Vegetation dynamics and erosion resistance of sea dyke grassland

J.T.C.M. Sprangers

Vegetation dynamics and erosion resistance of sea dyke grassland

J.T.C.M. Sprangers

Proefschrift

ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van de Landbouwuniversiteit Wageningen,
dr. C.M. Karssen,
in het openbaar te verdedigen
op vrijdag 12 februari 1999
des namiddags te 1.30 uur in de Aula.

ABSTRACT

The high erosion resistance of grass swards on clay dykes seems to be largely determined by the amount of roots and the root system architecture. Following on previous studies on river dykes which revealed high root densities and erosion resistance in unfertilised pastures and hay-meadows, we experimentally investigated the influence of cessation of fertiliser application in combination with different management regimes on factors affecting water erosion of sea dyke grassland in the Netherlands. From 1991 to 1994 a study was done on the botanical composition, vegetation cover, above- and belowground biomass production (root density) and chemical composition of the soil and plant tissue.The erodibility of the sward was tested in field and laboratory experiments, and shear strength was measured. Unfertilised, species-rich grasslands were investigated as a reference. After continuing the experiment till 1997, data on biomass production and chemical composition in 1997 were analysed as well.

Three to four years after cessation of fertilisation we observed a slight increase in species number (from 13 to 16 species per 25 m^2), a decline in cover or abundance of Lolium perenne and an increase of species of less nutrient-rich conditions. Also, a rather rapid decline was detected in the aboveground biomass production from 9-10 tonnes dry matter to 7 t $ha^{-1}y^{-1}$ after 4 years, and subsequently to 5-6 t $ha^{-1}y^{-1}$ after seven years. Shifting from grazing to haymaking without the use of fertiliser resulted in the most drastic drop in biomass, reaching the level of the reference dykes. Together with the decline in biomass, a drop in mineral nitrogen availability was measured . The total soil N pool, however, was not changed. No decline in the cover of the vegetation (cut back to a height of 2 cm) or shoot density was found.

In the mown treatments on both pastures and hayfields, cessation of fertilisation resulted in an increased root length and root weight, and lower shoot to root ratios. Species-rich old meadows exhibited relatively high root length and root weight values, and low shoot to root ratio's, and appeared to be characterised by a less steep decline of root density with depth than the species-poor fertilised pastures. Pastures were observed to have somewhat high specific root lengths (SRL, thin roots), and hayfields low SRL (thick roots), except for the species rich hay-meadow, characterised by high SRL.

No seasonal fluctuation in root mass was measured in both fertilised pastures and unfertilised old hay meadows, so that the root length fluctuation measured in both types is caused by growth and decay of fine roots. Spatial variation in root weights seemed to be higher in the floristically homogeneous fertilised pastures.

Shear strength measurements did not reflect soil cohesion due to higher root density and therefore the use of shear strength is not recommended as a parameter for erosion resistance. Although erosion spray experiments did not show significant effects between

treatments, the erosion centrifuge experiments showed a significant relation between resistance against internal erosion and the combined effect of root density and particle size.

In dyke grassland management we conclude that the main prerequisites for a high erosion resistance of the sod constitute avoiding the use of fertiliser in combination with haymaking or grazing and proper maintenance sustained over long periods. While judging the erodibility, more emphasis should be put on botanical composition than on clay quality.

Voorwoord

Het is niet vreemd dat in een land dat zonder dijken meteen voor de helft onder water zou lopen het verhaal van Hansje Brinker beklijft. Met één vinger de dijk redden spreekt aan: held worden als gevolg van de zwakke plek in de constructie. De vergelijking gaat natuurlijk niet helemaal op, buiten dan de overeenkomst in voornaam, maar 7 jaar lang onderzoek doen aan de kwetsbare plek van dijken (het gras), levert een behoorlijke dosis "Hansje Brinker gevoel". De realiteit is anders: onderzoekers zijn geen helden en het gevoel delen ze met de mensen met wie ze samenwerken. Die mensen wil ik hier noemen. Zij hebben bijgedragen aan dit zeedijkenonderzoek en de totstandkoming van dit proefschrift.

Graag bedank ik mijn promotoren Karlè Sýkora en Frank Berendse. Karlè, onze gemeenschappelijk belangstelling voor de vegetatiekunde vormde het begin van een inmiddels 10 jaar lange samenwerking. Hierin konden we onze wederzijdse interesse voor onderzoek naar wat nu modieus "multifunctionele natuur" wordt genoemd, verder ontwikkelen. Je hebt me daarin steeds gesteund en dit proefschrift is daar een tastbaar bewijs van. Bedankt voor al je begeleiding, betrokkenheid en vertrouwen. Frank, je was bereid een al langer lopend toegepast onderzoek kritisch tegen het fundamenteel-wetenschappelijke daglicht te houden. Jouw aanwijzingen en vooral je revisie van de conceptteksten hebben mij bijzonder geholpen. Op deze plaats wil ik ook Willem Vos bedanken. Door aan mijn aanstelling bij het IBN de voorwaarde van een promotie te verbinden en daarvoor ook daadwerkelijk faciliteiten te creëren, kon de knop definitief worden omgezet. Willem, het heeft gewerkt, zij het dat het toch weer iets langer duurde. Maar, het ligt er nu, en dat komt dus ook door jou !

Ook professor Piet Zonderwijk wil ik hier graag bedanken. Hij gaf destijds leiding aan het samenwerkingsverband Vakgroep VPO - Adviesgroep Vegetatiebeheer, en was als architect van deze "Kenniseenheid Groene Ruimte avant la lettre" zijn tijd vooruit. Ook na zijn emeritaat begeleidde hij het zeedijkenonderzoek en overtuigde menig betrokkene binnen TAW-verband van de noodzaak civiele techniek en ecologisch onderzoek te integreren.

Werkgroep A (belasting en bekleding) van de TAW wil ik hierbij bedanken voor het financieel mogelijk maken van het onderzoek. Jan Muijs en Jan-Willem Seijffert hebben vanuit DWW-Rijkswaterstaat waar mogelijk bijgedragen, en de resultaten steeds intensief gevolgd zowel op papier als in het veld. Met Jan heb ik bijna letterlijk strijd moeten leveren om de vaak ingewikkelde administratieve afwikkeling van contracten rond te kunnen breien. Jan, onze inspanning was niet voor niets, graag bedank ik je voor je inzet.

Zonder de hulp van waterschappen en pachters was het onderzoek niet mogelijk geweest. Waterschappen hebben kosteloos mankracht en materiaal ter beschikking gesteld voor inrichting, beheer en onderhoud van proefvakken. Pachters hebben – soms tegen een geringe vergoeding – letterlijk rare bochten moeten maken om het gewijzigde beheer van veelal kleine proefvakken in te passen. De gesprekken met HTD's, dijkbeheerders, opzichters en pachters hebben mij veel geleerd over de praktijk van het graslandbeheer. Ik wil hen allen hartelijk danken voor hun inzet en hulp bij het onderzoek.

Contents

1

General introduction

1.1 Dyke functions

The recent flooding of rivers in the Netherlands and near the Polish border in Germany has stressed the importance of dyke stability and safety (Anonymous 1995b, 1995c). Also the threat of a rising sea water level as a result of climatic changes (Anonymous 1990), urges civil engineers to reconsider present safety margins for the stability and erodibility of sea dykes. In the Netherlands this has led to renewed measures for reconstruction and maintenance care in several cases (Anonymous 1994a, 1994b, 1995c, 1995d). To guarantee dyke safety, features like stability and erosion resistance will be evaluated every five years according to official guidelines for the Dutch water management authorities, which have been recently published by the Technical Advisory Committee for Water Defences (Anonymous 1996a, 1996b, 1998).

Besides the height and width of the dyke body itself , the cover of the dyke and its resistance against erosion by waves or running water plays an important role in the safeguarding of dyke stability. This cover can consist of concrete (stones, cement blocks or asphalt) or turf. Management of the grass sward has a great impact on the quality of erosion resistance (Sýkora & Liebrand 1988, Sprangers et al. 1991, Van der Zee 1992, Coppin & Stiles 1995). From a civil engineering point of view a grass dominated plant community with a vigorous root growth and a closed sward must be maintained. Frequent defoliation by sheep grazing or frequent cutting usually results in a closed sward and reduction in root growth. Haymaking, on the other hand, leads to deeper root growth at the cost of shoot density (Coppin & Stiles 1995). Choosing the type and intensity of management currently depends on the other secondary function(s) of dykes like agricultural production and recreation, and their ecological functions as a part of the landscape (corridor, refugium, gene source, specific habitat). Intensive fertilizer application in agricultural production in both pasture and hayfields results in shallow-rooted or very open systems. Amenity turf management (7-8 x mowing per year) often done for recreation purposes near buildings and houses, also results in a shallow-rooted grass sward. To stimulate the occurrence of natural habitats or the connection between these habitats (corridors) haymaking without the use of fertilizer seems to be the preferred choice.

In line with modern practice in landscape and environmental planning in the search for an optimal combination of functions, as is the case with the construction of road borders and crossings (Anonymous 1995a) and river and canal banks (Anonymous 1994a,

1994b, 1995c), what is needed is dyke grassland management that results in a high erosion resistance that also fits in well with one of the other dyke grassland functions. To decide which measures are best more knowledge is needed of the relation between vegetation, management and erodibility of dyke grassland. This study endeavours to bridge this knowledge gap.

1.2 Erosion resistance of dyke grassland

Grass is the most common and maybe the best known cover of dykes. It is used to cover and protect the clay layer of river embankments and sea dykes, often combined with concrete blocks or columns in fixed settings or asphalt for the base. In large-scale experiment with turf taken from a Friesian dyke and exposed to waves of 1.5 m in height for 16 hours, intact grass sods proved to be extremely strong and capable of limiting soil erosion to approximately 0.4 cm h^{-1} (Smith 1993, Kruse 1994). This is low if erosion resistance is compared with the results of a layer of concrete blocks 20 cm thick. Here, blocks were sometimes dislodged by waves of one m height after two hours (Smith, 1993). Turf seems to possess a kind of 'elasticity' to better withstand the power of huge wave attacks than solid blocks (Kruse 1993, Anonymous, 1998). In experiments on internal erosion of grass sods, i.e. erosion of soil particles from the pores inside the sward, an erosion rate was found of 0.1-0.2 cm h^{-1} (Van Essen 1994).

The above mentioned-erosion rates are found in the upper soil layers at a depth 0-6 cm containing about 65 % of the total amount of roots (Coppin & Richards 1990, Sprangers 1994). At a depth of 6-15 cm with 20 % of the roots the estimated erosion rate was 2-3 cm h^{-1} (Smith 1993). Below 15 cm with only 15 % of the roots measured in a column up to 50 cm deep, the estimated erosion rate was more than 10 cm h^{-1}, corresponding with the results of wave experiments with uncovered clay. Furthermore, these experiments proved that soil under turf has a greater strength than soil under blocks, possibly due to the effect of roots on cohesion of soil particles to a depth of several dm (Kruse 1994a).

Erosion resistance of grassland seems to be not only dependent on soil structure (granular composition and the amount and size of clay aggregates), but also on the root density of the top layer (-10 cm). Porosity seems to play an important role in withstanding the forces brought about by severe wave attacks (Van Essen 1994).

To understand the significance of turf to erosion resistance, we need to look at the structure of the clay-root-complex in the upper soil layers and take into account the erosion mechanisms. Both aspects will be discussed.

Structure of grass sods

Sea and river dykes usually consist of a sand body covered with clay (Figure 1.1). Sometimes this clay layer can be divided in a top layer (0.3 m) consisting of a more sandy or humus material to benefit plant growth, and a lower layer of heavier clay (Anonymous 1996). Nowadays, while reconstructing the dyke, the top layer of the old dyke is often used to form the upper layer of the new dyke. Clay is used for its low permeability and high consistency (low distortion). The structure of the clay layer is influenced by climate (shrink and swell), root growth, and activity of soil fauna: different sized aggregates are formed with pores in between (Hartge 1994, Anonymous 1996). This soil structure lowers the clay
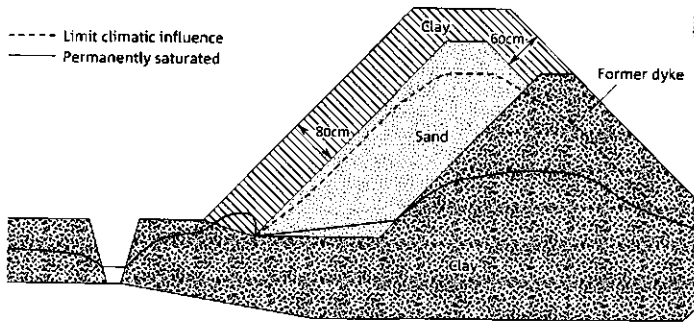
Figure 1.1 *Profile of a reinforced dyke with a permanently saturated zone and a zone under influence of climate. In the new dyke the former dyke is still visible (source: Anonymous 1996a).*
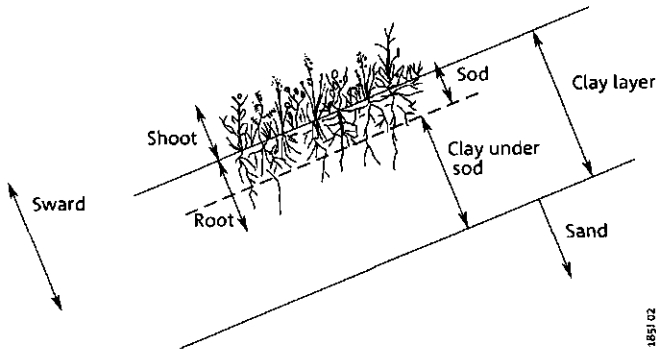
Figure 1.2 *Composition of clay layer with grass cover (Anonymous 1996a, figure modified)*

quality, because its permeability is increased. Plant growth, furthermore, contributes to the development of this soil structure, and enhances infiltration of the upper-layer (Coppin & Richards 1990, Hartge 1994). The development of soil structure continues even under concrete blocks or asphalt(Anonymous 1996). The smallest aggregates (0.002-2 mm) are found in the grass sod in the upper layer of the clay cover. Underneath the sod the structure is less developed and bigger angular aggregates occur up to 0.2 m (Figure 1.2).

Soil aggregates - the bigger ones sometimes composed of smaller ones - are held together by coagulation (aggregates < 0.002 mm); chemical bonding through organic matter from bacterial origin (0.002 - 0.02 mm); chemical bonding through organic matter (polysaccharides and lipids) from roots and mycorrhizae and cementation by carbonate,

silicium, ferro- and aluminium-compounds (0.02 - 0.25 mm); and through a fine network of roots and fungal hyphae (0.25 - 2 mm) (Kruse 1993 and references therein, Anonymous 1996a). Aggregates bigger than 0.5 mm, can be held together by fine roots, that penetrate the aggregates (Kruse 1993, Anonymous 1998). Particles of 3 - 5 mm are both enclosed and penetrated by the network of roots (Kruse 1993, Van Essen 1994).

The soil structure that develops in the rooting zone becomes highly cohesive through this binding and cementation of aggregates. The fineness and stability of the aggregates determines the porosity and permeability of the grass sod, which greatly influences the erosion resistance.

Root-clay interaction

Roots play an important role in developing both structure (fineness of aggregates and pores) as well as stability (bonding of aggregates by cementation, penetration and enclosure) in clay soils. The soil structure in the well-rooted layer of the sod is finer-grained than in deeper layers. In erosion experiments with grass sods a structure of fine aggregates was found in zones with high root density, and large, mechanically strong aggregates in zones with low root density (Van Essen 1994). By penetrating soil particles, roots contribute to a fine soil structure. Furthermore, the activity of soil fauna foraging on the roots also contributes to the fine-grained soil structure.

The soil under grass turf has a relatively stable structure, because of biomass production, rhizodeposition which stimulates microbial growth, and the supply of aggregate binding compounds (Lichtenegger 1985, Lynch 1990, Goss 1991, Gli'nsky & Lipiec 1993). The stability of aggregates and the mean root length and root weight are positively related (Perfect *et al.* 1990).When root length is high, there is a high coagulation of aggregates and rhizodeposition (Kruse 1993). Soil moisture depletion by evapotranspiration and desiccation around rootlets stimulates the formation of smaller aggregates: higher soil suction because off the lower pore-water pressure increases the attraction between soil particles through the effect of residual capillary water (Coppin & Richard, 1990). Since soil suction increases as the size of voids and capillary channels decreases, its contribution to cohesion is greater in finer-grained soils. Root hairs anchor the developing roots to soil particles. Hyphae, i.e. filaments in mycelium of fungi, also contribute to formation and maintenance of aggregates. The amount of stable aggregates larger than 2 mm is proportionate to the length of hyphae. The carbon-hydrogen cover of (dead) bacterial colonies can bind clay particles. Small aggregates formed this way are very stable in soils under old grasslands with a high content of lutum and organic matter (Kruse 1993).

There is a dynamic equilibrium between the formation and demolition of aggregates in soils under stable, well-developed vegetation. Roots influence the microclimate and changes in temperature and moisture content (Coppin & Richards 1990). Furthermore, roots can sometimes neutralize the effects of soil cracks in clay as a result of shrinkage after the construction of a dyke, are sometimes neutralized by roots (Anonymous 1996a, Muijs 1996). Seasonal effects and moisture content indirectly affect aggregate stability (Kruse 1993). Bacterial populations, influencing the stability of smaller aggregates, are at their peak at the end of the summer. The amount of fungi, which affect cohesion of aggregates, changes during the season. Just after winter, when the moisture content is high, the fraction of bigger aggregates (> 2 mm) is relatively small, but rather high at the end of

the summer. These aggregates are subject to an equilibrium with a constant renewal of bonding, maintained by rhizodeposition of fine roots in and around the aggregates. A network of such fine roots influences small-scale changes in moisture content, contributing to a fine structure in cohesive soil. Intensive tread (trampling), big changes in the salt content of pore water and some organic compounds may decrease the stability of this fine dynamic structure.

We may conclude that apart from the granular composition of the clay, depth and density of the root network in the grass sods largely determine the stability of the clay layer. Stability will be low in the absence of roots or when root density is low, no matter if in the upper layer the aggregates are large or the structure is fine. This means that factors that influence root density and rhizosphere, such as *botanical composition, soil nutrient level,* and *management type (fertilization, grazing and haymaking)* also have an impact on size and stability of the soil aggregates and their cohesion (cf. Kandeler & Murer, 1993). However, more research is needed to further clarify this relation between clay quality and root density.

Erosion mechanisms

One can distinguish different types of erosion that affect clay used as a cover in dyke construction: suspension of fine material in water; the removal of small particles like sand-grains and small aggregates by flowing water; and the breaking away of larger fragments through heavy wave attack (Anonymous 1996a). The first type is usually a long-term process, where even without any flow, particles absorb so much water that there is loss of cohesion between particles. In the second type, smaller particles loosen when vertical water movements and water pressure provoked by low waves overrule the adhesive forces in the soil. With high waves, the pressure built up lifts bigger fragments out of the soil, specially when the turf is missing or damaged (cf. Anonymous 1984, Seijffert & Philipse 1990, Smith 1993). The effectiveness of water flowing through grass sods by wave attack in removing soil particles is determined by pore structure, permeability and saturation. Erosion experiments have shown that the flow rates, reached by wave attack, on the surface and through the sods were not sufficient to remove particles held together by cementation. Erosion of smaller particles only occurs when the chemical bonding of one particle to another or to roots is weak, as is the case with sand grains or bigger aggregates. Fine particles with a somewhat large chemical reactive surface have a large amount of chemical bondings. The erosion of lutum-sized particles will be small. This means that the percentage of sand and the size of aggregates (structure) in soil determine the extent of internal erosion.

The presence of a fine network of roots prevents the erosion of sand grain-sized particles by inclusion (Van Essen 1994) and limits flow rates. In less cohesive soils severe erosion will take place when gaps in the root network occur. Also in cohesive soils erosion will increase when roots are not homogeneously distributed, because fewer surrounding particles will be kept in place, when one soil particle is washed away. Individual grass roots are strong enough (0.1 - 2.0 N, depending on root diameter and species) to resist high flow rates (Lichtenegger 1985, Kruse 1993). However, according to Kruse (1993), the permeability of the sod which is probably responsible for the specific properties ('elasticity') of grass swards to intercept the forces of severe wave attack, is not determined by the rooting system but by the pore structure. Nevertheless, roots have an

indirect effect: pores in the soil are formed by the dying off of old roots, among others. The total pore volume increases with rooting density (Coppin & Richards 1990).

At the surface, the flow velocity of water flowing up and down as a result of wave movements is reduced by the vegetation cover (Sykora & Liebrand, 1988). Moreover, soil particle movement is reduced. These retarding effects of the grass sward on runoff volume and velocity depends on the percentage canopy cover (Coppin & Richards 1990). However, when the vegetation is too long, e.g. where grazing or cutting before the winter season is insufficient, the sward can be damaged by waves seizing at long tussocks of grass and moving these tussocks to and fro (N. Bakker, pers. comm.).

The erosion resistance of grass swards on dykes seems to be dependent primarily on the type and intensity of root growth (the rooting system) and less on the quality of the clay that is used. There is an indirect effect of roots influencing soil structure, cohesiveness and pore volume, and a direct effect of the actual root network and physical strength of individual roots. This means that if we could stimulate root growth by manipulating factors that influence root density and rhizosphere, such as *botanical composition* and *soil nutrient level* by adjusting the type of management used for maintaining the sward, for example, we would have an important tool for improving the protective properties of grassland against water erosion. The canopy structure, i.e. vegetation cover and sprout density, influences surface erosion and should therefore be paid special attention, when adjusting management.

1.3 Vegetation type, sward characteristics (e.g. root density) erosion resistance and management

A variety of grassland types can develop on dykes and embankments depending on habitat factors (soil conditions and exposition) and management (grazing by sheep or cattle, haymaking or mowing without removing cuttings, use of fertilizer or herbicide). Previous investigations of the grassland vegetation of sea and river dykes showed a clear relationship between botanical composition, habitat factors, management, rooting density, canopy cover, and erosion resistance (Sýkora & Liebrand 1987, Sprangers 1989, Sprangers *et al.* 1991, Van der Zee 1992). Species-rich dyke grassland, extensively managed by sheep-grazing or hay-making without the use of fertilizer, is characterized by a relatively high root-density and high to moderate canopy cover (sprout density). This is the case with botanically well-developed relatively species-rich grasslands belonging to the phytosociological syntaxa *Medicagini-Avenetum*, *Arrhenatheretum elatioris* and *Lolio-Cynosuretum*. Species-poor, fertilized grassland, intensively managed by sheep grazing (*Poo-Lolietum*), and grassland mown twice a year without removal of cuttings (fragmentary *Arrhenatheretum*), are characterized by a high aboveground production but low root density and in the case of the poor *Arrhenatheretum* a very low shoot density.

Surface area

The total area of grassland on primary dykes comes to 80 km^2 equally divided over sea dykes and river dykes. About 90 to 95 % of the river embankments are covered by species-poor and agriculturally-managed, high-productive pastures, and abandoned and overgrown rough meadows (van der Zee 1992, Fliervoet 1992, Anonymous 1998). Less than 2 km^2 is

occupied by semi-natural species-rich grassland. Species-rich communities hardly occur on dykes along the coast: 85 % consists of species-poor agricultural grassland grazed by sheep, and 15 % of species-poor grassland used for hay-production. However, species-rich grassland is sometimes found on inland dykes (secondary dykes) and on dykes along the lakes of the southern estuary.

Roughly four types of grasslands could be distinguished on sea dykes (Sprangers 1989):

- Poo-Lolietum, species-poor and intensively grazed pastures, fertilized with approximately 100-150 kg N ha^{-1}yr^{-1} ;
- Lolio-Cynosuretum, less species-poor and less intensively fertilized (c. 90 kg N ha^{-1}yr^{-1}) periodically grazed grassland. In the northern parts of the Netherlands this type is maintained by well-organized maintenance measurements, like cutting of the non- or partly-eaten plants, the spreading of dung after a period of grazing, and trapping of moles (Bakker 1988);
- fragmentary Arrhenatheretum elatioris, fertilized hay-meadow (100-200 kg N ha^{-1}yr^{-1}) with two to three cuttings a year, with a very open sward and sometimes composed by only two to three species; and
- Arrhenatheretum elatioris brizetosum, species-rich and unfertilized hayfield, mown once a year, with many grass species and herbs.

Sward characteristics and management

Several studies have been conducted on the relationship between management, botanical composition, and above- and belowground biomass production of grassland (Bakker 1989, Olff & Bakker 1991, Berendse *et al.* 1992, Olff *et al.* 1994, Oomes *et al.* 1996). In species-poor , fertilized grasslands (*Poo-Lolietum*) the belowground biomass is relatively low, whereas in natural to semi-natural species-rich grassland communities the belowground biomass is high (Kmoch 1952, Fliervoet 1984, Sýkora & Liebrand 1987, Bakker 1989, Sprangers *et al.* 1991, Van der Zee 1992). The vegetation in species-rich grassland consists of many grass and herb species, each with its own rooting pattern, which is also affected by the nutrient level in the soil and competition between species (Kutschera & Lichtenegger 1982). A stratified root system is formed, with grass roots growing in the upper layers and roots of herbs growing in deeper layers of the soil (cf. Berendse 1982, Lichtenegger 1985, Schiechtl 1985). Soils of species-rich communities possess a greater spatial heterogeneity of nutrient availability. This greater variation stems from local differences in mineralization and microbial turnover of organic matter because of differences in the quantity and the decomposability of the dead root material that the various species produce (Miles 1987, Berendse 1990, Ozinga 1997). This phenomenon, in combination with a high root density, is favourable for aggregate-stability in clay soils.

The low belowground biomass in high-productive agricultural grasslands in contrast with the higher share of roots in the total mass of plants as a result of mineral deficiency, can be clearly explained using the work of Brouwer (1962, 1983). On the basis of experiments where the shoot/root ratio of barley and maize plants were investigated at different N-applications, he describes a *functional equilibrium* between shoots and roots, reflected by a constant shoot/root-ratio under separate sets of external conditions. Increasing the uptake of minerals, for example by fertilization, will increase shoot growth relative to root growth until shoot growth is limited when the maximum uptake of minerals

and moisture by the roots is reached (Brouwer 1962). Consequently, root growth will increase as a result of a higher supply of carbohydrates that cannot be converted into increased shoot growth. As root growth increases mineral and moisture uptake will increase and the cycle can be repeated until shoot growth and root growth are equally limited by carbohydrate and nutrient supply (cf. Van der Werff 1993). It appears that the carbon allocation to shoots and roots in relation to nitrogen supply is mediated by the production of cytokinins in the roots, which enhance photosynthetic capacity and leaf expansion (Lambers et al 1998). Cutting off the shoots (for example by grazing) will disturb the equilibrium. Shoot growth will increase again when mineral and moisture supply is abundant and the maximum uptake capacity of the roots is not reached. In the case of grasslands the continuously disturbed equilibrium results in a system with a rather low root density and a high shoot production.

The results of several investigations of the root system of agricultural or otherwise managed grassland are in line with this theory. To reach the maximum root mass considerably less N is needed than for maximum shoot production (Dirven & Wind 1980, Sibma & Ennik, 1988). Above a certain N level the root system will no longer increase, even though the maximum uptake of minerals and moisture has not yet been reached. Reduction of the leaf area decreases root growth (Througton 1981). Intensive grazing results in superficial root growth and a shorter life cycle of the roots (Fiala & Studeny, 1988). With mulching the root density remains low due to an increased soil fertility by mineralization of the organic matter, supported by favourable moisture conditions under the remaining cuttings (Sýkora & Liebrand, 1987). Ungrazed or very infrequently cut swards become tall-grass communities with a fairly dense growth, but an open sod. Regular cutting (sports turf and greens) as well as grazing stimulates tillering in grasses and results in a much shorter, more compact growth, with a higher shoot density, but also reduces depth and density of rooting (Coppin & Richards 1990, Coppin & Stiles, 1995).

Grassland management influences the moisture condition of the soil by its impact on roots. Dyke grassland is fed by rainwater. Their superficial root growth makes grazed and frequently cut swards more sensitive to drought than deeper rooting grass vegetation. Unfertilized hayfields have a more homogeneous distribution of roots along the soil profile (Sprangers *et al.* 1991) which results in a higher moisture content in the upper layers, and soil stability in terms of aggregate-bonding. In times of drought there is a transport of water from deeper layers to the upper-layers of the soil by roots (Caldwell *et al.* 1991). Unfertilized meadows may therefore be more drougth-tolerant.

If N is given in large quantities as is customary for high-productive agricultural grassland, the shoot density decreases and the sward becomes more open (Sibma & Ennik 1988). Intensive grazing creates open space in the grass sward, and species like *Urtica dioica, Stellaria media, Cirsium arvense, Cirsium vulgare* and *Hordeum murinum* become dominant along trodden and manured (dung) places (Sprangers 1989, Sprangers *et al.* 1991). The use of herbicides to control these plants usually has an adverse effect: open places are created that are again colonized by the same species which prefer the high nutrient level of the soil (Heemsbergen 1994). Insufficient maintenance of meadows, e.g. not dragging to spread out dung and molehills, or not cutting plants that are left behind after grazing, will lead to an irregular vegetation cover formed by tussocks of *Dactylis glomerata , Festuca arundinacea*, and *Elymus repens*. Mulching results in a species-poor tall-grass community dominated by *Arrhenaterum elatius, Elymus repens, Anthriscus*

sylvestris, Heracleum sphondylium, and *Urtica dioica* (Sýkora & Liebrand 1987, Van der Zee 1992).

An important and sometimes overlooked aspect for judging the erodibility of dyke grassland (cf. Anonymous 1996b) is the status quo of the sward under unfavourable growth conditions, i.e. at the end of the winter, after a period of minimal growth. In this period the heaviest storms can be expected, so that the grass cover must be in the right condition to provide the necessary erosion resistance. Another perhaps less overlooked aspect is the spatial variability in vegetation cover and root density. Open spots in the above- and belowground grass cover can function as weak spots from where erosion can spread out once the cover has been broken (Smith 1993, Kruse 1994b). Not much is known about the phenological patterns in root development or about spatial heterogeneity. The advantage of high root densities can be overruled if the distribution of roots is heterogenous.

Erosion resistance and vegetation types

The erosion resistance of the surface of turf of different communities was tested in a study of the vegetation of river dykes in small-scale experiments, by using a shower device and measuring the amount of washed out soil. Sýkora & Liebrand (1987) concluded that species-rich meadows originally occurring on sand dunes in the river basin (*Medicagini-Avenetum*), and pastures of the *Lolio-Cynosuretum-/Poo-Lolietum* type, have a similar resistance against superficial erosion. They also found a slight correlation between high resistance and low fertilization. Mulched grassland was shown to have a very low resistance in these experiments (Sýkora & Liebrand 1987, Van der Zee 1992). Laboratory experiments to test erosion in the grass sod, using a centrifuge to produce a water flow around soil core samples while measuring the loss of weight, showed a positive correlation between erosion resistance and a combination of clay content in the soil and root density (Van der Zee 1992).

To test the strength of grass sods of river dykes under standardized wave attack, large-scale experiments were carried out with turf of different vegetation types (Verheij *et al.* 1995, Anonymous 1998). The results are in line with the small-scale erosion tests: sods originating from the mulched species-poor *Arrhenatheretum* were considerably damaged, whereas the species-rich *Medicagini-Avenetum, Arrhenatheretum elatioris* and *Lolio-Cynosuretum* types resisted waves of 0.3 m for over 60 hours. The species-poor *Poo-Lolietum* type was not tested. While shoot density and erosion resistance were found to be negatively correlated, no significant correlation was found with root density. From these erosion experiments we may deduce the inadequacy of erosion resistance of grass swards managed by mulching or intensive grazing with fertilization. Field observations of sea dykes after heavy storms in february 1990 and river dykes after the high water period in 1995, support these findings: severe damage of the grass turf was observed in overgrazed and mulched dyke grassland (Johanson 1990, Anonymous 1995b, 1995c, 1995d).

Extensive management

The aim of cessation of fertilization in combination with the removal of biomass by grazing or haymaking is to decrease the nutrient level of the soil. The intention is two-fold: an increase in species diversity as well as a higher root density. To reach a sufficient vegetation cover and to stimulate regeneration of the vegetation, it is necessary to adjust

the grazing intensity to the biomass production and to maintain periods of rest (specially during winter). In case of haymaking, the times of mowing, at the maximum twice a year, should be adjusted according to the time of seed production of species that should be favoured. No herbicides should be used so as not to disturb the development of herbs.

Changes in productivity, nutrient availability and species composition have been described in several impoverishment experiments on former agricultural land (Oomes & Mooi 1985, Bakker 1989, Gough & Marrs 1990, Berendse *et al.* 1992, Olff *et al.* 1994, Oomes *et al.* 1996). In grassland on clay soils, cessation of fertilizer application results in a considerable decrease of biomass production during the first 2-3 years, followed by a more gradual decline over the next 5-8 years to the level of semi-natural species-rich grassland (Oomes & Altena 1987). Long term experiments in the Drentse A Nature Reserve show the same results. There was a decrease in the soil's nutrient level and in the annual production in fields that had not been fertilized over different periods of time (Bakker 1989, Olff & Bakker 1991, Olff *et al.* 1994). Cessation of fertilization leads to an increased growth of species typical to nutrient-poor soils (Oomes & Mooi 1985, Bakker 1989, Oomes *et al.* 1996). Because of the decreased aboveground biomass, the sward exhibits a more open structure (Coppin & Richard 1990) which is favourable for the settlement or regeneration of nutrient-poor species. A low productivity level results in an increase of species diversity (Bakker 1989, Olff 1991).

After stopping the application of fertilizer, the belowground biomass will increase (Olff *et al.* 1994). In accordance with the functional equilibrium between aboveground and belowground plant parts (Brouwer 1983, Lambers *et al.* 1998), plants invest more in their roots at a lower nitrogen availability to enhance their absorption capacity (Boot 1990). More carbohydrates are allocated to the roots resulting in a morphological change in the root system: root/shoot ratio, root length, root diameter and length and density of root hairs all increase. Boot (1990) suggested that the change in size and morphology of the root system after a decline in nutrient supply is a consequence of a change in both species composition and the effect of altered environmental conditions like water and nutrient availability. For example, species of nutrient-poor habitats have a greater root length and root hair density at low N levels.

Plants react to local differences in N supply by proliferation of roots in zones with increased nutrient content (Grime *et al.* 1991, De Kroon & Hutchings 1995). Dominant species like *Arrhenatherum elatius* develop an extensive root system, using a large volume of the soil in contrast to subordinates characterized by fine-rooted systems, which exhibit an intensive and precise exploitation of localized parts of the resource mosaic (Grime *et al.* 1991). Increasing heterogeneity of N availability in the soil by impoverishment practices (cf. Boot 1990) probably results in a complete occupation of the topsoil by the root system, to which the different coexisting dominant and subdominant species contribute, each with its own rooting strategy.

Plant species have different effects on mineralization and the turn-over of organic matter (Miles 1987, Berendse, 1992). Thus, increase of species-richness as a result of reduced soil nutrient levels enhances spatial soil heterogeneity, which has a positive effect on soil stability. When species of nutrient-poor habitats like *Festuca rubra* with a low root turnover compared to *Lolium perenne* (Throughton 1981) become dominant after cessation of fertilization, the effect will probably be additional to the decrease of nutrient levels in the soil, because the lower rhizodeposition of these species limits the mineralization

Fertilized grassland (c. 150 kg N h⁻¹y⁻¹)

competition of dominant species for light and moisture.
low nutrient use efficiency

high N and P, light and moisture limiting

large production of plant material, with high decomposibility, high root turnover
(Lolium perenne: 40 days)

high N and P mineralisation

species-poor (grazing)
Lolium perenne
Poa pratensis
Poa trivialis
Trifolium repens
Taraxacum species

High root density
in upper layer 0-5 cm
thin roots

Not using fertilizer

competion of species for N (higher N-level possible with good moisture conditions)

low N and P, N limiting.

small production of plant material with low decomposibility
low root turnover
(Festuca rubra: 120 days)

low N and P mineralisation

species-rich
Festuca rubra
Cynosurus cristatis
Anthoxanthum oderatum

High root density
in layer 0-20 cm
thick and thin roots

Figure 1.3 Processes governing plant growth in fertilized and unfertilized grassland

process. Figure 1.3 summarizes some of the processes that may govern plant growth in fertilized and unfertilized grasslands.

Botanical and landscape ecological values

This study is focused on the effects of the extensive grassland management on vegetation cover and soil stability primarily to improve the resistance of the sward against erosion. In nature conservation impoverishment practices are used for the restoration of species-rich grassland. A zero-null situation exists when both the civil-technical quality and botanical or landscape-ecological value of dyke grassland can be increased simultaneously. In this section the last mentioned values are considered.

While a decrease in productivity might result in a higher species diversity, it cannot guarantee successful restoration of species-rich meadows (Berendse *et al.* 1992). A high species diversity as a result of extensive grassland management can be achieved only in the long term and within the confines of the necessary habitat conditions, probably after 15 to 20 years (Oomes & Mooi 1985, Bakker 1987, 1989), assuming the establishment of species either from seed bank or seed dispersal (Strykstra *et al.* 1998). Compared to cutting, grazing is expected to extend this period, because only a small quantity of nutrients will be removed (Fliervoet 1992, Bullock *et al.*1994). A period of 10-15 years has been mentioned as being necessary for the regeneration of species-rich grassland on river dykes, depending on soil composition and other habitat factors (Sýkora *et al.* 1990). South exposed slopes are dryer and have a lower nutrient availability and thus are more favourable for the development of species-rich grasslands (Sýkora & Liebrand 1988).

At present species-rich grasslands and some rare and less common species like Torilis nodosa, Sherardia arvense, Lathyrus nissiola, Lathyrus tuberosus, Orobanche lutea, Galium verum, Briza media, Koeleria macranta, Campanula rotundifolia, do occur on a few dykes along the sea coast and the estuary Westerschelde. If indeed the erosion resistance improves by impoverishment practices and extensive management becomes a commonly accepted instrument for dyke grassland maintenance, a significant potential area will be created for restoration of species-rich grassland. Like other linear elements, e.g. road verges, ditch banks, railway lines, and field boundaries, dykes covered with semi-natural grasslands can function as ecological corridors for the migration of certain plants, insects and mammals (Zonderwijk 1979, Koster 1991, Sykora *et al.* 1993, Anonymous 1995a, Kleijn 1997, Hermy & Blust 1997). Through their specific location in agricultural landscapes they can provide sustainable habitats for the population of species that otherwise would not survive. Since dykes have an important role in linking the greater recreational centres along the coast, extensive management resulting in flower-rich grasslands will also contribute to their recreational function as well. It is clear that the restoration of species-rich dyke grasslands should be one of the aims in landscape-planning, where dykes can play an important role in the multifunctional design of cultural landscapes in the near future.

1.4 Hypotheses and questions

The soil physical properties of the clay layer covering the sand body of dykes cannot be changed directly. However, indirect change in abiotic circumstances by influencing biotic processes in the soil such as root growth and microbial activity is very likely. These processes have a considerable impact on soil structure, aggregate stability, and permeability, and thereby on the erosion resistance of the rooted clay zone.

Hence, species composition, shoot and root density, soil fertility and microbial activity can be controlled by changing grassland management. However, it will probably take at least 3-4 years to reach some of the desired effects, depending on the status quo of the grassland. Most of the sea dyke grasslands are currently intensively managed for agricultural purposes in the firm believe that it will result in a good dyke cover. In many places, however, the erosion resistance of the sward is low and the dyke authorities have difficulties in maintaining a good closed vegetation cover, because of overgrazing or intensive haymaking with the use of fertilizer.

The aim of this study is to investigate whether extensive management of sea dyke grassland improves erosion resistance through the expected changes in botanical composition and rooting density of the sward. The following deducible hypotheses are formulated and will be tested:

1) Stopping the use of fertilizer followed by a less intensive grazing or cutting regime leads to an increase in the number and/or cover of grass and herb species indicative of less nutrient-rich soil conditions. Haymaking on former pastures will have the most impact.

2) These management strategies result in a slight decrease and in some cases to an increase of vegetation cover and shoot density.

3) As a result of cessation of fertilization, there will be a decrease in aboveground biomass production and an increase in root biomass and root density. Grazing and cutting have a different effect on the profile of the rooting system.

4) Species-rich unfertilized hayfields have less seasonal fluctuation in root density compared to fertilized sheep-grazed pastures.

5) A spatial homogeneous vegetation cover reflects a homogeneous distribution of underground biomass.

6) A high shoot density, and a higher root density in grassland developing after cessation of fertilization, results in a higher erosion resistance.

In order to verify these hypotheses the following questions need to be answered:

1) Can the species composition of dyke grassland be altered towards communities of nutrient-poor habitats by stopping fertilization and which management systems would be appropriate?

2) How do cessation of fertilization and different management regimes influence vegetation cover, shoot density, above- and belowground biomass and chemical composition of soil and plants?

3) Will root density of dyke grassland be enhanced by the cessation of fertilizer application ? What time period and environmental conditions are needed to achieve this objective and what are the most appropriate management systems?

4) What are the differences between the root growth and seasonal dynamics of root biomass of fertilized sheep-grazed dyke grassland and that of unfertilized hayfield?

5) What differences are there in spatial heterogeneity in vegetation cover, shoot and root density between fertilized pasture and unfertilized hay-meadow ?

6) How do cessation of fertilization and different management practices affect erosion resistance of dyke grassland?

