for the available seed sources is a necessary prerequisite in this phase of restoration.

This stage often includes reducing the former impacts of community degradation, e.g., in case of abandonment or fertilization, the removal of the aboveground phytomass, possibly including the litter layer. In practice, this often includes mowing one or more times in the growing season and removing the hay in order to lower the soil fertility. This activity must result in an optimal vegetation structure for increasing species density (Mitchley & Willems 1995; Bobbink & Willems 1993).

Consolidation Stage

When a number of conditions for restoration of species diversity are fulfilled, regular management can be started. Preferably, this management must reflect the former agricultural practice which maintained the calcareous grasslands as a sustainable natural resource until the introduction of the artificial fertilizer.

During this phase, which might last for many years, both immigration of characteristic species and increase of present species to viable populations can contribute to a higher biodiversity of the community. This also holds for the faunistic aspects of the ecosystem (e.g., pollinators) in this stage (Brown & Gibson 1994). In this stage it is also necessary to monitor vegetation development by permanent plots, since small-scale vegetation inventory is an appropriate method to study succession processes (Willems et al. 1993; Bakker et al. 1996). Restoration goals can be tested in this way, as well as probable negative external influences, e.g., atmospheric nutrient input.

Long-Term Conservation

This stage includes creating a suitable ecological infrastructure in the landscape in South-Limburg, in order to enhance the gene flow between the small and isolated chalk grassland sites (van Treuren 1993; Oostermeijer et al. 1996). These sites can be considered islands of wildlife in an ocean of highly productive arable fields and monotonous grasslands. The role of amenity grasslands on roadside verges as corridors for diaspore migration, in combination with a number of flocks of sheep moving around, can contribute to the cessation of isolation of the chalk grassland sites (Fischer et al. 1996; Poschlod et al. 1998).

These conclusions based on the past and present position of the chalk grassland sites in South-Limburg may hold for successful restoration attempts of different manmade ecosystems in other parts of the world, too, possibly with some modifications.

At present, the approximately 25 calcareous grassland sites scattered in South-Limburg are managed well and are not threatened directly in the near future. It is important that all fragments be preserved, since each site has a number of characteristic chalk grassland species of its own, often Red List species (Willems 1995). The evaluation of the consequences of the newly introduced sheep grazing management for biodiversity of the rare and vulnerable chalk grassland ecosystem in The Netherlands is a future challenge for both scientists and conservationists.

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LITERATURE CITED

Bakker, J. P., H. Olff, J. H. Willems, and M. Zobel. 1996. Why do we need permanent plots in the study of long-term vegetation dynamics? Journal of Vegetation Science **7:**147–156.

Bakker, P. A. 1979. Vegetation science and nature conservation. Pages 247–288 in M. J. A. Werger, editor. The study of vegetation. Junk Publishers, The Hague.

Bekker, R. M., J. P. Bakker, U. Grandin, R. Kalamees, P. Milberg, P. Poschlod, K. Thompson, and J. H. Willems. 1998. Seed size, shape and vertical distribution in the soil: indicators of seed longevity. Functional Ecology **12:**834–842.

Bobbink, R. 1989. *Brachypodium pinnatum* and the species diversity in chalk grassland. Ph.D. thesis. Utrecht University, Utrecht, The Netherlands.

Bobbink, R. 1991. Effects of nutrient enrichment in Dutch chalk grassland. Journal of Applied Ecology **28:**28–41.

Bobbink, R., and J. H. Willems. 1987. Increasing dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grasslands: a threat to a species-rich ecosystem. Biological Conservation **40:**301–314.

Bobbink, R., L. Bik, and J. H. Willems. 1988. Effects of nitrogen fertilization on vegetation structure and dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grassland. Acta Botanica Neerlandica **37:**231–242.

Bobbink, R., and J. H. Willems. 1991. Impact of different cutting regimes on the performance of *Brachypodium pinnatum* (L.) Beauv. in Dutch chalk grassland. Biological Conservation **56:** 1–21.