1.5 Outline of the thesis

The first chapter of this book begins with a general introduction to the various aspects of the erodibility of dyke grasslands. Special attention has been paid to the construction of the grass-clay complex and technical aspects of erosion and the mechanism of protection of the clay layer by grass sods. The aims of the investigation have been worked out into a precise formulation of the problem, with the emphasis on the increase of root density by lowering the nutrient level in soils. Chapter 2 describes the study sites and experimental

design. It gives a general outline of the experiment, which is basically a survey of successional processes after the cessation of fertilizer application on agricultural grassland, while continuing sheep-grazing or haymaking or shifting from grazing to hay-making, or a combination of the two management treatments, over a course of four years (1991-1994). The experiment is still being continued, and some of the data collected in 1997 has been analysed and described in this thesis (see Chapter 4). In Chapters 3 to 6 the results are given and discussed of the various investigations that are being carried out to answer the general research questions. A detailed description is also provided of the methods used for data sampling and analysis.

Chapter 3 examines the changes in floristic composition of dyke grassland after four years of succession, including the changes in percentage cover of herbs compared to grasses. The possible increase of species diversity and the occurrence of rare species are analysed and compared on a national scale. Because it is important to know if and to what extent extensivity of management leads to a more open vegetation, this chapter contains an analysis of the total cover of the vegetation, cut back to a height of 2 cm, as well as shoot density, expressed by the score of classified distances between 100 measuring points and nearest sprout. Here, attention is also paid to the threat of moles related to the different management practices that have been investigated.

In Chapter 4 the changes in biomass production, root density and nutrient levels in plant and soil are analysed. Information about successional processes derived from the data are discussed with respect to the results of old species-rich hayfields on (former) sea dykes, which function as a reference. The question as to whether the root system is expanding as a result of cessation of fertilization is answered in this chapter.

The condition of the sward in unfavourable periods of the year (wintertime, late autumn, early spring: periods of heavy storms) is important for dyke management. Also crucial is the homogeneity of the grass cover. In Chapter 5 seasonal variability and spatial heterogeneity are examined, by comparing the grass swards of fertilized pastures and unfertilized hayfields (references).

In Chapter 6 is analysed to which extent grass cover and root systems contribute to erosion resistance. Emphasis is placed on the relation between dyke grassland management and erosion resistance and the influence of edaphic factors. The impact of short-term changes in management (cessation of fertilization and extensive grazing or haymaking) on erosion resistance are tested and discussed.

Finally, Chapter 7 aims at integrating the results of the different experimental studies and the consequences of these findings for dyke grassland management. The focus is more on the practical implications of the results of this investigation.

2

Experimental design

2.1 Study sites, management treatments and set-up of the experiment

In this chapter a general outline of the experiment is given. A description of methods used for sampling and analysis is included in the following chapters (Chapters 3-6).

In 1991, 24 study sites were selected on dykes along the coast of the Dutch Wadden Sea (5), the North Sea (7), the IJsselmeer (3) and on dykes along the Westerschelde (8) and Oosterschelde (1) in the south-western estuary (see Figure 2.1); 14 sites were located on sheep grazed dykes and 9 on mown dykes (see Tables 2.1 and 2.2). The criteria for selection of the sites were:

1) the sward had to have been at least five years old and had the same management during those five years, i.e. fertilized and intensively managed by sheep grazing (15-40 animals ha^{-1}) or mowing (mulching with 4-8 cuttings a year or hay-making with 2-3 cuttings a year);
2) the site had to represent the grass cover of a considerable dyke length;
3) the sites had to be similar in exposure to sun and sea. The sites in the southern part of Noord- en Zuid-Beveland, along the Westerschelde, and some other locations, however, are an exception to this rule);
4) carrying out the different management practices, had to be easy.

To investigate the effect of fertilizer cessation and the adjustment of grazing or mowing intensity, as well as the effect of shifting from grazing to hay-making or a combination of both practices, four treatments were started on grazed dykes and two treatments on dykes that were mown. These treatments were closely related to the most common management practices of dyke grasslands by farmers and dyke management authorities. The four treatments on dykes grazed by sheep at the beginning of the experiment were:

- **Treatment G+**: *annual fertilization with 100-150 kg N ha^{-1}* and 10-20 kg P and K ha^{-1} and continuous (or in periods of 4 to 9 weeks) grazing by sheep with an average of about 15 ewes ha^{-1}, which can temporarily come up to 40 sheep ha^{-1} (ewes and lambs);
- **Treatment GG-**: *no fertilizer application*, grazing in two periods of about 4 weeks in April-May and August-September with an average of about 10 - 12 ewes ha^{-1}, or continuous grazing with 7 ewes (with lambs) ha^{-1}.
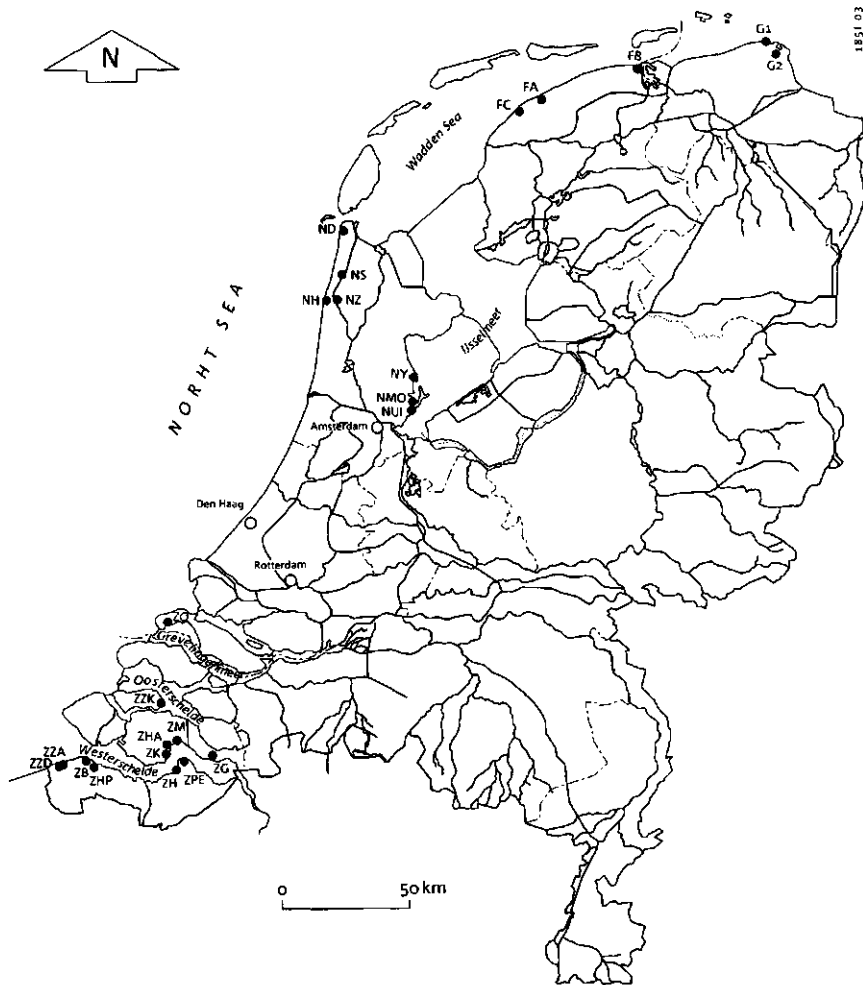
Figure 2.1 *Study sites. For explanation of codes see Tables 2.1 and 2.2*

- **Treatment HG-**: *no fertilizer application*, mowing of the first cut for hay-making after June the 15th, followed by grazing in a 4 weeks period (August-September).
- **Treatment HH-**: *no fertilization*, mowing twice a year with removal of cuttings (hay-making) the first cut after 15 June, the second cut before 15 September.

In treatment 2-4 the use of herbicides was prohibited. In treatment G+, which is a continuation of the grassland management at the start of the experiment, sometimes an additional cutting was carried out for hay-making in the beginning of June after a period of grazing in March. In both treatments G+ and GG- where necessary, additional mowing took place of ungrazed material shortly after a grazing period. For practical reasons it was not possible to realize all four treatments on each site. In Table 2.1 a list is given of sites with their exact location, exposure to the sea, and treatments with starting date.

Two treatments were applied on the sites with mown grassland:

- **Treatment H+** : annual *fertilization with 100 -150 kg N ha^{-1}* and one or two cuttings a year for hay-making, at the beginning of June and at the end of August. Management practices as mulching 3-4 times a year or mowing 5-7 times a year without removal of cuttings and additional fertilization of about 50 kg N ha^{-1} are also considered to belong to this treatment, because of the extra nutrient-input to the soil from the biomass left behind.
- **Treatment H-**: *no fertilizer application* and mowing twice a year (in the beginning of July and in mid-September) with removal of cuttings for haymaking or removal of green cuttings.

Sites and treatments on mown grassland are listed in Table 2.2.

Table 2.1 *Study sites and management treatments (indicated by shading) on dyke grassland grazed by sheep at the beginning of the experiment. G+ = fertilized, sheep grazing in periods or continuously; HH- = not fertilized, 2x cuts a year for hay-making; HG- = not fertilized, 1 cut for hay-making + 1 period sheep grazing; GG+ = not fertilized, 2 periods sheep grazing; sec = secondary dyke, not directly exposed to the sea.*

Location	Dike marking point	Exposure outer slope	Management treatments fertilized G+	HH-	unfertilized HG-	GG-	Starting date
G1 (Groningen-Eemshaven)	103 - 104	NW					4/91
G2 (Groningen-Eemshaven)	harbour	NE (sec)					8/91
FB (Friesland-Lauwersmeer)	94	N					4/91
FA (Friesland-Boonweg)	35-36	NW					4/91
FC (Friesland-Koehool)	23	NW					4/91
NH (Hondsbossche zeewering)	Camperduin A+B	W					4/91
NZ (Hazedijk 2ᵉdijk HBZ)	sect. A+B	E (sec)					4/91
NS (Zijperzeedijk)	sect. A	W					4/91
NY (Zeevangzeedijk-Edam)	95 - 97	E (sec)					9/91
ZG (Zimmermanpolder-Rilland)	20 - 24	ZW					4/91
ZM (W-Annapolder-ZakvZuidBev)5c		ZW					4/9
ZK (Hoedek.kerke-ZakvZuidBev)	24 - 29	E					5/91
ZH (Nijspolder-Ossenisse)	14 - 16	W					5/91
ZB (Nr. Eén)	3 - 5	NW					8/91

Table 2.2 *Study sites and management on dykes maintained by mowing.Reference =
hayfield for > 20 years; H^+ = fertilized 1-2x cuts a year for hay-making or m = mulching
and g = 4-8x mowing as in greens; H^- = not fertilized, 1-2x cuts a year for hay-making.*

Location	Dyke marking point	Exposure outer slope	Management H^+	H^-	Starting date
ND (Den Helder)	139 -147	Northwest	g		4/91
NMO (Monnickendam)	51 - 53	North (sec)	m		9/91
NUI (Uitdam)	59 - 61	East (sec)	m		9/91
ZHA (Biez.Ham-Noordpolder)	9 - 11	South			5/91
ZK (Biez.Ham-Moert.dijk)	13 - 15	East			4/91
ZPE (Perkpolder-Honten.)	73 - 76	North			5/91
ZHP (Hoofdplaat)	50 - 52	North			6/91
ZZA (Zwartepolder-oost)	11 - 13	West			6/91
ZZD (Zwartepolder-zuid)	7 - 8	Northwest			6/91
ZO (Oudelandse zeedijk) - reference	-	Southwest (sec)			± 70
ZZK (Zandkreekdam) - reference	-	Northeast (sec)			75
ZK (Biez.Ham-Moert.dijk) - reference	12 - 13	East (sec)			65

The treatments were started in 1991 and were continued until the end of 1997. On
some sites the introduced treatments are still being continued. In this thesis we present the
data collected in the period 1991-1994, except for the data on aboveground biomass
production, covering the period 1991-1997. Each treatment was applied to dyke sections
35-150 m in length at an average width of 40 m, which corresponds to 0.14 - 0.6 ha. In
every section two permanent plots of 5 x 5 m^2 were laid out, exactly in the middle of each
dyke slope. This was done to take into account any effects of salt spray and drought as a
result of exposure to the sun, see Figure 2.2 for a simple scheme of treatments (4 in this
example) and plots on a site that was grazed by sheep at the beginning of the experiment.
All measurements were in the plots.

Reference plots were studied on three sites that were mown once a year for haymaking
and had not been fertilized over the past twenty-five years. These sites are located on dykes
in the south-western estuary along the Grevelingenmeer (code ZO), Oosterschelde (ZZK)
and Westerschelde (ZK) (see also Table 2.2).

To investigate the seasonal and spatial variation in cover and root density of fertilized
and unfertilized dyke grasslands, additional plots were set up in the fertilized sections of
three sites (FA, NH, ZH) and in the sites functioning as an unfertilized reference (ZO,
ZZK, ZK).

This investigation of sea dyke grassland can be viewed mainly as a study of two
experiments on the impoverishment of the soil top layer: one experiment on sheep-grazed
dykes and one on mown dykes. In both experiments we can distinguish two compartments
that differ in habitat factors: one compartment representing the outer slope of the dyke,
with a possible exposure to salt spray, and the other compartment representing the inner
slope of the dyke, characterized by a probably low salt effect. Since most of the slopes
facing the land side are south or southwest exposed slopes, another factor (high sunlight
influence) must be taken into account when studying differences between the two
compartments.

Figure 2.2 *Scheme of treatments and permanent plots on grazed dykes.*

The treatments on grazed dykes were replicated on 14 locations on both the inner and outer slope of the dyke, except for the secondary dykes. Here the plots are situated only at one slope. Because of management restrictions, the unfertilized treatments (HH-, HG- and GG-) could not be realized on all the sites (see Table 2.1). The two treatments on mown dykes (H+ and H-) were replicated on either the inner or outer slope in 9 locations (see Table 2.2). All measurements were carried out fourfold. For practical reasons the results of experiment I and experiment II are often presented in the same diagram or table.

Besides these two experiments a descriptive study was carried out of the seasonal and spatial differences in vegetation cover and root density between fertilized grassland and unfertilized hayfield (reference).

2.2 Organization and time schedule of measurements

One of the main difficulties in realizing the desired management treatment was the inconsistency of the sheep grazing on the different experimental sections. On fertilized dyke grassland the occupation with sheep varies with each season. The average number of ewes comes to about 15-20 per hectare. After giving birth to the lambs in February-March, however, the actual occupation at the end of the grazing period just before the lambs are separated from the ewes (June-July) can be as much as 40 animals per hectare.

The period of grazing depends on the length of the dyke section, generally about three to four weeks for 600 m section. Since sections were grazed by the same group that occupied the rest of the dyke, the grazing intensity was adjusted to the lowered production in the experimental sections by manipulating the grazing period, which varied from one to three weeks. From an ecological point of view of dyke grassland maintenance, it is better to have a rather short period of grazing with a high occupation (cf. Sýkora *et al.* 1990). The adjustment of intensity and grazing period was not always successful during the

experiment. For example, where a section with treatment GG- had not been properly grazed in April-May, an additional cut was done in June. Samples taken in these sections were not analysed separately.

The experiment started in 1991. In early spring (March) measurements were made of the vegetation cover, shoot and root density and shear resistance in the plots. For practical reasons this was done only on the fertilized plots. It was assumed that at the beginning of the experiment average values for these parameters did not differ along the dyke sections where the treatments were laid out. In June 1991 the botanical composition was recorded and biomass production and soil composition were measured in all treatments. At that time the extensive plots remained unfertilized at the beginning of the season in contrast with the intensive plots. Thus, the measured parameters in June do not express the null-situation in the plots. Measurements of biomass production was repeated each year except in 1996, and the change of productivity during this period in fertilized and unfertilized plots was calculated.

In March 1994, the measurements of vegetation cover, shoot and root density, and shear resistance were repeated and recordings of botanical composition and soil parameters were made in June. This means that apart from productivity, a comparison was made between fertilized and unfertilized plots in 1994. Comparison with the 1991 data was only possible with the fertilized plot data. In March 1994, small-scale erosion experiments were carried out and the results were analysed to compare differences between treatments in that year.

To determine the seasonal variation, root and shoot density, shear resistance, vegetation cover and biomass were measured every six weeks during 1992 in three fertilized and three unfertilized plots (references). Recordings of spatial variability were made in early spring and the summer of 1993.

3

Vegetation

Changes in botanical composition and vegetation cover after four years without fertilizer application

With K.V. Sýkora and A.P. Schaffers

3.1 Introduction

When fertilization has been terminated, the growth conditions change rapidly and consequently the botanical composition of the grassland changes as well. The productivity decreases (Oomes & Altena 1987, Olff & Bakker 1991, Berendse *et al.* 1992), the soil nutrient content declines, and the number of species increases (Bakker 1989, Olff *et al.* 1991). As already pointed out in Chapter 1, species-rich communities probably have a higher erosion resistance. The species of nutrient-poor soil conditions that occur in such communities probably have deeper-rooting systems. Plants in these communities exhibit a rather low shoot-root ratio. The unproductive soil conditions results in an expansion of the rooting system as a whole. Also, a high species diversity contributes to an increased soil heterogeneity and stability. The development of species-rich communities, however, is a long-term process (Bakker 1989, Berendse *et al.* 1992, Olff *et al.* 1994). Although low productivity levels (4-6 tonnes ha⁻¹) are essential for a high species-diversity, it is not a guarantee for restoration of species-rich communities on former highly fertilized agricultural grassland (Berendse *et al.* 1992).

According to Bakker (1989) changes in botanical composition are mainly due to changes in canopy structure by time and frequency of aboveground biomass removal (management practises) and its influence on growth and germination of seedlings, rather than soil impoverishment. The last mentioned is a protracted process if practised by biomass removal. Soil fertility in the long run is determined by the balance between nitrogen input and output. To maintain the lower levels of primary production in impoverishment experiments, a continuous removal of nutrients is necessary (Berendse *et al.* 1992).

In anticipation of these long-term developments and their effects on grassland on clay dykes, we could focus on short-term processes as well. During the restoration succession there will be a rather slow overall increase in species diversity but a rather rapid increase of species on nutrient-poor sites (Oomes & Mooi 1985, Bakker 1989, Olff *et al.* 1991). The rapid appearance of these species might have an impact on the erosion resistance of grassland through their specific rooting properties. Stopping the use of fertilizer will rapidly diminish the standing biomass, and results in a more open canopy structure (Bakker

1989, Coppin & Richards 1990), and a subsequent increase in the biomass of nutrient-poor species that were already present.

Such changes in botanical composition and vegetation structure can have a direct impact on erosion resistance of the dyke grasslands. In this chapter we examine the changes in botanical composition as well as sward characteristics of sea dyke grasslands after four years of sheep grazing and haymaking without the application of fertilizer. We try to answer the following questions in particular: (i) does the number of species increase and is there a shift in the dominant grassland species towards species indicative of nutrient-poor conditions?; (ii) does the proportion of herbs in the grass sward increase?; (iii) what are the effects of the different management systems on the botanical composition and how do habitat factors, such as exposure, soil texture, geographical location interact?; and (iv) what are the changes in vegetation cover and to what extent is sward structure related to the vegetation composition?

From a of civil engineering point of view it is important to know the kind of changes that occur, shortly after stopping the use of fertilizer, not only in botanical composition but also in vegetation cover. This knowledge can help us to predict the erosion resistance of grassland under different management regimes.

3.2 Methods

Botanical composition

In 1991 and in 1994 a total of 291 relevés were made in the second half of June in the permanent plots of all sites (see Chapter 2 for study sites and management treatments) according to the Braun-Blanquet method (Westhoff & Van der Maarel 1973, Werger 1974, Schaminée *et al.* 1995) with the use of a refined ordinal scale (Barkman *et al.* 1964, Van der Maarel 1979). Plant nomenclature follows Van der Meijden (1990) for phanerogams and Margadant & During (1982) for bryophytes.

The rough Table composed of all relevés has been structured by TWINSPAN (Hill 1979b, Jongman *et al.* 1987) and a synoptic Table has been calculated. The species were grouped into syntaxonomic elements according to their syntaxonomic status. Using the proportion of the different syntaxonomic elements the different clusters were assigned to syntaxa as described by Westhoff & Den Held (1975), Ellenberg (1978) and Oberdorfer (1990). Species were considered to be differential within the table, if the difference in frequency between clusters was at least 30 per cent. When it was found impossible to assign the derived cluster at the association level, they were described as so-called trunk communities (t.c.) were recognized (Sykora & Westhoff 1979) and names were given using the deductive method (Kopecký & Hejný, Schaminée *et al.* 1991). Trunk communities are "unsaturated", i.e. they miss the character species of an association but species of higher syntaxonomical levels are present.

Detrended Correspondence Analysis (DCA) was used for ordination of the relevés (DECORANA, Hill 1979a, Hill & Gauch 1980). The mean decorana-score for each community was calculated and depicted in an ordination diagram. For an ecological interpretation of the diagram axis the co-ordinates of the relevés of the first two axis were correlated with weighted averages of species indicator values (Kruijne *et al.* 1967,

Ellenberg 1978, Sýkora & Liebrand 1987) by calculating the Pearson correlation coëfficient.

Habitat factors

In July 1991 soil samples were taken between 2 and 12 cm from the fertilized plots, each of which composed of a mixture of 12 subsamples. The texture of these samples was measured by the gravimetrical method, organic matter by the Kurmies procédé, and $CaCO_3$ by the method of Scheibler (Houba *et al.* 1994, 1995). The following fractions were determined: clay (percentage particles < 2 μ), silt (2 - 63 μ), and sand (63 - 2000μ). The granular composition of the soil was determined in the fertilized plots at the beginning of the experiment, with the assumption that this factor did not differ substantially from the nearby unfertilized plots. Differences in texture between communities were tested using a simple analysis of variance.

For each community the distribution of relevés as a percentage of the total number of relevés were computed over north/south region and inner/outer dyke slope. Differences were analysed by using a Chi-square test. Differences occurring in the botanical composition between the northern and southern region were justified by the two floristically different areas distinguished: the Northern Clay District (Van der Meijden, 1990) with dykes along the Wadden Sea, North Sea and IJsselmeer; and the Estuary District covering dykes in the south-western part of the Netherlands. Another difference between the northern and southern region, that may affect species composition or the results of the extensification experiment, concerns the types of management used and the accuracy of maintainance. Detailed information about management and maintenance practises, like duration and intensity of grazing and mowing dates were made note of for all the plots. Also differences in texture between communities as well as between the two regions were analysed, since waterboard authorities mentioned differences in clay content of the soils used for dyke construction.

The position on the inner or outer dyke slope is linked to the likely influence of salt water. The concentration of soluble Na in the soil samples was is measured and differences of this factor between inner /outer dyke slope and between communities were analysed. Another factor that interferes with the position on the dyke and which possibly influences vegetation growth and composition, is the exposure to sunlight. Most inner dyke slopes have a southern to south-eastern exposure, except for the dykes along the north bank of the Westerschelde where the situation is the opposite. For each plot the duration of direct solar radiation was calculated (h day^{-1}), based on measurements of slope angle and exposure, using the radiation diagram of Grime & Loyd (1973). The effect of this factor on species composition and vegetation cover was analysed. The relevés of 1994 were used to compare the habitat factors between communities.

Changes in species composition and species abundance

To obtain a general impression of the phytosociological changes within each management treatment, a comparison was made for each suntaxonomic unit between the number of relevés of 1991 and that of 1994. This gave an indication of how many relevés have "moved" from one community to another as a result of the altered management (cf. Sýkora *et al.* 1990).

Multivariate techniques were used for analysing the effect of management on species composition. Data from 1991 were compared with data from 1994, but also data of the different treatments in 1994 were analysed separately. From the ordination of relevés, which is to be regarded as an indirect DCA of species data (DECORANA, Hill 1979a) the average first and second axis coordinates of relevés of permanent plots were calculated for each management treatment in 1991 and 1994. Average scores are depicted in the ordination diagram. Corresponding values from the same management treatment but from different years are connected by arrows, indicating the direction of the vegetation change. Differences between the scores from 1991 and 1994 were tested for each management treatment with Wilcoxon's signed ranks test (Sokal & Rohlf 1995).

Using the software package CANOCO (Ter Braak 1987), a Redundancy Analysis (RDA) was carried out on the floristic data of 1994 with management treatments as environmental variables and *location* of the study sites, *dyke slope position, Na content in the soil* and duration of *received sunlight* as covariables. RDA is the canonical form of Principal Component Analysis (PCA). RDA provides the technique for selecting the linear combination of environmental variables that gives the smallest total residual sum of squares, so that species data can be regressed on the restricted (constrained) sites, in contrast with PCA, where sites are not restricted (Jongman *et al.* 1987). Monte Carlo Permutation tests were used to determine the significant contribution of treatments, habitat factors and interactions to the total variance in species composition. Resulting correlation coefficients of species as well as environmental variables with the first two axis of the RDA are represented as arrows in a biplot of species and treatments.

Changes in species frequency and abundance were investigated by: (1) comparison of values in permanent plots in 1991 and 1994 for all the treatments, and (2) comparison of values between treatments in 1994. In analysis (1) the average cover/abundance of species in permanent plots was determined for each treatment in 1991 and 1994. Differences in species cover/abundance between the two years were tested using a paired comparison test. In analysis (2), relevés from 1994 were clustered for each management treatment and the frequency of species assigned to five classes (present in 0-20, 21-40, 41-60, 61-80, 81-100 % of the relevés) and average abundance (using ordinal values) for each treatment were calculated. On comparing the frequencies and (weighted) average abundance of species from unfertilized and fertilized treatments, species with a difference of at least two classes were considered to have increased or decreased after fertilization had ceased.

Species-richness

Species-richness was calculated as the mean number of species in 5 x 5 m^2 plots for each treatment. To express the contribution of herbs to the vegetation, the ratio between the cover of herbs and total cover was determined, and the effects of the different management treatments on species-richness and the ratio herbs-cover/total-cover in 1994 were analysed.

Vegetation cover and sward structure

Measurements were made in February and March in 1991 and 1994. This time of the year is preferable for testing the erodibility of the grass turf since high wave attack can be expected during storms often occurring in February, while the condition of the grass turf will be the poorest in this period.

The cover of the vegetation clipped to 2 cm above ground level was determined by measuring the point frequency of shoots in a 0.5 x 0.5 m² screen with 81 points. At each point a note was made of whether it was occupied by a shoot or leaf. The method can be regarded as a modified 'point-frequency-method' (cf. Mueller-Dombois & Ellenberg, 1974, Kent & Coker, 1992). Only living plant parts (grasses and forbs) were recorded. Mosses and dead plant material were not considered to contribute to the cover of vegetation. The measurement was carried out four times at random positions in the plots.

Sod compactness was determined by calculating two parameters, *shoot density* and *average open spot size* using concentric rings with an increasing radius, thus forming size classes with different areas (Figure 3.1). In each plot 100 measurements were made at points equally distributed over the 5x5 m² area. At each point the class matching the distance to the nearest shoot was recorded, where $F_k\%$ is the frequency of rooted grass and forb tiller bases in class k. To determine the *shoot density* the frequency of the absence of rooted plant bases for each class was calculated ($100 - \Sigma F_k\%$) and plotted on a logarithmic scale against class-radius r. The coefficient of the resulting curve (c_{SD}) calculated using linear regression, was the measure used for the sward structure. Low values for c_{SD} indicate high sod compactness, whereas relatively high values indicate open sods.

The *average size of open spots* in the sod (OSS, see equation 1) was calculated by summarizing the product of class score ($F_k\%$) and average class area (s_k, see Table 3.1) divided by the total score (100).

$$OSS = \sum_{0}^{k}(F_k\% \cdot s_k)/100 \qquad (1)$$

The average surface of a class (s_k) was determined by the area of the preceding class augmented by half the difference in area between present class and preceding class.

Mole-hills were counted along dyke sections of 50 m in length at all study sites to investigate the relation between mole activity and treatments.

Figuur 3.1 *Device with rings used for measuring sod compactness (cf. Neuteboom et al. 1992)*
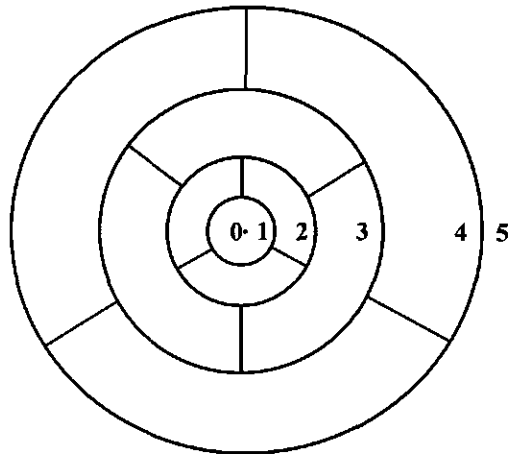
Table 3.1 *Average areas of different diameter classes corresponding to the rings used for measuring sod compactness*

Class k	radius r (cm)	average area s_k (cm²)
0	r < 0.125	0.02
1	0.125 < r < 0.7	0.79
2	0.7 < r < 1.4	3.85
3	1.4 < r < 2.8	15.39
4	2.8 < r < 5.6	61.58
5	r > 5.6	246.3

Statistics

Several parameters were tested using a simple analysis of variance (ONEWAY-ANOVA) in combination with a Least Significant Difference test (LSD) to derive the differences between communities. The data on granular composition (percentages) were converted using an arcsine transformation before analysis of variance (Sokal & Rohlf 1995). Differences in percentage relevés between habitat factors were analysed using a Chi-square test. The relation between vegetation cover, shoot density and species richness was determined using Pearson correlation coefficients. Wilcoxon's signed rank test (Sokal & Rohlf 1995) was applied to compare DCA-scores of relevés and species cover/abundance values between 1991 and 1994. For these statistical analyses the computer package SPSS PC$^+$ (Norusis 1986) was used.

Analysis of the effects of the different treatments (fertilization combined with management) and the separate effects of fertilizer use and management practise was done using a REML-analysis (Restricted Maximum Likelihood) from the computer package GENSTAT (Payne *et al.* 1993). This method was chosen since the practical arrangements of the experimental design made it impossible to create a fully balanced data set. Data are analysed in two ways. Different contrasts were used to test separately the effects on the investigated parameters: (former) pastures and meadows; stopping and continuing the use of fertilizer on pastures as well as hayfields; grazing and haymaking on former pastures; grazing or haymaking against haymaking followed by grazing on former pastures; and meadow grassland against long-term unfertilized meadows (references). Then, a REML analysis was carried out with 'treatment' (combination of fertilization and management) as factor, followed by a pair-wise comparison with t-statistics for all distinguished treatments. In both analyses *duration of received sunlight* and *Na content in the soil* were used as covariates to correct for the position on inner/outer slope of the dyke, after the effect of dyke slope on these factors had been tested. REML was also used to test the effect of *region* (northern or southern located dyke grassland plots) on texture.

3.3 Results

Plant communities

Phytosociological classification

In total 194 species were recorded in the 291 relevés made in 1991 and 1994. Nine communities were distinguished from the phytosociological analysis.Tabel 3.2 gives the frequencies of differential species of the distinguished communities. A full synoptical table is printed in Appendix 1. Four communities of the *Lolio-Cynosuretum* type and five of the *Arrhenatheretum elatioris* type were recognized, the names, codes (between brackets) and a short description of the communities are as follows:

1. Geranium molle variant of the Lolio-Cynosuretum cristati (LG).

Number of species:14. The community could be assigned to the *Lolio-Cynosuretum* because of the presence of *Cynosurus cristatus, Bellis perennis, Lolium perenne, Phleum pratensis*, and *Leontodon autumnalis. Geranium molle* is abundant. The coenon can be considered as a relatively species-poor, degraded variant of the *Lolio-*

Cynosuretum, with a rather high share of species of the very species-poor *Poo-Lolietum*. It is typical of the less intensively fertilized grasslands occurring on dykes along the Wadden Sea.

2. Ranunculus bulbosus variant of the Lolio-Cynosuretum cristati (LR).

Number of species: 18. Relatively well developed *Lolio-Cynosuretum* with an abundance of *Ranunculus bulbosus*, occurring on dykes in Friesland, Noord-Holland and Zeeland, characterized by a relatively low input of fertilizer.

3. Trunk community of *Festuca rubra* and *Cirsium arvense* [Molinio-Arrhenatherertea / Plantaginetalia] (LF).

Number of species: 18. This community is a fragmentary *Lolio-Cynosuretum*, characterized by species of *Molinio-Arrhenatheretea* as well as *Plantaginetalia*. Typical for dykes in Noord-Holland along the North Sea, characterized by abundance of *Festuca rubra* and the presence of *Cirsium arvense*.

4. Poo-Lolietum (PL)

Number of species: 12. Very species poor community without differential species and characterized by the occurrence of the species group formed by *Lolium perenne, Poa trivialis, Poa pratensis, Taraxacum spec., Trifolium repens, Ranunculus repens* and *Plantago major*. The community has been described recently as t.c.of *Poa trivialis - Lolium perenne* -[Plantaginetea majoris/Cynosurion cristati] by Sýkora *et al.* 1996. The community is typical of high fertilizer application. Other species seldom occur, unless nitrophilous species indicative of overgrazing like *Stellaria media* and *Hordeum murinum*.

5. Trunk community of *Arrhenatherum elatius* and *Heracleum sphondylium* [Arrhenatherion/Artemisietea] (AH).

Number of species: 8. Very species-poor community with very few character species of *Arrhenatheretum* and *Arrhenatherion*. Differential species of *Arrhenatheretum elatioris, group A inops* are present, which indicate an affinity with this community. The community is highly comparable with the t.c. of *Anthriscus sylvestris - [Arrhenatheretalia]* as described by Zuidhoff *et al.* (1996). Typical community of mulched, strongly fertilized or abandoned hayfield with species of *Artemisietea*.

6. Trunk community of *Festuca arundinacea* and *Elymus repens* [*Plantaginetalia/Molinio-Arrhenatheretea*] (AF).

Number of species: 12. Species-poor community on fertilized and hardly grazed or mown grassland, mainly in Zeeland and IJsselmeer dykes. Because of the absence of character species this community could not be assigned to the *Arrhenatheretum elatioris*, nor be regarded as a *Poo-Lolietum*, although species of *Arrhenatherion* as well as *Poo-Lolietum* are present. In fact it is a poor and heterogeneous community, which develops on fertilized meadows without sufficient management. *Elymus repens* as well as *Festuca arundinacea* are indicative of this situation.

28   *Chapter 3*

Tabel 3.2 *Differential species of the distinguished communities. I - V: species present in 2-20 (I), 21-40 (II), 41-60 (III), 61-80 (IV), 81-100 % (V) of the relevés, + = present in 1% of the relevés; species are differential between communities if frequencies differ at least 30 % (figures in bold).*

Community number	4	1	2	3	5	6	7	8	9
Code:	PL	LG	LR	LF	AH	AF	AC	AO	AB
Number of relevés :	66	57	27	55	7	9	36	23	11
Number of species (av.)	12	14	18	18	8	12	13	25	34
Geranium molle	II	**V**	II	III	-	I	-	+	I
Cynosurus cristatus	-	**IV**	**III**	+	-	-	+	I	II
Veronica arvensis	II	II	**III**	II	-	-	I	I	I
Ranunculus repens	I	II	-	III	I	II	+	I	-
Leontodon autumnalis	-	-	-	II	-	-	-	+	-
Plantago coronopus	-	-	-	II	-	-	-	-	-
Cirsium arvense	II	I	I	**IV**	I	I	**III**	I	I
Alopecurus pratensis	-	-	-	-	**III**	-	+	+	-
Heracleum sphondylium	-	-	-	+	III	-	I	+	II
Phragmites australis	-	-	-	-	II	-	-	+	-
Urtica dioica	-	-	-	-	**III**	-	I	+	-
Fissidens species	-	-	-	+	**III**	-	-	+	-
Glechoma hederacea	+	-	-	I	**III**	**III**	I	I	I
Polygonum amphibium	-	-	-	+	II	II	-	-	-
Festuca arundinacea	I	-	+	+	-	**V**	**III**	**IV**	I
Crepis capillaris	I	I	I	II	-	II	I	**IV**	II
Festuca pratensis	I	-	-	-	-	-	I	**III**	I
Lathyrus nissolia	-	-	-	-	-	-	+	**II**	-
Origanum vulgare	-	-	-	-	-	-	-	**II**	-
Allium vineale	-	-	-	+	I	-	I	**III**	V
Daucus carota	-	-	+	I	-	-	I	**IV**	V
Geranium dissectum	II	I	II	I	-	II	II	**IV**	IV
Senecio erucifolius	+	-	-	-	-	-	I	**III**	III
Vicia sativa ssp. nigra	-	-	+	I	-	-	II	III	V
Holcus lanatus	+	-	II	II	-	-	I	II	IV
Anthoxanthum odoratum	-	-	-	-	-	-	-	+	IV
Briza media	-	-	-	-	-	-	-	-	II
Carex flacca	-	-	-	-	-	-	-	I	II
Leucanthemum vulgare	-	-	-	-	-	-	-	-	III
Cirsium vulgare	I	I	I	I	-	-	I	+	IV
Eryngium campestre	-	-	-	-	-	-	-	-	IV
Galium verum	-	-	+	+	-	-	-	-	IV
Avenula pubescens	-	-	-	-	-	-	-	-	III
Luzula campestris	-	-	-	-	-	-	-	-	II
Medicago arabica	I	-	I	+	-	-	-	I	III
Myosotis arvensis	-	-	-	-	-	-	-	-	III
Ononis repens ssp. spin	-	-	I	+	-	-	-	-	III
Pastinaca sativa	-	-	-	+	-	-	-	-	II
Potentilla reptans	-	-	I	I	-	-	-	+	IV
Rumex acetosa	-	+	I	+	-	-	-	I	III
Centaurea jacea	-	-	-	-	-	-	-	-	III
Pseudoscleropodium purum	-	-	+	-	-	-	+	-	II
Trifolium repens	I	IV	III	V	-	I	I	+	-
Poa annua	I	II	I	I	-	-	+	-	-
Hordeum murinum	II	I	II	I	-	-	-	-	-
Lolium perenne	V	V	V	V	I	V	I	II	III
Poa trivialis	V	V	V	IV	-	IV	V	IV	IV
Elymus repens	IV	I	III	V	V	V	III	IV	III
Poa pratensis	III	IV	IV	IV	II	II	IV	V	V
Dactylis glomerata	IV	+	IV	II	V	V	V	V	V
Agrostis stolonifera	III	III	IV	IV	-	III	I	I	III
Festuca rubra	IV	IV	IV	V	-	II	IV	V	V
Arrhenatherum elatius	I	-	-	+	V	III	IV	IV	IV
Ranunculus bulbosus	I	I	**III**	+	-	-	I	II	V

7. *Cirsium arvense* variant of the *Arrhenatheretum elatioris* (AC).

Number of species: 13. Because of the presence of the number of species belonging to the *Arrhenatherion* and *Arrhenatheretum elatioris* (see Appendix I), this coenon is assigned to this community. It can be regarded as a relatively species-poor, not well developed *Arrhenatheretum* with the abundance of Cirsium arvense.

8. *Festuca pratensis* and *Origanum vulgare* variant of the *Arrhenatheretum elatioris* (AO).

Number of species: 25. Moderately species-rich *Arrhenatheretum* with the presence of Origanetalia species like *Origanum vulgare* differential to community 9. According to the recent classification of grassland vegetation the community can be assigned to the *Arrhenatheretum festucetosum arundinaceae* (as described by Zuidhoff *et al.* (1996).The type is characteristic of not or hardly fertilized dykes in the south-west part of The Netherlands (Zak van Zuid-Beveland).

9. *Arrhenatheretum elatioris brizetosum* (AB).

Number of species: 34. Species-rich hayfield with *Briza media*, unfertilized for at least 20 years. Well developed *Arrhenatheretum* with the presence of character species of the association as well as differential species of the subassociation. The association has some affinity with the *Arrenatheretum luzeletosum campestris* as described by Zuidhoff *et al.* (1996). The community functions as a reference for this study.

Ordination

Figure 3.2 shows the result of a Detrended Correspondence Analysis (DCA) of all relevés made in 1991 and 1994 based on species cover and abundance. The cluster centroïds (= average DCA score of all the relevés within each community) that have been plotted, show a clear difference between pastures (communities 1-4) on the left of the diagram and hayfields (communities 5-9) on the right. The species-poor mulched or strongly fertilized *Arrhenatheretum* (community 5) is located along axis 2 at the upper part of the diagram and the over 20 years unfertilized species-rich *Arrhenatheretum* (reference community 9) at the lower part of the diagram. This suggests that axis 2 can be interpreted as a scale from relatively nutrient-poor to relatively nutrient-rich conditions, and axis 1 as a scale of explicit pasture to explicit hayfield species. This is in agreement with the correlation between calculated indicator values (Kruijne *et al.* 1967, Ellenberg 1978, Sýkora & Liebrand 1987) and the *DCA scores of the species* along the axes. Axis 1 is correlated ($r = 80$; $p < 0.001$) with indicator-values for pasture (low values) and hayfield (high values) species. Axis 2 is correlated with indicator values for the soil fertility of species ($r = 0.75$, $p < 0.001$) ranging from nitrogen-poor to nitrogen-rich.

There is a significant difference in average DCA scores of relevés along axis 1 between community 9 and communities 6, 7,8 and 5 (Oneway Anova) , indicating that this community has the most hayfield indicator species. Also community 1, characterized by pasture species, is significantly different from community 2, 3 and 4 ($p < 0.05$). Along axis 2 the average DCA score of community 4 differs significantly from the average DCA score of community 1 ($p < 0.05$). Generally three groups can be distinguished from the ordination diagram: I *Lolio-Cynosuretum* variants, II *Poo-Lolietum*, and III
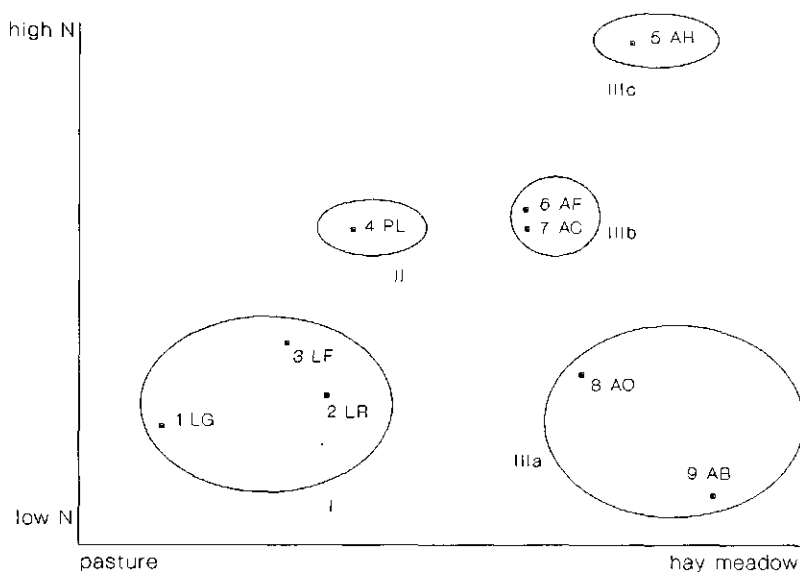
Figure 3.2 *Detrended Correspondence Analysis (DCA) of the relevés of sea dyke grasslands with different management regimes. The average score of relevés has been plotted for each community. See text for full names of plant communities.*

Arrhenatheretum variants with three subgroups: IIIa species-rich, not fertilized communities, IIIb species-poor, fertilized hayfields and IIIc the abandoned type (see Figure 3.2).

Habitat factors

With Chi-square tests no significant difference between communities was revealed in the distribution of the relevés over inner and outer dyke slope. Communities did not differ in duration of received sunlight (Oneway-ANOVA). Also, there appeared to be no significant difference in the average duration of received sunlight between inner and outer dyke slope, or between the northern and southern region (REML).

There is, however, a clear geographical effect on the occurrence of communities (Chi-square, $p < 0.001$, see Table 3.3). Plots representing the *Lolio-Cynosuretum* occur mainly in the northern region (dykes along the Wadden Sea, North Sea and IJsselmeer), whereas the *Poo-Lolietum* plots and plots belonging to the *Cirsium arvense* variant (AC) and the *Festuca pratensis and Origanum vulgare* variant of the *Arrhenatheretum* (AO) are more frequent in the southern region (dykes in the south-western estuary). This difference is probably based rather on differences in management than on different geographical features like temperature and floristic boundaries. In the northern regions less fertilizer is used on average (85 -120 kg N ha^{-1} y^{-1}) compared to the southern region (100 - 150 kg N ha^{-1} y^{-1}), mown grassland occurs less frequently and pastures are maintained more carefully by dragging to spread dung, mowing after periods of grazing, and extra cuttings when productivity is very high.

Table 3.3 *Distribution of relevés (% of the total number of relevés in 1994) for each community in the northern (Wadden Sea, North Sea and IJsselmeer) and southern region (south-western estuary) of Dutch sea dykes. Average soluble Na content per community is indicated as well. Different letters denote significant differences at p < 0.05*

Community	relevés frequency (%)		Soil Na content
	northern region	southern region	(mg kg^{-1})
1 LG	23		66.6^{bc}
2 LR	10	5	31.3^{ab}
3 LF	10	6	78.4^{c}
4 PL		17	20.8^{a}
5 AH	3		29.6^{abc}
6 AF	2	2	29.5^{abc}
7 AC	1	13	21.4^{a}
8 AO	1	5	33.5^{abc}
9 AB	0.7	1.3	19.8^{a}

On average the soil Na content is higher in the plots in the northern region (REML-analysis, $p < 0.05$). This is probably because the northern dykes are exposed to salt water, whereas the southern dykes, situated along the Westerschelde, are exposed to more brakkish water. This is in agreement with the higher soluble Na concentrations found in the soils of the northern *Lolio-Cynosuretum* communities LG and LF (Oneway-ANOVA, followed by LSD, $p < 0.01$, see Table 3.3). The difference in soluble Na content between the inner and outer dyke slope was weakly significant (REML-analysis, $p < 0.06$) in 1994, but significant in 1997 ($p < 0.05$).

On the community level the granular composition is significantly different (Oneway-ANOVA, $p < 0.001$, see Figure 3.3): the three *Lolio-Cynosuretum* variants (LF, LG and LR) as well as the species-rich hayfield (AB) have a higher sand fraction and lower silt and lutum fractions compared with the other communities. No significant difference was found with a REML analysis of average lutum and sand content between the two regions. Also there was no significant difference in granular composition at the inner and outer slope of the dyke.

Effects of management treatments on species composition, species abundance and species richness

Species composition

The changes on the community level as a result of four years cessation of fertilizer application are demonstrated in Table 3.4. Within each community the number of relevés in the different treatments in both years 1991 and 1994 is shown. Comparing the figures per treatment indicates in which community the number of relevés is increased or decreased from 1991 to 1994. In the column *D* is a summary of changes pertaining to the unfertilized treatments on grazed dykes (GG-, HG- and HH-).
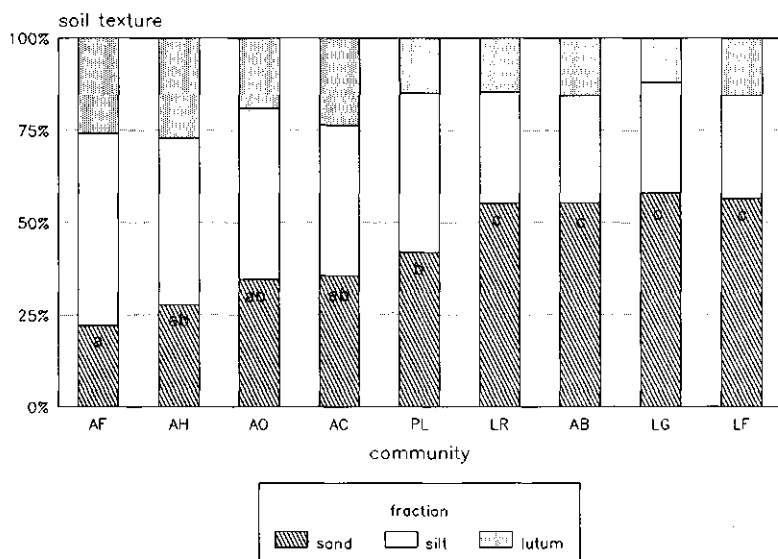
Figure 3.3 *Soil texture for each community. Small letters denote the significant differences (Oneway ANOVA after arcsine transformation, followed by a LSD test at p < 0.05).*

The number of relevés of the species-poor communities (LG) (*Geranium molle* variant of the *Lolio-Cynosuretum*) and PL (*Poo-Lolietum*) decreased (-4 and -9 respectively), whereas the number of relevés increased (+9) in the relatively species rich community LR (*Ranunculus bulbosus* variant of the *Lolio-Cynosuretum*). The *Arrhenatheretum* communities 6 (AF),7 (AC) and 8 (AO) also show a slight increase. From Table 3.4 it is furthermore clear that treatment HH- (unfertilised 2 cuttings a year) has the highest impact on changes in number of relevés: 30 % of the relevés from 1991 are placed in 1994 in another community, towards 13% and 19 % for the treatments GG- and HG-.

One can see from Table 3.4 that in 1991 relevés of fertilized treatments (G+ and H+) occur in all the communities, with the exception of the *Arrhenatheretum elatioris brizetosum* (AB), consisting of reference relevés of unfertilized old dyke grasslands. This indicates that the same communities were already in existence at the beginning of the experiment. In column *"%fert."* the percentage of fertilized relevés in 1994 is given. It indicates to what extent stopping the use of fertilizer is reflected by the distinguished plant communities. The *Poo-Lolietum* (PL) consists of 56 % of relevés of fertilized plots, against 22 % for the *Lolio-Cynosuretum with Ranunculus bulbosus* (LR).

Table 3.4 *Distribution of relevés from 1991 and 1994 over the communities for each treatment. G+ = fertilized with sheep grazing; GG- = unfertilized, 2 periods of grazing; HG- = unfert. 1 cut followed by grazing; HH- = unfert. 2 cuts haymaking; D = difference in number of relevés 94 - 91, cumulative over the unfert. treatments; % fert. = relevés of fertilized plots as a percentage of the total number of relevés in 1994 for each community; % change = percentage relevés that in 1994 belonged to a different community than in 1991*

	G+		GG-		HG-		HH-		D	H+		H-		% fert.
Year	91	94	91	94	91	94	91	94		91	94	91	94	94
1 LG	10	9	9	9	8	6	8	6	-4					30
2 LR	3	4	2	4	2	5	1	5	+9					22
3 LF	4	2		1	2	2	7	6	0	3	2	3	3	25
4 PL	11	12	9	5	4	3	5	1	-9	2	2	2	2	56
5 AH										3	2	3	1	66
6 AF	1	1	2	2			1	2	+1	1	1	1		33
7 AC		1		1			1	2	+2	3	5	3	6	40
8 AO								1	+1	2		3	3	0
9 AB										-	-	4	4	0
Total	29	29	22	22	16	16	23	23		14	12	15	15	
% change	10		18		19		30			25		20		

In an ordination diagram of relevés (indirect correspondence analysis, Figure 3.4) the effects of a changed management on botanical composition is demonstrated by arrows connecting average DCA scores of the 1991 and 1994 relevés for each treatment. The diagram shows a general shift towards less nitrogen-rich environmental conditions and the presence of more hayfield species. Cessation of fertilization in former pastures together with grazing (treatment GG-) or haymaking (treatment HH-) results in a significant decline in both treatments of DCA scores along axis 2 (see Figure 3.4), indicating a decrease of nitrogen-rich indicator species in the relevés between 1991 and 1994. Cessation of fertilization on mown dykes (treatment H-) leads also to a decrease of nitrogen-rich indicator species in the ordination diagram, but the change is not significant, comparable with the change along axis 2 between reference plots in 1991 and 1994. Although differences in position along axis 2 are shown between fertilized and unfertilized treatments after four years without fertilization, these differences are relatively small, when compared to the position of the reference plots in the diagram,.

Along axis 1 the unfertilized treatments GG- (grazing) and HH- (haymaking) show a significant change towards more hayfield species (axis 1), as well as the fertilized and grazed treatment G+. Probably the lowering of grazing intensity in GG- leads at the short term to an increase in hayfield species. A temporary decrease in grazing intensity between 1991 and 1994 probably causes the same effect in treatment G+. The change along axis 1 for treatment HG- is not significant. After fertilisation cessation the species-poor hayfields on sea dykes in the diagram positioned between pastures and long term unfertilized hayfields do not immediately show a clear shift towards more hayfield species.

Redundancy analysis (CANOCO)

To analyse the effect of fertilizer application and management after four years and of possible interactions with habitat factors on species data (cover-abundance in an ordinal
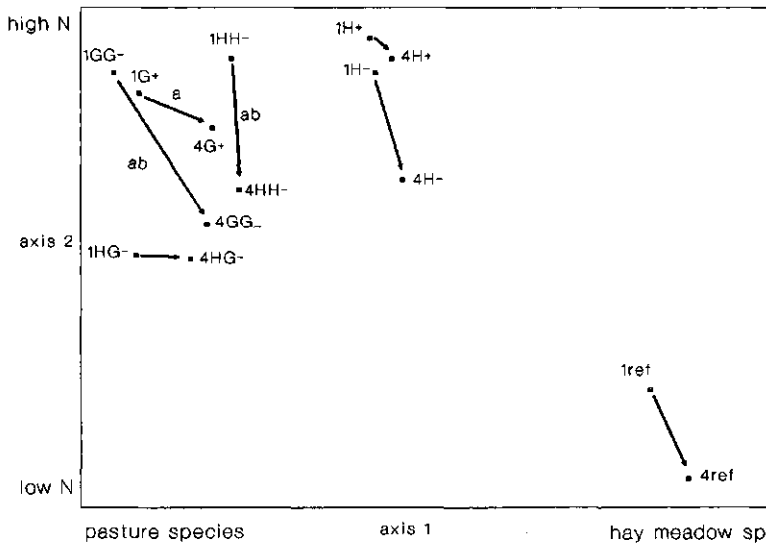
Figure 3.4 *Ordination diagram with averaged DCA scores of relevés in 1991(1) and 1994 (4) for each treatment. Arrows indicate the direction of change; a = significant change along axis 1, b = significant change along axis 2 (Wilcoxon's paired analysis of DCA-scores of 1991 and 1994 relevés along axis 1 and axis 2 , p < 0.05).*

scale), a Redundancy Analysis (RDA) was carried out. In a RDA, which is in fact a constraint PCA, the site scores are restricted to a linear combination of the environmental variables. The contribution and significance of each environmental variable to the total variance in species data, was determined, using forward selection of environmental variables followed by Monte Carlo permutation tests.

In this way a model was constructed of the most important environmental variables, which explained about 74 % of the total variance in species cover/abundance values. The differences between sites, and inner/outer dike slope, explain 68.7 % of the total variance in species data. Duration of received sunlight appeared to be a significant factor, but explained only 2.3 % of the total variance when sites were treated as covariates. Na content ("salt influence") had no significant effect on species composition. With sites combined with inner or outer dyke slope ("blocs"), and management as covariates, application of fertilizer is a significant factor, explaining 2.1 % of the total species variance. Management significantly (p < 0.005) explained 2.8 % with blocs and fertilization as covariates, and both management and fertilization as variates 4.1 %. The combination of management and fertilization, which are the treatments used in this investigation (G+, H+, HH-, H-, HG-, GG-) significantly (p < 0.005) explained 6 % of the total variance in species cover/abundance, which is 19.2 % of the rest variance after fitting the covariables 'site' and 'dyke slope'.

Although the differences between locations together with position on the dyke (effects of received sunlight and salt spray) have a considerable impact on the variance of species data (c. 70 %), cessation of fertilization together with the applied management practises still has a significant effect on the variation in the species composition (19.2 % of the rest variance).

Table 3.5 *Redundancy analysis of species data and management treatments with 'blocs' (= sites + dyke slope) as covariates (a). Only four axes are shown explaining 16.2 % of the rest variance (31,3 % = sum of all unconstrained eigenvalues). Total explained variance is 74.7 %, 6 % is explained by management treatments (p < 0.005, Monte Carlo permutation test). Canonical coefficients and intra-set correlations of the nominal variabels "management treatments" with the first two axes are given as well (b).*

a)

	axes				total
	1	2	3	4	
Eigenvalues	.024	.011	.009	.007	1.000
Species-env correlations:	.735	.784	.701	.654	
Cum. % of var.of spec.data	7.6	11.1	13.9	16.2	
of spec.-env. relation:	39.5	57.8	72.1	84.0	
Sum of all unconstrained eigenvalues (after fitting covariables)					.313
Sum of all canonical eigenvalues (after fitting covariables)					.060

b)

Treatment	coefficients		correlations	
	axis 1	axis 2	axis 1	axis 2
HG+	-0.37	-0.42	0.56	0.06
GG+	-0.80	-1.31	0.37	-0.54
H+	-0.99	-0.97	0.12	-0.41
HH-/H-	-1.86	-0.68	-0.51	0.52
HG-	-1.42	-0.58	-0.38	0.22
GG-	-1.10	-1.08	-0.04	-0.32

In Table 3.5 coefficients and correlations with the first two environmental axes are given, explaining 11.2 % of the rest variance. Although the coefficients do not differ much between treatments, and the correlations are weak (-0.51 and 0.52 for HH- and 0.56 and -0.54 for HG+ with axis 1 and GG+ for axis 2 respectively), the first axis can be interpreted as a fertilizer gradient and the second a gradient between grazing and hay-making.

This image is reflected by the biplot of the RDA of species and treatments (Figure 3.5). Unfertilized treatments are situated on the left side of the diagram and fertilized on the right, whereas pasture-treatments are located in the lower side of the biplot and meadow-treatments in the upper part.. It is obvious that *Lolium perenne, Poa trivialis, Bromus hordeaceus ssp. hordeaceus* as well as *Dactylis glomerata* are correlated with fertilized plots, whereas *Trifolium dubium, Festuca rubra, Brachythecium rutabulum, Agrostis stolonifera* and *Cynosurus cristatus* are correlated with unfertilized plots. *Festuca rubra* as well as *Lolium perenne* have an intermediate position towards 'management'-axis 2. *Trifolium dubium* is strongly correlated with haymaking and haymaking on former pastures in particular, but also *Arrhenatherum elatius* and *Elymus repens* are correlated with less fertilized grassland used for haymaking. *Cynosurus cristatus, Bellis perennis* and *Agrostis stolonifera* and *Dactylis glomerata* are linked with treatments on pastures.
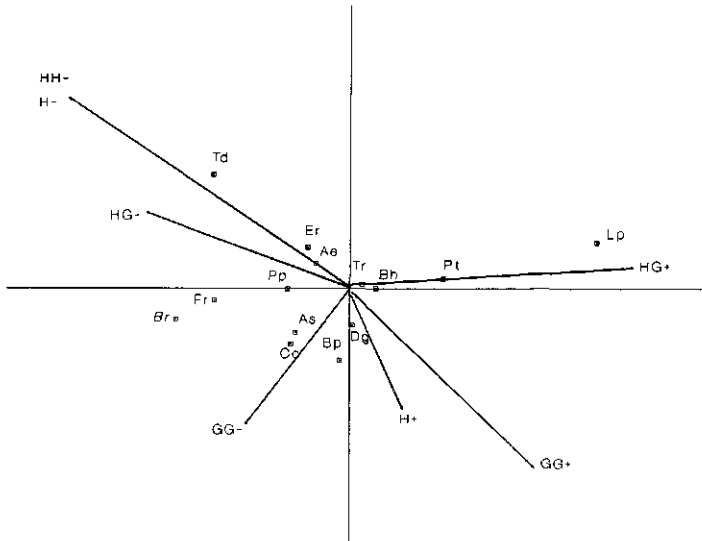
Figure 3.5 *RDA ordination diagram with the first two axes, showing the relative position of the species , based on cover/abundance, and the different treatments represented as vectors. Lengths of the arrows is indicative for the correlation of treatments with the axis. Lp= Lolium perenne, Pt = Poa trivialis, Bh = Bromus hordeaceus, Tr= Trifolium repens, Dg= Dactylis glomerata, Bp = Bellis perennis, As = Agrostis stolonifera, Cc= Cynosurus cistatus, Br= Brachythecium rutabulum, Fr = festuca rubra, Pp = Poa pratense, Ae = Arrhenatherum elatius, Er = Elymus repenms, Td = Trifolium dubium. For treatment codes see table 3.4. Only species with high variance contribution are indicated.*

Changes in species cover/abundance and presence

In a paired analysis using Wilcoxon's signed rank test (Sokal & Rohlf 1995) for statistical significance, the cover of species in 1991 plots is compared with the cover of species in the same plots in 1994. This was done for each treatment. The results are presented in Table 3.6. Only species that show a significant decrease or increase are presented.

The three unfertilized treatments on formerly grazed dykes showed an increase of *Trifolium dubium* and a strong decline in cover of *Lolium perenne*. The increase of *Poa trivialis* as well as the decrease of *Poa annua,* may not be the result of cessation of fertilization, since the same changes in cover also took place in the fertilized treatment. *Cynosurus cristatus,* however, showed a larger increase in cover percentage in both unfertilized grazed treatments GG- and HG- compared to the fertilized grazed and unfertilized mown plots. It is obvious from Table 3.6 that most changes in species cover occurred in treatment HH-. The grass species *Holcus lanatus* increases and *Dactylis glomerata* and *Bromus hordeaceus ssp. hordeaceus* showed a decline in cover in this treatment. Except for *Plantago lanceolata* which also increases in HG-, the herbs *Taraxacum species, Ranunculus repens, Leontodon autumnalis* and *Cirsium arvense* increase in HH-, and *Geranium molle* and *Capsella bursa-pastoris* decrease.

The unfertilized treatment on mown dykes (H-) in plots of 1991 and 1994 had only two species that exhibited a significant change in cover: an increase of 8 % cover of *Poa*

Table 3.6: Increase or decrease in average percentage cover of each species between 1991 and 1994 for the different treatments on grazed dykes. Wilcoxon paired analysis with p < 0.001 (****), p < 0.005 (***), p < 0.01 (**) and p < 0.05 (*). Figures represent the difference in average percentage cover in 5x5 m² plots, number of plots between brackets.

Species	G+			HH-			GG-			HG-		
					Treatments							
Increased % cover												
Trifolium dubium				+5	****	(20)	+3	**	(11)	+9	***	(14)
Taraxum species				+1.5	***	(23)						
Poa trivialis	+14	****	(30)	+6	**	(24)	+5.5	*	(14)	+5.5	*	(16)
Ranunculus repens				+3.9	**	(8)						
Holcus lanatus				+3	**	(7)						
Cynosurus cristatus	+2.5	*	(8)	+3	**	(10)	+7	**	(9)	+6	**	(9)
Plantago lanceolata				+2.4	*	(9)				+2	*	(5)
Leontodon autumnalis				+2.4	*	(5)						
Cirsium arvense				+2.4	*	(12)						
Cerastium fontanum										+2	*	(16)
Decreased % cover												
Lolium perenne				-33	****	(25)	-29	**	(14)	-29	**	(16)
Geranium molle				-1.5	***	(16)						
Poa annua	-2.4	*	(10)	-2.5	**	(8)				-2.5	*	(5)
Dactylis glomerata				-1.5	*	(11)						
Capsella bursa-pastoris	-2.4	*	(8)	-4	*	(6)						
Bromus hordeaceus -h.				-3	*	(23)						
Stellaria media	-1.5	*	(8)									
Brachythecium rutabulum	-8	***	(21)									

trivialis (n=10) and a decrease of 4 % of the moss *Eurhynchium praelongum*. In the fertilized hayfield (H+) the cover of *Poa trivialis* also increased (+4 % , n = 10), but the cover of *Festuca rubra* decreased by 13 %.

Unfertilized treatments are compared with fertilized treatments in 1994, and the differences in frequency and average abundance of the species are shown in table 3.7. Frequencies and average abundance (average ordinal scale) have been calculated separately for relevés in the northern region and the southern region, because of the observed floristic difference between the regions. This method was used to obtain additional information to the data presented in Table 3.6, to compare the differences between fertilized and unfertilized plots in 1994 as well as the difference between dykes from the northern and southern region.

As a result of the cessation of fertilizer application a higher frequency and average abundance in relevés was found of the grasses *Festuca rubra* (particularly on south-located dykes with mown as well as grazed treatments), *Cynosurus cristatus* (mainly in grazed plots), *Arrhenatherum elatius* (mainly on mown dykes) , *Agrostis stolonifera* (grazed dykes in the northern region), *Poa pratensis* (continuously grazing), and *Hordeum secalinum* (periodicaly grazing). On dykes in the northern region the number of relevés with *Elymus repens* increased in the HH- plots, but decreased in the H- plots. The abundance of *Lolium perenne* was lower in the unfertilized haymaking-treatments on formerly grazed dykes in both regions (HH-), and the treatment with a combination of haymaking and grazing (HG-), compared to the fertilized plots (G+).

The occurrence of the following herbs had a higher frequency and /or average abundance in the relevés of unfertilized plots: *Plantago lanceolata, Ranunculus bulbosus, Sonchus asper, Leontodon autumnalis* and *L. saxatile* (only in the northern region),

Table 3.7 *Differences in species frequency and average abundance in relevés of fertilized and unfertilized treatments on all sites of the northern and southern regions, four years after fertilizer application had been stopped;* + = *higher frequency, and* +a = *higher average abundance with a difference of at least two classes compared to the fertilized plots;* +n= *new species in more than 30 % of the relevés;* n = *new species in max. 20 % of the relevés;* - = *lower frequency, and* -a = *lower average abundance with at least two difference in class.*

Species	Treatments							
	Northern region				Southern region			
	G+/HH- (19)	G+/GG- (9)	G+/HG- (12)	H+/H- (5)	G+/HH- (6)	G+/GG- (6)	G+/HG- (4)	H+/H- (8)
Leontodon autumnalis	+	+n	+n					
Leontodon saxatile	+n	+	+n					
Elymus repens	+			-				
Agrostis stolonifera		+a						-a
Plantago lanceolata			+				n	
Cynosurus cristatus		+a		-n		n		n
Cerastium fontanum				+	+a			
Sonchus asper	n			n	+		+	
Hordeum secalinum		n	n			+n	+	
Arrhenatherum elatius				+a	+		+n	
Festuca rubra					+	+a	+a	
Trifolium dubium			+a	+	+	-a	+	
Brachythecium rutabulum					+	+	+	
Ranunculus bulbosus		n			+n	+	+	n
Taraxacum species	-	+			+			
Lolium perenne	-a		-a		-a		-a	
Bellis perennis			-a	-a		+a		+

Cerastium fontanum and *Taraxacum spec. Trifolium dubium* was shown to occur more frequently and abundantly in haymaking variants (HH- , HG-, and H-), but had a lower average abundance in the southern unfertilized grazed plots (GG-). On the contrary, the average abundance of Bellis perennis was higher in unfertilized grazed plots (GG-) and lower in mown (H-) or partly mown (HG-) plots. The species also occurred more frequently in meadows, when fertilization was halted for four years (treatment H-). On southern grazed dykes Brachythecium rutabulum occurred more frequently in the unfertilized plots, but this difference may be also due to the decline in percentage cover in the fertilized treatment (see Table 3.6).

Species richness

The species richness of sea dyke grassland is low. At the community level, the average number of species was shown to vary between 12 and 13 for the trunk community of *Festuca arundinacea* and *Elymus repens* (AF), the trunk community of *Arrhenatherum elatius* and *Heracleum sphondylium* (AH), the *Poo-Lolietum* (PL), the *Cirsium arvense* variant of the *Arhenatheretum elatioris* (AC) and the *Geranium molle* variant of the *Lolio-Cynosuretum* (LG); and between 18 and 19 for the trunk community of *Festuca rubra* and *Cirsium arvense* (LF) and the *Ranunculus bulbosus* variant of the *Lolio-Cynosuretum* (LR,

see Table 3.8). Only the well-developed Arrhenatheretum communities (AO, AB) on dykes that had not been fertilized for the last 20 years had higher species numbers, 25 and 35 respectively.

In the less species-poor communities (LF, LR, AO and AB) herbs were discovered to take a greater share in the total cover of the vegetation. Calculation of the Pearson correlation coefficients shows a weak, but statistically significant negative correlation between species number ($r = 0.51$, $p < 0.001$) and H/T ratio (cover of herbs as a percentage of the total cover; $r = 0.45$, $p < 0.001$), and average N indicator values of Ellenberg of relevés. On sea dykes a higher species number with more herbs is indicative of less fertile soil conditions.

Table 3.8 also gives the number of less common and rare species, which is relatively high in LF and the reference communities AO and AB. In these two communities some less common species occur, typical of dyke vegetation in riverine and coastal areas, like *Eryngium campestre, Koeleria macrantha, Avenula pubescens, Lathyrus nissiola, Lathyrus tuberosus, Verbena officinalis, Dipsacus fullonum, Orobanche lutea, Agrimonia eupatoria, Senecio erucifolius, Briza media, Crepis vesicaria, Origanum vulgare, Carex flacca*. The rare species of LF (*Trunk community* of *Festuca rubra* and *Cirsium arvense*) are typical of (dyke) grassland in coastal areas: *Torilis nodosa, Sherardia arvensis, Juncus gerardii, Alopecurus bulbosus*.

Tabel 3.8: Average number of species, ratio herbs cover/ total cover and number of less common and rare species for each community (i.e. species belonging to frequency class five or less of the number of hour-squares of 25 km² were the species have been recorded in the Netherlands since 1950, cf. Mennema et al., 1985).

Community	species number	herbs/total cover	number of less common and rare species
AF	12.0[a]	0.07[a]	0
AH	12.3[a]	0.14[ab]	0
PL	12.9[a]	0.12[a]	2
AC	13.3[a]	0.11[a]	2
LG	13.5[a]	0.24[bc]	2
LR	18.9[b]	0.36[c]	3
LF	19.5[b]	0.33[c]	8
AO	25.3[c]	0.34[c]	5
AB	35.3[d]	0.34[c]	6

A REML analysis was carried out of the number of species and the ratio herb cover/total cover, to determine the effect of cessation of fertilization after a period of four years and that of the different management regimes. The duration of received sunlight and Na content in the soil were used as covariates. For both parameters there was a significant effect of fertilizer use in the plots on grazed as well as mown dykes ($p < 0.05$), but no significant difference between grazing or haymaking was found. Table 3.9 shows the results of a paired analysis of the different treatments in 1994. Compared to the fertilized plots (G+, H+), all treatments on previously grazed dykes (HH-, HG-, and GG-), as well as the unfertilized treatment on mown dykes (H-) , had a significantly ($p < 0.05$) higher species number, four years after cessation of fertilization. However, the species number

Table 3.9: Average number of species and relative cover of herbs (H/T ratio = cover of herbs divided by total cover) in fertilized and unfertilized treatments. One asterix denotes a significant difference (p < 0.05) between unfertilized and fertilized plots on formerly grazed dykes; two asterixes indicate this significant difference on mown dykes. The species number and H/T-ratio of the reference dykes are given as well.

Treatment	n	species number	herbs cover / total cover
G+	25	13.5	0.16
HH-	19	15.6 *	0.26 *
GG-	14	15.3 *	0.21
HG-	15	15.9 *	0.26 *
H+	10	13.6	0.14
H-	10	16.9 **	0.24 **
ref	4	31.4	0.40

was still lower than the species richness on mown dykes (reference dykes) after at least 20 years without fertilization. This increase in species number is not caused only by the number of herbs. In the unfertilized treatments there is no significant increase of this figure (data not shown). The H/T ratio (herbs cover / total cover) however is higher ($p < 0.05$) in treatment HH-, HG- and H- compared to G+ and H+ respectively, which means that herbs contribute more to the total vegetation cover when fertilization is stopped.

Sward structure

Plant communities

Vegetation cover, mean open spot size and shoot density of the dyke grassland communities are presented in Table 3.10. The average value of these parameters in 1994 was calculated for each community. They give an impression of the sward structure of the distinguished communities. The two variants of the *Lolio-Cynosuretum* characterized by *Geranium molle* (LG) and *Ranunculus bulbosus* (LR), and the trunk community of *Festuca rubra* and *Cirsium arvense*, with affinity to the *Lolio-Cynosuretum* (LF) provided a relatively high vegetation cover (shoot frequency), a small mean open spot size, and high shoot density (i.e. low shoot density coefficient). The *Poo-Lolietum* (PL) together with the two *Arrhenatheretum* communities (AF and AC) gave a low vegetation cover, high values for open spot size and low values for shoot density. The species-rich Arrhenatheretum community (AB) had a low vegetation cover, but a small open spot size and high shoot density, similar to the *Lolio-Cynosuretum* communities, indicating a more diffuse spreading of shoots compared to the two other Arrhenatheretum variants, as well as the Poo-Lolietum.

Treatments

REML analysis of shoot frequency, average open spot size, sod density and average number of molehills, did not reveal significant effects of fertilization or management treatment. Only a significant difference ($p < 0.05$) in shoot frequency and average open spot size was found between formerly grazed dykes and mown dykes. Apparently stopping the use of fertilizer and continued grazing or haymaking or changing the management from

Table 3.10: Average shoot frequency, shoot density, open spot size, and number of molehills (ha⁻¹) *of the sampled communities. Differences are tested with a oneway ANOVA followed by a Least Significant Difference (LSD) test. Different letters indicate significant differences at p=0.05. No measurements were made in the trunk community of Anthryscus sylvestris and Heracleum sphondylium (AH).*

Community	number of relevés	shoot frequency (% vegetation cover)	open spot size (cm²)	coefficient of shoot density-curve (sod density)	number of molehills ha⁻¹	
LG	17	89^f	0.90^d	-1.40^c	30^b	(22)
LR	8	88^{ef}	1.87^{cd}	-1.02^b	300^b	(11)
LF	10	81de	2.81^{bc}	-1.04^b	510^b	(13)
PL	11	65^{bc}	4.24^{abc}	-0.64^a	1920^a	(13)
AF	2	45^a	6.56^a	-0.45^a	690^b	(2)
AC	4	55^{ab}	6.23^a	-0.51^a	430^b	(6)
AO	3	65^{bc}	4.79^{abc}	-0.41^a	800^b	(3)
AB	2	72^{cd}	1.67^{cd}	-1.2^{cb}	1090^{ab}	(2)

grazing to haymaking does not lead to a significant change in the sward characteristics after a period of four years. In the paired analysis of treatments (Table 3.11) no differences were found between fertilized (G+, H+) and unfertilized treatments (GG-, HG-, HH-, H-).

From Table 3.11 we may conclude that fertilization together with grazing results in a relatively high sod compactness (high shoot frequency and low values for open spot size and coefficient of shoot density), and this quality remains almost unaffected when fertilization is stopped. Fertilized dyke grasslands used as hayfields have a lower shoot frequency and sod density, and larger open spots in the sward, compared to fertilized grazed dykes. In the unfertilized species-rich hayfields of the reference dykes, however, the sward characteristics are not significantly different from those of the (formerly) grazed dykes. The sod is more open than the grazed dykes but the values for shoot density and average open spot size indicate an even distribution of shoots, with relatively small open spots. In the unfertilized plots on haymaking dykes (treatment H-) there seemed to be a slight increase of sod quality.

Compared to the fertilized treatment on grazed dykes (G+) less molehills were counted in the unfertilized treatments GG- and HH- (tabel 3.11), except for treatment HG-. On mown dykes there was no significant difference in the number of molehills between treatments.

Correlations

There is a significant correlation (p < 0.001) between shoot frequency (after arcsines transformation, r = - 0.46), coefficient of shoot density curve (r = 0.43 with logarithmic transformation) and mean open spot size (r = 0.52, log transformation), with the average N-indication values of relevés. This means that species present at high vegetation cover or shoot density are indicative for relatively low soil fertility. *Vice versa*, a low vegetation cover or shoot density is indicated by species growing under conditions of a rather high soil fertility.

Tabel 3.11: Shoot frequency (= % vegetation cover), average size of open spots, sod density (as expressed by c_{SD} = coëfficient of shoot-density-curve) and number of molehills in permanent plots in 1994 with different treatments. Different letters indicate significant difference at p< 0.05 between treatments (REML paired analysis followed by a t-test). I = fertilized +grazing; GG- = unfert. with two periods of grazing; HG- = unfert. first cut haymaking followed by grazing; HH- = unfertilized two cuttings for haymaking; H+ = fertilized haymaking; H- = unfertilized haymaking; ref = unfertilized, 20-25 years haymaking.

Treatment	N	shoot frequency	open spot size (cm^2)	coefficient of shoot density	number of molehills ha^{-1}
G+	15	83^b	1.7^c	-1.07^b	870^a
GG-	7	79^b	2.1^c	-1.12^b	450^b
HG-	7	80^b	1.6^c	-1.06^b	600^a
HH-	13	79^b	2.5^c	-0.91^{ab}	320^b
H+	5	63^a	6.3^a	-0.59^a	580^a
H-	5	65^a	5.6^{ab}	-0.70^{ab}	730^a
ref	3	73^{ab}	3.7^{bc}	-0.89^{ab}	770^a

Shoot frequency is positively correlated ($r = 0.35$, $p < 0.001$) and c_{SD} ($r = -0.38$, $p < 0.001$) and OSS ($r = -0.31$, $p < 0.01$) negatively to the ratio H/T (cover of herbs divided by total cover). These weak, but significant correlations indicate that a relatively high cover of herbs (measured during summer) goes along with a high sod compactness (measured during winter).

3.4 Discussion

Plant communities, habitat factors and botanical diversity

A phytosociological classification of relevés of differently managed study sites from both 1991 and 1994 gives insight into the changes in the botanical composition of the plots as a result of changed management dependent on the different habitat conditions (cf. Sýkora *et al.* 1990). A great number of sites have been investigated so that the relevés provide a general description of grassland communities on sea dykes, which is similar to that of a previous survey of Dutch sea dyke grassland (Sprangers *et al.*, 1990).

Van der Zee (1992) made an inventory of dyke vegetation in the Netherlands using relevés of sea dykes as well as river dykes. In his classification the majority of relevés of grazed sea dykes were assigned to the *Poo-Lolietum*. The grazed grasslands described in this study have been assigned to the Lolio-Cynosuretum or to the Poo-Lolietum. In the recently revised study of Dutch plant communities (Schaminée *et al.* 1996, Sýkora *et al.*, 1996), the *Poo-Lolietum* is no longer recognized at the association level, but it has been considered to be a trunk community, the *Trunk community of Poa trivialis and Lolium perenne [Plantaginetea/Cynosurion]*. In this study a community has been assigned to the *Lolio-Cynosuretum* if apart from the species group that is typical of the *Poo-Lolietum* sufficient species occur, which are characteristic of the *Arrhenatherion*, or (following the revised classification) of the *Cynosurion*. Variants have been distinguished below the association level. This subdivision allows the recognition of small differences between or

changes within phytocoena as determined by various habitat factors including management.

Although the *Lolio-Cynosuretum* variants occur more frequently on northern dykes and *the Poo-Lolietum* and *Arrhenatheretum* variants are more frequent in the south-western part, the difference between the various communities and variants must be attributed mainly to differences in management, i.e. the amount of fertilizer used in combination with sheep-grazing or haymaking. The botanical composition of the northern and southern region may differ on the basis of the two floristically different areas that can be distinguished, the Northern Clay District with dykes along the Wadden Sea, North Sea and IJsselmeer, and the Estuary District, covering dykes in the south-western part of the Netherlands (Van der Meijden, 1990). They both belong to the group of Haf Districts, man-made land, characterized by clay and peat soils. However the difference between the fertilized sheep-grazed grassland types belonging to the *Lolio-Cynosuretum* in the north and *Poo-Lolietum* in the south can be explained by the smaller amount of fertilizer that is used in the northern region and the higher accuracy of maintenance on these dykes. This is in line with the occurrence of relevés of Lolio-Cynosuretum variants also on southern dykes in plots that have been left unfertilized for the last four years. Contrary to the *Lolio-Cynosuretum* variants, the variants of *Arrhenatherum elatioris* occur more on dykes in the southern region, because of the management practise of haymaking without grazing in the south, which is not applied on northern dyke grasslands.

Other habitat factors that may contribute to the differences between the distinguished communities are the exposure to salt water influence and the granular composition of the soil. The two communities that are characterized by a higher Na content in the soil, the *Geranium molle* variant of the *Lolio-Cynosuretum* (LG), occurring on dykes in Groningen and Friesland, and the trunk community of *Festuca rubra and Cirsium arvense* (LF), occurring in the north-western part of the Netherlands (Hondsbossche Zeewering, Amsteldiepdijk and Helderse Zeewering) are indeed exposed to higher salt spray influences, compared to the *Arrhenatheretum* communities and *Poo-Lolietum* occurring on dykes along the Westerschelde. The *Ranunculus bulbosus* variant of the *Lolio-Cynosuretum* (LR), characterized by a relatively low soil Na content, occurs mainly on inner dyke slopes in the north and on unfertilized grasslands in the south. However, relevés of the trunk community of *Festuca rubra and Cirsium arvense* (LF) also occur on (unfertilized) plots on Westerschelde dykes in the south. This community and the *Geranium molle* variant of the *Lolio-Cynosuretum* (LG) are characterized by somewhat higher sand fractions, but only the sand fraction of LF differs significantly from most of the other communities. The higher sand fraction may be a distinguishing factor of this community, it is not linked with its occurrence on northern or southern dykes: relevés of LF also occur on southern located dykes and generally no significant differences have been found in granular composition between northern and southern located dykes.

The species-rich vegetation type that functions as a reference, the *Arrhenatheretum elatioris brizetosum*, grows on secondary dykes in the southern region and on one northern location. It includes the largest number of species and herbs and has a low average N indication value. The *Festuca pratensis and Origanum vulgare* variant of the *Arrhenatheretum elatioris* (AO), consisting of relevés of a reference dyke along the Westerschelde, is also relatively species-rich. In these communities a number of rare species occur, such as *Koeleria macrantha, Eryngium campestre, Avenula pubescens,*

Lathyrus nissolia, Briza media, Carex flacca. The other communities - in the ordination diagram there is a distinct separation between hayfields and pastures - are less species-rich and indicative of moderate to high nutrient levels in the soil. Some species typical of coastal areas occur: *Torilis nodosa, Sherardia arvensis, Medicago arabica.* The botanical diversity on primary dykes is low, although some less common and threatened species occur. Through cessation of fertilizer application, and less intensive grazing or haymaking, these species could maintain and spread out. These management measures will increase the botanical value of dykes.

Changes in botanical composition

The period of four years during which the treatments were applied is relatively short and has had just some minor effects on botanical composition. The results of other studies reveal that a much longer period of at least 10 years is required for the desired development towards a species-rich community (Bakker 1989, Oomes 1990), if this plagioclimax is ever to be reached (Berendse 1992). Nevertheless, changes did occur, which might have implications on the erosion resistance of dyke grassland. The methods used to analyse the effects of the different treatments on species composition and the clear trends that are visible will now be discussed.

At the community level a noticeable shift was observed in the number of relevés towards relatively species-rich communities at the cost of the species-poor communities. The largest effect occurred in plots on formerly grazed dykes that are now mown twice for haymaking (treatment HH-). This treatment as well as grazing twice a year without the use of fertilizer (GG-) has been shown to increase species indicative of a lower soil fertility, as depicted in the ordination diagram. This is in line with experiments on level grassland where the proportion of species growing on nutrient-poor soils increased when fertilisation was ended (Bakker 1989). However, the assignment of a number of relevés of unfertilized plots to relatively species-poor communities, indicates that the vegetation is still in a transition phase. Bakker (1989) found that 15 years after the new management was imposed, plant communites were not constant and succession was still going on.

Besides an increase of hayfield species in haymaking plots, an increased proportion of hayfield species was also observed in the grazed plots (Figure 3.4). This is probably a direct result of a decreased grazing activity, or an insufficient removal of standing crop by the lack of careful management on some locations. The change in species composition on dykes that were already mown before the start of the experiment, does not indicate a decline in soil fertility in the ordination diagram. Apparently cessation of fertilizer use has less effect in these grassland types after four seasons.