Bobbink, R., and J. H. Willems. 1993. Restoration management of abandoned chalk grassland in the Netherlands. Biodiversity and Conservation **2:**616–626.

Brown, V. K., and C. W. D. Gibson. 1994. Re-creation of species-rich calcicolous grassland communities. Pages 125–136 in R. J. Haggar, and S. Peel, editors. Grassland management and nature conservation. British Grassland Society, Maidenhead (Berkshire), United Kingdom.

de Kroon, H. 1990. In search of a foraging plant: the clonal growth of *Brachypodium pinnatum* and *Carex flacca*. Ph.D. thesis. Utrecht University, Utrecht, The Netherlands.

Dierschke, H., and M. Engels. 1991. Response of a *Bromus erectus* grassland (Mesobromion) to abandonment and different cutting regimes. Pages 375–397 in G. Esser, and D. Overdieck, editors. Modern ecology: basic and applied aspects. Elsevier, Amsterdam.

Diemont, W. H., and A. J. H. M. van de Ven. 1953. De kalkgraslanden van Zuid-Limburg. Publicaties Natuurhistorisch Genootschap in Limburg **VI:**3–20 (with a summary in French).

Dutoit, Th. 1996. Dynamique et gestion des pelouses calcaires de Haute-Normandie. Ph.D. thesis. University of Rouen, Rouen, France.

Dutoit, Th., and D. Alard. 1995. Permanent seed banks in chalk grassland under various management regimes: their role in the restoration of species-rich plant communities. Biodiversity and Conservation **4:**939–950.

Dzwonko, Z., and S. Loster. 1998. Dynamics of species richness and composition in a limestone grassland restored after tree cutting. Journal of Vegetation Science **9:**387–394.

Ellenberg, H. 1988. Vegetation ecology of Central Europe. Cambridge University Press, Cambridge, United Kingdom.

Fischer, F., P. Poschlod, and B. Beinlich. 1996. Experimental studies on the dispersal of plants and animals by sheep in calcareous grassland. Journal of Applied Ecology **33:**1206–1222.

Green, B. H. 1990. Agricultural intensification and the loss of habitat, species and amenity in British grasslands: a review of historical change and assessment of future prospects. Grass and Forage Science **45:**365–372.

Hakes, W. 1988. Vergleich der Pflanzenbestandesstruktur genutzter und brachliegender Kalk-Halbtrockenrasen in Nordhessen. Phytocoenologia **16:**289–314.

Hennekens, S. M., J. H. J. Schaminée, and V. Westhoff. 1985. The development of chalk grassland on abandoned fields in South Limburg, The Netherlands. Colloques Phytosociologiques **11:**471–485.

Keymer, R. J., and S. J. Leach. 1990. Calcareous grassland - a limited resource in Britain. Pages 11–17 in S. H. Hillier, D. H. W. Walton, and D. A. Wells, editors. Calcareous grasslands: ecology and management. Bluntisham Books, Bluntisham, United Kingdom.

Kull, K., and M. Zobel. 1991. High species richness in an Estonian wooded meadow. Journal of Vegetation Science **2:**711–714.

Meusel, H., E. Jäger, and E. Weinhert. 1965. Vergleichende Chorologie der zentral-europäischen Flora. Fischer, Jena, Germany.

Milberg, P. 1995. Soil seed bank after eighteen years of succession from grassland to forest. Oikos **72:**3–13.

Mitchley, J., and P. J. Grubb. 1986. Control of relative abundance of perennials in chalk grassland in southern England. 1. Constancy of rank order and results of pot- and field-experiments on the role of interference. Journal of Ecology **74:**1139–1166.

Mitchley, J., and J. H. Willems. 1995. Vertical canopy structure of Dutch chalk grasslands in relation to their management. Vegetatio **117:**17–27.

Muller, S., T. Dutoit, D. Alard, and F. Grévilliot. 1998. Restoration and rehabilitation of species-rich grassland ecosystems in France: a review. Restoration Ecology **6:**94–101.