The difference in the frequency of relevés per community between 1991 and 1994 and the shift in average site scores per treatment in the ordination diagram between the two years, demonstrate the general effects of treatments on the basis of species composition, apart from effects of environmental variables. In the redundancy analysis the species-environment correlation was calculated on the basis of linear combinations of environmental variables. Although the variance in species composition has been determined largely by location of the study sites and linked habitat factors (soil texture, exposure to sunlight and salt spray, local differences in management), the redundancy analysis of species cover and data on environmental factors in 1994 revealed a small but strongly significant effect of management, i.e. fertilization in combination with sheep-

grazing or haymaking. Apparently cessation of fertilizer application on sea dyke grassland does affect species composition, even after a short period of time in spite of strong effects of habitat factors. It is possible that the decline in nutrient availability develops faster on dykes because of their low soil moisture than in flat grassland.

From the canonical correlations between species and management types in 1994 it is obvious that the cover of *Lolium perenne* and *Poa trivialis* and to a lesser extent *Bromus hordeaceus ssp. hordeaceus* and *Trifolium repens* is correlated with fertilization and grazing in combination with mowing, whereas the cover of *Trifolium dubium*, and to a lesser extent *Elymus repens* and *Arrhenatherum elatius* is related to haymaking without fertilization. The cover/abundance of *Festuca rubra, Brachythecium rutabulum* and *Poa pratense* is correlated to unfertilized dyke grasslands that are either grazed by sheep or mown for haymaking. *Cynosurus cristatus* and *Agrostis stolonifera* are related to unfertilized grazing, and *Bellis perennis* and *Dactylis glomerata* have an intermediate position towards fertilizer use and management type.

Species cover and abundance

The results of the canonical analysis are in agreement with the observed differences in cover/abundance of species in plots of 1991 and 1994. Four years after fertilization was stopped, species like *Cynosurus cristatus, Holcus lanatus, Festuca rubra, Arrhenatherum elatius, Trifolium dubium, Leontodon autumnalis, Ranunculus bulbosus, Plantago lanceolata, Hordeum secalinum* increased, while *Lolium perenne, Bromus hordeaceus spp. hordeaceus*, and *Capsella bursa-pastoris* decreased (Tables 3.6 and 3.7), indicating a rather short period of changes in species cover and species replacement.

In level grassland similar processes were observed after cessation of fertilization, together with a relatively rapid increase of species indicating nutrient-poor soil conditions. In these studies the time span required for new species to appear is about 3-10 years (Oomes 1990, Olff & Bakker 1991). Oomes (1990) describes a fast decrease of Lolium perenne and Stellaria media within three years, after stopping the use of fertilizer on grass on clay with cutting twice a year and removal of cuttings, but an increase of species like *Anthoxanthum odoratum* as was reported for experiments on sandy soil, did not occur even after 10 years. Only the biomass of *Holcus lanatus* increased but decreased again in a further successional stage (Oomes *et al.* 1996). In an experiment on the drier parts of brook grasslands in the Drentse Aa, where fertilization was stopped while cutting for haymaking once a year was continued, many species initially present, like *Holcus lanatus, Bromus hordeaceus, Lolium perenne*, and *Taraxacum spp.* disappeared and were replaced by *Agrostis capillaris, Anthoxanthum odoratum, Plantago lanceolata, Ranunculus repens* and *Leontodon autumnalis* within a period of 10 years (Olff & Bakker 1991). Some species like *Trifolium dubium, Rumex acetosa, Plantago major* appeared and disappeared within this period, with maximum cover 4-5 years after the experiment was started. On the drier parts the grassland type with *Lolium perenne, Bromus hordeaceus* and *Rumex obtusifolius*, developed through a *Festuca rubra* phase to an *Agrostis capillaris* sward, 25 years after fertilization was stopped (Olff *et al.* 1994).

The species replacement during succession after fertilization application is ceased, seems to be caused mainly by changed competitive relationships depending on the nutrient supply rate and changed vegetation structure, while soil fertility hardly declines (Bakker,1989, Olff & Bakker 1991). The changes in vegetation structure, resulting either

from aboveground standing crop removal through grazing or haymaking, or from different structural features of invaded or expanded grassland species, affect germination strategies (Olff *et al.* 1994, Bekker 1998) and strongly influence the establishment of species during the grassland succession.

Both in our experiments on sea dykes as in the experiments in dry grassland mentioned above (Bakker, 1989, Oomes 1990), Lolium perenne strongly declined. This short term process may be regarded as a direct effect of reduced nutrient availability, which is favourable for species with a lower growth rate such as *Festuca rubra*, that now can expand. Because of the changed leaf structure of the less productive sward (cf. Fliervoet 1984) other species can expand or invade. The appearance and expansion of species as *Holcus lanatus, Festuca rubra* and *Trifolium dubium* in the haymaking treatment probably indicate this transition from a highly productive to low productive grassland (see Mountford *et al.* 1993, Oomes *et al.* 1996 for the appearance of *Holcus lanatus* during succession).

Small changes in canopy structure can also have an important effect on the establishment of new species. The management in HH- was changed from fertilized grazing to unfertilized mowing. By stopping regular grazing and postponing the first cut (to the end of June), grasses are able to form flowering stems, but produce less shoots and rhizomes. The sward becomes less dense. As competition for light increases, rosette-plants *like Bellis perennis* will disappear, whereas other plants like *Trifolium dubium* and *Plantago lanceolata* settle or expand. Similar changes occur in the unfertilized treatment on mown dykes (H-). Competition for light becomes less important by a lower standing crop. The vegetation is less high and more open, which enables shorter species to establish and develop. With continued haymaking these grasslands could develop towards the species-rich meadows now occurring on sea dykes (reference grasslands), and characterized by - amongst others - species such as *Agrostis capillaris* and *Anthoxantum odoratum.*, if establishment of new species takes place either from seedbank or seed rain (Strykstra *et al.*, 1998)

Grazing is reported to have a greater impact on succession than haymaking. In the dry brook grassland experiment little grazing had a bigger effect on the poor to rich species ratio than haymaking (Bakker 1989). On sea dyke grassland, however, the haymaking treatment on formerly grazed and fertilized grassland had the greatest impact on species cover/abundance. Usually, grazing positively influences species richness through its impact on vegetation structure. Bullock *et al.* (1994) concluded that because of their high seed production together with the increasing gap frequencies as a result of grazing, dicotyledonous species are favoured by grazing. The density of large gaps ($> 25 \text{ cm}^2$) decreased during the dry succession when haymaking was applied in the brook grassland experiment (Olff *et al.* 1994). Smith & Rushton (1994) found that species richness in old meadows was maintained by grazing and that species numbers were reduced after cessation of grazing. The minor effects on species cover and composition of unfertilized grazed plots on sea dyke grassland compared to the mown plots can probably be explained by the relatively high grazing intensities employed on sea dykes, and consequently, the higher nutrient availability from sheep dung.

Four years after stopping fertilization only a slight, but significant increase of species number was observed: from 13 to 16 species per 25 m^2 in the unfertilized treatments on grazed dykes and 14 to 17 species on mown dykes. The number of species growing in the

long-term unfertilized hayfields (reference dykes) is about 2-3 times higher than the fertilized grasslands. The increase of species numbers after the four years in question, indicate that this period is far too short for the development of a species-rich community. Extensive management should be continued for several decades to approach the diversity in the reference plots.

Sward structure

The observed changes in presence and cover/abundance of species influence the stability of the vegetation. Grassland dominated by *Lolium perenne* is more sensitive to frost, over-grazing and drought than vegetation with less drought-sensitive species like *Cynosurus cristatus* and *Festuca rubra*. The change in species dominance can also affect root density and erodibility. *Cynosurus cristatus* and *Festuca rubra*, for example, have deeper rooting patterns than *Lolium perenne* (Kutschera & Lichtenegger 1982, Van der Zee 1992). When *Lolium* declines together with superficially rooting herbs as *Stellaria media* and *Capsella bursa-pastoris* in favour of deeper-rooting grasses and herb species like *Trifolium dubium* and *Plantago lanceolata*, the overall root density is likely to increase.

In this study, sod characteristics like vegetation cover (shoot frequency), shoot density, average open spot size, have been measured in the plots to judge erosion resistance of the grass cover under different management regimes after fertilization was ended. A dense sod on clay soil has a higher erosion resistance than a grass sward with many open spaces (Anonymous 1984, Verheij *et al.* 1995, Anonymous 1998). As shown above, the change in vegetation structure has an important effect on species replacement during succession towards species rich-grassland. Therefore, vegetation structure influences erosion resistance in both a direct and indirect way.

In general, shoot frequency, mean open spot size, and shoot density did not differ significantly between the fertilized and unfertilized treatments. Only the fertilized or mulched hayfields had a significantly more open sward compared to the other treatments. Thus the extensivity of management in the short term does not lead to a strong lowering of vegetation cover. Regarding the sod quality of the reference dykes (unfertilized hayfield), we can expect the vegetation cover in the mown treatments on grazed as well as mown dykes to also remain equal or even increase in the long run. Data on the sward parameters measured in 1997 (Sprangers & Ramaekers 1998) confirm these expectations. In the unfertilized treatment on mown dykes the level of vegetation cover (measured as shoot frequency) remained the same (low) at the end of the four years, but there was a slight increase of shoot density and a decrease of the open spot size. This is in agreement with the decrease of large gaps during the restoration succession of species-rich hayfield (Olff *et al.* 1994). No clear relation was found between fertilization or management and the occurrence of molehills. On grazed dykes two of the three unfertilized treatments had significantly less molehills than the fertilized plots, suggesting that mole activity is higher in fertilized grasslands (Knight 1989). On mown dykes no such difference was found between fertilized and unfertilized dykes, including references. Probably mole activity is very variable depending on climatic circumstances and local conditions as type of landuse near to the dyke. Regardless of the management type, the control of mole activity seems to remain a contstant focus of care for safeguarding the erosion resistance of dyke grasslands.

The present data clearly shows that a dense sod is correlated with a high cover of herbs. Furthermore, high sod compactness appears to be correlated with low average N

indicator values. Species of dense turf are indicative of nutrient-moderate to nutrient-poor conditions. This concerns mainly hemicryptophytes. Annuals like *Stellaria media* and *Capsella bursa-pastoris*, sometimes with high cover present in fertilized grassland, do not contribute to sod density. This means that the development of species-rich grasslands on dykes by extensive management practises favour sod density and thus erosion resistance of dykes.

These findings are confirmed by the different vegetation types that are recognized. Dyke grasslands of the *Lolio-Cynosuretum* type (with fertilized as well as unfertilized plots) are characterized by a high vegetation cover and shoot density, whereas species-poor hayfields (fertilized or mulched plots) and the productive *Poo-Lolietum* (mostly fertilized plots) have low values for these parameters. The difference between the *Lolio-Cynosuretum* pastures, occurring mainly in the North, with a maximum turf height of c. 25 cm, and the *Poo-Lolietum* of the South, that sometimes reaches heights of over 40 cm requiring a hay-cutting before grazing, can also be a matter of sward maintenance. In fertilized amenity turf of Lolium perenne tiller density is inversely related to tiller height (Lush & Rogers, 1992). Apart from this maintenance factor, vegetation cover seems to be a reliable criterion for the compactness of the turf (Anonymous 1984, Sýkora & Liebrand, 1987, cf. Anonymous 1996b). However, in the unfertilized species-rich hayfields of the reference dykes the shoot frequency (vegetation cover) is low compared to the *Lolio-Cynosuretum*, but the shoot density is relatively high with the same values as the *Lolio-Cynosuretum*, because of a diffuse distribution of shoots over the surface and the occurrence of small open spots. Therefore, to determine erosion resistance of a sward, it would appear useful to take shoot density into account as well (cf. Anonymous 1998).

Conclusions.

Returning to the questions that are asked at the beginning of this chapter, the following answers can be given. After four years, fertilizer cessation on dyke grasslands results in a slight increase of species numbers, and, moreover, a rapid decline in cover/abundance of *Lolium perenne* followed by an increased abundance of species indicative of less nutrient-rich conditions like *Festuca rubra, Cynosurus cristatus, Trifolium dubium.* The proportion of herbs in the grass sward increases. At the community level this species replacement causes an expansion of species-rich communities at the cost of species-poor communities.

Although there are large differences in habitat factors between study sites, characterized by Na content in the soil, soil granular composition and amount of received sunlight, differences in management are most determinant of the species composition of the sites. After correcting for habitat factors, the effect of cessation of fertilizer application combined with extensive grazing or haymaking on species composition could be clearly demonstrated at the end of four growing seasons. We argued that the rather rapid response to the changed management when compared to other experiments, was the result of the specific moisture conditions of dyke grasslands, resulting in a drastic lowering of the nutrient availability when fertilization was ended. The change from grazing with fertilization to haymaking without fertilizer application, showed the largest effects on botanical composition.

Species replacements, as observed in this study, that occur during vegetation succession after fertilizer application has stopped, can be considered to be the result of a process of continuous interaction between nutrient availability and vegetation structure

(competition for light). The succession does not lead to a strong decrease in density of the sward, even not after a longer period without fertilizer as is demonstrated by the case with the reference dykes. The development of species-rich grasslands on dykes through extensive management will therefore result in relatively dense swards, which is considered to be good for erosion resistance. Apart from vegetation cover, shoot density must also be measured to judge the sward quality.

Productivity and root growth

Effects of cessation of fertilization on aboveground productivity, root growth, and nutrient contents in plants, roots and soil

With K.V. Sykora

4.1 Introduction

One of the aims of this study is to investigate the feasibility of establishing species-rich grassland on sea dykes for reasons of their presumed high root density and resultant erosion resistance (cf. Sykora & Liebrand 1987, Van der Zee 1992). This chapter discusses the short-term effects of cessation of fertilization on above- and belowground production and nutrient levels in soil and plant tissue.

Cessation of fertilizer application to grassland on clay-on-peet soils leads to a slow decrease in production when compared to sandy soils (Berendse 1992). A combination of fertilizer cessation and haymaking did not change the productivity in grassland on clay soils within two years (Oomes 1990). A level of unfertilized grassland was reached only after a period of five years. The N-concentration in the aboveground biomass showed a slight decrease after two years, which dropped to a level of species-rich nutrient-poor grassland after ten years. These and other experiments (cf. Olff *et al.* 1994) demonstrate that the process of decreasing nutrient availability in the soil can be described by the decline in the dry matter and nutrient yield, and consequently, data on nutrient contents are necessary to identify possible causes of this decline (Oomes *et al.* 1996). Fluctuations in productivity as a result of changes in weather conditions must be taken into account (De Leeuw *et al.*1990). These fluctuations could be quite marked because of the poor moisture conditions on dykes in the summer, causing a significantly reduced release of mineral nitrogen (Sprangers, unpublished data).

A deficiency of nutrients or water in the soil leads to an increased root growth compared to the growth of shoots, thus decreasing the shoot/root-ratio (Brouwer 1962, Noordwijk 1987, Wilson & Tilman 1991a, Fitter 1994, Olff *et al.* 1994, Ericsson 1995, Lambers *et al.* 1998). This relation however, is ambiguous. Species of nutrient-rich habitats showed a greater allocation to roots, resulting in lower shoot/root ratios than species from nutrient-poor habitats (Berendse & Elberse 1989, Boot 1990, Olff *et al.* 1990, Elberse and Berendse 1993, Schippers & Olff 1998). Berendse & Elberse (1989) found the species from poor habitats to have a higher specific root length (length per unit root weight), which could compensate for the low root weight. Schippers & Olff (1998) on the

other hand found that species from more fertile sites had a higher or equal specific root length, resulting in a higher relative growth rate and total biomass.

The ratio between aboveground and belowground production expresses possible changes in allocation of carbohydrates to above and below ground compartments of vegetation. Plants follow the functional equilibrium between root and shoot allocation defined by Brouwer (1962), which explains the decrease in shoot to root ratio when nitrogen supply is limited. Wilson and Tilman (1991a) stated that this was demonstrated by individual plants as well as by plant communities, indicating that a greater root allocation is required at low resource supply rates. This is in agreement with the results of studies on grassland communities, where the species-rich types, occurring at low soil nutrient levels are characterized by relatively high root densities (Sýkora & Liebrand 1987, Van der Zee 1992, Fiala 1993). While reduced nutrient availability is expected to affect the plant's functional equilibrium and enhance root growth, disturbances provoked by grazing and haymaking will reduce root growth, because of reallocation to the shoot of part of the root carbon and nitrogen after aboveground biomass loss (Brouwer 1962).

The probable impact of cessation of fertilization and the adjustment of the grazing and haymaking regime on above and belowground productivity at different nutrient levels can be described in terms of the above-mentioned processes. Although they indicate the potential of this type of extensive grassland management for the expansion of rooting systems and resulting soil stability of dyke grassland, little is known of the short-term effects at the community level. The change in species dominance following the cessation of fertilization (Olff & Bakker, 1991, Olff *et al.* 1994, cf. Chapter 3) will also influence rooting patterns and soil stability (Goss, 1991). The questions we tackle in this chapter are: (1) what are the changes in aboveground biomass and chemical composition of soil and plants, four and seven years after fertilizer application has been stopped?; (2) what are the effects of four years discontinued fertilization on below-grond production and root length densities?; (3) what are the differences in effects of grazing and haymaking on root system properties when nutrient availability decreases?; (4) how is root density correlated to soil texture, shoot density, and chemical composition of soil and plant? Much attention will be paid to the changes in distribution of roots along the soil profile. This is an undiscussed aspect so far in this survey, but very significant to soil stability and soil structure (see Chapter 1).

4.2 Methods

Biomass

From the end of June till the beginning of July, the aboveground vegetation was clipped in 4 replicate plots of 0. 25 m² in each permanent quadrat (see Chapter 2 for study sites and management treatments). This was done each year from 1991 up to 1997. The harvested material was weighed after it had been dried for 48 hours at 70 °C. The biomass was harvested in grazed plots in exclosures next to the permanent quadrats. From the dried material in each permanent plot a representative sample was taken for analysis of N, P, K, Na and Ca by digestion of ground material using a mixture of sulfuric acid, salicylic acid, hydrogen peroxide and selenium, following the methods described by Walinga *et al.* (1995).

Once, namely in 1994 the regrowth was assessed at several locations by clipping the aboveground vegetation at the end of September. This was done in pastures in exclosures that were replaced at the beginning of July (and cut at the same time to remove ungrazed material), and in hayfields just before the second cutting.

To analyse the effect of duration of daily received sunlight on productivity, the plots were divided into locations with predominant sun influence (> 2.8 h radiation day^{-1}) and locations with less sun radiation (< 2.8 h day $^{-1}$). The duration of direct solar radiation (h day $^{-1}$) was calculated for each plot by measuring the slope angle and exposition by using the radiation diagram of Grime & Loyd (1973).

Roots

For root measurements, samples were taken in each permanent plot in March 1994 using an auger of 4 cm diameter provided with a sample removing device. Three replicate samples were chosen randomly in the grass turf avoiding the open spots. The samples were taken to a depth of 50 cm and divided in 8 layers after removal of the upper part of the sod (about 0.5 to 1 cm below soil surface): 0 to 3 cm, 3 to 6 cm, 6 to 10 cm, 10 to 15 cm, 15 to 20 cm, 20 to 30 cm, 30 to 40 cm and 40 to 50 cm. In order to calculate the ratio aboveground/belowground production auger samples were taken again in June/July to a depth of 30 cm and stored at - 20 °C. In the laboratory, the soil cores were thawed in water and gently shaken for about six hours, then washed with tap water over 250 μm sieves and transferred into a water-filled tray. Roots were separated from dead material and soil particles by a flotation method (repeatedly pouring off floating matter), stained in a solution of methylene blue (50 mg l^{-1}) for about 6 hours and spread out in water trays, after which they were scanned using a high resolution scanner (up to 354 pixels per cm, TRUVEL TZ-3, Vidar system corporation, Herndon, USA). Excessive dye was rinsed off with water before scanning.

Root length of the samples and subsamples gathered in March was measured by analysing the scanned images with the interactive image analysis package TCL-Image V4.6 (TNO Institute of Applied Physics, Delft, The Netherlands). This method has proved to be much more accurate when compared to the line-intersect method (cf. Tennant, 1975) and more reliable when measuring very thin roots (< 0.1 mm) than other methods using image analysis (Smit *et al.* 1994). After scanning root dry weight was measured after drying of the root samples at 70 °C. From the June /July samples only root dry weight was measured. The following parameters were determined: *root density* (m dm^{-3}), *average root biomass* (g dm^{-2} in a 50 cm layer), *average root length* (m dm^{-2}), *specific root length* (SRL in m g^{-1}) and *shoot to root ratio* (SRR g g^{-1}). Calculation of the specific root length of the sampled permanent quadrats in the different treatments provided information on wether or not many relatively thin or a few relatively thick roots are present. The shoot/root ratio was determined here by calculating the ratio of above-and belowground average production (peak biomass in g m^{-2} and root mass to a depth of 30 cm in g m^{-2}) per community or treatment.

To analyse the vertical distribution and to compare distribution patterns between treatments, the change in root length and root weight per volume of soil with the depth of the rooted profile, is expressed by the following equation:

$$y = a + (b - a)r^{(x-1.5)} ,$$

where y = root length dm^{-3}, x = depth and a, b and r are constants indicating the root quantity at a depth of 50 cm (a), which is assumed to become zero in deep layers, root quantity at the surface (b, at -1.5 cm) and the degree of root decrease with depth (r) respectively. The values a, b and r were calculated for each root auger sample at average values of x in each layer (1.5; 4.5; 8; 12.5; 17.5; 25 ; 45 cm). In this way one parameter for the distributions of roots along the profile was obtained.

Soil

In the summer period 15 June to 5 July of 1994 ten random soil samples were taken at a depth of 1 to 11 cm below the soil surface in each permanent plot and combined into one mixed sample. After drying at 40 °C for 48 hours, 10 g of the fraction < 2mm was extracted in 100 ml 0.01 M CaCl$_2$ solution, and NO$_3$-N, NH$_4$-N, dissolved organic N, Na and K were determined after dialysis in a continuous flow analysis system, and dissolved orthophosphate in a plasma emission spectrophotometer (Houba *et al*. 1994, 1995). The contents of total N, P and K in the soil were determined by digestion at 300 °C using a mixture of sulfuric acid, salicylic acid, hydrogen peroxide and selenium. Organic matter was measured according to Kurmies (Houba *et al*. 1994) and calciumcarbonate according to Scheibler (Houba *et al*. 1994). The percentage of carbon was calculated as the 0.58 fraction of organic matter (Houba *et al* 1994).

Statistics

Statistical analysis was carried out using a REML analysis (Residual Maximum Likelihood) from the computer package GENSTAT (Payne *et al*. 1993)., followed by a Wald-test for significance of effects. This method was chosen because of the unbalanced set of data, which made it impossible to carry out a threefold ANOVA with the factor management nested within fertilizer application, nested within (former) grazed or mown dykes. Using REML the effects of fertilization and management were tested separately by comparing and contrasting: plots of formerly grazed and mown dykes; fertilized and unfertilized dykes; grazed and mown dykes; grazed or mown dykes and mown dykes combined with grazing; and finally, reference and non-reference hayfields. The duration of exposure to direct sunlight ('sun') and the Na content in the soil ('salt') have been treated as covariates, to correct for differences between inner and outer slope of the dykes. Additionally, to make a direct comparison of the different treatments, a REML analysis was done, with 'treatment' (referring to the combination of fertilizer use and management practice) as factor, and 'sun' and 'salt' as covariates, followed by a t-test on paired differences of means. Because of the unbalanced data set, analysis of the data on biomass was done for each year, separately. With a one factor ANOVA followed by a posteriori LSD test, the differences between communities for the investigated parameters are analysed.

4.3 Results

Aboveground biomass

Table 4.1 shows the results of the REML analysis of the calculated peak aboveground biomass for the different comparisons carried out separately for each year of the investigated period of 1991 to 1997. Except for 1991 on the formerly grazed dykes, and 1991 and 1992 on mown dykes, a significant effect of fertilization was observed on both

Table 4.1 *REML analysis of contrasts in average peak biomass for each year and regrowth in 1994 (RG94) between (former) pastures and meadows (d), and the following treatments on (former) pastures: +/- fertilizer application (f1), haymaking or grazing (m2), haymaking followed by grazing versus haymaking or grazing (m1), and two treatments on mown dykes: +/- fertilizer application (f2) and reference plots vs. experimental plots (r). Duration of received sunlight ('sun') and Na content in the soil ('salt') have been treated as covariates. Significant differences between contrasts are indicated by *** (p < 0.001), ** (p < 0.01) and * (p < 0.05), according to the calculated t-values.*

Year	'sun'	'salt'	Pasture vs. hayfield (d)	Pastures: +/- fertilizer (f1)	Pastures: haymaking vs. grazing (m2)	Pastures: haymaking + grazing (m1)	Hayfields: +/- fertilizer (f2)	Exp. plots vs. reference plots (r)
91	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
92	n.s.	n.s.	n.s.	***	*	n.s.	n.s.	n.s.
93	n.s.	n.s.	n.s.	*	n.s.	n.s.	***	n.s.
94	*	n.s.	n.s.	***	n.s.	n.s.	**	n.s.
95	n.s.	n.s.	n.s.	**	n.s.	n.s.	**	***
97	n.s.	n.s.	n.s.	***	n.s.	n.s.	***	**
RG94	*	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

types of dykes, but hardly any effect of management type. Grazing or haymaking without the use of fertilizer did not show significant differences in the aboveground biomass except in 1992. The effect of received sunlight appeared to be only significant in 1994. In 1995 and 1997 the aboveground biomass of the reference dykes differed significantly from fertilized and unfertilized mown dykes.

In Figure 4.1 the peak aboveground biomass over the years is given for the different management treatments on pastures(4.1a) and hayfields (4.1b). The continuation of fertilizer application led after three and two years to significant higher peak biomass in the fertilized plots than compared to the unfertilized treatments. In 1997, the average peak biomass on (formerly) grazed dykes (Figure 4.1a) amounted to 7.2 tonnes ha^{-1} in the fertilized plots and 3.7 to 4.6 tonnes ha^{-1} in the unfertilized plots, indicating a decline in production after cessation of fertilizer application of about 3 tonnes ha^{-1}. The peak biomass on mown dykes (Figure 4.1b) amounted to 6.5 tonnes ha^{-1} in the fertilized and 3.8 tonnes ha^{-1} in the unfertilized treatment, indicating a similar reduction of peak biomass production of about 3 tonnes ha^{-1}.

Both fertilized and unfertilized treatments on pastures (Figure 4.1a) show substantial annual fluctuations, but the variation in the unfertilized plots seems to be smaller. During the experimental period there was no clear decline in peak biomass in the unfertilized treatments in the years following the first growing season without fertilizer (4.2 to 4.8 tonnes ha^{-1} in 1991 and 3.7 to 4.6 tonnes ha^{-1} in 1997). There was no significant trend of the differences in peak biomass between the unfertilized treatments. The haymaking treatment (HH-) in 1992 had a higher peak biomass than the grazed variants (GG-, HG-), whereas the biomass values of the periodically grazed type (GG-) has higher than the treatment with haymaking followed by grazing in 1994. No difference was observed between the unfertilized treatments in the other years. The same pattern shows up in the hayfield experiment (Figure 4.1b): relatively large fluctuations in peak biomass in the fertilized treatment, and a relatively smaller variation in the unfertilized treatment.
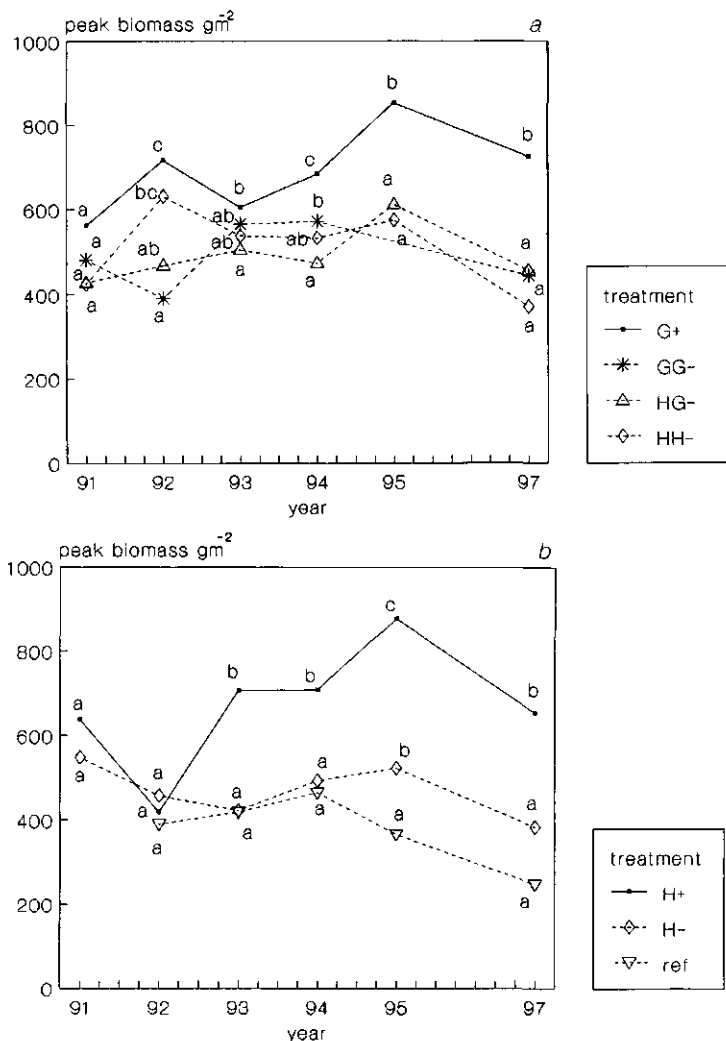
Figure 4.1 *Peak aboveground biomass in the fertilized (G+, H+) and unfertilized (GG-, HG-, HH-, H-, ref) treatments on dyke pastures (a) and hayfields (b) from 1991 to 1997. G+ = periodic or continuous grazing, GG-= two periods grazing.; HG-= haymaking followed by grazing; H+, HH-,H- = two cuttings for hay-making, ref = reference dyke - unfertilized for 25 years in combination with hay-making (one cutting). Different letters denote significant differences (p < 0.05) between treatments in each year. No measurements were made in 1996.*

Compared to the unfertilized treatments on pastures, a larger difference in peak biomass showed up after seven years without fertilizer (3.8 tonnes ha⁻¹ in 1997) compared to the peak biomass in the first season without fertilizer (5.5 tonnes ha⁻¹ in 1991). The peak aboveground biomass of the 25 years unfertilized reference dykes remained fairly constant over the years at about 4 tonnes ha⁻¹, with a lower value in 1997 - similar to all dyke locations - of 2.5 tonnes ha⁻¹.

In 1994 the biomass regrowth was measured on 15 september after cutting in hayfields and in replaced exclosures in pastures at the beginning of July (cf. Table 4.2). Although in the REML-analysis of contrasts no significant overall effect of fertilization could be found (see Table 4.1), from the paired analysis of treatments it became obvious that the regrowth was significantly smaller in the unfertilized haymaking treatment on grazed dyke grasslands (HH-) as well as in the unfertilized treatment in meadows (H-) compared to the fertilized plots (G+ and H+). The regrowth in other three unfertilized treatments (GG-, HG- and ref) did not differ significantly from the fertilized plots.

By adding the regrowth to the peak biomass measured at the first cut, we can calculate total annual aboveground productivity. The relative regrowth in all treatments was c. 25 %, except for the treatment haymaking with subsequent grazing (HG-) which was 30.3 % regrowth of the total production (Table 4.2). Four years after fertilization had been stopped, the annual productivity varied from 6.5 to 7.7 t ha^{-1}y^{-1}, while in the plots that were still fertilized it was 9.3 t ha^{-1}y^{-1}, which is a difference of c. 1.5 to 2.5 t ha^{-1}y^{-1}. After seven years, the total production calculated on the basis of peak biomass and extrapolated percentages regrowth was about 5 t ha^{-1}y^{-1} in the haymaking treatments, and 6 to 6.5 t ha^{-1}y^{-1} in the grazed treatments. In the fertilized plots the total annual productivity was c. 8.5 and 9.9 in mown and grazed grassland respectively, indicating a decline in productivity of c. 3.5 t ha^{-1}y^{-1}. Since both reference plots and fertilized plots show a substantial difference between the years 1994 and 1997, it is believed that these figures may have been influenced by climatic year to year fluctuations.

Table 4.2 *Peak standing crop, regrowth and total aboveground productivity in 1994 for each treatment. The calculation of the total production in 1997 was based on peak biomass in 1997 and percentage regrowth in 1994. Significant differences between treatments are indicated by different superscripts (REML paired analysis of treatments with t-test at p = 0.05, with duration of received sunlight and Na content in the soil as covariates). Treatments on (former) pastures: G+/ GG- = grazing with/without fertilizer use, HG-/HH- = hay-making with grazing and hay-making in two cuttings without fertilizer use. Treatments on meadows: H+/H- = hay-making with/without fertilizer use, ref = long-term unfertilized hay-meadow.*

Treatment	n	peak biomass 94 g m^{-2}	regrowth g m^{-2}	total prod. 94 g m^{-2}	% regrowth of total prod.	total prod.97 g m^{-2} (extrapolated)
G+	15	683^c	246^c	929^b	26.5	985
GG-	9	571^b	199^{abc}	770^a	25.8	597
HG-	5	473^a	206^{abc}	679^a	30.3	653
HH	15	533^{ab}	178^{ab}	711^a	25.0	493
H+	9	709^c	231^{bc}	940^b	24.5	866
H-	9	493^{ab}	162^a	655^a	24.7	509
ref	4	465^{ab}	173^{abc}	638^a	27.1	340

A significant effect of duration of daily received sunlight on peak biomass was shown using a REML analysis on contrasts (Table 4.1). Plots on southern exposed sites that received relatively more sunlight, had a higher peak biomass than slopes with less sunlight (see Figure 4.2a). The difference between the two categories was significant in the treatments on (former) pastures, contrary to the treatments on mown dykes (results not shown). A REML analysis on biomass regrowth averaged over the different contrasts also revealed significant effects of received sun radiation and Na content in the soil. The last-
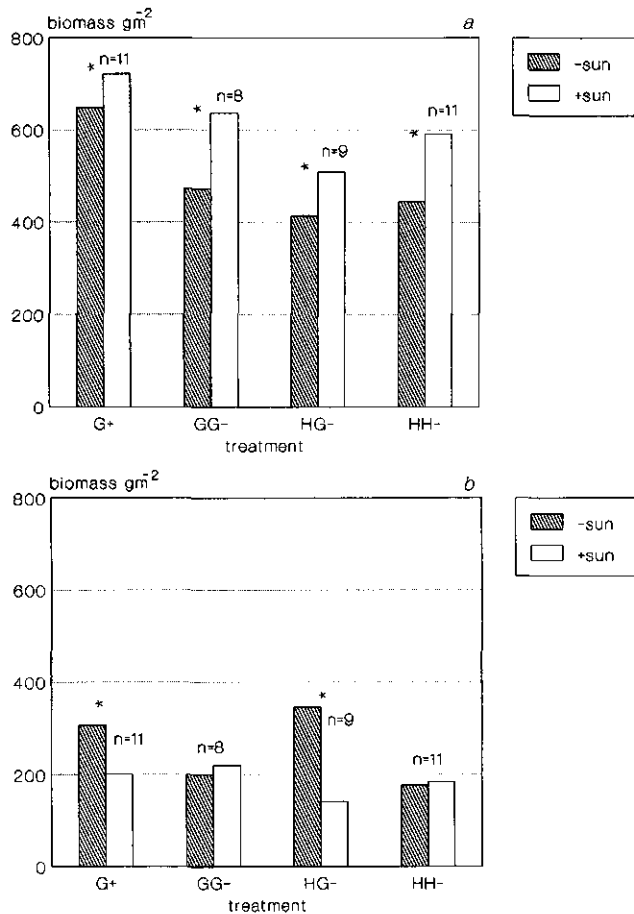
Figure 4.2 *Average peak biomass (a) and regrowth (b) of plots on slopes predominantly exposed to sunlight and slopes with a less exposure to sunlight, for the different treatments on (former) pastures in 1994. For an explanation of the different treatments see figure 4.1.*

mentioned effect was caused only by the higher levels of Na in the soil of slopes of the fertilized mown plots (treatment H+), exposed to the sea. The effect of sunlight on regrowth resulted in a significantly higher productivity during the period July-September in the fertilized grazed plots (treatment G+) and unfertilized mown plots with subsequent grazing (treatment HG-), at sites with a less exposure to sunlight (Figure 4.2b).

Differences in aboveground productivity between plant communities

Figure 4.3 gives the total annual productivity as well as peak biomass in 1994 for the distinguished plant communities (see Chapter 3). The species-poor hayfield communities, the *Festuca arundinacea* variant (AF), the *Heracleum sphondylium* variant (AH), and the *Cirsium arvense* variant (AC) of the *Arrhenatheretum*, are characterized by a significantly higher biomass production (9 to 14 tonnes ha^{-1}y^{-1}) than the two grazed communities LR (*Ranunculus bulbosus* variant of the *Lolio-Cynosuretum*) and LG (*Geranium molle* variant)

(5.8 to 6.8 tonnes ha^{-1}y^{-1}), and the unfertilized species-rich *Arrhenatheretum elatioris brizetosum* (AB). The total annual production of the remaining pastures *Poo-Lolietum* (PL) and the *Festuca rubra* variant of the *Lolio-Cynosuretum* (LF) and the hay meadow community *Arrhenatheretum with Origanum vulgare* (AO) is in between with about 8 tonnes ha^{-1} y^{-1}. These communities do not differ significantly from other communities, except from the species rich, low productive AB and the species-poor, extremely high productive hayfield AF as well as AH

The differences between communities in peak biomass follows more or less the same pattern. The species-poor hayfield communities with a peak biomass 6.5 to 8 (10) tonnes ha^{-1}) differ from the species-rich meadow AB (3.3 tonnes ha^{-1}) and the pastures LR and LG (4.5 tonnes ha^{-1}). From among the group of pasture communities with a peak biomass of 4.5 to 6 tonnes ha^{-1}, the *Poo-Lolietum* (PL) has a significant higher peak production then the *Lolio-Cynosuretum with Ranunculus bulbosus* (LR), and the fragmentarily developed *Lolio-Cynosuretum* LF (the *Festuca rubra and Cirsium arvense* variant) has a higher peak biomass than the two *other Lolio-Cynosuretum* communities (LG and LR).
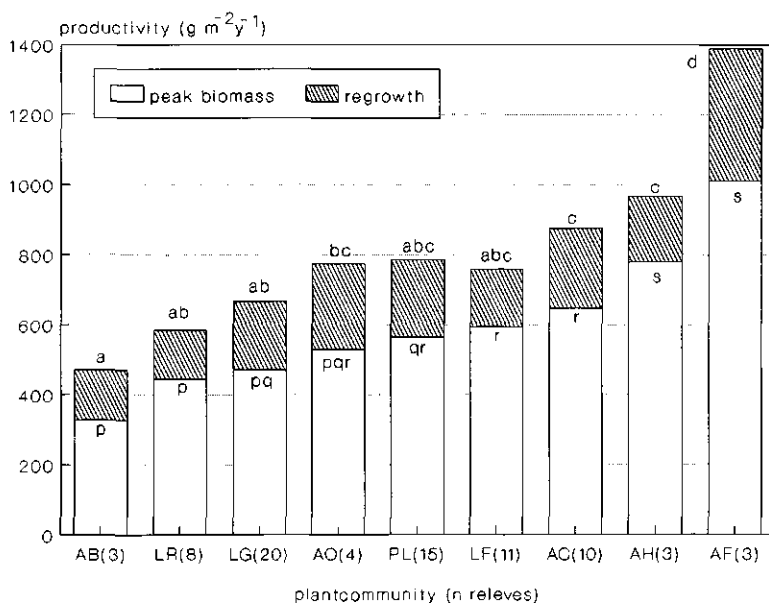
Figure 4.3 Total annual aboveground productivity and peak biomass in 1994 in different plant communities. Mean values that have no superscripts in common differ at p = 0.01 (one factor ANOVA followed by a LSD-test) . AB = Arrhenatheretum elatioris brizetosum; AO =A. variant Origanum vulgare; AC = A, variant Cirsium arvense; AH = A. variant Heracleum sphondylium (trunk community); AF = A. variant Festuca arundinacea (trunk community); LR = Lolio-Cynosuretum variant Ranunculus bulbosus; LG = L. variant Geranium molle; LF = L. variant Festuca rubra; PL = Poo-Lolietum.

Root length and root weight and their vertical distribution

Total root length and root weight, specific root length and shoot to root ratio

The effect of cessation of fertilization and different management regimes on root length and root weight was tested by a REML analysis of contrasts between plots of different dyke categories and management type, followed by a REML analysis with 'treatment' as factor and a paired t-test of the different treatments. All analyses were carried out with duration of exposure to sunlight and Na content in the soil as covariates.

Except for a weak difference ($p < 0.06$) in total root length between the two dyke categories (former) pastures and hayfields, no significant overall effect of fertilization or management was found in the total root length, total root weight, specific root length and shoot/root ratio of the contrasting groups studied. A REML analysis of these parameters with 'treatment' as factor (which is in fact a combination of fertilization and management), however, showed clear significant effects. The results of the paired t-test on the different treatments and the values for the tested parameters are given in Table 4.3.

Table 4.3 *Total root length (TRL, m dm^{-2}) and total root weight (TRW, g dm^{-2}) measured in a 50 cm deep soil profile, specific root length (SRL m g^{-1}) and shoot/root ratio (SRR g g^{-1}) for the different treatments (for a full description see table 4.2). Values with at least one superscript letter(s) in common, are not significantly different (p < 0.05, REMLPAIR with t-test).*

Parameter	Treatments						
	G[+]	GG[-]	HG[-]	HH[-]	H^{+}	H[-]	ref
Number of plots	13	5	5	11	5	5	3
TRL (m dm^{-2})	1608[a]	1690[a]	1798[ab]	1655[a]	1834[ab]	1963[ab]	2263[b]
TRW (g dm^{-2})	5.84[a]	6.25[ab]	5.65[ab]	7.42[bc]	8.10[bc]	9.07[c]	7.92[abc]
SRL (m g^{-1})	275[ab]	270[ab]	318[b]	223[a]	226[a]	216[a]	286[b]
SRR	0.94[c]	0.72[abc]	--	0.71[ab]	0.90[bc]	0.60[ab]	0.47[a]

There are no significant differences in total root length (TRL, Table 4.3) between treatments, except for the reference dykes, where the average value was higher than in the treatments G+ (grazing with fertilization), GG- (grazing without fertilization) and HH- (haymaking without fertilization) on (former) pastures (see also Figure 4.4a). The mowing treatment HH- on former pastures and treatment H+ (haymaking with fertilization) on meadows had significantly higher total root weights (TRW, Table 4.3) than the fertilized grazing treatment (G+). Also the haymaking treatment without fertilizer use (H-) had a significant bigger root weight than the treatments G+, GG- and HG- (haymaking and subsequent without fertilization) on pastures (see also Figure 4.4b). This may indicate that haymaking results in heavier roots compared to grazing practices. The haymaking treatments H+, H- and HH- (on former pastures) also have lower values for specific root length (SRL, Table 4.3) than the grazing treatments. Together with the larger root weights this points to the presence of relatively thicker roots, whereas the grazing treatments with relatively high SRL values are characterized by relatively thin roots. The value of SRL and the total root weight of the reference meadow was high. This would indicate the presence of a root system consisting of many thin roots. Sod compactness would most probably be greater in these grassland types, because of a dense and homogeneous rooting pattern.

In spite of lower productivity and in treatment HH- a higher root weight in the unfertilized plots compared to the fertilized plots, the shoot/root ratio (SRR, Table 4.3) did not differ significantly between both treatment types. Only in the reference dyke grassland was the SRR significantly lower than in the fertilized grasslands, because of a low aboveground biomass and high root weight. The value SRR was relatively high in the fertilized grazed (treatment G+) and mown (treatment H+) plots, indicating a low investment in the rooting system. In this way the lower SRR value in the unfertilized plots (treatments GG-, HH- and H-) could indicate a shift in the growth strategy of the vegetation: more investment in the belowground parts at the cost of aboveground biomass production.

Vertical distribution of roots under different treatments

Root length (m dm^{-2}) and root weight (g dm^{-2}) of the various sampled strata are given cumulatively over the 50 cm deep soil profile (Figure 4.4a-b), to enable comparison of the total amount of roots and the amount of roots in each layer in the different treatments and the reference grasslands, and analysis of the vertical distribution. A REML analysis of average root length and average root weight of contrasts and a paired analysis of treatments was carried out for each layer. There was a significant difference ($p < 0.05$) in both root length and root weight between pastures and hayfields at depths of 3 to 6, 6 to 10 and 10 to 15 cm. A significant effect on root length of fertilizer use on mown grassland was shown at a depth of 6 to 10 cm. No other significant differences between contrasting groups were found. The paired analysis, however, revealed significant differences between fertilized and unfertilized treatments on both pastures and meadows (see Table 4.4 for significance between the different treatment values in each layer)

Except for the greater root length of the reference dykes, there was no significant difference in root length between treatments at a depth of 0 to 3 cm. In the layer 3 to 6 cm the reference grassland had higher root length values than all other treatments, except for the unfertilized haymaking treatment with higher values than the grazing treatments G+ and HG-. Also at a depth of 6 to 10 cm both reference dykes and unfertilized mown plots (H-) had significantly greater root lengths than all the other treatments. At this depth the unfertilized haymaking plots on both pastures (HH-) and meadows (H-) showed a significantly greater root length than the fertilized treatments (G+ and H+). In the layer 10 to 15 cm the reference dykes had higher root length values than all treatments on pastures. The fertilized and unfertilized treatment on meadows (H+ and H-) had higher values than G+ and HH- in this layer. From 15 to 20 cm only the unfertilized haymaking treatment (H-) differed from the treatments G+, GG- and HH- on (former) pastures. At a depth of 20 to 50 cm differences were hardly significant (see Table 4.4 and Figure 4.4a). Only treatment HG- was observed to have had a higher root length than the fertilized treatment G+ at a depth of 30 to 40 cm.

Significant differences in root weight between grazing treatments and haymaking treatments (including the haymaking treatment on pastures) occurred throughout the whole profile (Table 4.4, Figure 4.4b) resulting in greater root weights in mown grasslands (except for treatment HG-). The root weights at 0 to 20 cm in both fertilized and unfertilized hayfield (H+ and H-) were not different from the average root weight of the reference dykes, however, here the average root weight was lower at 20 to 40 cm. Similar to the results for root length, higher root weight values were also found in the unfertilized plots (HH-, H-) compared to the fertilized treatments (G+, H+) at depth of 3 to 10 cm. In
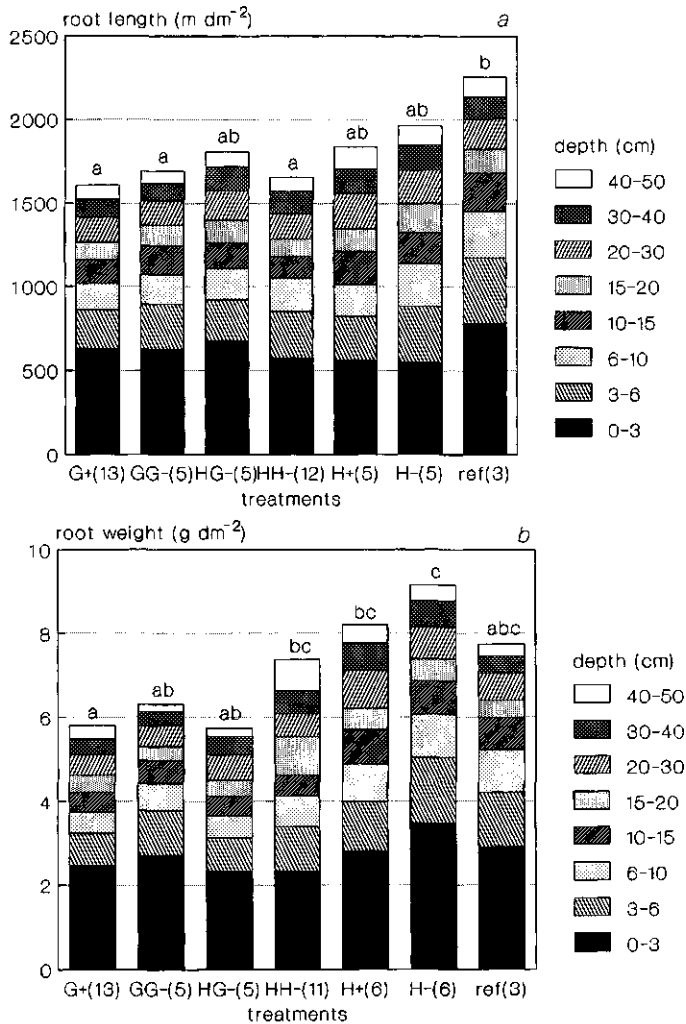
Figure 4.4 *Cumulative average root length (a) and average root weight (b) of eight layers of a 50 cm deep soil core, per treatment. Significant differences between total values are indicated by different letters a,b,c (REML paired analysis with t-test, p < 0.05). For an explanation of the different treatments see figure 4.*

treatment HH- root weights greater than G+ were also found at depths of 15 to 20 and 30 to 50 cm. Like the results for root length, with the exception of HG- at 30 to 40 cm, the other unfertilized treatments on pastures (GG-, HG-) did not differ from the fertilized grazing treatment (G+).

Although there were remarkable differences between the amount of roots per layer in each treatment, the relative distribution of roots, i.e. the percentage root length and root weight per stratum of the total value, did not differ much between treatments. About 53 to 55 % of the total root length or root weight was located in the first 6 cm and about 75 to 80 % in the layer 0 to 20 cm, except for the mown treatments H+ and H-, with fewer roots in

Table 4.4 *REML paired analysis with t-test of root length and root weight in different treatments (see Table 4.2) for each sampled layer. Values are given in Figure 4.4a and 4.4b. Significant difference (p < 0.05) is indicated by different letters (a,b,c).*

Depth (cm)	Treatments root length							Treatments root weight						
	G+	GG-	HG-	HH-	H+	H-	ref	G+	GG-	HG-	HH-	H+	H-	ref
0-3	ab	ab	ab	a	a	a	b	a	ab	a	a	ab	b	ab
3-6	a	ab	a	ab	ab	bc	c	a	ab	a	b	b	c	bc
6-10	a	ab	ab	b	ab	c	c	a	ab	a	b	bc	c	c
10-15	a	abc	ab	a	bc	bc	c	a	a	a	a	b	b	b
15-20	a	a	ab	a	ab	b	ab	a	a	ab	b	ab	ab	ab
20-30	a	a	ab	ab	b	ab	ab	a	a	ab	a	c	bc	ab
30-40	a	a	b	ab	ab	ab	ab	a	a	a	b	b	b	a
40-50	a	a	a	a	a	a	a	a	ab	ab	b	ab	ab	ab

the upper layers.(relative distributions of 45 % (0 to 6 cm) and 75% (0 to 20 cm). The biggest differences in vertical distribution between treatments was found at depths of 0 to 20 cm.

The curves obtained by calculations of the change of root density with depth according to the exponential function $y = a + (b - a)r^{(x-1.5)}$ fitted well with measured data in each plot (with r^2-adjusted varying from 94.3 to 99.9). Low values for r ($0 < r < 1$) resulted in a rapid decrease of root density with depth. Parameter b represents the density (m dm^{-3}) at the ground level (-1.5 cm), a is the root density at a depth of 50 cm. The decline in roots below this depth is not included in the model. The average values for a, b and r are calculated have been calculated for each treatment (Table 4.5).

The differences between the parameters, tested with REML, showed a significant difference in r between pastures and hayfields (p < 0.05). No differences in other contrasts (effect of fertilization or management) were found. A REML paired analysis on treatments revealed significant differences (p < 0.05) between the r-value of G+ and the r-values of the treatment H+, H-, and 'ref' (see Table 4.5), resulting in less steep curves in these treatments compared with G+ (see Figure 4.5), and thus a less steep decline in root length density with depth. However the density in the upper layer (at a depth of 1.5 cm) must be taken into account. The largest differences in decline occurred at depths of 5 to 20 cm. Also the r-value of treatment HH- (on pastures) was significantly higher than the fertilized grazed grassland (G+). This indicates - in agreement with the results of root length per

Table 4.5 *Average parameter-values per treatment, describing the change of root density (m dm^{-3} and g dm^{-3}) with depth in the soil profile. b = root density in the upper layer (at depth 1.5 cm), r = slope; a = root density at a depth of 50 cm; difference in superscripts denote significant differences between parameter values (REML paired analysis with t-test at p < 0.05). See table 4.2 for treatments.*

Treatments		G$^+$	GG$^-$	HG$^-$	HH$^-$	H$^+$	H$^-$	ref
Number of plots		13	5	5	11	5	4	3
Root	b	1937[ab]	1916[ab]	2056[ab]	1790[a]	1668[a]	1662[a]	2366[b]
Length	a	154[ab]	160[ab]	187[ab]	129[a]	195[b]	160[ab]	175[ab]
	r	0.71[a]	0.74[ab]	0.70[a]	0.78[bc]	0.77[bc]	0.83[c]	0.79[bc]
Root	b	7.6[a]	8.6[ab]	7.2[a]	6.9[a]	8.6[ab]	10.9[b]	8.9[ab]
Weight	a	0.55[a]	0.47[a]	0.56[a]	0.81[a]	0.79[a]	0.68[a]	0.59[a]
	r	0.67[a]	0.72[ab]	0.66[a]	0.72[ab]	0.76[b]	0.75[ab]	0.78[b]

stratum - that four years after stopping the use of fertilizer on pastures in combination with haymaking leads to a less steep decline of root length density with depth. The difference between the curves measured in the HH- and G+ plots was very small (Figure 4.5b).

In the analysis of *r*-values between treatments using the same model for the decline of root weight (Table 4.5), significant differences were also found between the haymaking treatments H+ and 'ref' and the treatments G+ and HG-, but there was no significant difference in decline of root weight with depth between the fertilized and unfertilized treatments G+ and HH- on pastures

From these results we may conclude that four years after stopping fertilizer application in combination with haymaking (on both formerly grazed and mown dykes) an increase of root density (root length and root weight) occurred mainly at a depth of 3 to 10 cm, leading to a less steep decline of root length density on pastures. Moreover, the differences in root density between fertilized and long-term unfertilized dyke grassland occurred at a depth of 0 to 15 cm, the latter with greater root lengths and root weight than fertilized pasture from 3 to 15 cm, and greater root length and comparable root weight from 0 to 10 cm, but lower root weight at 20 to 40 cm than fertilized hayfield. . It is also shown that mown dykes have larger root weights than grazed dykes, and a less steep decline of root length and root weight density with depth.
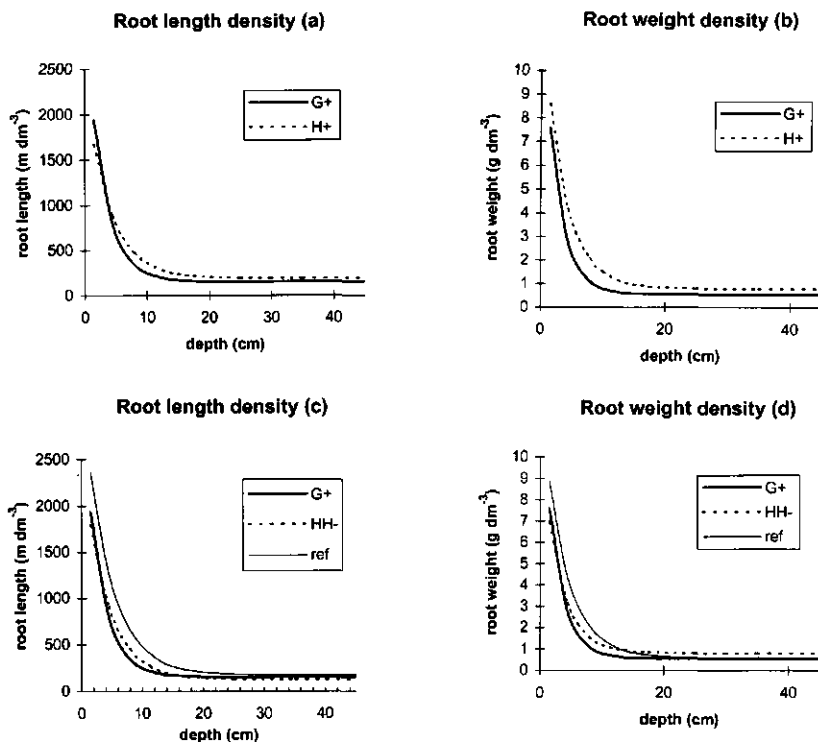
Figure 4.5 *change of root length density (a,c) and root weight density (b,d) with depth in different treatments. a,b: fertilized pasture (G+) and fertilized hay-meadow (H+); b,d: fertilized pasture (G+), unfertilized mowing on former pasture (HH-) and long-term unfertilized hay-meadow (reference dykes).*

Differences in rooting system between plant communities

Although there is was a considerable overlap between treatments and sea dyke plant communities (see Chapter 3), most communities still consisted of both fertilized and unfertilized relevés (plots). Comparison of root characteristics of investigated plots, grouped on a phytosociological basis, gives insight into root properties of different plant communities.

In order to characterize the rooting system of the distinguished communities on sea dykes, total root length and root weight, specific root length and shoot/root ratio (Table 4.6), and cumulative root lengths and root weights of the layers in the sampled soil profile (Figure 4.6) are calculated for each community[1]. Differences between communities have been analysed using Oneway ANOVA followed by a LSD test.

Tabel 4.6 *Total root length (TRL, m dm^{-2}) and total root weight (TRW, g dm^{-2}) measured in a 50 cm deep soil profile, specific root length (SRL, m g^{-1}), and shoot to root ratio (SRR, g g^{-1}) of the distinguished plant communities. Different superscripts indicate significant different values (p < 0.05. For further legends see Figure 4.3.*

Community	LG	LR	LF	PL	AF	AC	AO	AB
number of sampled plots	10	8	9	11	2	6	2	2
TRL m dm^{-2}	2080^c	1382^a	1890^{abc}	1567^{ab}	1459^a	1515^{ab}	1918^{bc}	2339^c
TRW g dm^{-2}	6.67^{ab}	5.75^a	6.74^{ab}	5.82^{ab}	11.39^c	8.62^{bc}	8.16^{abc}	8.24^{abc}
SRL m g^{-1}	312^c	240^b	280^{bc}	269^{bc}	128^a	176^a	235^b	284^{bc}
SRR g g^{-1}	0.7^a	0.8^a	0.8^a	0.97^a	0.97^a	0.89^a	0.51^a	0.42^a

The *Arrhenatheretum* meadows are characterized by higher total root weights than the *Lolio-Cynosuretum* and *Poo-Lolietum* variants (Table 4.6). The difference is not large: only the trunk community of *Festuca arundinacea* and *Elymus repens* [*Plantaginetalia/ Molinio-Arrhenatheretea*] (AF) and the *Cirsium arvense* variant of the *Arrhenatheretum elatioris* (AC) differ significantly (p < 0.05) from the *Ranunculus bulbosus* variant of the *Lolio-Cynosuretum cristati* (LR). In the species-poor *Geranium molle* variant of the *Lolio-Cynosuretum cristati* (LG) and the species-rich *Arrhenatheretum elatioris brizetosum* (AB) significantly (p < 0.05) higher values of total root length were found than in the *Ranunculus bulbosus* variant of the *Lolio-Cynosuretum cristati* (LR), the species-poor *Cirsium arvense* variant of the *Arrhenatheretum elatioris* (AC), the *Poo-Lolietum* (PL) and the trunk community with *Festuca arundinacea and Elymus repens* (AF), where the total root length is comparatively low (Table 4.6; Figure 4.6). Also the *Origanum vulgare* variant of the *Arrhenatheretum elatioris* (AO) has a significant higher root length than LR and AF (p < 0.05).

The relatively low total root length value and high total root weight value of the species-poor *Arrhenatheretum* variants AF and AC, resulted in low specific root lengths (SRL) in these communities. The species-rich meadow *Arrenatheretum elatioris brizetosum* (AB) has a relatively high SRL, but in the species-rich *Origanum vulgare* variant of the *Arrhenatheretum elatioris* (AO) the SRL is lower.

---

[1] No measurements were made in the *Heracleum sphondylium* variant of the *Arrhenatheretum elatioris* (AH).
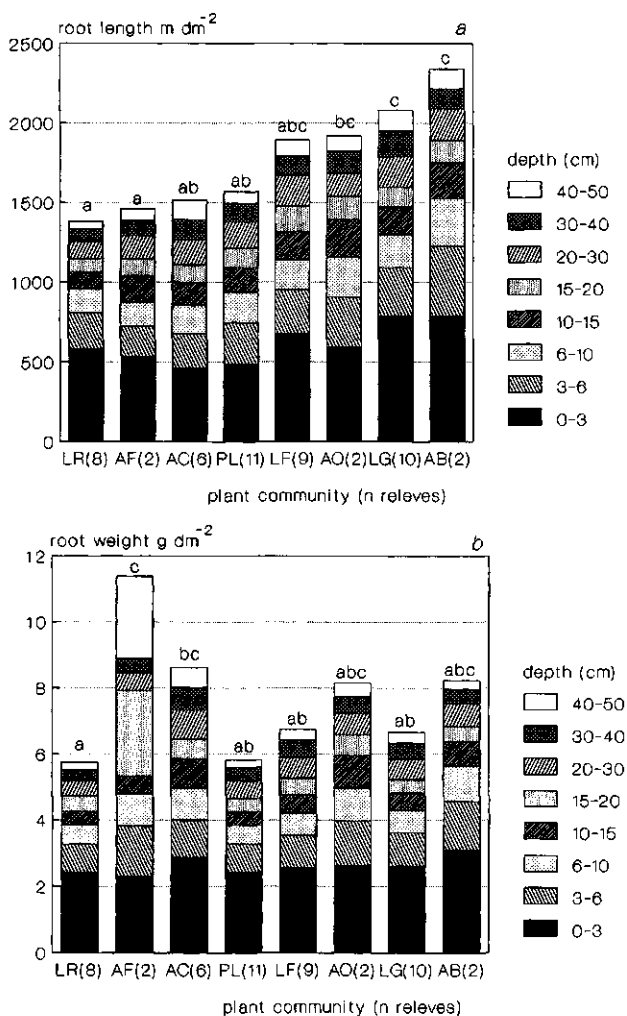
Figure 4.6 *Cumulative average root length (a) and average root weight (b) of eight layers of a 50 cm deep soil core, for different plant communities. Significant differences between total values are indicated by different letters a,b,c (LSD after Oneway ANOVA, p < 0.05). For legends see Table 4.6.*

In the species-poor *Poo-Lolietum* (PL) as well as in the *Ranunculus bulbosus* variant of the *Lolio-Cynosuretum cristati* (LR) total root length and root weight values were low, and the values of SRL of these communities were average. This points at a less developed root system.The *Geranium molle* variant (LG) and the *Festuca rubra and Cirsium arvense* variant of the *Lolio-Cynosuretum cristati* (LF) showed rather high specific root lengths (Table 4.6). Plant communities did not differ significantly in shoot/root ratio (SRR, Table 4.6). Relatively high values were found in the communities with a high biomass production, like the *Poo-Lolietum* (PL) and the *Festuca arundinacea* variant of the *Arrhenatheretum elatioris*(AF).

The differences in root length between the communities are manifest mainly in the upper layers (0 to 3 cm, 3 to 6 cm, 6 to 10 cm and 10 to 15 cm) of the soil profile (Figure 4.6a). The *Geranium molle* (LG) and the *Festuca rubra and Cirsium arvense* (LF) variants of the *Lolio-Cynosuretum cristati* had a significant greater root length in the top layer (0 to 3cm) than the species poor communities *Poo-Lolietum* (PL) and *Arrhenatheretum, variant Cirsium arvense* (AC) (p < 0.005). The *Geranium molle* variant of the *Lolio-Cynosuretum cristati* (LG) with also more roots (m dm^{-2}) than the *Ranunculus bulbosus* variant was thus characterized by a great root length in the top layer of 3 cm. The species-rich *Arrhenatheretum brizetosum* (AB) had also high root length values in the top layer (significantly different from PL, p < 0.05). At a depth of 3 to 6 cm this community had a significant greater root length (p < 0.05) than most of the other communities (AF, AC, LR, LF, PL). At a depth of 10 to 15 cm the root length in the *Ranunculus bulbosus* variant (LR) was significantly smaller (p<0.05) than in the two other, relatively species-poor *Lolio-Cynosuretum* variants (LF and LG) as well as the species-rich *Arrhenatheretum* communities (AO and AB).

Differences in root weight were noticeable at a depth of 6 to 10 cm (the *Arrhenatheretum* communities having higher values than the *Ranunculus bulbosus* variant of the *Lolio-Cynosuretum* (LR), and 10 to 15 cm (AB having larger root weight than LR and AC larger than other communities, p < 0.001). At 15 to 20 cm and 40 to 50 cm the species-poor *Festuca arundinacea* variant of the *Arrhenatheretum* (AF) had a larger root weight than all other communities (p<0.005).

Nutrient concentrations in soil and vegetation

Nutrient concentrations in the soil

A REML analysis on contrasts showed an effect of grazing or mowing on the NO$_3^-$ concentration in the 1994 plots (Table 4.7a, REML contrast m2, p < 0.05). In the mown plots (treatments HH- and HG⁻) on (former) pastures NO$_3^-$ concentrations were significant lower than in the grazed plots (G+ and GG-). In the paired analysis however, a significant difference was found only with the unfertilized grazed plots (G+).

On the hayfield dykes there was a significant effect of fertilization (REML contrast f2, p < 0.01). The NO$_3^-$ concentration in the fertilized H+ treatment was higher than in the unfertilized plots of treatment H- and the reference dykes. The differences in concentrations of NH$_4^+$ between fertilized and unfertilized plots are less obvious compared to differences in NO$_3^-$, except for treatment H- and 'ref'. The relatively higher concentration of NH$_4^+$ in these two treatments and the lower concentration of NO$_3^-$ probably points at a lower nitrification rate. The concentration of organic soluble N was relatively low in these treatments, but only significantly different from the fertilized grazed plots (G+). Also the soluble P concentration in the soil was considerably lower in the reference plots, compared to all other treatments (REML contrast r, p < 0.05). In the unfertilized mown treatment H- soluble P concentration was significantly lower than in the fertilized mown plots (H+). However, no significant difference was found between fertilized and unfertilized plots on pastures. The relatively high values for extractable K in the mown plots H+ and H- can be explained by the heavy clay soils with relatively large lutum percentages of the study sites where these plots are located (see Table 4.7b).

Table 4.7 *Mean concentrations of nutrients in the soil in different treatments on dyke grasslands in 1994 en 1997 (four and seven years respectively after cessation of fertilization). Those indicated are: soluble nutrients mg kg^{-1} (after extraction with $CaCl_2$) in 1994 (a) and 1997 (c), and total nutrient concentrations g kg^{-1} (after digestion) in 1994 (b, with C/N ratio and percentage lutum fraction) and 1997 (c). Significant differences (REML analysis on contrasts, p < 0.05) between grazed and mown plots (m2) or mown+grazed plots and grazed/mown plots (m1), with and without fertilization on (former) pastures (f1) and hayfields (f2), reference and other mown dykes (r), are indicated in the second column. Superscripts (a,b,c,d) denote significant differences between treatments (REML paired analysis with t-test p < 0.05). For an explanation of treatments see Table 4.2.*

a) Soluble soil nutrients mg kg^{-1} (1994)

	REML contrast	G+ n = 20	GG- n = 14	HG- n = 16	HH- n = 19	H+ n = 9	H- n = 9	ref n = 4
N-NO$_3$	m2, f2	15.41^c	14.34^b	12.94^a	12.14^{ab}	17.02^c	9.59^a	10.02^{ab}
N-NH$_4$	-	5.86^{ab}	6.02^{abc}	7.05^{bc}	5.62^a	6.51^{abc}	7.66^c	7.91^{bc}
Norg.	-	4.94^b	3.68^{ab}	2.94^{ab}	3.35^{ab}	2.44^{ab}	0.61^a	0.47^a
sol. P	r,f2	3.58^b	4.08^b	3.80^b	3.90^b	4.39^c	2.93^a	1.41^a
sol. K	-	65^a	85^b	72^{ab}	69^{ab}	102^b	98^b	90^{ab}

b) Total soil nutrient concentrations g kg^{-1} (1994)

	REML contrast	G+ n = 20	GG- n = 14	HG- n = 16	HH- n = 19	H+ n = 9	H- n = 9	ref n = 4
N	m2,r	2.30^c	2.31^c	2.34^c	2.00^{ab}	2.37^{bc}	2.53^c	1.87^a
P	r	0.69^c	0.68^c	0.67^{bc}	0.60^{ab}	0.64^{bc}	0.63^{bc}	0.43^a
K	m1,r	6.84^b	6.80^b	6.98^b	6.01^a	9.32^c	9.40^c	6.30^a
		n = 17	n = 10	n = 6	n = 16	n = 9	n = 6	n = 3
C	-	23.64^a	25.27^{ab}	27.84^b	25.92^{ab}	27.01^{ab}	29.61^b	21.71^a
C/N		10.52^a	11.20^a	11.96^{ab}	13.33^b	11.60^a	11.14^a	10.94^a
%lutum		12.7	13.4	10.5	13.5	20.2	26.6	15.8

c) Soluble soil nutrients mg kg^{-1} (1997)

	REML contrast	G+ n = 10	GG- n = 8	HG- n = 7	HH- n = 10	H+ n = 9	H- n = 9	ref n = 3
N-NO$_3$	f1,m2	8.17^d	4.24^{bc}	3.27^{abc}	2.15^a	4.42^c	2.57^{ab}	1.86^a
N-NH$_4$	-	6.07^{ab}	6.35 ^{ab}	6.63 ^{b}	5.60^a	6.32^{ab}	6.50 ^{ab}	6.78 ^{ab}
Norg	not measured							
sol. P	f1	3.15^b	2.46^{ab}	1.96^a	1.95^a	1.67^{ab}	1.06^a	0.89^a
sol. K	-	29^a	51^b	38^{ab}	36^{ab}	55^b	56^b	49^{ab}

d) Total nutrient concentration in soil g kg^{-1} (1997)

	REML contrast	G+ n = 10	GG- n = 8	HG- n = 7	HH- n = 10	H+ n = 9	H- n = 9	ref n = 3
N	m2	2.33^{ab}	2.45^b	2.25 ^{ab}	2.01 ^{a}	2.24^{ab}	2.26^{ab}	2.05^{ab}
P	-	0.77 ^{b}	0.77^b	0.73 ^{b}	0.68 ^{ab}	0.64^{ab}	0.66^{ab}	0.51^a
K	f2	5.63^a	6.85 ^{a}	6.34 ^{a}	5.80 ^{a}	11.07^b	8.50^a	6.64^a

The total N, P and K concentrations in the soil of the reference plots were significantly lower than the two other haymaking treatments (REML contrast r, p < 0.001), as well as the treatments on pastures with the exception of the unfertilized haymaking treatment HH- (Table 4.7b). Here concentrations of total N, P and K were significantly lower than the

concentrations in the fertilized grazed plots (treatment G+). The difference between this treatment and the other treatments on (former) pastures, shows in a significant effect on the total N and K concentration of management type (grazing or mowing, REML contrast m1 and m2, p < 0.05). Apparently, haymaking without fertilization after four years leads to a small, but significant decline in N, P and K concentrations in the soil. Like the soluble K concentration, the concentration of total K in H+ and H- was also significantly higher compared to all other treatments, probably due to the higher clay content of these soils. The rather low total N concentration in treatment HH-, together with a somewhat higher percentage of carbon, resulted in a significantly higher value for C/N ratio in this treatment compared to all other treatments except one (HG-). This may indicate a slower mineralization of accumulated organic material in the unfertilized mown plots on former fertilized pastures.

In Tables 4.7c and 4.7d the results are given of soil chemical analysis of soil nutrients in 1997. The NO_3^- concentration in the soil in 1997 appeared to be considerably lower than in 1994 in all treatments, but the concentration in treatment G+ is still significantly higher than in the unfertilized treatments (REML contrast f1, p < 0.05). As in 1994 NO_3^- concentrations were higher in the grazed plots than in the mown plots (REML contrast m2, p < 0.05). In the paired analysis significantly higher NO_3^- concentrations were found in the fertilized meadows compared to the unfertilized meadow and reference dykes. NH_4^+ values did not differ much between 1994 and 1997. The values in treatment H- and 'ref' were somewhat lower, and there was no significant difference between fertilized and unfertilized treatments.

Values of soluble P and K were lower in 1997, specially in the treatments H+ and H-. On (former) pastures fertilization had a significant effect of (REML contrast f1, p < 0.05): the values of soluble P were lower here in the treatments H- and HG- than in the fertilized treatment G+ compared to 1994. The concentrations of total N, P and K in the soil show hardly any difference between 1994 and 1997 (Table 4.7d), with significantly lower values for P in the reference dyke grasslands in both years, compared to the grazed dykes. In 1997 there is no difference between fertilized and unfertilized plots, except for the total concentration of K, which is now significantly higher in the fertilized haymaking treatment than in H- and 'ref' (REML-contrast f2, p < 0.05). Like in 1994, there is a significant difference between the grazed and mown plots on pastures (REML-contrast m2, p < 0.05).

These results reveal that the total pool of soil (immobile) nutrients barely has changed after cessation of fertilizer application.

Nutrient concentrations in plant tissue

Shoot tissue N concentrations in the unfertilized haymaking treatment HH- were significantly lower than in the fertilized grazed treatment G+ (Table 4.8a). The other treatments, including the reference dykes did not show significant differences in shoot N concentration. The concentration of total P in shoots was significantly lower in the reference plots, compared to all other plots. A small but significant difference in tissue P concentration was observed between the unfertilized grazed treatment (GG-) and the unfertilized treatments HG- and HH- on former pastures. The total K concentration in shoots in the unfertilized meadow treatment H- was significantly lower than in the fertilized treatment H+. No other significant differences in K tissue concentration were discovered between treatments. Total K concentration in shoots is high and exceeds the concentration range given for land plants by Larcher (1983).

Table 4.8 *Concentrations of nutrients in shoots (a) and roots (b) in different treatments in 1994 and in shoots in 1997 (c), four and seven years respectively after cessation of fertilization. N/P ratios are indicated as well. Values with the same superscript letters are not significantly different (p < 0.05); * = estimated value in g m⁻²y⁻¹ based on the percentage regrowth in 1994; n.a. = not analysed; d = significant difference between (former) pastures and meadows (REML-contrast p < 0.05). For other legends see Table 4.7*

a) Total nutrient concentration in shoots (g kg⁻¹) in 1994 and the total amounts (g m⁻²) removed at cutting of peak biomass; for shoot N between brackets the total annual amounts (g m⁻²y⁻¹, regrowth included).

	REML contrast	G+ n = 15	GG- n = 10	HG- n = 12	HH- n = 13	H+ n = 6	H- n = 6	ref n = 4
N (g kg⁻¹)	-	14.2ᵇ	13.5ᵃᵇ	13.4ᵃᵇ	12.2ᵃ	12.5ᵃᵇ	13.5ᵃᵇ	13.2ᵃᵇ
P (g kg⁻¹)	d, r	2.77ᵇᶜ	2.86ᶜ	2.58ᵇ	2.62ᵇ	2.61ᵇᶜ	2.44ᵇ	1.88ᵃ
K (g kg⁻¹)	f2	66.8ᵃᵇ	71.3ᵃᵇ	67.9ᵃᵇ	71.0ᵃᵇ	73.2ᵇ	57.9ᵃ	59.5ᵃᵇ
N/P ratio	d, r, f2	5.27ᵇᶜ	4.78ᵃ	5.28ᵇᶜ	4.74ᵃ	4.87ᵃᵇ	5.81ᶜ	7.15ᵈ
N at cutting (g m⁻²)	n.a.	9.7ᵇ	7.7ᵃᵇ	6.3ᵃ	6.5ᵃ	8.9ᵇ	6.7ᵃ	6.1ᵃ
(tot N g m⁻²y⁻¹)		(13.2)	(10.4)	(9.1)	(8.7)	(11.8)	(8.8)	(8.4)
P at cutting (g m⁻²)	n.a.	1.89ᵇ	1.63ᵃᵇ	1.22ᵃ	1.33ᵃ	1.85ᵇ	1.20ᵃ	0.87ᵃ
K at cutting (g m⁻²)	n.a.	45.6ᵇ	40.7ᵃᵇ	32.2ᵃ	37ᵃᵇ	52ᵇ	29ᵃ	28ᵃ

b) Total nutrient concentration in roots (g kg⁻¹) in 1994 and the total amounts (g m⁻²) removed at cutting

	REML contrast	G+ n = 11	GG- n = 7	HG- n = 0	HH- n = 13	H+ n = 5	H- n =4	ref n = 3
N (g kg⁻¹)	d,f1	12.8ᶜ	11.8ᵇᶜ	-	11.4ᵇ	11.2ᵇᶜ	10.1ᵃᵇ	9.1ᵃ
P (g kg⁻¹)	d	1.56ᵇ	1.60ᵇ	-	1.51ᵇ	1.08ᵃ	1.12ᵃ	0.97ᵃ
K (g kg⁻¹)	-	2.80ᵃᵇ	2.59ᵃ	-	3.05ᵃᵇ	3.54ᵇ	3.53ᵇ	2.93ᵃᵇ
N at cutting (g m⁻²)	n.a.	7.42	7.53	-	8.41	9.19	9.25	7.05
P at cutting (g m⁻²)	n.a.	0.90	1.01	-	1.12	0.89	1.03	0.75
K at cutting (g m⁻²)	n.a.	1.62	1.64	-	2.25	2.91	3.23	2.27

c) Total nutrient concentration in shoots (g kg⁻¹) in 1997and the amounts at cutting of peak biomass (g m⁻²) in 1997 and - between brackets - annual shoot N production (g m⁻²y⁻¹).

	REML contrast	G+ n = 10	GG- n = 8	HG- n = 7	HH- n = 10	H+ n = 8	H- n = 9	ref n = 3
N (g kg⁻¹)	-	17.4ᵃ	12.1ᵃ	15.1ᵃ	13.9ᵃ	17.4ᵃ	13.4ᵃ	14.2ᵃ
P (g kg⁻¹)	d	2.78ᵇ	2.55ᵃᵇ	2.54ᵃᵇ	2.60ᵇ	2.44ᵃᵇ	2.38ᵃᵇ	1.82ᵃ
K (g kg⁻¹)	f2	20.9ᵃᵇ	19.7ᵃᵇ	19.7ᵃᵇ	19.5ᵃ	23.5ᵇ	19.8ᵃ	20.8ᵃᵇ
N/P ratio	d, r, f2	6.07ᵇᶜ	5.02ᵃᵇ	6.11ᵇᶜ	4.87ᵃ	7.45ᶜᵈ	5.94ᵃᵇ	8.75ᵈ
N at cutting g m⁻²	n.a.	12.6ᵇ	5.4ᵃ	6.9ᵃᵇ	5.1ᵃ	11.4ᵇ	5.1ᵃ	3.5ᵃ
(tot. N g m⁻² y⁻²)*		(17.1)	(7.2)	(9.7)	(6.9)	(15.1)	(6.8)	(4.8)
P at cutting	n.a.	2.01ᵇ	1.13ᵃ	1.16ᵃ	0.96ᵃ	1.60ᵇ	0.91ᵃ	0.45ᵃ
K at cutting	n.a.-	15.2ᵇ	8.9ᵃ	9.1ᵃ	7.4ᵃ	15.4ᵇ	7.6ᵃ	5.2ᵃ

Furthermore, N concentrations in roots were significantly lower in treatment HH-, compared with treatment G+ (Table 4.8b), which results in a significant effect of fertilization in the pasture treatments (REML contrast f1, p < 0.05). In the hay meadows left unfertilized for 25 years (reference dykes) the root N concentration was significantly lower than all treatments except for treatment H-. Root P and root K concentrations did not

differ between fertilized and unfertilized treatments on both pastures and meadows. Root P concentration, however, was significantly lower on mown dykes compared to (former) grazed dykes (REML contrast d, $p < 0.01$). In spite of the low P values in plant tissue in the reference plots relative to the N concentrations, N still remains the limiting factor, since a N/P ratio < 14 was calculated for these plots (cf. Koerselman & Meuleman, 1996). In all other treatments the N/P-ratios were lower than in the reference plots (Table 4.8a), which implies a N limitation in all treatments.

The shoot N concentrations were higher in 1997 than in 1994 in the treatments G+, HG-, HH- and H+ (Table 4.8c), but treatments in 1997 do not differ significantly. Although the shoot P concentration values were comparable, the shoot P concentration in the reference plots in 1997 was only significantly lower than the P concentration in treatment G+ and HH-. While the measured K tissue concentrations in 1997 were in line with ranges for land plants given by Larcher (1983), they were considerably lower than in 1994. Soluble K in the soil was also lower in 1997 compared to 1994. This could imply a decrease in availability of K with time. The difference between treatments, however, was not changed: the shoot K concentration in the unfertilized meadow treatment H- was significantly lower in 1997 than in treatment H+, whereas other treatments showed no significant differences. As in 1994, the reference plots were found to have the highest N/P-ratio, significantly different from all other treatments, but with N/P < 14, N is a limiting nutrient in these long-term unfertilized sea dyke grasslands.

Nutrient quantities at cuttings and removal of biomass

The differences in soil and plant tissue nutrients between G+ and HH-, and H+ and H- suggest that haymaking without fertilization has had the largest impact on reducing nutrient levels in the soil. The decline in production as a result of the cessation of fertilization in the treatments HG-, HH- and H- resulted in significantly lower quantities of shoot N, P and K (not in treatment HH-) in the aboveground peak biomass (g m^{-2}) compared to the fertilized treatments G+ and H+ (Table 4.8a). However,the total amount of N, P and K removed with cuttings was almost equal in the different unfertilized treatments. The reduced quantity of N, P and K in the biomass of treatment GG- did not differ sifnificantly from G+.

In 1997, seven years after cessation of fertilization (Table 4.8c) the total amounts of N in peak biomass were somewhat higher in the fertilized treatments compared to 1994, and lower in the unfertilized treatments, due to lower production than in 1994, as well as to higher tissue concentrations in some cases (see Tables 4.8a and 4.8c). In 1997, the total amount of N in the removed biomass of treatment GG- differed significantly from the quantity of N in the biomass of G+, while treatment HG- was not significantly different. As in 1994, shoot P content at cutting in 1997 was also significantly higher in the fertilized treatments, with somewhat lower values in the unfertilized treatments in 1997 due to the lower production. The quantity of K in the shoot biomass is much lower than in 1994, which is in line with the measurements of lower concentrations in soil (extractable) and plant tissue.

There seemed to be a small increase of total N, P and K (significant) in the roots in treatment HH- compared with G+ in 1994 (Table 4.8b). Although the tissue N concentration was lower in HH-, the total amounts of nutrients in the plant was higher as a result of an increased root biomass.