Oomes, M. J. M., and H. Mooi. 1981. The effect of cutting and fertilizing on the floristic composition and production of an *Arrhenatherion elatioris* grassland. Vegetatio **47:**233–239.

Oostermeijer, J. G. B., A. Berholz, and P. Poschlod. 1996. Genetical aspects of fragmented plant populations. Pages 93–101 in J. Settle, C. R. Margules, P. Poschlod, and K. Henle, editors. Species survival in fragmented landscapes. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Pärtel, M., M. Zobel, K. Zobel, and E. van der Maarel. 1996. The species pool and its relation to species richness: evidence from Estonian plant communities. Oikos **75:**111–117.

Peet, R. K., D. C. Glenn-Lewin, and J. W. Walker-Wolf. 1983. Prediction of man's impact on plant species diversity. Pages 41–54 in W. Holzner, M. J. A. Werger, and I. Ikusima, editors. Man's impact on vegetation. Junk Publishers, The Hague, The Netherlands.

Poschlod, P. 1993. Die Dauerhaftigkeit von generativen Diasporenbanken in Böden am Beispiel von Kalkmagerrasenpflanzen und deren Bedeutung für den botanischen Arten- und Biotopschutz. Verhandlungen der Gesellschaft für Ökologie **22:**229–240.

Poschlod, P. S., S. Kiefer, U. Tränkle, S. Fischer, and S. Bonn. 1998. Plant species richness in calcareous grasslands as affected by dispensability in space and time. Applied Vegetation Science **1:**75–90.

Pottier-Alapetite, G. 1943. Recherches phytosociologique et historiques sur la végétation du Jura central et sur les origines de la flore jurassienne. SIGMA Communication 81. La Rapide, Tunis.

Rose, F. 1981. The wild flower key: British Isles - N. W. Europe. Frederick Warme Publishers, London, United Kingdom.