Table 4.9 *Estimated annual nitrogen balance (kg N ha^{-1} year^{-1}) of dyke grassland treatments in 1994 (1997). * Estimated values based on measurements by different authors as is described by Berendse et al., 1993. ;** measured by Berendse et al. 1994;+ estimated on the basis of the contribution of 1-2 % to total biomass of legumes in the fertilized treatments and the increased contribution of 2-6 % to total biomass by legumes in the unfertilized treatments, assuming an annual fixation of 40 kg N ton^{-1} by legumes (cf. Berendse et al. 1994) ; ++estimation based on calculations of (netto) excretion/consumption balance of sheep (cf. Bokdam & Piek, 1998); # see table 4.8a and 4.8c. See table 4.2 for legends.*

	G+	GG-	HG-	HH-	H+	H-	ref
Inputs							
atmospheric deposition*	50	50	50	50	50	50	50
N fixation+	4 (4)	8 (7)	20 (15)	15 (10)	3 (3)	12 (8)	4 (4)
fertilizer	110	0	0	0	130	0	0
dung++	50 (60)	40	20	0	0	0	0
Outputs							
denitrification**	18	18	18	18	18	18	18
harvest#	132 (171)	104 (72)	91 (97)	87 (69)	118 (151)	88 (68)	84 (48)
Balance I-O	+64 (+35)	-24 (+7)	-19 (-30)	-40 (-27)	+47 (+14)	-44 (-28)	-48 (-12)

Nitrogen balance in different treatments

Table 4.9 gives an estimated input/output N balance in the different treatments in 1994 and 1997. In 1994 all unfertilized treatments showed a net negative nitrogen input, with the mown grasslands HH-, H- and 'ref' showing the highest values. In the grazed unfertilized treatments GG- and HG-, the balance was influenced by N input through sheep dung and also a substantial increase of legumes (e.g. *Trifolium dubium*). In 1997, the net nitrogen input in the fertilized treatments was found to be much lower than in 1994, owing to the higher amounts of removed nitrogen with cuttings, probably resulting from more favorable climatic circumstances. The negative N-balance of the unfertilized mowing treatments was less, as a result of a lower annual productivity. In the reference dyke grasslands, which had been unfertilized for at least 25 years, a net withdrawal of nitrogen was still present which might have compensated for the atmospheric nitrogen input. In the grazed unfertilized treatment GG- the small positive N input in 1997 found was attributable to sheep dung input. In treatment HG- the balance remained negative through the relatively higher amount of removed N with cuttings and a somewhat lower N-fixation by legumes.

Differences between communities in soil and plant tissue nutrient concentrations

The differences in nutrients concentrations at the community level are shown in Table 4.10. A low mineral N (N-NO$_3$ and N-NH$_4$) concentration in the soil (Table 4.10a) was found in the relatively species rich meadow communities *Arrhenatheretum elatioris brizetosum* (AB) and the *Festuca pratensis and Origanum vulgare* variant of the *Arrhenatheretum elatioris* (AO). In the species-poor *Arrhenatheretum* communities (AH, AF and AC) we measured relatively high concentrations of mineral N. The grazed dyke grassland communities (LG, LR, PL) were also characterized by rather high values of soluble N, except in the case of the *Festuca rubra and Cirsium arvense* variant of the *Lolio-Cynosuretum* (LF). The high value of the C/N ratio together with low values for soluble N as well as total N (Table 4.10b) suggest an accumulation of organic matter and a low mineralization in this community. The *Arrhenatheretum* communities (AH, AF, AO and AC) demonstrate high values of soluble K (Table 4.10a) has except for the species-rich

Table 4.10 *Concentrations of various nutrients in soil, shoot and roots in the different plant communities on sea dyke grassland in 1994. See Table 4.6 for full names of plant communities. Nmin= N-NO₃⁻ + N-NH₄⁺. Values given with the same superscript letter were not significantly different (Least significant difference at p = 0.05 after One-way ANOVA).*

a) Soluble *soil* nutrients (mg kg⁻¹)

	LG	LR	LF	PL	AF	AC	AO	AB	AH
n	28	16	18	20	5	10	5	3	3
Nmin	19.9ᵇ	19.9ᵇ	10.7ᵃ	21.2ᵇᶜ	22.8ᵇᶜ	22.6ᵇᶜ	15.6ᵃᵇ	17.4ᵃᵇ	29.7ᶜ
sol. P	6.40ᵇ	2.78ᵃ	5.35ᵇ	1.91ᵃ	4.12ᵃᵇ	2.94ᵃ	2.05ᵃ	1.37ᵃ	2.57ᵃᵇ
sol. K	49ᵃ	50ᵃ	60ᵃᵇ	68ᵇ	151ᶜᵈ	102ᶜ	116ᶜᵈ	77ᵃᵇᶜ	173ᵈ

b) Total nutrient concentration in *soil* (g kg⁻¹), C/N-ratio

	LG	LR	LF	PL	AF	AC	AO	AB	AH
n	28	16	18	20	5	10	5	3	3
N	2.6ᵇᶜ	2.0ᵃ	1.8ᵃ	2.0ᵃ	3.1ᶜ	2.1ᵃ	2.1ᵃ	2.1ᵃᵇ	3.4ᵈ
P	0.8ᶜᵈ	0.5ᵃ	0.5ᵃ	0.6ᵃᵇ	0.9ᵈ	0.7ᵇᶜ	0.6ᵃᵇ	0.4ᵃ	0.8ᵇᶜᵈ
K	6.3ᵃᵇ	5.4ᵃ	5.1ᵃ	7.0ᵇᶜ	9.2ᵈ	8.9ᵈ	8.8ᵇᶜᵈ	6.1ᵃ	13.9ᵉ
C/N	11ᵃᵇ	12ᵃᵇ	14ᶜ	11ᵃᵇ	11ᵃᵇ	11ᵃᵇ	11ᵃᵇ	10ᵃ	11ᵃᵇᶜ

c) Total nutrient concentration in *shoots* (g kg⁻¹)

	LG	LR	LF	PL	AF	AC	AO	AB	AH
	15	13	12	16	2	5	3	3	1
N	12.3ᵃ	14.8ᵃ	13.8ᵃ	13.0ᵃ	11.0ᵃ	12.6ᵃ	12.5ᵃ	13.1ᵃ	11.5ᵃ
P	2.9ᶜ	2.6ᵇᶜ	2.7ᵇᶜ	2.5ᵇ	2.7ᵇᶜ	2.6ᵇᶜ	2.7ᵇᶜ	1.7ᵃ	2.6
K	78ᵇ	57ᵃ	67ᵃᵇ	68ᵃᵇ	87ᵇ	70ᵃᵇ	68ᵃᵇ	61ᵃᵇ	76
N/P	4.2	5.7	5.1	5.2	4.1	4.8	4.6	7.7	4.4

d) Total nutrient concentration in roots (g kg⁻¹)

	LG	LR	LF	PL	AF	AC	AO	AB
n	14	5	8	8	2	4	3	2
N	13.1ᶜ	12.1ᵇᶜ	11.0ᵃᵇ	11.5ᵃᵇ	10.0ᵃᵇ	10.0ᵃᵇ	9.4ᵃ	9.1ᵃ
P	1.8ᶜ	1.6ᵇᶜ	1.3ᵃᵇ	1.2ᵃᵇ	1.2ᵃᵇ	1.1ᵃ	1.1ᵃ	0.9ᵃ
K	3.0ᵃ	3.3ᵃ	3.0ᵃ	2.9ᵃ	2,1ᵃ	2.6ᵃ	3.0ᵃ	3,3ᵃ

Arrhenatheretum elatioris brizetosum (AB). The total K (Table 4.10b) in these communities was also high which was probably caused by the high clay content of the soil in these plots.

The Poo-Lolietum was characterized by a relatively high concentration of mineral N (Table 4.10a) and low concentration of total N in the soil (Table 4.10b), as a result of the application of fertilizer. P fertilization is probably responsible for the somewhat high concentrations of soluble P in the *Lolio-Cynosuretum* variants LG and LF.

Total N and total P are high in the *Geranium molle* variant of the *Lolio-Cynosuretum cristati* (LG), and the *Arrhenatheretum elatioris* variants *Festuca arundinacea and Elymus repens* (AF) and *Heracleum sphondylium* (AH), indicating the relatively nutrient-rich conditions of these communities. The *Cirsium arvense* variant of the *Arrhenatheretum elatioris* (AC) and the pasture variant *Ranunculus bulbosus* (LR) (apart from the above-mentioned *Lolio-Cynosuretum* variant LF), exhibited low concentrations of total N, but relatively high mineral N concentrations, suggesting a relatively low N accumulation in these communities. Mineral N and soluble P as well as total N and P concentrations were low to moderate in the species-rich hay meadows *Arrhenatheretum elatioris brizetosum*

(AB) and the *Origanum vulgare* variant of the *Arrhenatheretum elatioris* (AO), including most of the reference plots in this study. The low C/N ratio of AB (Table 4.10b) suggests a considerable mineralization of organic matter in this community, but N remains a limiting factor with N/P < 14 (Table 4.10c). The low tissue concentration of P in shoots and N and P in roots indicate the relatively nutrient-poor conditions of these communities.

No significant difference was observed in shoot N concentration between the distinguished communities. Shoot K concentration was low in the *Ranunculus bulbosus* variant of the *Lolio-Cynosuretum* (LR) - like the concentration of K in the soil - probably because of the occurrence of this community on more sandy clay soils (see Chapter 3). The root tissue concentration of N and P was higher in the *Lolio-Cynosuretum* variants *Geranium molle* (LG) and *Ranunculus bulbosus* (LR) than in the species-rich *Arrhenatheretum* communities AB and AO.

Root density and some vegetation and soil characteristics

We studied the factors that enhance root density, and thus ameliorate erosion resistance of the grass cover on sea dykes. To investigate the relation between the characteristics of roots, aboveground vegetation and soil, Pearson correlation-coefficients were calculated between root densities and different parameters measured in 1994 (Table 4.11). Only parameters with significant correlations are shown.

This analysis revealed several significant correlations that explain a greater (40 %, r = 0.63) or smaller (14 %, r = 0.37) proportion of the variation in root parameters. There is a negative correlation (r = -0.37) between the sand fraction and total root weight (*TRW* g m^{-2}) in the sampled profile (0 to 50 cm), but also between sand fractions and root weight at depths of 3 to 6 cm (*RW2*, r = -0.43) and 10 to 15 cm (*RW4*, r = -0.38). Root weight on the other hand was positively correlated with percentage lutum at a depth of 10 to 15 cm (*RW4*, r = 0.48), 20 to 30 cm (*RW6*, r = 0.41) and 30 to 40 cm (*RW7*, r = 0.38). The specific root length (*SRL*) was positively correlated with sand percentage (r = 0.45). Grasslands with a high specific root length occurred on the more sandy clay soils of dykes in the north of the Netherlands.

There is a negative correlation between N concentration in root tissue (*Nr*) and root weight (*TRW*, r = -0.44, *RW2*, r = -0.47, *RW3*, r = -0.53, and *RW4*, r = -0.45). The specific root length (*SRL*) is positively correlated with N concentration in roots (r = 0.42), indicating that the N tissue concentration is relatively low in thicker roots.

A positive correlation was found between *SRL* and vegetation cover (VC, r = 0.49), *SRL* and shoot density (i.e. a negative correlation with shoot density coefficient: SDc, r = -0.39), and a negative correlation between *SRL* and open spot size (OSS, r = -0.49. Grasslands with a high *SRL* also had a high vegetation cover, small average open spot size, and high shoot density. This could illustrate the importance of the arrangement of the rooting pattern at the surface on the one hand, and shoot density and vegetation cover on the other. So, it is not surprising to find a highly significant positive correlation of *root length* in the upper layer of 0 to 3 cm (*RL1*) with vegetation cover (VC, r = 0.54) and shoot density (i.e. a negative correlation with shoot density coefficient, *SDc*, r = - 0.63), and a negative correlation with open spot size (*OSS*, r = - 0.61). When shoots grow close together, roots of neighbouring shoots strongly overlap, resulting in a dense network of roots in the upper 1 to 3 cm of the soil profile.

Table 4.11 Pearson correlation coefficients of root parameters with some soil and vegetation characteristics. TRL, TRW= total root length (m dm^{-2}) and root weight (g dm^{-2}) in 0-50 cm; SRL= specific root length (m g^{-1}); RL1..RL8, RW1..RW8 = root length (m dm^{-2}) and root weight (g dm^{-2}) at a depth of 0-3, 3-6, 6-10, 10-15, 15-20, 20-30, 30-40, 40-50 cm ; LUT, SAND, SILT= % lutum, sand, silt after arcsinus transformation; VC = vegetation cover after arcsinus transform.; OSS = open spot size; Sdc = shoot density coëfficient; SRR = shoot to root ratio; Nmin = soil mineral N (mg/kg, N-NO$_3$ and N-NH$_4$); Nr = total N concentration (g kg^{-1}) in root tissue. Correlations are significant at p = 0.01 (*) and p = 0.001 (**), N = 37.

	LUT	ZAND	SILT	VC	OSS	SDc	SRR	Nmin	Nr
TRL	0.11	0.08	-0.07	0.20	-0.32	-0.37	-0.47*	-0.29	-0.15
TRW	0.19	-0.37*	0.37	-0.36	0.22	0.10	-0.35	-0.28	-0.44*
SRL	-0.25	0.45*	-0.38	0.49**	-0.49**	-0.39*	0.17	-0.02	0.42*
RL1	-0.21	0.35	-0.28	0.54**	-0.61**	-0.63**	-0.36	-0.40*	0.10
RL2	0.11	-0.03	0.04	0.13	-0.22	-0.28	-0.56**	-0.26	-0.21
RL3	0.21	-0.15	0.13	-0.06	-0.02	-0.11	-0.53**	-0.07	-0.36
RW1	0.14	-0.07	0.05	0.023	-0.19	-0.27	-0.46*	-0.38*	-0.20
RW2	0.11	-0.43*	0.43*	-0.30	0.22	0.10	-0.50*	-0.12	-0.47*
RW3	0.26	-0.36	0.33	-0.35	0.29	0.16	-0.39	-0.09	-0.53**
RW4	0.48**	-0.38*	0.33	-0.32	0.27	0.18	-0.32	0.03	-0.45*
RW6	0.41*	-0.24	0.16	-0.14	0.12	0.07	-0.20	0.03	-0.33
RW7	0.38*	-0.22	0.13	-0.21	0.19	0.20	-0.19	-0.02	-0.26
RW8	-0.04	-0.28	0.32	-0.40*	0.29	0.23	0.03	-0.23	-0.22

There is a weak but significant negative correlation between mineral N in the soil and root length (*RL1*, r = -0.40) and root weight (*RW1*, r = -0.38) at a depth of 0-3 cm of the rooted soil profile. This means that the concentration of mineral N is low when root length and root weight are high in the upper layer of the rooting system. The total root length (*TRL*) and root lengths at a depth of 3 to 6 cm (*RL2*) and 6 to 10 cm (*RL3*), as well as root weights at a depth of 0 to 3 cm (*RW1*) and 3 to 6 cm (*RW2*) were negatively correlated with the shoot to root ratio (*SRR*), with r values -0.47, -0.56, -0.53, -0.46, -0.50, respectively. The expansion of the root system at the cost of aboveground production apparently takes place in this part of the rooted profile.

4.4 Discussion

Biomass production and nutrient concentrations in soil and vegetation

The annual biomass production of 4 to 5 tonnes ha^{-1} of the unfertilized species-rich meadow on reference dykes is similar to the annual production of other hayfields that have not been fertilized for a long period of time (Elberse *et al.* 1983, Bakker 1989, Olff & Bakker 1991). The annual production of 9 to 10 t ha^{-1} in the fertilized dyke grassland plots is somewhat lower than the production in most other fertilized hay meadows (10 to 12 t ha^{-1}, Oomes 1990, Berendse *et al.* 1992, Oomes *et al.*1996), probably due to poor moisture conditions in the summer period, which reduces nutrient mineralization. On grazed dyke grassland cessation of fertilization led to a decline in production from 9 to 7 t ha^{-1} y^{-1} after four years and a further decline up to 6 t ha^{-1} y^{-1} after seven years. Continuing haymaking after cessation of fertilizer application on meadows led to a production of 5 t ha^{-1} y^{-1} after seven years. A similar decline has been observed in a restoration experiment of species-rich meadows on clay-on-peat soils. Here a rather rapid fall in production (from 11

to 7 t ha^{-1} y^{-1}) was found in the first 3 to 4 years after stopping fertilizer application, followed by a more slow decline to 5 to 6 t ha^{-1} y^{-1} in the subsequent ten years (Berendse *et al.* 1992, Oomes *et al.* 1996). Stopping fertilizer application and starting haymaking on sheep grazed dykes (treatment HH⁻, Table 4.2) resulted in a production of 5 t ha^{-1} y^{-1} after seven years. On dykes the decline in production to levels as found on the reference dykes seems to occur more rapidly than in flat grassland.

The measured low productivity levels in unfertilized hay meadows (4 to 5 t ha^{-1}y^{-1}) comply with the conditions necessary for the development of species-rich grassland (Olff & Bakker 1991), although the fulfillment of this requirement does not guarantee success (Berendse *et al* 1992). Other factors, like the invasion of species either from seed bank or seed dispersal are necessary (cf. Bullock *et al.* 1994, Olff *et al.* 1994, Bakker *et al.* 1996, Strykstra *et al* 1998, Bekker *et al.* 1998).

Nutrient removal by haymaking after cessation of fertilizer application to grassland seems to be marginal with respect to the total nutrient pool in the soil, which makes reducing the nutrient pool in the soil a long-term process (Bakker 1989, Olff & Bakker 1991). Year after year variations in climate conditions influence productivity (Bakker, 1989, De Leeuw *et al.* 1990, Olff & Bakker 1991). In the different treatments of our experiment there were considerable annual fluctuations in the production (Figure 4.1). In the first two to three years of the experiment the difference between treatments was not significant. Only from 1993 onwards on meadows, and from 1994 on pastures, did the fertilized plots have significant higher biomass productions than the unfertilized plots, independent of annual weather fluctuations. It is likely that an immobile N pool is present in the clay soils of sea dykes, responsible for an additional N supply by increased mineralization under favourable moisture conditions. In dry years, however, productivity would be low, but then N offtake by cutting or grazing would hardly reduce the N pool of the unfertilized plots, if there were to be a net N offtake at all. The nutrient-pool in the reference dyke (at least 25 years of unfertilized meadows) must be smaller, since the productivity was more constant over the years (Figure 4.1b).

An estimation of the annual nitrogen balance (Table 4.9) revealed a net N output of about 40 to 50 kg N ha^{-1} y^{-1} in 1994 in the unfertilized mowing treatments (HH-, H- and reference), and about 20 kg N ha^{-1} y^{-1} in the unfertilized grazed plots (GG-and HG-). In 1997 input and output in the unfertilized grazed plots (GG-) were almost balanced, so that especially in treatments HH- and H- there should have been a slight decrease of the nitrogen-pool in the soil. Measurements of nitrogen concentrations in soil and tissue (Table 4.4 and 4.5) do not confirm these estimations. Although in 1994 the total N was significantly lower in treatment HH- compared to most of the other treatments, resulting in a significantly higher C/N ratio, in 1997 no significant difference in total N concentration was found between the treatments (except a higher total N concentration in GG- compared to HH-), suggesting that cessation of fertilization and haymaking had no effect on the nitrogen pool in the soil yet. In 1997 we found lower values of nitrate in all treatments compared with 1994, but as no change could be observed in the total N concentration in the soil, no decrease of the N-pool could be demonstrated.

The significant lower values for total N in shoots and roots of treatment HH- compared to the fertilized treatment G+, indicate a lower N uptake and N availability. Indeed, direct available nitrate was significantly lower in unfertilized treatments than in the fertilized treatment on pastures as well as meadows in both years (excepting for GG- in 1994). In the reference dykes total N concentration in the soil was significantly lower in

1994 compared to the other treatments (excepting for HH-), but no difference was found in 1997. Here the concentrations of nitrate, soluble P, total P and K in the soil, total P in shoots and total N and P in roots, were significantly lower than in most other treatments in both years. The lower P concentrations supports the assumption that there is a limitation of P in these grasslands. Also Gough and Marrs (1989) found significantly lower soluble P concentrations in soils of semi-natural grassland compared to agricultural plant communities. Olff *et al* (1994) found that hay-fields that were not fertilized for 45 years had the lowest tissue phosphorus concentration in compared to fields left unfertilized fertilized for two years. However, the N/P ratio of the reference dyke grasslands indicates a limitation of N in these species-rich meadows (Koerselman & Meuleman 1996). The concentrations of K in soil and plant tissue did not much differ between fertilized and unfertilized treatments. Relatively high K concentrations in soils of the mown dyke grasslands before the start of the experiments coincide with high lutum percentages of these soils.

The effect of drought, temperature and possibly light intensity on the production is illustrated by the differences in peak biomass and regrowth on slopes with a relatively longer and shorter period of received sunlight (Figure 4.3). The peak biomass on sun exposed slopes, measured at the end of June, was higher than the non exposed slopes, as a result of higher light intensities and where drought not yet hampered growth. In the much dryer period July - September the shaded slopes had the better growing conditions, resulting in a higher regrowth.

Whereas no significant difference was found in total N concentration in the soil between treatments, obvious differences in chemical composition of the soil were demonstrated between communities. The soil in which high productive species-poor *Arrhenatheretum* communities were found, had significantly higher concentrations of total N, P and K, than that of the less productive hay meadow and pasture communities. Apart from the species-rich meadows, characterized by relatively low mineral N concentrations, the soil were some of these pasture and meadow communities grew contained relatively high concentrations of mineral N, but low total N concentrations, expressing the effects of fertilization. The phytosociological characterization of dyke grassland types appears to be a reliable instrument for distinguishing different chemical properties of the soil of these types.

Root length, root weight and management practices

After four years the cessation of fertilization in combination with haymaking on formerly grazed dyke grassland (treatment HH-) resulted in an increase of root length and root weight at a depth of 6 to 10 and 3 to 10 cm respectively (Figure 4.5). Mown dyke grassland (H-) also demonstrated a significant increase of root length and root weight at these depths following discontinued fertilization.. It seems likely that the observed effects are caused by the decline in nutrient availability. Olff *et al.* (1994) also recorded an increase of belowground biomass after cessation of fertilization in hayfields. In the other treatments (GG-, HG-), where N availability was less affected after fertilization was stopped, no significant changes in root length or root weight were measured.

The increased *root weight* in the mown treatment on pastures (HH-) however, could have been caused by changes in management (e.g. the shift from grazing to haymaking) rather than by the decline in nutrient availability (the latter being responsible for the

increase in *root length*). Apparently, mowing is a most efficient tool for the removal of biomass and nutrients. Infrequent removal of above ground biomass, enables a greater allocation to roots, resulting in an increase of root weight, while intensive grazing results in a superficial rooting pattern (Fiala & Studeny 1988), characterized by a higher specific root length and a higher shoot to root ratio (Table 4.3).

Shoot/root ratio

When growing under conditions of nutrient stress, plants invest relatively more in their roots, usually expressed by a decline in shoot/root ratio (Tilman 1988, Berendse *et al.* 1989, Boot 1990, Olff *et al.* 1990, Wilson & Tilman 1991a, Olff *et al.* 1994, Fitter 1994, Ericsson 1995, Mamolos *et al.* 1995, Reynolds and D' Antonio 1996, Schippers & Olff 1997). This follows a functional equilibrium between root and shoot growth, regardless of the size of the root system (Brouwer, 1962, 1983, Van Noordwijk 1987, Lambers *et al.* 1998). However, this relation is ambiguous. Bakker (1989) did not find an overall decrease in the ratio aboveground /belowground production of the vegetation after fertilization was stopped in hayfields. Wilson & Tilman (1991b) found an increase of shoot/root ratio with N application, but an increase of root biomass as well. In pot experiments with species of nutrient-rich and nutrient-poor habitats the fast-growing species of fertile sites invested rather more dry weight in roots than did species from infertile sites under suboptimal nutrient conditions (Berendse & Elberse 1989, 1990, Boot & Mensink 1991, Olff 1990, Elberse and Berendse 1993, Schippers & Olff 1998). A possible explanation for this reverse relationship is the difference in phenotypic response to low nutrient conditions of the two species groups (Boot 1990, cf. Schubert 1991). The lower root/shoot ratio found in nutrient-poor species in these pot experiments was shown to be compensated by a higher specific root length (length per g root weight) of these species (Berendse & Elberse 1990), so that the most important difference between the two groups seems to be the smaller root diameter of the species of the nutrient-poor sites (Berendse *et al.* 1998).

In agreement with an expected influence on the functional equilibrium of the grassland plants after cessation of fertilization, a significantly lower ratio aboveground /belowground production was found after four years in the haymaking treatment on (former) pastures (HH-) compared to the fertilized grazed treatment (G+), as a result of a significantly higher total root weight and lower peak biomass. Total root length, however, was not significantly different in spite of a greater root length in the unfertilized treatment at a depth of 6 to 10 cm. In the unfertilized meadow treatment H- root length was significantly higher at a depth of 6 to 10 cm than in the fertilized treatment H+, but total root length, total root weight and the shoot/root ratio did not differ significantly from H+. Also between the grazing treatments no significant difference was found in total root length, root weight and shoot/root ratio. The unfertilized species rich old meadow was characterized by a relatively low shoot/root ratio, high total root length and total root weight. All haymaking treatments had significantly higher total root weights than the fertilized grazed dykes. Haymaking or grazing would seem to have had an impact on root weight, whereas root length seemed to have been influenced by nutrient availability in the soil.

Root length/root weight ratio

In general one could say that root biomass is only a poor indicator of root activity. Root length data provide information about nutrient uptake, and root weight about changes in carbon allocation and vertical distribution (Boot 1990). For this reason root length and the

ratio of root length and root weight (specific root length, SRL) will probably express more satisfactory changes in root proliferation and the rooting system of differently managed grassland communities as a result of decreased soil nutrient levels. SRL is used as an indicator of the gross morphology of the roots (Fitter 1985): plants with high SRL values are expected to have a low mean root diameter and vice versa (Boot, 1990). In this study root length was measured to get a rough idea of (changes in) densities of the grassland rooting system and its vertical distribution. The calculated ratio of root length to weight (SRL at the community level) can be a good measure for morphological features, thus expressing the difference in effects of grazing or haymaking on the rooting system at high and low N availability. This is shown by the differences in the root length/root weight ratios between treatments. The low SRL values and high root weights in the haymaking treatments HH- (on former pastures) , H+ and H- (on meadows) indicate the presence of mainly thick roots (Table 4.3). High values of SRL and low root weight values (in the grazing treatments G+ , GG- and HG-) indicate the presence of relatively thin roots. High values of SRL are also calculated for the species rich old meadows, indicating a large proportion of thin roots.

The presence of mainly thick roots in hay-fields in both treatments H+ and H- can be influenced by factors other than management. The habitats of these grasslands are characterized by high clay content. It is possible that species with thicker roots (e.g. *Dactylis glomerata*) are favoured by heavy clay soils or that species growing on heavy clay grow thicker roots due to the mechanical impedance (Atwell 1993).

To compare root morphology between communities the calculated SRL-ratio seems to be a good parameter. While the species rich *Arrhenatheretum elatioris brizetosum* is characterized by a large proportion of thin roots (high values of SRL), the species poor *Arrhenatheretum* variants are characterized by the presence of thick roots (low SRL values). Mainly fine roots can be found in the *Lolio-Cynosuretum* variants and the *Poo-Lolietum* (high SRL values).

Vertical distribution of roots

Hardly any difference was found between treatments in the amount of roots in the top layer, making up about 30 to 40 % of total root lengths and root weights, so that differences become obvious below a depth of 5 cm. In an experiment that measured the depth of root uptake of coexisting grassland species at different depths Mamolos *et al.* (1995) found that the relative activity differed with depth between species, but all species had an increased root activity at a depth of 5 cm. The differences in vertical distribution of root density between the fertilized grazed plots and the unfertilized old hay-field is well demonstrated in Figure 4.5. A sharp decline of root length density occurs in the fertilized pasture, whereas the species rich meadows are characterized by a less steep decline of root density. In the unfertilized mowing treatments HH- (on pastures) and H- (on meadows) the distribution of roots seemed to become similar to that in the species rich grassland. The difference in root system between species-poor pastures and species-rich meadows seemed to be greatest at a depth of 3 to 15 cm. This difference would appear to be largely caused by differences in nutrient availability, resulting in dominance of slow-growing species with large root systems, while fast-growing shallow-rooted species characterize the (grazed) fertilized, nutrient-rich habitats.

The mechanisms behind these observed differences in root activity between the two species groups and habitats is still subject for study. Low nutrient supply requires a greater root allocation (Wilson & Tilman 1991b). Due to a different root morphology of species

(deep rooting systems vs. superficial rooting systems, Berendse1982) a spatial niche segregation is created. The greater the number of species the larger the number of niches required to enable coexistence (Rosenzweig 1995). In chalk grassland, for example, species experience a high degree of soil heterogeneity on a small scale (Stark 1994). The nutrient uptake rate differs between species and genotypes (McMichael & Quisenberry 1993, Marschner 1995). In general the possibilities for niche differentiation and the development of species-rich communities increase when nutrient supply declines.

Van der Werff (1993) stated that in low nitrogen environments fast-growing species show a relatively large investment in root biomass at the beginning of the decline in nutrient availability. In the long run the competitive ability of slow-growing species will increase because of a lower turnover rate of biomass. This means that both species groups respond differently to the decline in nutrient availability, although they exhibit a similar increase in root allocation in response to nitrogen shortage (Reynolds and D'Antonio 1996). This is in agreement with the conclusions of Ryser *et al.* (1995), in which is stated that low density of plant tissues is responsible for the faster growth of *Dactylis glomerata* (nutrient-rich species group) at all nutrient levels, but that the high biomass density and slow turnover of *Brachypodium pinnatum* (nutrient-poor species group) from the unfertile habitats, result in a lower N requirement and advantage in the long term (cf. Berendse & Elberse, 1990).

One of the conclusions of our experiment is that within a rather short period (four years) of haymaking after cessation of fertilizer application on pastures as well as meadows, a substantial extension of the rooting system at a depth of 3 to 10 cm had occurred. This coincides well with the observed shift in dominance in the pasture plots of a.o. *Lolium perenne*, with a small root biomass and high turnover towards species such as *Festuca rubra* characterized by a large root system with a low turnover (cf. Troughton 1981). Furthermore, the decline in concentration of N in roots is probably a result of changes in morphological and physiological strategies of plant roots to changed nutrient availability. Fine roots with high turnover have generally a high nitrogen concentration. The observed decline of N concentration in roots in treatment HH- (Table 4.8) is probably attributable to the increase of the percentage thicker roots and a decrease of root-turnover.

Root foraging strategies

The observed differences in root characteristics can be the result of different strategies in nutrient capture. Plants are able to increase their competitive ability for soil nutrients by increasing root length or root surface area per unit biomass (Berendse *et al.* 1998). Boot (1990) distinguishes two categories: (I) *exploration*, characterized by a low SRL, large soil volume explored, low root density, fine and thick roots, shoot/root ratio lower at low nutrient supply; and (II) *exploitation*, characterized by high SRL, small soil volume explored, high root density, fine roots and a higher SRL at low nutrient supply. The species-poor *Arrhenatheretum* communities seem to follow strategy (I) on the basis of their root characteristics, while the species-poor *Lolio-Cynosuretum* communities follow strategy (II). Haymaking seems to favour species with a strategy of exploration, whereas grazing favours a strategy of exploitation. It is possible that species-rich meadow communities, characterized by both types of root traits combine both strategies, resulting in a root system where a relatively large soil volume is explored and a large number of niches are exploited by the coexisting species. The root system of the unfertilized hayfield on

formerly grazed dykes, with root properties resembling those of the species-rich meadow, will probably develop into a stable, well developed rooting system.

Different strategies for nutrient acquisition uptake have also been described by other authors (De Kroon & Hutchings, 1995). The root system can respond to nutrient-rich patches with morphological changes (Fitter 1994), especially to enhance P uptake, and physiological changes like elevated uptake kinetics, causing, among others, an increased NO_3^- uptake (Jackson & Caldwell 1996). Another factor that enhances nutrient uptake capacity is mycorrhyzal interference (Grime *et al.* 1987, Evans & Miller 1990, Cui & Caldwell 1996, Ozinga *et al.* 1997). Mycorrhizal activity contributes to species coexistence by enlarging niche differences or creating common networks (Grime *et al.* 1987, Ozinga *et al* 1997). The resource-ratio hypothesis (Tilman 1982, 1986) is not contradictory to the concept of *niche differentiation*, since spatial heterogeneity is included in this theory, assuming trade-offs between the competitive ability for different resources (Tilman, 1986, 1997, Bengtsson *et al.* 1994). We could regard this as *niche exploitation*. Additionally, Tilman's spatial competition hypothesis describes coexistence on the basis of trade-offs between competitive ability, colonizing capacity and longevity of species (Tilman 1994).

Synthesizing the information on root dynamics described by several authors and the results of this study we can formulate the following hypothetical mechanisms for the observed effects of changes in nutrient supply in the field. A decline in nutrient availability after fertilizer cessation will enhance the investment in root biomass of both fast-growing species (FG) and slow-growing species (SG). The FG will show a greater aboveground growth reduction than the SG. Due to the high turnover the FG will exploit the available soil N-pool resulting in a nutrient-stress (cf. Van der Werf, 1993). Because of their lower nutrient requirement resulting from a higher biomass density and slower turnover (Ryser & Lambers 1995, Schippers & Olff 1997), the SG will outcompete the FG species resulting in a dominance shift from FG towards SG. No longer hampered by the FG the SG root system will proliferate and thus enhance exploration, and increase niche differentiation between the species that become dominant.

Conclusions

On dykes, cessation of fertilization in pastures and hay-fields leads to a decrease in production from 9 to 10 t ha^{-1} year^{-1} to 6.5 to 7 t ha^{-1} year^{-1} after four years and to 6 to 6.5 t ha^{-1} year^{-1} in unfertilized grazed and 5 t ha^{-1} year^{-1} in unfertilized mown dyke grasslands after seven years. The peak biomass at the beginning of July is higher on sun-exposed slopes, whereas regrowth from July till October is higher on slopes with less received sunlight. The decrease in production is caused by a decline in availability of mineral nitrogen. Although, according to our estimations, the net N input is slightly negative in the unfertilized treatments with the highest N-offtake in the mown treatments, total soil N pool did not change compared to the fertilized plots..

Four years after cessation of fertilization, root length and root weight at a depth of 3 to 10 cm in the unfertilized haymaking treatments were significantly higher than in the fertilized treatments on pastures and meadows. We made comparisons of soil and root parameters in the treatments with those of long-term unfertilized species-rich meadows (reference), characterized by significantly high values of root length and root weight at a depth of 3 to 15 cm and low N and P concentrations in soil and tissue. Also, total root length was higher than in all the pasture treatments. In general pastures had low, and

hayfields high total root weight values. The ratio aboveground/belowground production (SRR) was smaller in the unfertilized mowing treatments and reference plots than in the fertilized pasture. The ratio root length/root weight (specific root length, SRL) differed between treatments exhibiting high values in grazed grasslands (fine roots) and low values in hayfields (thick roots). The SRL was also high in old meadows.

At the community level, high productive species-poor Arrhenatheretum communities were recognized, characterized by relatively high concentrations total N, P and K in the soil, low SRL (thick roots) and high SRR compared to less productive meadow and pasture communities, like the *Geranium molle* variant of the *Lolio-Cynosuretum* (high SRL and high SRR). The *Poo-Lolietum* and the *Ranunculus bulbosus* variant of the *Lolio-Cynosuretum* were characterized by relatively low root lengths and root weights values, indicating a less developed rooting system. The species-rich *Arrhenatheretum elatioris brizetosum* was characterized by a low SRR, high values of total root length and root weight and the presence of thin roots (high SRL).

It is argued that management (haymaking or grazing) has an impact on root weight and that root length is influenced by N availability, according to different (root)strategies of grassland plants, as a reaction to the cessation of fertilization.

5

Temporal and spatial variation

Seasonal variability in shoot and root biomass and spatial variation in vegetation cover and root weight

5.1 Introduction

In both natural and managed ecosystems, factors that affect plant growth exhibit a large temporal and spatial variation at all scales, from less than that of the individual plant to greater than that of the habitat as a whole (Bell & Lechowicz 1994, Stark 1994).

The most important temporal variation is probably the seasonal fluctuation in environmental factors, with its effects on nutrient availability. During the summer the root biomass in grassland increases simultaneously with the enhanced aboveground biomass (Matthew *et al.* 1991, Fiala 1993). In an experiment with hard and lax grazing of a ryegrass sward, Matthew *et al.* (1991) showed that the seasonal variation in root parameters were large in comparison to the differences in grazing regimes. In our study of the influences of different management practices on above and belowground vegetation of sea dyke grassland (Chapters 3 and 4), shoot and root density were always measured at the end of the winter the period when high water levels are most likely to occur, and sea dyke grass swards are most vulnerable to erosion. The results collected during this period provide the necessary information about differences in vegetation cover and rooting patterns between plant communities or management practices and the possible consequences for soil stability and erodibility.

However, since several authors mention different seasonal dynamics of root biomass production in different grassland types (Matthew *et al.* 1991, Dumortier 1991, Scholand 1991) it is conceivable that circumstances on sea dyke grasslands in November and December, when the chances for high water are also likely, differs from the circumstances in February and March. Seasonal fluctuations can either compensate for or enhance the measured differences in root parameters of the grasslands under study.

Another difficulty when evaluating the erosion resistance of grassland is the spatial heterogeneity in sod characteristics (quality), because of spatial differences in plant growth and species-specific interactions (cf. Thórallsdóttir 1990a, 1990b, Tuzinkevich & Frisman 1990, Hook *et al.* 1994), nutrient availability (Rorison 1987, Pegtel 1987, Jackson & Caldwell 1993, Caldwell 1994, Bell & Lechowicz 1994, Gross *et al.* 1995), and effects of management practices and herbivory (Chaneton & Facelli 1991, Hill *et al.* 1992, Bullock et al 1994, Silvertown *et al.* 1994). Nutrients are heterogeneously distributed in the soil and generally not at random (Robertson & Gross, 1994) but at multiple scales (Gross *et al.* 1995), varying from ranges at the rhizosphere level (less than 1cm) to levels of less than

one metre (Thórhallsdóttir 1990a) or even more than that (100 m) (Rorison 1988, Jackson & Caldwell 1993, Robertson 1994). The largest sources of organic material in the soil constitute of turnover of fine roots and root exudation. These organic matter additions to the soil can be responsible for local and short-lasting immobilization or mineralization of nutrients. This creates heterogeneity in nutrient supply over a spatial range of a few centimetres during a period of a few weeks (Stark, 1994).

Spatial variation on a larger scale can be the result of activity of moles or sheep at high or irregular grazing intensities resulting in a sward of tussocks, and on an even larger scale it can be the result of differences between higher and lower situated spots on a dyke slope, or the inner and outer slope of a dyke. Large open spaces in grassland or places with large numbers of ruderal plants that reduce the sod quality, such as *Stellaria media*, *Cirsium arvense*, *Capsella bursa-pastoris*, *Hordeum murinum*, *Urtica dioica* are easy to recognize. But how homogeneous is the root and shoot density over a certain area of dyke grassland with an apparently closed canopy? Are there 'weak' spots in the grass cover and in which type of management do these occur? Perhaps in species-rich unfertilized grassland, where plants are part of a more stable vegetation, the distribution of roots over a certain area is less heterogeneous compared to the unstable fertilized vegetation types.

To seek answers to these questions we studied the seasonal variation in aboveground production and root parameters as well as spatial heterogeneity in vegetation composition, cover and rooting pattern of fertilized grazed dyke grassland and unfertilized old dyke meadow (reference). By comparing the two differently managed grassland types, we were able to determine the effects of management practices on temporal and spatial heterogeneity as well.

5.2 Methods

Temporal variation

Temporal variation was determined in the 'fertilized pasture' treatment plots of three study sites and in the plots of three reference dykes (unfertilized hayfield). Two extreme types of grassland management were compared. For the intensive management plots, the following sites were selected (see Chapter 2 for a site description and geographical location and Chapter 3 and Appendix 1 for the dominant plant community at the site): (1) Zeeland-Ossenisse (*Poo-lolietum*, code ZH-G+), (2) Friesland-Boonweg (*Geranium molle* variant of the *Lolio-Cynosuretum*, code FA-G+), and (3) Hondsbossche zeewering (*Geranium molle* variant of the *Lolio-Cynosuretum*, code NH-G+). These sites were fertilized with 100-150 kg N ha^{-1}y^{-1} and periodically grazed, sometimes varied with one hay-cutting, or mown just after grazing to remove ungrazed plant parts. Measurements were made on both the inner and outer slope of the dyke. For the extensive haymaking management, the following reference dykes were sampled: (1) Oudelandse zeedijk (*Arrhenatherum elatoris brizetosum*, code ZO-ref), (2) Zandkreekdam (*Arrhenatherum elatoris brizetosum*, code ZZK-ref), and (3) Biezelingse Ham (*Festuca pratensis* and *Origanum vulgare* variant of the *Arrhenatherum elatoris*, code ZK-ref). These sites which had not been fertilized for the past 25 years were mown once a year (end of June, or the beginning of July) for haymaking.

The measurements started in February 1992 and continued until February 1993. Biomass and root samples were taken every six weeks. The aboveground biomass was determined by harvesting four plots of 50 x 50 cm within a permanent quadrate and measuring the dry weight (expressed as g m^{-2}). The biomass of the grazed sites was measured in permanent exclosures. Root data were collected by taking three 50 cm deep soil cores, which were cut into eight segments (0-3 cm, 6-10 cm, 10-15 cm, 15-20 cm, 20-30 cm, 30-40 cm and 40-50 cm). After separating the roots from the soil by washing with water, the root weight and root length were measured. For a detailed description of the methods for determining biomass and root density see Chapter 4.