Ryser, P., B. Verduyn, and H. Lambers. 1997. Phosphorus alloca-

tion and utilization in three grass species with contrasting response to N and P supply. New Phytologist **137:**293–302.
Schamineé, J. H. J., A. H. F. Stortelder, and E. J. Weeda. 1996. De vegetatie van Nederland, deel 3. Plantengemeenschappen van graslanden, zomen en droge heiden. Opulus Press, Uppsala, Sweden - Leiden, The Netherlands.
Schenkeveld, A. J., and H. J. Verkaar. 1984. On the ecology of short-lived forbs in chalk grasslands. Ph.D. thesis. Utrecht University, Utrecht, the Netherlands.
Scherrer, M. 1925. Vegetationsstudien im Limmattal. Veröffentlichungen des Geobotanisches Institut Rübel - 2, Zürich, Switzerland.
Schleumer, H. 1934. Die Pflanzenwelt des Kaiserstuhls. Pflanzensoziologie Band 8, Fischer Verlag, Jena, Germany.
Tansley, A. G. 1939. The British Isles and their vegetation. University Press, Cambridge, United Kingdom.
Thompson, K., S. R. Band, and J. G. Hodgson. 1993. Seed size and shape predict persistence in soil. Functional Ecology **8:**29–35.
Tutin, T. G., V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters, and D. A. Webb. 1964–1980. Flora Europaea. Cambridge University Press, Cambridge, United Kingdom.
van Dam, D. 1990. Atmospheric deposition and nutrient cycling in chalk grassland. Ph.D. thesis. Utrecht University, Utrecht, The Netherlands.
van der Hoeven, E. C. 1999. Do chalk grassland bryophytes compete? Ph.D. thesis. Utrecht University, Utrecht, The Netherlands.
van Speybroek, D. 1989. Synecology of the chalk and limestone grasslands in Belgium, Luxemburg and northern France. Ph.D. thesis. Free University, Brussels, Belgium.
van Tooren, B. F. 1989. The ecological role of the bryophyte layer in Dutch chalk grasslands. Ph.D. thesis. Utrecht University, Utrecht, The Netherlands.
van Treuren, R. 1993. The significance of genetic erosion for the extinction of locally endangered plant populations. Ph.D. thesis. University of Groningen, The Netherlands.
Verbeke, W., and M. Lejeune. 1998. Quatre carrés permanents dans une pelouse calcaire de la Montagne Saint-Piere. Resultats sur douze années. Pages 61–69 in O. Decocq, and L. Woué, editors. La gestion des pelouses calcaires. Cercles des Naturalistes de Belgique, Vierves-sur-Viroin, Belgium.
Wells, T. C. E. 1974. Management and mowing. Pages 190–196 in E. M. Duffey, G. Morris, J. Sheail, L. K. Ward, D. A. Wells, and T. C. E. Wells, editors. Grassland ecology and wildlife management. Chapman and Hall, London, United Kingdom.
Westhoff, V. 1979. Phytosociology in The Netherlands: history, present state, future. Pages 81–122 in M. J. A. Werger, editor. The study of vegetation. Junk Publishers, The Hague, The Netherlands.
Willems, J. H. 1978. Observations on north-west European limestone grassland communities: phytosociological and ecological notes on chalk grasslands of southern England. Vegetatio **37:**141–150.
Willems, J. H. 1980a. Observations on N.W. European limestone grassland vegetation I. Limestone grassland vegetation in the central part of the French Jura, South of Champagnôle (dept. Jura). Koninklijke Nederlandse Akademie van Wetenschappen, series C **76:**231–244.
Willems, J. H. 1980*b*. Limestone grassland in north-west Europe. Ph.D. thesis. Utrecht University Utrecht, The Netherlands.
Willems, J. H. 1982. Phytosociological and geographical survey of Mesobromion communities in western Europe. Vegetatio **48:** 227–240.
Willems, J. H. 1983. Species composition and above-ground phytomass in chalk grassland with different management. Vegetatio **52:**171–180.
Willems, J. H. 1987. Kalkgrasland in Zuid-Limburg. Wetenschappelijke Mededelingen KNNV, Hoogwoud, Nr. 184 (with summary in English).
Willems, J. H. 1988. Soil seed bank and regeneration of a *Calluna vulgaris* community after forest clearing. Acta Botanica Neerlandica **37:**313–320.
Willems, J. H. 1990. Calcareous grasslands in Continental Europe. Pages 3–10 in S. H. Hillier, D. H. W. Walton, and D. A. Wells, editors. Calcareous grasslands. Ecology and management. Bluntisham Books, Bluntisham, United Kingdom.
Willems, J. H. 1995. Soil seed bank, seedling recruitment and actual species composition in an old and isolated chalk grassland site. Folia Geobotanica et Phytotaxonomica **30:** 141–156.
Willems, J. H., and R. Bobbink. 1990. Spatial processes in the succession of chalk grassland on old fields in The Netherlands. Pages 237–249 in F. Krahulec, A. D. Q. Agnew, S. Agnew, and J. H. Willems, editors. Spatial processes in plant communities. Academia Press, Prague, Czech Republic.
Willems, J. H., R. K. Peet, and L. P. M. Bik. 1993. Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. Journal of Vegetation Science **4:** 203–212.
Willems, J. H., and K. G. A. Huijsmans. 1994. Vertical seed dispersal by earthworms: a quantitative approach. Ecography **17:**124–130.
Willems, J. H., and M. L. G. van Nieuwstadt. 1996. Long-term after effects of fertilization on above-ground phytomass and species diversity in calcareous grassland. Journal of Vegetation Science **7:**177–184.
Willems, J. H., and J. Ellers. 1996. Plant performance and population characteristics of *Orchis simia* (Orchidaceae) in two extremes of its distribution area. Flora **191:**41–48.
Willems, J. H., and L. P. M. Bik. 1998. Restoration of high species density in calcareous grassland: the role of seed rain and soil seed bank. Applied Vegetation Science **1:**91–100.
Zobel, M., E. van der Maarel, and C. Dupré. 1998. Species pool: the concept, its determination and significance for community restoration. Applied Vegetation Science **1:**55–66.