The software package SPSS/PC+ (Norusis 1986) was used for the statistical analyses. With a simple analysis of variance (Oneway ANOVA), optionally followed by an LSD test for pair-wise comparison, differences between periods and management practices were examined for the various parameters. In spite of site-specific differences, the plots on each of the two dyke slopes and the various locations within each management type were treated as replicates of the treatments.

Spatial variation

Measurements of spatial variation were conducted in spring and summer of 1992 at three sites: the fertilized dykes Zeeland-Ossenisse (ZH-G+) and Friesland-Boonweg (FA-G+) were compared to the long-term unfertilized control dyke Oudelandse zeedijk (ZO-ref). In addition to these sites the treatment plot at the location Friesland-Boonweg which has not been fertilized since 1991 (*Ranunculus bulbosus* variant of the *Lolio-Cynosuretum*, code FA-HH-), was examined. To determine the variation in species composition ten Braun-Blanquet relevés were made along a 100 m transect lengthways and halfway down the inner slope of the dyke. Additional relevés were made perpendicular to the dyke to a total of five relevés on the inner slope and two on the outer slope. In these relevés the vegetation cover at a height of 2 cm and open-spot size were measured as described in Chapter 3.

The variation in root density was determined in a 5 x 5 m grid halfway down the inner slope (ZH-G+ and FA-G+) or outer slope (ZO-ref) of the dyke. Using a soil auger, 50 cm deep root samples were taken in each of the 1 m^2 cells of the grid, which were divided into eight soil layers. Additionally, from the cell at the middle of the grid four root samples were collected, resulting in a total of 29 samples. In the treatment FA-HH- two samples were taken in each grid. For practical reasons only the root weight in each soil layer of these samples was determined. The species composition of the cells in these grids was also recorded.

The similarity between both the transect relevés as the grid relevés was calculated using the DENDRO program (Schaffers 1991), which uses the cover values of the species in the relevés according to the following equation (Sörensen-index):

$$PS_{A,B} = \frac{2 * \sum \min(a,b)}{\sum A + \sum B} * 100\%$$

In this equation $PS_{A,B}$ stands for the percentage similarity between relevé A and B, min(a,b) for the lowest cover value of a species occurring both in A and B, and ΣA, ΣB for the sum of the values of the species in A and B. For comparison of the management practices the

average similarity index per treatment was calculated for the relevés of the 100m transect, the cross transect and the 5 x 5 m grid. This method was also used for calculating the average similarity in rooting pattern between the 25 grid samples, using the root weight values of the different layers in each sample.

As a measure for the variation in vegetation cover, open spot size, shoot density and root density the variation-coefficient (= standard deviation as a percentage of the mean) was calculated for each treatment. A test for auto-correlation (Moran's I) was done to analyse the potential patterns in root density in the 5 x 5 m grid.

The relation of root density with soil depth (based on root weight) was expressed using a modified version of the equation in Chapter 4: $y = b * e^{-ax}$

where x stands for the depth of the sampled soil profile, y for the root weight at depth x (g dm^{-3}), b for the value of the top layer and a for a coefficient describing the decline in root weight with depth. The greater the value for a, the larger the decrease in root weight with soil depth. Differences in a-values between the 1 m^2 plots were tested against position on the dyke slope using a one-way analysis of variance. Next, the average values and variation-coefficient of a and b were calculated for the different treatments. Differences in average a-values between treatments were tested using a one-way analysis of variance. These analyses were conducted with the aid of the GENSTAT statistical package (Payne & Lane 1993).

5.3 Results

Temporal variation

Biomass

The seasonal fluctuation in aboveground plant growth of the investigated sites is presented in Figure 5.1. In Zeeland (ZH-G+, Figure 5.1a), where fertilizer was applied in early spring, the peak production at the inner dyke slope was found in May. In Noord-Holland (NH-G+, Figure 5.1a) and Friesland (FA-G+, Figure 5.1a) where fertilizer was added later in spring, the largest production was recorded in June, just before mowing in early July. Depending on the amount of fertilizer the peak standing crop at the inner slope varied from 650 g m^{-2} in Friesland and Noord-Holland to 920 g m^{-2} in Zeeland. At the sites in Zeeland (ZH-G+) and Noord-Holland (NH-G+) the peak production on the outer slope was found to be lower, in comparison with the observed differences between inner and outer slope at all investigated locations in 1994 (Chapter 4). This difference in peak biomass between inner and outer slope of the dyke was not found in Friesland.

The measurements taken in late June and shortly thereafter (early July) the vegetation was harvested, and the regrowth was measured in autumn. The maximum regrowth at the inner dyke slope was 350 g m^{-2} in ZH-G+, 250 g dm m^{-2} in NH-G+, and 170 g dm m^{-2} in FA-G+, resulting in a total aboveground production at the inner dyke slope of respectively 1270, 1000 and 850 g m^{-2}. More regrowth was found on the outer dyke slope in Friesland and Noord-Holland. The annual production on the outer slope was 880 g m^{-2} (ZH-G+), 750 g m^{-2} (NH-G+) and 980 g m^{-2} (FA-G+). In Friesland the annual production was largest on the outer slope.
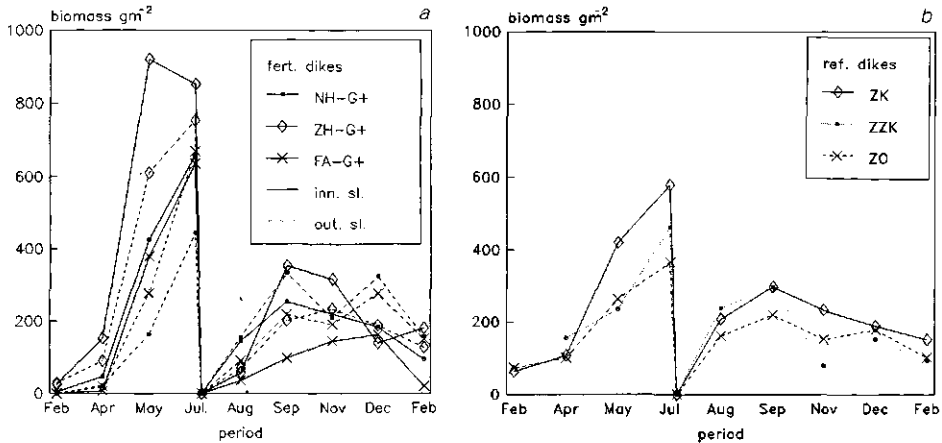
Figure 5.1 *Seasonal variation (February 1992 - February 1993) in aboveground biomass at both inner and outer dyke slope of fertilized pastures (a) and at the outside slope of unfertilized old dyke meadows (b). Legends: ZH-G+ = Zeeland-Ossenisse (150 kg N ha⁻¹y⁻¹, periodically grazed, sometimes altered with one hay-cutting), NH-G+ = Hondsbossche Zeewering (100 kg N ha⁻¹ y⁻¹ , periodically grazed) and FA-G+ = Friesland-Boonweg (100 kg N ha⁻¹ y⁻¹, periodically grazed); ZO = Ouddorp (unfertilized meadow, one hay-cut in July), ZZK = Zandkreekdam, unfertilized, two cuttings for haymaking July and October, ZK = Biezelingse Ham, unfertilized, hayed once at the end of June).*
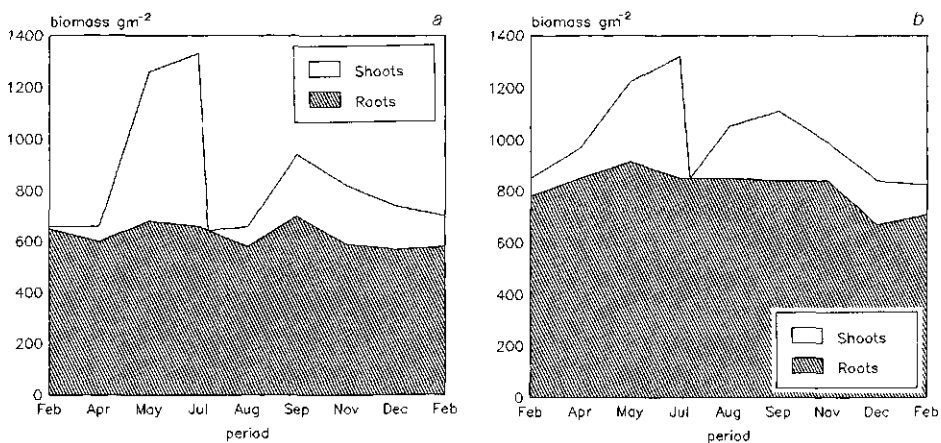
Figure 5.2 *Seasonal variation in above- and belowground biomass in a) fertilized pasture (n=6) and b) unfertilized meadow (n=3).Depth of the sampled profile is 0-50 cm.*

The maximum biomass production in the unfertilized hayfields was also recorded in July and measured approximately 400 g m^{-2}, with the exception of the dyke located at the Biezelingse Ham (ZK, Figure 5.1b) where a small amount of fertilizer was accidentally applied by the local tenant farmer. In comparison with the fertilized pasture the growth rate was lower in April-May (the slope of the curve is less steep). The regrowth (200 to 300 g dw m^{-2}) did not differ much from the fertilized and grazed treatments, with 230 to 300 g m^{-2} on the outer dyke slope. The difference in biomass production in July between fertilized pastures (average 670 g m^{-2}) and unfertilized hayfield (average 470 g m^{-2}) is statistically significant (p < 0.05).

Root growth

Figure 5.2 shows the seasonal the variation in above and belowground biomass of the fertilized pastures (a) and the unfertilized hayfields (b). The differences between the root biomass measured at different sampling dates in both pasture and meadow were not significant. The fluctuation in the ratio between aboveground and belowground production (SRR = shoot/root ratio, Figure 5.3) therefore strongly resembles the seasonal variation in aboveground biomass production for both grassland types. Both the aboveground production and the SRR measured in July were significantly higher in the fertilized pasture than in the reference dykes (p < 0.05). Averaged over all sample periods the root biomass in the fertilized pasture is about 600 g m^{-2} and 800 g m^{-2} in the unfertilized hayfield. On the sample dates 'April', 'July' and 'August' the root biomass in the unfertilized hayfield was significantly higher than in the fertilized pasture (p < 0.01, see also Table 5.1).

These results clearly show that more material is allocated to the roots at the cost of aboveground production of the unfertilized meadows, when compared to the fertilized pastures. Furthermore the unfertilized species-rich meadows show a lower productivity during the season , but they do not differ from the fertilized meadows concerning the time at which peak biomass is reached and in the amount of regrowth.

Figure 5.4 gives the seasonal fluctuation in *total root length* in the sampled soil profile (0 to 50 cm) of the fertilized and the unfertilized grassland. A Oneway analysis of variance followed by an LSD test indicated that at all sample times, with the exception of February and August 1992, the total root length in the unfertilized hayfield was significantly higher than the root length of the fertilized pastures (p<0.05; see also Table 5.1). In the pasture, the seasonal fluctuation in root length was marginally significant (effect of sampling date: p < 0.07). Increase in root length occurs from February until May (Figure 5.4), and remains at this level until it starts to decline again in November. Because the root weight hardly changes (Figure 5.2a) – there is no significant difference in root weight between the sampling dates – this is most likely to be the result of an increase and subsequent decrease of the fraction of fine roots. The root-length/root-weight ratio (specific root length, SRL, Figure 5.5a) does indeed increase in April and May, indicating an increased growth of fine roots in this period, which decreases after November.

The variation in total root length during the year is greater in the unfertilized hayfield than in the fertilized pasture (effect of sampling date: p < 0.02), with relatively high values in May and September. The differences between root biomass measured at different times, however, were also not significant. Here, the constant root weight during the year implies an increase in fine roots (and thus SRL) particularly between February and April, and
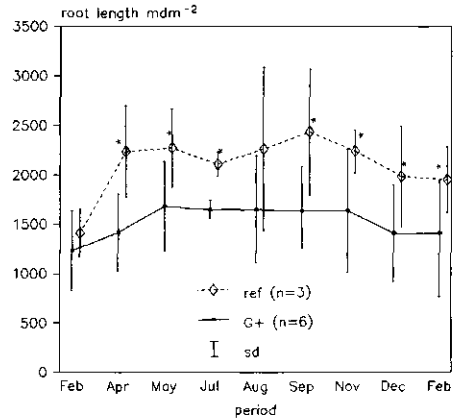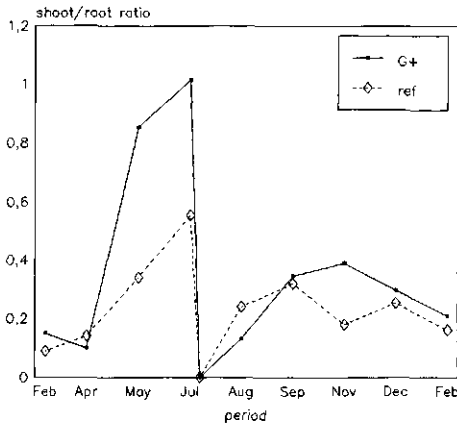
Figure 5.3 *(left) Seasonal variation in the ratio between above and belowground biomass (shoot/ root ratio) in fertilized pasture (G+, n=6) and unfertilized meadows (ref, n=3).*

Figure 5.4 *(right) Seasonal variation in total root length (m dm^{-2}) in the sampled profile (0-50 cm) in fertilized pasture (G+) and unfertilized hayfield (ref). Mean and standard deviation are shown; * : significant difference between G+ and ref (p < 0.05.).*
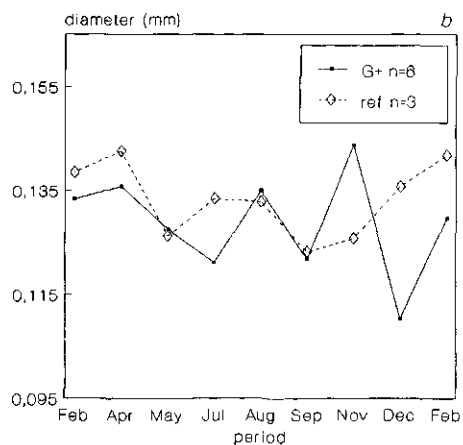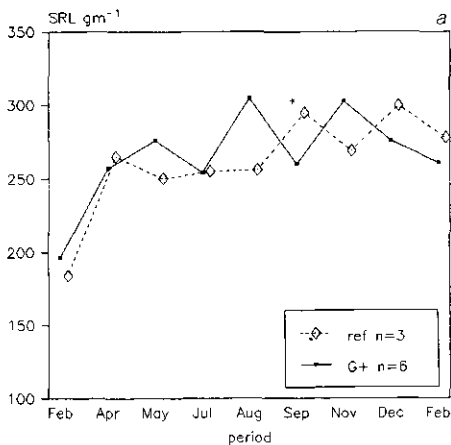
Figure 5.5 *Seasonal variation in a) the ratio root length/root weight (specific root length) and b) average root diameter in the fertilized pasture (G+) and unfertilized meadow (ref).*

between August and September. Only in September was the SRL found to be is larger in the hay meadow. In spite of the difference in total root length and total root weight, the ratio length/weight and probably the ratio fine roots/thicker roots is roughly similar in both grassland types.

Table 5.1 *Overview of periods and soil layers showing the values of root length and root weight of unfertilized hayfield (ref) to be significantly higher than in fertilized pasture (G+). Oneway ANOVA followed by LSD test for each period; * : significant difference at p < 0.05; **: significant difference at p < 0.01; n.s. not significant.*

Soil layer		F	Apr	May	Jul	Aug	Sep	Nov	Dec	Feb
Total root length (0-50 cm)			**	**	**		**	*	*	**
Total root weight (0-50 cm)			**		**	**				
Root length	0-3 cm									
	3-6 cm			**		**		**	*	*	**
	6-10 cm	*	*	*	**		**	**		**
	10-15 cm	*	**	*	**		**	**	**	**
	15-20 cm	*	**	**	**		**			
	20-30 cm		**	**			**		*	
	30-40 cm		**	**			**	**	*	*
	40-50 cm		*	*			*	**		
Root weight	0-3 cm					*				
	3-6 cm	*	**		**		*	*	*	*
	6-10 cm		*		**	**	**	*		*
	10-15 cm	*	**		**	*	**	*	**	**
	15-20 cm	*	**	**	**	**	**			
	20-30 cm	*	**		**				*	
	30-40 cm		**						*	
	40-50 cm		*	*	*					

This agrees with measurements of root diameter (Figure 5.5b). Little difference was observed in average root diameter between the two grassland types. Root diameter also varied little during the year. On the reference dykes the average root diameter declined somewhat in May and September while in the fertilized treatment the average root diameter decreased in July, September and December. Reduction of the average root diameter, and the concurrent increase in the percentage fine roots is apparently correlated to the increase in aboveground production.

Assessment of the average root length and root weight *per soil layer* (Table 5.1) revealed that the difference between the fertilized and unfertilized grassland was most pronounced between 3 and 20 cm in the soil layers, and that this difference changed little during the year. Where differences were significant, root length and root weight values were significantly higher in the unfertilized hayfield. In the soil layers at depths of 20 to 50 cm significant differences in root length were found at sampling dates in April, May and September, and differences in root weight at dates in April and July. At a depth of 0–3 cm the difference in root length between both grassland types was not significant on any of the sampling dates. Only the root weight measured at this depth in August showed a difference.

Examination of the seasonal fluctuation in root length per soil layer revealed a significant (effect of sampling date: p < 0.01) variation in root length at a depth of 0-3 cm in the fertilized pastures, with relatively high values in the periods July and September-November (Figure 5.6a). Up to a depth of 30 cm the other layers displayed no significant fluctuation in root length. This variation in the surface layer agrees with the increase in aboveground production in May-July and the regrowth in September-November. There was some change in root length in the layers 30 to 40 and 40 to 50 cm, but the absolute values were low at this depth. In the unfertilized hayfield the variation of root length in the
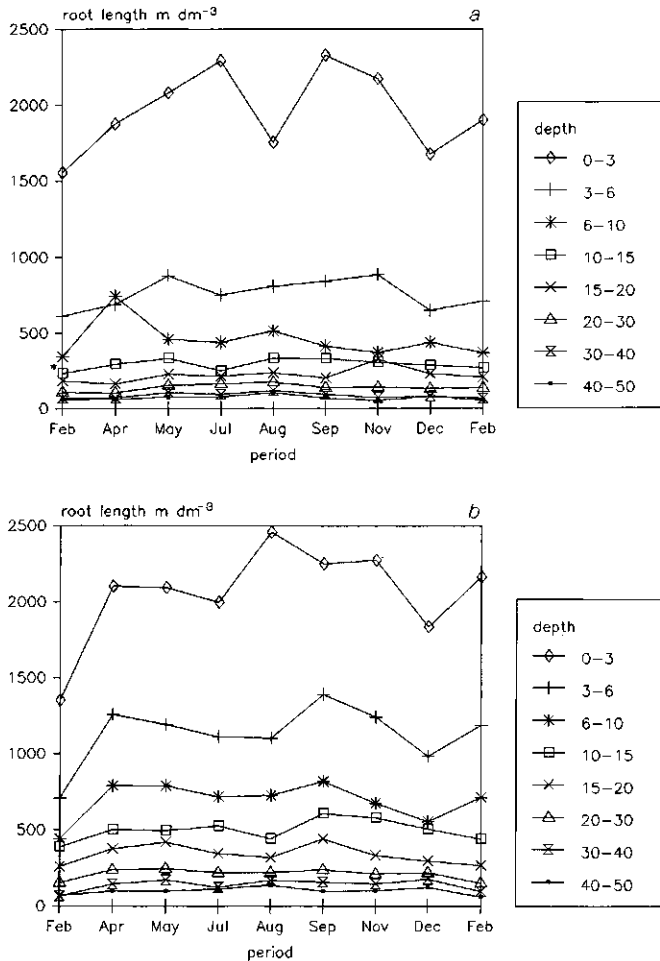
Figure 5.6 *Seasonal variation in root length for all soil layers of a) fertilized pasture (G+) and b) unfertilized meadow (ref).*

uppermost soil layer was not significant (Figure 5.6b). However a significant difference in root length was demonstrated between the different sample dates at depths of 3 to 6 cm (p < 0.05), 6 to 10 cm (p < 0.05), 15 to 20 cm (p < 0.001), 20 to 30 cm (p < 0.05) and 30 to 40 cm (p < 0.05), with relatively high values in April and September. Growth of the root system through development of fine roots appeared to precede an increase in aboveground production with a peak in July. The increase in root length in September however coincided with the higher aboveground production. In the pasture the root weight only fluctuated at a depth of 40 to 50 cm (p < 0.05, high values in August and December) and in the hayfield at a depth of 15 to 20 cm (p < 0.05, high values in May and September) and 40 to 50 cm (p < 0.05, high value in August).

Spatial variation

Vegetation

The similarities (Sörensen index) were calculated of the 25 relevés of $1m^2$ in the 5x5 m grid, the 10 relevés of the 100 m longitudinal transect, and the 7 relevés of the transect perpendicular to the dyke. The average value of this index is a measure of the homogeneity of a site. The results are presented in Table 5.2. The unfertilized old meadow (ZO-ref, belonging to the *Arrhenatheretum elatoris brizetosum*) revealed the most variation in composition of the vegetation, demonstrating a noticeable difference between the inner and outer slope. This can be attributed to the extremely sandy inner slope at this site, characterized by an open vegetation, which is not representative of the sites investigated in this study. In the other treatments the floristic homogeneity along the cross transect did not differ from the homogeneity in the 5x5 m grid (ZH-G+, FA-HH-) or 100 m transect (FA-G+) of the inner slope. At the outer slope of the reference dyke (ZO-ref) the heterogeneity was more pronounced in the 100 m transect than in the 5x5 m grid. This means that floristical heterogeneity is greater when a larger scale is considered.

This phenomenon was also found at the other sites, with the exception of the unfertilized haymaking treatment (FA-HH-, assigned to the *Ranunculus bulbosus* variant of the *Lolio-Cynosuretum*). Here the similarity between relevés in the 25 m^2 patch was smaller than the similarity along the 100m transect (Table 5.2). The unfertilized treatment (FA-HH-) was also more homogeneous along the 100 m transect compared to the fertilized treatment at the same site (FA-G+). Moreover, the number of species is higher in FA-HH-, indicating a more even distribution of species on a larger scale, whereas in FA-G+, species occurred in more homogeneous patches that slightly differed on larger scales. A greater homogeneity and a small species number on both scales (5x5 grid and 100 m transect) are found in the fertilized treatment ZH-G+ (*Poo-Lolietum*). The unfertilized hayfield ZO-ref accommodated the largest number of species. The relatively large variation in species composition implies a larger occurrence of species in mosaic-like patterns.

Vegetation cover and shoot density

Table 5.3 gives the average cover and open spot size in the relevés along the 100m transect and along the transversal transect together with their variation coefficient. A somewhat high and homogeneous average cover of the relevés in the fertilized pasture treatment in Friesland (FA-G+) and in the two years unfertilized haymaking treatment at the same site (FA-HH-) was observed over the 100 m transect (low values of the variation coefficient). The transects perpendicular to the dyke in these treatment areas also displayed high values of cover and continuity. Open spots in the vegetation were comparatively small. In the fertilized treatment (FA-G+) these spots appeared to vary considerably in size (32 %), whereas in the haymaking treatment (FA-HH-) the percentage (variation coefficient) was lower (17 %).

The vegetation cover in both the longitudinal and the perpendicular transect of the fertilized pasture ZH-G+ is characterized by low values, and a much variation. Here the species composition of the vegetation was homogeneous, and the vegetation cover heterogeneous. This can be attributed to the large activity of moles at this site. Furthermore the management differed: in contrast to FA-G+ partly grazed or ungrazed patches were not

Table 5.2 *Similarity indices and average numbers of species in a 25 m² sample grid, a 100 m transect (10 relevés) and a cross-transect (7 relevés). Legends: ZH-G+ = Zeeland-Ossenisse, 150 kg N ha⁻¹ y⁻¹, periodically grazed, sometimes altered with one hay-cutting; FA-G+ = Friesland-Boonweg, 100 kg N ha⁻¹ y⁻¹, periodically grazed; FA-HH- = Friesland-Boonweg, two years without fertilizer, two cuts for haymaking); ZO-ref = Ouddorp, unfertilized old meadow, one hay-cut in July); LG = Lolio-Cynosuretum, variant Geranium molle; LR = Lolio-Cynosuretum, variant Ranunculus bulbosus; PL = Poo-Lolietum; AB = Arrhenatheretum elatioris brizetosum.*

Site	Veg. type	25 m² sample grid		100 m transect		cross transect	
		Similarity index %	Number of species (m⁻²)	Similarity index %	Number of species (m⁻²)	Similarity index %	Number of species (m⁻²)
FA-G+	LG	79.6	10	70.5	9	72.6	8
FA-HH-	LR	78.3	13	83.0	15	79.0	12
ZH-G+	PL	81.1	7	80.1	6	81.4	8
ZO-ref	AB	69.6	24	60.2	28	58.1	24

Table 5.3 *Average vegetation cover (COV) and open spot size (OSS) with variation coëfficients (VAR) in the 100m transect and the cross-transect. Different superscript letters denote sigfnificant differences between sites (p = 0.001). See Table 5.2 for legends of sites*

Site	Veg.type	100 m transect				Cross-transect			
		COV %	VAR %	OSS cm²	VAR %	COV %	VAR %	OSS cm²	VAR %
FA-G+	LG	81,2[c]	6	2,14[a]	32	89,4[c]	6	3,40[a]	22
FA-HH-	LR	91,4[c]	2	3,32[a]	17	90,9[c]	2	2,06[a]	18
ZH- G+	PL	44,9[a]	19	16,9[c]	43	53,0[a]	26	13,8[c]	30
ZO- ref	AB	68,6[b]	14	9,29[b]	91	70,7[b]	17	6,40[b]	32

always mown after a grazing period at this site, with the result that the grass plants (mainly *Agrostis stolonifera*) were overgrown and lying on and choking the grass shoots. Cut back to a height of two centimetres the open sward has an extremely low vegetation cover. The vegetation cover of the species-rich hayfield (ZO-ref) was average in size with a fairly large variation. The open spot size varied considerably, but the spots were smaller on average than in the ZH-G+ treatment. Here too the presence of molehills, creating large open spots in some of the sample plots, could explain the high variation.

Root growth

In Table 5.4 the average root weight (g dm⁻² in a 50 cm deep profile) and variation coefficient of 25 plots in the 5x5m grid is given for each location, together with the calculated average similarities between root weights. Root weights of the different soil layers were treated as variables.

The fertilized pasture treatment in Zeeland (ZH-G+) exhibited a low average root biomass and a relatively large spatial variation (40%). In the fertilized pasture treatment in Friesland (FA-G+) the average root weight was higher, with a fairly small variation (24%). The similarity between root cores was also higher (81%) compared to ZH-G+ (72%). Both treatments were characterized by a homogeneous species composition of the vegetation (see Table 5.2). The vegetation cover (over the 100m transect) however was much lower in ZH-G+ than in FA-G+ (see Table 5.3). The species-rich hayfield type ZO-ref had a high root biomass while the spatial variation in root weight was rather low (30%). The similarity

Table 5.4   Average root weights (g dm^{-2}) with standard deviation (SD) and variation coefficient (VAR%) and similarity coefficients calculated using the Sörenson-index on the basis of similarity in root weights of the sampled soil layers of n cores in 25 cells of the 5x5 m^2 grid for the four sites (see Table 5.2 for legends). Different letters denote significant differences (p < 0.005).

Site	Veg type	n	Root weight (g dm^{-2})	SD	VAR %	Similarity coefficient %
FA-G+	LG	29	11.23[b]	2.67	24	81
FA-HH-	LR	50	7.68[a]	3.24	41	71
ZH-G+	PL	29	7.89[a]	3.12	40	72
ZO-ref	AB	29	20.79[c]	6.32	30	80

*Table 5.5   Average values for parameters **b** (root density g dm^{-3} of the top soil layer) and **a** (decline of root weight with depth) in $y = b \cdot e^{-ax}$ and their variation coefficient (VAR %) per site (see Table 5.4 for legends). Different characters denote significant differences at p < 0.05.*

Site	Veg. type	n	b (g dm^{-3})	VAR %	a	VAR %
FA-G+	LG	29	27,14[c]	37	0.27[c]	8
FA-HH-	LR	50	15,24[a]	68	0.21[b]	8
ZH-G+	PL	29	15,49[a]	76	0.22[b]	11
ZO-ref	AB	29	23,17[b]	38	0.13[a]	5

between the sampled plots was assessed as relatively high (80%) like FA-G+. These two sites are thus distinguished by a somewhat less heterogeneous root distribution. The vegetation composition and the shoot density in the species-rich meadow, however, were fairly heterogeneous (see Tables 5.2 and 5.3). An uneven species distribution and shoot density can apparently occur with a spatially uniform root density. The haymaking treatment in Friesland FA-HH- exhibited a low root weight with a relatively high variation, while the vegetation composition, vegetation cover and turf density were spatially homogeneous. This was possibly the result of the change in management from grazing and fertilizing to haymaking without fertilizer application after two years, leading to a (temporal) reduction of root mass.

The spatial variation in the root weights of all 25 plots of the Poo-lolietum (ZH-G+) and the species-rich hayfield (ZO-ref) is illustrated in Figure 5.7. Clearly visible are the differences between average root weight and the spatial variation between the two plots. To give an impression of the range of values in the four sampled sites, the data in Figure 5.8 are divided over a number of weight classes. Most of the observations in the treatments ZH-G+ and FA-HH- contribute to the lower weight classes. The variation is small, with many data points belonging to one weight class. The data of treatment FA-G+ appear on average in higher weight classes, with a greater range of values. At ZO-ref the values are distributed over the highest weight classes. Analyses of variance per site do not show any significant change in root weights when moving in horizontal or vertical direction on the dyke slope. Neither can a significant clustering of high or low values be observed (auto-correlation, Morans's I).
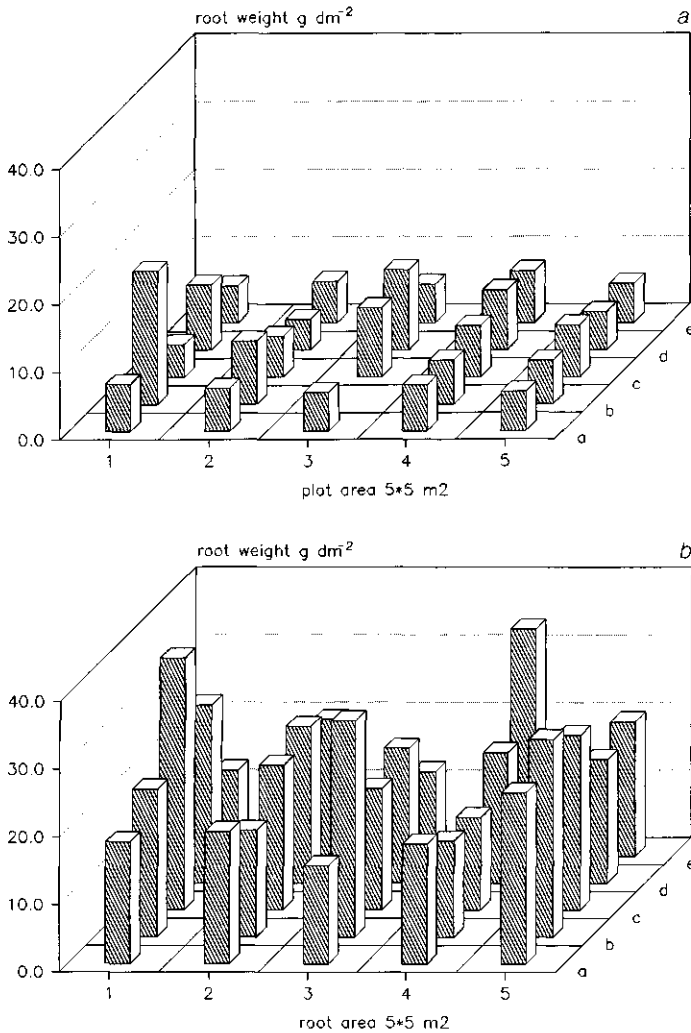
Figure 5.7 *Spatial distribution of root weight (g dm^{-2}) of 50 cm deep soil cores in a 5x5 m^2 grid in a) fertilized pasture (ZH-G+) assigned to the Poo-Lolietum, and b) unfertilized hay meadow (ZO-ref), belonging to the Arrhenatheretum elatioris brizetosum*

The average a-value (describing the decrease in root weight with soil depth; high a-values indicate a rapid decrease with depth) in the species-rich hayfield (ZO-ref) differs significantly from the a-values of the other sites (Table 5.5). The a-value is lowest in this treatment resulting in a less steep decline in root density, corresponding with a higher root mass at depths of 5 to 25 cm in comparison with the fertilized pasture FA-G+. Here the a-value is highest, leading to a steep decline in root biomass with increasing depth. Figure 5.9 graphically displays the relation between depth and root density (root mass per volume of soil) for the different treatments.

number of releves
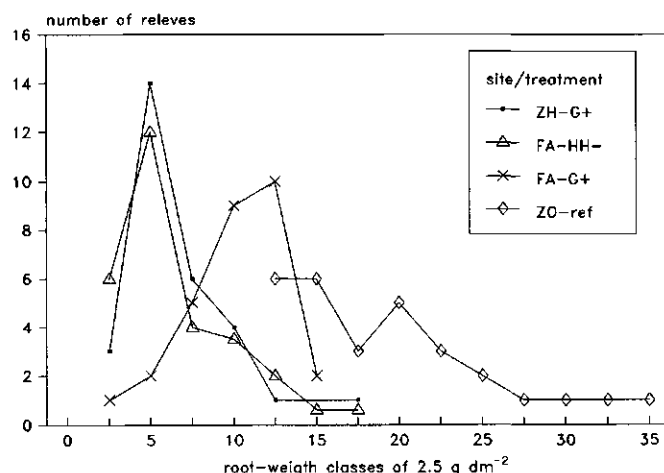
Figure 5.8 *Distribution of relevés over root-weight classes of 2.5 g dm^{-2} of the different investigated sites.*

root—weight g dm^{-3}

$$y = b.e^{-ax}$$
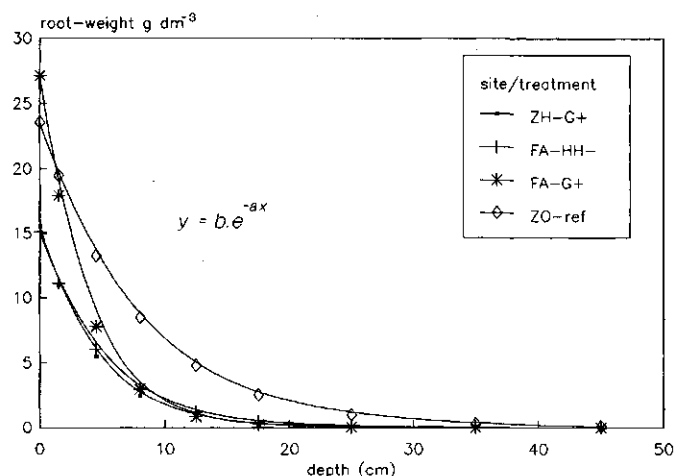
Figure 5.9 *Relationship of root density (g dm^{-3}) with soil depth at the different sites.*

The *b*-values (root density of the top soil layer) in the species-rich hayfield (ZO-ref) and the moderately fertilized pasture FA-G+ are significantly higher than the *b*-values in the fertilized pasture ZH-G+ and the unfertilized haymaking variant on the Frysian dyke (FA-HH-; Table 5.5). This means that more roots occur in the top soil layer, and the low variation coefficients indicate a small spatial variation. The root density in this layer at the treatments FA-HH- and ZH-G+ shows a large spatial variation. The spatial variation in the decline of root density with soil depth is relatively small at all sites. Analysis of the parameters *a* and *b* within the sites does not reveal any significant variation or auto-correlation between sample points.

5.4 Discussion

Seasonal variation

The lower aboveground productivity at the Hondsbossche Zeewering and the Frysian dyke (10 ton and 8.5 ton ha^{-1} respectivily) in comparison with the seasonal production at the Zeeland site (12.5 ton ha^{-1}) corresponds with the lower amount of fertilizer used at these locations (100 kg N ha^{-1} y^{-1} vs. 150 kg N ha^{-1} y^{-1} in Zeeland). The yearly production of the unfertilized dykes was about 5 to 7 ton ha^{-1} y^{-1}, which agrees with the yield of a 30 year unfertilized grassland on a clay-on-peat soil (Berendse *et al.* 1992).

The period of maximum aboveground production also appears to depend on the amount of fertilizer. In heavily fertilized grassland the growth rate is relatively high during April-May with the highest dry weight yield in June (Sibma & Ennik, 1988). In Zeeland the peak production occurred in May, while at the sites with a lower fertilizer gift peak biomass was reached at the time of mowing (late June / early July). In an experiment on level grassland Olff *et al.* (1994) measured the maximum biomass in May two years after cessation of fertilizer application, while four years later the peak biomass was reached in June. However, it is believed that the differences in soil temperature between the southern and northern provinces in The Netherlands in early spring, could also influence the time at which peak biomass is reached.

In Friesland and at the Hondsbossche Zeewering the regrowth on the outer dyke slope was observed to be larger than on the inner slope. This could have been caused by the second fertilizer gift in August, which was more effective at the north-west facing outer slope, because of smaller drought stress. This agrees with the higher regrowth found on slopes that received less sunlight (Chapter 4). In Zeeland, with a north-south position of the dyke, this difference is less obvious. Disregarding the second fertilizer application, it may also be that the higher production at the outer slope was the result of the superior soil moisture conditions and extra mineral input due to the spraying of

The belowground biomass in fertilized dyke grassland amounts to about 6 ton ha^{-1} (both dead and living material). At a root turnover rate of 1-2 times per year this indicates a yearly root production of 6 to 12 ton ha^{-1}, which is considerably more than the 4.5 ton ha^{-1} reported for level production grassland (Sibma & Ennik 1988, cf. Matthew *et al.* 1991). The dykes with unfertilized hayfield were distinguishable by a high root biomass of about 8 ton ha^{-1}. The lower belowground and higher aboveground plant biomass in the fertilized pasture compared to the unfertilized hayfield (Figure 5.2) agrees with described mechanism for the greater allocation to belowground parts in plants at low nutrient supply (Brouwer 1962, Boot 1990). In the pasture relatively little is invested in the belowground biomass, whereas in the unfertilized situation a balance between a low aboveground biomass and a sustained large root mass appears to have been reached. The difference in root mass between the two grassland types can also be partly attributed to the effect of grazing. Matthew *et al.* (1991) found a slightly greater root mass on lax grazed swards compared to hard grazed swards. In both grassland types no significant fluctuation in root mass during the year was measured. Variation in the shoot/root ratio therefore equals the variation in aboveground biomass.

Furthermore, the seasonal fluctuation in root length appeared to be less important than the difference between the two grassland types, almost all periods exhibiting greater root

lengths at a soil depth of 3 to 20 cm in the unfertilized type. The main variation in root length in the fertilized pasture during the season took place in the top layer of 0-3cm, where the increase of the predominantly fine roots paralleled the aboveground growth. Both seasonal variation as root length showed a strong similarity with the variation and root length measured in a grazed *Poo-Lolietum* in New-Zeeland (Matthew *et al.* 1991). In both cases the root length at a depth of 0-25 cm was about 800 to 850 m dm^{-2}. Moreover, a decrease in average root diameter during the growing season was also found by Matthew *et al.* (1991).

In the unfertilized hay meadow significant changes in root length during the season were most pronounced below the top layer, at a depth of 3 to 20 cm, with increasing values in April and September, preceding an enhanced growth of the rather low aboveground biomass. Olff *et al.* (1994) described an enhanced growth of fine roots in the period April-May. This increase in the growth of fine roots appeared to be positively correlated with the number of years after stopping fertilization. Since root weight did not show significant seasonal changes in both nutrient-rich pastures and nutrient-poor meadows, the turnover of fine roots in both systems determine the seasonal fluctuations in root densities. The higher root densities at most of the sampling dates as well as greater fluctuations in root quantities just under the top layer of the soil in the less nutrient-rich ecosystems may be related to an optimal exploitation of a lower and probably more heterogeneously distributed nutrient supply (cf. Rorison, 1987, Stark 1994, Ozinga 1997).

Spatial variation

The greater floristic heterogeneity of the hayfield (*Arrhenatheretum elatioris brizetosum*) and the Frisian pasture (*Lolio-Cynosuretum*) at the 100m transect compared to the 25 m^2 grid, suggests a more mosaic pattern of vegetation at these sites. Miller *et al.* (1995) also described mosaics as the more common pattern of spatial heterogeneity in grassland. The fertilized pasture in Zeeland (*Poo-Lolietum*) was observed to be characterized by a strongly homogeneous composition (similarities of 80 % between relevés), a relatively large variation in average open spot size (43%), and – in a 5x5m grid – a large variation in root growth (40 %). The spatial variation in root biomass agrees with the 40 % coefficient of variation for root weight auger samples in grasslands, mentioned by Noordwijk *et al.* (1985). The species-rich hay meadow displayed a more heterogeneous species composition (70 % similarity), a strong variation in average open spot size (91%), but a less variable root density (30%), whereas in the lightly fertilized pasture (*Lolio-Cynosuretum*) the variation in species composition (80 % similarity), open spot size (32%) and root growth (24%) was fairly small. This means that the aboveground homogeneity in species composition and shoot density is not necessarily correlated with a small spatial variation in root density and vice versa.

Patterns in the (horizontal) spatial distribution of roots were not detected in this survey. Such patterns could be the result of clusters of soil properties (Robertson & Gross 1994). Thórhallsdóttir (1990a) argued that variation in spatial arrangements of plants in grassland at the scale of 1m must be attributed to species interactions, since no correlation with environmental variables was found.

Compared to the vertical distribution of roots in a moist hayfield (Dumortier 1991), the root mass in the grazed dyke grassland in our study showed a more rapid decline, and in the unfertilized (dry) hayfield a less rapid decline of root mass with depth. This

difference between pastures and meadows corresponds with the results showing the decline of root *length* with depth (Chapter 4). Also root length declined more rapid with depth in pastures than in meadows. Irrespective of a steep or a gradual decline of root weight with soil depth, the spatial variation in distribution of roots over the soil profile was small for both grassland types. The unexpectedly low root weights in the two years unfertilized haymaking treatment in Friesland (FA-HH-) are possibly a temporal decrease caused by weather conditions or a still unstable vegetation. Already in February of the next year (1994) higher root weights were measured in the 'HH-' treatment compared to the 'G+' variant.

Summary and conclusions

In heavily fertilized grassland the maximum aboveground biomass is reached in May, while in non-fertilized grassland peak biomass is delayed until June. After mowing in July, all types showed a peak in regrown biomass in September. There was no significant fluctuation in root mass during the season. Fertilization resulted in an increased aboveground production, but reduced the investment in belowground biomass. Unfertilized grassland is therefore characterized by a lower aboveground production, but a larger investment in root biomass.

In the fertilized pasture, the largest fluctuations in root length during the year took place in the upper 3 cm of the soil, with peaks in July and September. In the unfertilized hayfield, variation in root length was below this top layer (from 3 to 40 cm), with an increase in April and September. In both types of grassland the growth and decay of fine roots were responsible for the variation in root length. In the top 3 cm of the soil profile there was no difference in root length between the grassland types, but in the deeper soil layers the unfertilized hayfield contained more roots per unit soil volume. This difference did not alter during the season.

In vegetation types with a homogeneous vegetation composition like the *Poo-Lolietum* the spatial distribution of roots can vary considerably. In species-rich grassland where the species composition is patchy and the shoot density is uneven, the relatively high root biomass displayed less variation. In the *Lolio-Cynosuretum*, both above- and belowground biomass was distributed homogeneously.

No patterns in the horizontal distribution of roots were detected, and there was little variation in the vertical distribution of roots within one vegetation type over the soil profile. However, in the unfertilized hayfield the root mass and root length declined less steeply with depth than in the other communities.

6
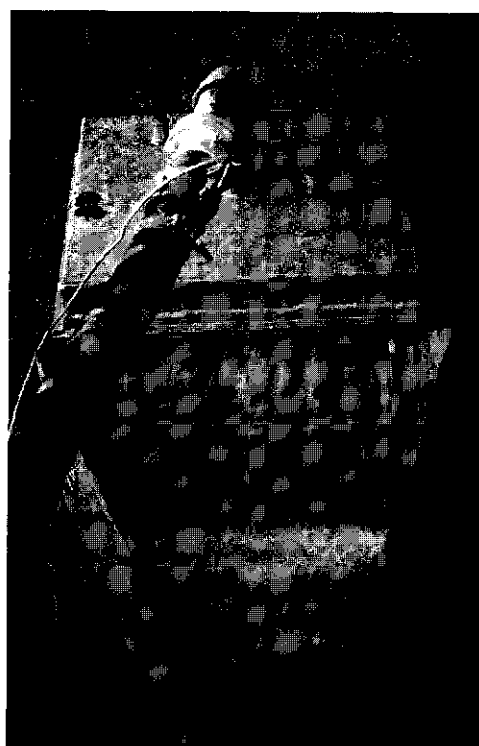
Erosion

The effects of vegetation management on the erodibility of dyke grassland

With K.V. Sýkora and J.C.M. Withagen

6.1 Introduction

Herbaceous vegetation has proved to be an important tool for slope stabilization and erosion control (Schiechtl, 1985, Lichtenegger 1985, Hewlett et al. 1987, Thorne 1990, Coppin & Richards 1990, Hrabe & Halva, 1993, Coppin & Stiles, 1995). On sea and river dykes in The Netherlands, grass vegetation is very commonly used to cover and protect the clay layer against erosion by runoff or wave-attack. Large-scale experiments testing the strength of grass sods taken from both sea and river dykes with experimentally provoked waves, revealed that these sods were able to withstand large waves. Hardly any disintegration took place, except for very sandy and poorly vegetated swards, in contrast to a cover of concrete blocks exposed to the same waves (Smith 1993, Kruse 1994a, 1994b, Anonymous 1998).

This relatively high erosion resistance of the clay with grass cover of dykes can be attributed to: (1) the soil properties (Van Essen 1994, Anonymous 1996a); (2) the tensile strength and the architecture of the root system, (Schiechtl 1985, Barker 1986, Styczen & Morgan 1995, Wu 1995); (3) the mutual interaction between roots and soil and microbiological processes, influencing soil structure (porosity and aggregation) and stability (Glinski & Lipiec 1993, Bencough & Mullins 1991, Passioura 1991, Kandelar & Murer, 1993, Dorioz et al. 1993, Hartge 1994, Wu 1995); and (4) to the plant cover reducing the energy of the water flow (Hewlett et al. 1987, Coppin & Richards 1990).

Previous studies, including small-scale erosion experiments, described a clear relationship between plant species composition, management, and erosion resistance of the grass sward (Lichtenegger 1985, Sýkora & Liebrand, 1988, Coppin & Richards 1990, Van der Zee 1992). Species-poor, heavily fertilized pastures or mulched grasslands were much more sensitive to erosion than extensively used or unfertilized pastures or hay meadows , mainly because of their shallow rooting system or open sod. As is discussed in Chapter 4 and 5, the relationship between above- and belowground plant biomass is strongly influenced by management type and by the input of fertilizers. Cessation of fertilization together with haymaking resulted after four years in an increased root growth at a depth of 5 to 15 cm, but root densities were still much lower than the root densities of hay meadows that had not been fertilized for several decades. Stopping fertilizer use in combination with

grazing, did not result in a significant increase in root growth in our experiments (Chapter 4). Both fertilization and frequent removal of aboveground biomass result in reduced root growth relative to the growth of the aboveground parts (Brouwer 1962). More frequent cutting or grazing will encourage a denser sward, but at the expense of root development (cf. Coppin & Stiles 1995). Indeed, some sea dyke pastures showed a considerably higher vegetation cover but lower root densities than the long-term unfertilized hay meadows. The equal distribution of shoots over the surface in the species rich hay-meadows (see Chapter 3), however, could compensate for the somewhat lower vegetation cover in these grasslands and therefore reduce runoff susceptibility.

To investigate the effects of management and cessation of fertilization on erodibility of the grass sward, small-scale erosion tests were carried out on a number of sites with different management treatments as described in Chapter 2, including the long term unfertilized hay meadows. As in the study of river dyke vegetation (Van der Zee, 1992), two types of tests were carried out: (1) one field experiment using a spraying device to test susceptibility for superficial run-off (*wear erosion*) at the site (cf. Hornung 1990); and (2) one laboratory experiment using a specially developed centrifuge device for turning water around auger samples at different speeds (Anonymous 1994), to test the resistance against *internal erosion*. The second type of erosion mentioned is described as the mechanism whereby a water flow, running through soil pores in the sod, leads to removal of soil particles (Kruse 1993, Van Essen 1994). This water flow is induced by high water pressure generated on the slope of the dyke as a consequence of wave attacks (Van Essen 1994). The first experiment tests erodibility related to sward characteristics as vegetation cover and shoot density. The second experiment tests the possible relation between erosion resistance and root densities. This relation is based on the influence of roots on pore structure and aggregate stability (Glinski & Lipiec 1993, Dorioz et al. 1993, Kandeler & Murer 1993, Kruse 1993) and the hindering of particle entrainments by a dense network of rootlets (Van Essen 1994).

Since both types of erosion not only depend on vegetation characteristics but are also strongly related to soil characteristics such as granular composition, soil compaction and soil reinforcement (Van der Zee, 1992, Styczen & Morgan 1995 , Anonymous 1996a), some soil physical parameters as granular composition, Atterberg limits, and shear strength were also measured. According to the sand fraction and the Atterberg limits, soils can be classified into three categories of erosion susceptibility (Anonymous 1996a). The shear strength can be regarded as an easy-to-measure parameter for resistance of the soil to erosion caused by waves and running water (Scholand et al. 1991). This parameter is determined by both soil and vegetation characteristics, since roots contribute to the mechanical strength of the soil (Thorne 1990, Morgan & Rickson 1995). Zhang and Horn (1996) found an increase of shear strength after the stocking rate in salt marshes was increased to the maximum of 1.0 sheep unit /ha, probably due to changes in root density and soil structure caused by grazing. Scholand et al. (1991) did not find a clear relation between shear strength and underground biomass in both grazed and ungrazed salt marsh. Shear strength, however, increased with depth of the soil. These results strongly suggest that soil properties had a dominant effect on shear strength. The reliability of this parameter is tested and discussed in this study.

In this chapter we try to answer the following questions: (1) To what extent is erodibility of dyke grassland determined by vegetation cover, soil plasticity and root

density and how do these parameters interact? (2) Does erosion resistance increase after cessation of fertilizer application, and how is it affected by different management types? (3) How is shear strength related to the soil and root characteristics of the grass swards, and is it a useful parameter for estimating the erosion resistance of dyke grassland? (4) Do erosion experiments as applied in this study provide sufficient information for the estimation of the erosion resistance?

6.2 Methods

Research area and study sites

In Chapter 2 a detailed description is given of study sites and treatments on both pastures and hay meadows on dykes along the Dutch sea coast. Shear strength measurements were carried out at all sites and treatments three years after cessation of fertilization, including the long-term unfertilized meadows (reference dykes). Granular composition was determined in soil samples taken in 1991 in plots of the reference dykes and in the fertilized treatment at all sites, assuming that this parameter does not differ between treatments, carried out on one site. Erosion 'spray'-experiments and auger sampling for the erosion centrifuge laboratory tests and determination of Atterbergs limits were carried out in close proximity to each other in a selected number of sites and treatments, as listed in table 6.1.

Soil shear strength and granular composition

The shear strength was measured using a vane tester from the company Geonor, which consists of a torsion spring around a steel pin with a four bladed (16 x 23 mm) vane at the end. To measure the torsion force (N cm^{-2}), the instrument is required to be pushed downwards into the soil at the desired depth and firmly turned clockwise but not too fast until the movement of the vane is felt, when the reading can be made. These and the measurements of shoot and root density (see Chapter 3 and 4) were carried out in the first two weeks of March 1994, when the soil was water saturated (at field capacity) so that strength measurements were not hampered by different moisture conditions of the soils. In each plot 20 replicated measurements were made at depths of 3, 9 and 20 cm. At depths of 9 and 20 cm dummy measurements using a steel pin without vane were also made to correct for the torsion provoked by the steel pin.

The content of particle fractions less than 2 μm (clay), greater than 2 μm but less than 63 μm (silt) and greater than 63 μm (sand), was determined in soil samples at a depth of 2 to 12 cm according to standard methods using sedimentation and wet sieving (Houba et al. 1995).

Erosion spray test

The spray experiment was carried out to test superficial erosion (run-off) using a 50 to 50 cm spray head with 625 holes of 2 mm in diameter. The spray head was placed on a metal frame that was hammered into the soil. A sediment trap, attached to the frame for gathering water and eroded material, was connected by a hose to three large vessels, interconnected by overflow pipes, allowing the eroded material to sink (see Figure 6.1 for a schematic overview of the experimental set-up). A hose connected the last vessel to the

crown
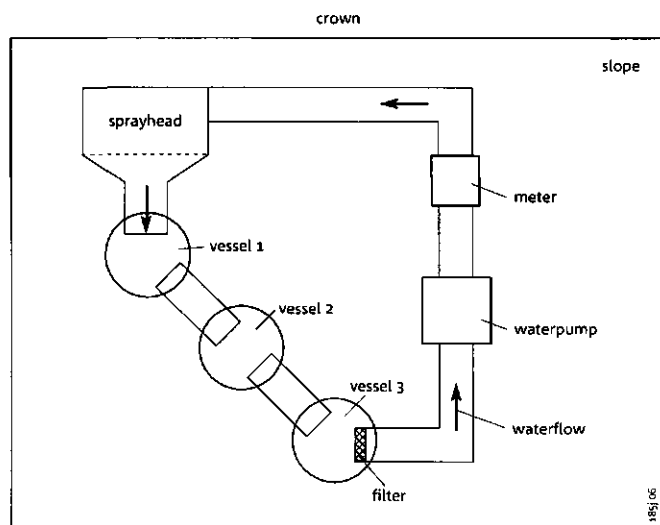
Figure 6.1 Schematic overview of the set-up of the erosion 'spray'-experiment.

spray head via a pump thus creating a closed system in which a continuous water flow could be maintained at a certain speed once it was filled (cf. Anonymous 1987). The volume of the vessels 1 to 3 (see Figure 6.1) was 500, 250 and 250 l respectively, the rest of the system measured about 350 l. The speed of the water pump was used to regulate the water flow through the spray head can be regulated.

The experiments were carried out at two pump speeds of 2 l s^{-1} and 4 l s^{-1}. This corresponds with flow rates of 1.05 m s^{-1} and 2.10 m s^{-1} respectively, based on a total area of openings of 1963.5 mm^{-2}. Each experiment lasted 30 minutes. Before and after spraying the soil relief was measured at 100 points within the 50x50 cm^2 test plot using an erosion measuring frame (cf. Hornung 1990) placed on top of the spray head frame. After the experiment both the sediment in the vessels and samples of the vessel water were collected to determine the total amount of washed out material (after drying). Samples of the system water while running the experiment were also taken and the amount of added water was registered to correct for the suspended material in water that was lost during the experiment. The two different erosion parameters that were measured, were the change in soil-relief and the loss of soil material by superficial run-off.

Erosion centrifuge test and Atterberg limits

After the collection of auger samples in the field (see Table 6.1) using stainless steel tins (diameter 6.6 cm) driven into the soil by a hammer, the soil cores were removed from the tins and divided into two parts of exactly 5 cm each after discarding the upper 0.5 cm. The resulting two core samples per plot from depths of 0.5 to 5.5 and 5.5 to 10.5 cm were tested separately in the erosion centrifuge. Each sample clasped between two pinned blocks was put into a metal cylinder filled with water, on a device specially developed for measuring weight and torsion of the sample during the experiment. The sample was then left to saturate for 15 minutes. In the cylinder are blades connected to an electrically driven servomotor, which can be rotated to act like a centrifuge moving the water at speed and

Table 6.1 *Sites and treatments where erosion spray experiments were carried out (rastered) and auger samples were taken for the erosion centrifuge tests and measurements of Atterbergs limits (marked with 'x') on pastures (a) and mown dyke grassland (b). G+ = fertilized, periodical or continuous sheep grazing; HH- = not fertilized, 2 cuts a year for haymaking ; HG- = not fertilized, 1 cut for haymaking + 1 period of sheep grazing; GG- = not fertilized, 2 periods of sheep grazing;; H+ = fertilized + 1-2 cuts a year for haymaking , or 7-8 cuts (ND) without removal of cuttings; H-= unfertilized + 1-2 hay-cuts a year; ref = reference dyke: long-term unfertilized hay-meadow, 1 cut a year. Total number of plots are given in the last row with total number of plots where erosion centrifuge samples were taken within parentheses.*

a) Pastures

Location	Dyke mark	Exposure	Management treatments G+	HH-	HG-	GG-
G1 (Groningen-Eemshaven)	103 - 104	North-West	x			
G2 (Groningen-Eemshaven)	harbour	South	x			x
FA (Friesland-Boonweg)	35-36	North-West	x	x		
NH (Hondsbossche zeewering)	Camperduin A+B	West	x	x		
ZG (Zimmermanpolder-Rilland)	20 - 24	South-West				
ZK (Hoedek.kerke-ZakvZuidBev)	24 - 29	East				x
ZH (Nijspolder-Ossenisse)	14 - 16	West			x	
ZB (Nr. Eén)	3 - 5	North-West	x		x	x
Total number of plots			8 (6)	7 (6)	5 (5)	5 (4)

b) Hay meadows

Location	Dyke mark	Exposure	Treatments H+	H-
ND (Den Helder)	139 -147	North-West	x	x
ZK (Biez.Ham-Moert.dijk)	13 - 15	East	x	x
ZPE (Perkpolder-Honten.)	73 - 76	North	x	x
ZZD (Zwarte Polder)	7 - 8	North-West	x	x
Total number of plots			4 (4)	4 (4)

c) Reference dykes

Location	Dyke mark	Exposure	ref
ZK^{ref} (Biez.Ham-Moert.dijk)	12 - 13	East	
ZO^{ref} (Oudelandse zeedijk)	-	secondary dyke	x
ZZK^{ref} (Zandkreekdam)	-	secondary dyke	x
Total number of plots			3 (2)

causing torsion. The effect of this torsion on the sample could then be read off, together with ten-minute registering of the soil loss caused by soil washing. Each experiment was carried out with a stepwise increase of the number of revolutions per minute up to 1200, which took three hours, and was continued at this speed for three hours. This implies that the total duration of the experiment was 6 hours, unless samples disintegrated earlier or a weight loss of 50 % was reached, assuming a maximum root (weight) content of the samples of 50 %. The experiments were carried out at Delft Geotechnics (Anonymous 1994).

The Atterberg limits of parallel samples were also determined by Delft Geotechnics, measuring the liquid limit according to the method of Casagrande, and the plastic limit by means of a rolling-clay-bar (Anonymous 1994).

Analysis and statistics

The average shear strength of the treatments and the distinguished communities (see Chapter 3) was calculated based on the plot averages at three depth of 3, 9 and 20 cm. Data were analysed using a REML (Residual Maximum Likelihood) analysis on contrasts between: formerly grazed and mown dykes; fertilized and non-fertilized dykes; grazed and mown dykes; grazed or mown and mown dykes followed by aftergrazing; and, finally, reference and non-reference hay meadows. Differences between treatments were tested with a one-factorial REML analysis, including a pairwise t-test of differences of means, based on the s.e.d matrix of REML (REMLPAIR). The duration of exposure to direct sunlight ('sun') and the Na content of the soil ('salt'; see Chapter 3 for measurement and calculation of these parameters) were treated as covariates, to correct any differences between inner and outer slope of the dykes. Differences between communities were tested using Oneway ANOVA followed by calculation of the least significant difference. Calculation of the Pearson correlation coefficient and multiple regression was used for analysing the relation between shear strength and soil parameters, vegetation cover and root densities, at corresponding depths.

The results of the erosion spray test were analysed by calculating the average decrease in soil relief and the amount of eroded material for each treatment. The results of the centrifuge experiments provided by Delft Geotechnics (Anonymous 1994) consist of sample weights measured after every 10 minutes while the experiment was in progress and the measured torsion against revolutions per minute. These results include graphs of the percentage weight loss plotted against time. Most of the graphs follow a 'broken stick'-pattern, caused by a sudden change in erosion rate (weight loss with time) during the course of the experiment. For further analysis the relation between percentage weight loss of samples (y) and the time that samples were exposed to the water forces provoked in the centrifuge (x) was expressed by:

$$y = y_c + (x < x_c)*b_1*(x - x_c) + (x > x_c)*b_2*(x - x_c)$$

The parameters b_1 and b_2 of this 'broken stick' -model represent the erosion rates before and after the point (x_c, y_c) at which the erosion rates change. In Appendix II a full list is given of the calculated model parameters of each sample, together with the values of r^2-adjusted. Average parameter values were calculated for each treatment. No analyses were made on the community level.

For both erosion experiments significance of treatment effects were tested using a REML analysis on contrasts and a REML analysis with 'treatment' as factor, and 'sun' and 'salt' as covariates, followed by a pairwise comparison of treatments (REMLPAIR). The correlation between superficial erosion and centrifuge parameters on the one hand, and soil granular composition, vegetation cover and root density on the other, was analysed using calculation of Pearson correlation coefficients and multiple regression.. For ANOVA, the statistical package SPSS-PC[+] (Norusis, 1986) is used. All other analyses were carried out using the GENSTAT statistical package (Payne & Lane 1993).

Soil samples can be classified into three categories of erosion resistance (good, moderate, bad) based upon plasticity index (based on liquid limit and plastic limit), liquid limit and sand content (Korzilius et al. 1991, Anonymous 1996a). These criteria were used

to classify the dyke samples and to make comparisons with corresponding values of root densities and erosion rate.

6.3 Results

Shear strength

At depths of 3, 9 and 20 cm a significant difference was found in shear strength between mown and grazed or previously grazed dykes (REML-analysis on contrasts, $p < 0.05$). The reason for this difference could be attributable to the low sand content of the heavy soils in Zeeland, where the hay meadows are predominantly located. Figure 6.2a shows the mean shear strength for each management type at three depths. The difference in shear strength between the pastures and the long-term unfertilized reference hay meadow characterized by a dense root system is not significant at depths of 9 and 20 cm. The values of shear strength measured in the fertilized (H-) and unfertilized (H+) treatments on hay meadow dykes, as well as the reference dykes are not significantly different. Measurements of shear strength at depths of 3 cm and 9 cm in fertilized and unfertilized treatment plots on (former) pastures, however, show a significant difference after four years of treatment (REML-analysis on contrasts, $p < 0.05$). The unfertilized treatment types on grazed dykes (HG-, HH-, GG-) have lower shear strength values at these depths than the fertilized treatment G+ (REML-PAIR, $p < 0.05$, see Figure 6.2a).On comparing the communities (Figure 6.2b), significant differences in shear strength at 9 and 20 cm were found between the *Poo-Lolietum* (PL) and the *Arrhenatherum elatioris* communities (AO, AC, AB) on the one hand, and the *Lolio-Cynosuretum* communities (LG, LF, LR) on the other. Given the large difference in root density between the *Poo-Lolietum* and *the Arrhenatherum elatoris brizetosum*, both showing similar values, it is unlikely that root density is the main factor determining shear strength. The difference seems to be explained by differences in soil grain size: the *Poo-Lolietum* and the *Arrhenatherum elatoris* communities occur mainly on the heavy soils of Zeeland, while the *Lolio-Cynosuretum* communities are found mainly on the slightly loamy dykes in the northern part of the Netherlands.

Since the root density declined with depth, and the shear strength appeared to increase, a negative correlation between roots and shear strength values could be expected. Table 6.2 shows that no relation was found between root length density and shear strength. At depths of 3, 9 and 20 cm, a significant negative correlation was observed between the shear strength and the percentage sand. A high sand content would appear to be linked with low values for shear strength. At all depths, the percentage of loam correlated positively with shear strength, while the percentage of clay showed a significant correlation at 3 and 9 cm. In addition, low values for vegetation cover, large open spot size and low shoot density indicate high values for shear strength. A negative correlation with shear strength was also apparent for specific root length (see Table 6.2). This would mean a low shear strength in a sod characterized by a high cover and many thin roots, and a high shear strength in an open sod with large open spots and few roots. However, at depths of 3 and 9 cm a positive correlation with root weight was found (Table 6.2), possibly caused by the thicker roots being responsible for the higher resistance in the soil. No correlation was found between shear strength and number of mole hills.
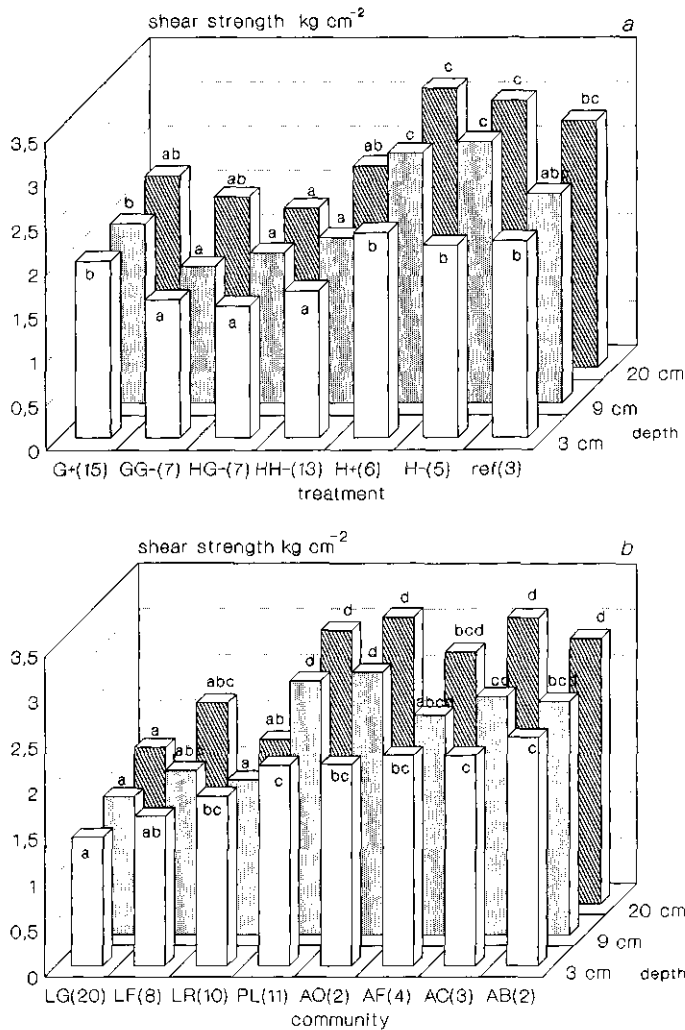
Figure 6.2 *Average values of shear strength per treatment (a) and community (b) at depths of 3 cm, 9 cm and 20 cm. Different superscripts denote significant differences (p < 0.05).*

a) Treatments on pastures: G+ = continuously or periodically grazed + fertilizer; GG- = unfertilized, two periods of grazing; HG- = unfertilized, haymaking (1 cut) followed by grazing; HH- = unfertilized, two cuts for haymaking . Treatments on meadows: H+ = fertilized, 2-3 cuts for haymaking or unfertilized + mulching; H- = unfertilized, 2 cuts for haymaking ; ref = unfertilized for at least 25 years, one cut for haymaking . The number of plots is given within brackets.

b) LG = Lolio-Cynosuretum with Geranium molle; LF= idem with Festuca rubra; LR= idem with Ranunculus bulbosus; PL = Poo-Lolietum; AO = Arrhenatheretum with Origanum vulgare; AF = idem with Festuca arundinacea; AC= idem with Cirsium arvense; AB = Arrhenatheretum brizetosum.

A stepwise multiple regression of shear strength at a depth of 3 cm with soil granular fractions, root length and root weight resulted in a model with one term, the percentage of loam, explaining 36 % of the variance (see Table 6.3). At a depth of 9 cm, 50.4 per cent of

Table 6.2 *Pearson-correlation coefficients between shear strength, and root and soil parameters. Levels of significance: *: p<0.05; **: p<0.01.[1]) at depth of 0-3, 6-10, and 15-20 cm; [2]) at depth of 3-6, 10-15, 20-30 cm.*

Parameters	shear strength at depth of		
	3 cm	9 cm	20 cm
% clay	0.38*	0.40*	0.40
% loam	0.57**	0.61**	0.61**
% sand	- 0.56**	- 0.60**	- 0.60**
rootlength[1] (m dm^{-3})	-0.22	0.25	0.04
rootlength[2] (m dm^{-3})	0.10	0.36	0.11
root weight[1] (g dm^{-3})	0.10	0.48*	0.17
root weight[2] (g dm^{-3})	0.38*	0.54**	0.34
specific root length	- 0.54**	- 0.38*	- 0.37
vegetation cover	- 0.52**	- 0.51**	- 0.53**
open spot size	0.59**	0.64*	0.65**
shoot density-coeff.	0.47**	0.54**	0.57**
Mole hills	0.17	0.20	0.15

the variance in shear strength was explained by the percentage of loam ánd root weight in the 6 to 10 cm deep soil layer (Table 6.3). When root weight was added to the one-term-model with percentage of silt, the value of r^2-adjusted increased by about 10 %. Root length was not included in the model, since no increase in r^2-adjusted was found. Forty per cent of the variance in the shear strength measured at a depth of 20 cm was explained away by percentage loam. From these results it can be concluded that shear strength is determined largely by loam content of the soil, and at a depth of 9 cm also by root weight density.

Table 6.3 *Multiple regression models of shear strength at different depths with sand, loam and silt fractions, and root weight (g dm^{-3}) and root length (m dm^{-3}) at corresponding depths, after stepwise selection of parameters. R^2-adjusted and coefficients and t-values of terms that contribute significantly to the model are given.*

Model parameters	Shear strength at 3cm		Shear strength at 9 cm		Shear strength at 20 cm	
	Coefficie	t(41)	Coefficient	t(41)	Coefficient	t(40)
Constant	1.049	5.70	0.177	0.58	1.045	3.79
% loam	0.029	5.02	0.039	5.14	0.044	5.10
Root weight (m dm^{-3})	-	-	0.426	2.90	-	-
R^2-adjusted	0.360		0.504		0.373	

Erosion spray experiments

In Figure 6.3 the mean *soil decline* (mm) of the different management treatments are shown for the flow rates of 4 and 2 l s^{-1}. The average erosion per management type ranged from 1.9–4.8 mm in 30 minutes for the 4 l s^{-1} experiment and 1.7–2.6 mm per 30 minutes at 2 l s^{-1}. The differences between treatments are not significant at 2 l s^{-1}. In the 4 l s^{-1} experiment, however, the erosion in the unfertilized treatment GG- appeared to be higher
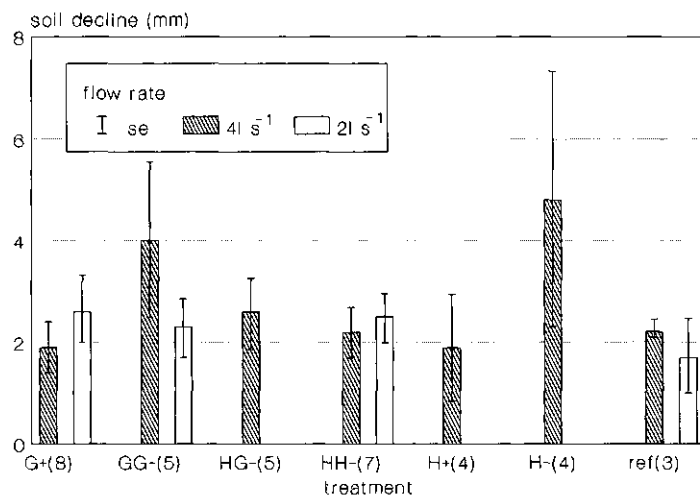
Figure 6.3 *Average soil decline per treatment in the erosion spray experiment at flow rates of 2 l s⁻¹ and 4 l s⁻¹. Soil decline per plot (0.25 m²) is the average of the decline at 100 measuring points.*

than in fertilized treatment G+ and the unfertilized haymaking treatment HH-(REMLPAIR, $p < 0.05$, 'sun' and 'salt' are covariates).

The amount of *washed out material* clearly differs between experiments with flow rates of 2 and 4 l s⁻¹ (Figure 6.4). The differences between management types do not appear to be significant in the 2 l s⁻¹ experiment, but in the 4 l s⁻¹ experiment the amount of *washed out material* was significantly higher in treatment HG- than in the other treatments on pastures and in the reference dykes (REML PAIR, $p < 0.05$, 'sun' and 'salt' are covariates). At a flow rate of 2 l s⁻¹ the amount of *washed out soil matter* was 40 to 75 g (Figure 6.4a). The quantity of *washed out material* in the test plots on grazed dykes is averaged 170 to 420 g and on mown dykes 170 to 630 g at a flow rate of 4 l s⁻¹ (Figure 6.4b). On the reference dykes the least amount of soil was lost in the test. Doubling the flow rate produced the largest impact on soil loss in the intensive treatment G+ (+426%), while the impact on the unfertilized grazed treatment GG- (+275 %) and haymaking treatment HH-(+100 %) was considerably smaller. The reference dykes were only slightly affected (+48%). Figure 6.4 show the three fractions of the washed out material (sediment; floating matter present at the end of the experiment; and the floating matter lost during the experiment). In the HG- treatment (Figure 6.4b) a relatively large fraction of the eroded material did not precipitate. This large amount of floating material in the overflow containers at the end of the experiment implies a high clay or loam content.

In the 2 l s⁻¹ experiment a negative correlation was found between erosion (decline of the soil surface) and loam content ($r = 0.64$, $p<0.05$). For the experiments with a showering rate of 4 l s⁻¹ no correlation was found between decline of soil surface and soil particle size, nor could a correlation be detected in both experiments between decline of the soil surface and shoot and root density. The amount of material washed out in the 2 l s⁻¹ experiment did not correlate with any of these parameters. At a showering rate of 4 l s⁻¹, however, there was a significant negative correlation between soil loss and vegetation cover ($r = -0.49$)
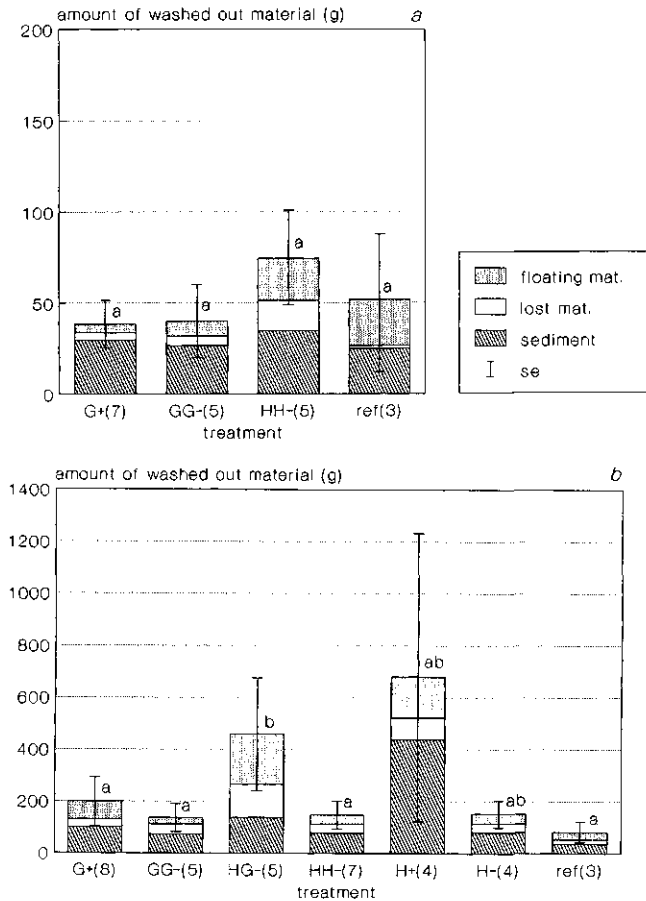
Figure 6.4 *The amount of washed out material (g per 0.25 m²) per treatment in the erosion spray experiment at flow rates of 2 l s⁻¹ (a) and 4 l s⁻¹ (b). Three fractions are given: sedimented material and floating material after the experiment and suspended material in lost water while the experiment was in progress.*

and root length in the upper layer ($r = -0.52$), and a positive correlation with the loam fraction ($r = 0.41$, see Table 6.5). This means that both soil granular composition, vegetation cover and root density of the top layer are determining factors of the erosion resistance of dyke grasslands.

Regression models with multiple factors revealed significant correlations in the 4 l s⁻¹ experiment. Here, the decline of the soil surface proved to be correlated positively with the percentage sand in the soil, when the vegetation cover was low ($r^2 = 0.56$). Half of the variation in the amount of eroded material was attributable to the clay content (negative) and the open spot size (positive). A fair bit of soil material is flushed away when clay content is small, in combination with large open spots or a low vegetation cover. The amount of superficial erosion is therefore largely determined by the parameters for vegetation cover and soil particle size. For the 2 l s⁻¹ test not enough replicated measurements were available to carry out a multiple regression analysis.

Centrifuge experiments

Relation between centrifuge time and sample weight loss

Figure 6.5 shows the percentages of accumulated weight loss plotted against the centrifuge time, according to the parameters of the broken stick model, averaged for each management treatment (Table 6.4). Although obviously different patterns of erodibility are visible between treatments (Figure 6.5), REML analyses on contrasts revealed only a weak significant difference ($p < 0.08$) in parameter x_c in both layers of 0-5 and 5-10 cm between fertilized and unfertilized pastures and a weak significant difference in y_c ($p < 0.08$) between pastures and meadows. Indeed, in a paired analysis of differences in erosion parameters between treatments, the value of x_c at a depth of 0-5 cm in the unfertilized hay-making treatment on previous pasture (HH-) appeared to be significant higher than in the fertilized pasture (treatment G+, REMLPAIR $p < 0.05$, see Table 6.4), indicating a slightly higher erosion resistance in HH- in the first half of the experiment. The value of x_c in HH-was also significantly higher than GG- (unfertilized pasture), but here the value of yc was significantly lower compared to HH-, resulting in a lower weight loss with time (see Figure 6.5a). At a depth of 0-5 cm the value of yc in HH- was also higher than yc in the unfertilized meadows (H- and ref, see Table 6.4), resulting in a higher erosion resistance in these treatments (see Figure 6.5a and 6.5c).

However, these differences are not reflected by significant differences between treatments in the parameters b_1 and b_2 in the layer 0-5 cm, whereas these parameters are assumed to be good indicators of erosion resistance in this experiment. Low values of b_1 and b_2 means low weight losses with time and thus high erosion resistance. A weak significant difference in b_1 was found between the reference dykes and the fertilized pastures (REMLPAIR $p < 0.07$, see Table 6.4). In spite of the lack of sufficient significant

Table 6.4 *Average parameter values of the 'broken stick model'*

$$y = y_c + (x < x_c)* b_1 *(x - x_c) + (x > x_c)* b_2 *(x - x_c),$$

*describing the relation between time period (x) and percentages of accumulated weigth loss (y) of samples at depths of 0-5 and 5-10 cm in different treatments in the erosion centrifuge experiment. The model consists of two linear curves with coefficients b1 and b2, connected to eachother at (x_c, y_c). See appendix II for the parameter values of each sample. Different superscripts denote significant differences between treatments (REMLPAIR, $p < 0.05$). Values marked by * are significantly different at $p < 0.07$. See Table 6.1 for meaning of treatment codes.*

parameters	treatments (number of samples)						
	G+(6)	GG-(4)	HG-(5)	HH-(6)	H+(4)	H-(4)	ref(2)
0-5 cm							
b1	0.11[a]*	0.05[a]	0.05[a]	0.06[a]	0.05[a]	0.02[a]	0.01[a]*
b2	0.09[a]	0.03[a]	0.03[a]	0.03[a]	0.102[a]	0.06[a]	0.01[a]
yc	11.4[abc]	6.7[ab]	13.2[b]	15.7[c]	8.8[abc]	1.3[a]	2.2[ab]
xc	131[a]	143[a]	177[ab]	216[b]	152[ab]	108[ab]	190[ab]
5-10 cm							
b1	0.09[a]	0.08[a]	0.08[a]	0.05[a]	0.07[a]	0.03[a]	0.01[a]
b2	13.7[ab]	6.3[ab]*	31.1[b]*	11.4[ab]	1.4[ab]	1.0[ab]	0.02[a]
yc	14.4[a]	16.4[a]	17.1[a]*	10.2[a]	13.7[a]	3.7[a]	3.2[a]*
xc	140[a]	194[ab]	232[b]*	191[ab]	202[ab]	147[ab]	138[ab]*
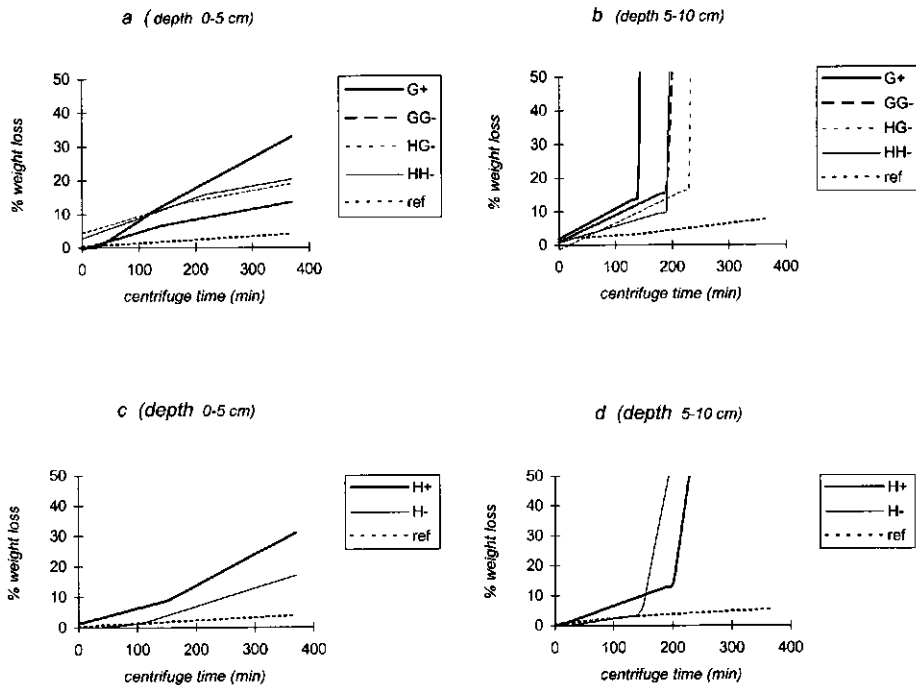
Figure 6.5 Relation between time period and percentages of accumulated weight loss in different treatments on previous pastures (a, b), including reference dykes, and on hay meadows (c, d) at depths of respectively 0-5 cm and 5-10 cm in the erosion centrifuge experiment. The curves are calculated according to the 'broken-stick' model and average parameter values per treatment as given in Table 6.4. The results of the reference dykes are included in each figure. For further legends see Table 6.1.

difference in all cases, the erodibility of the fertilized treatments on both pastures and meadows was higher than that of the unfertilized treatments in the layer 0 to 5 cm. The highest erosion resistance was found in the reference dykes. Extensive management practices have therefore not yet led to noticeable changes in erosion resistance, but there is a visible trend towards an increased erosion resistance in species-rich hay meadow.

At a depth of 5 to 10 cm a similar pattern emerges: low weight losses with time in the reference dykes and relatively higher weight losses in the fertilized treatments compared to the unfertilized treatments (see Figure 6.5b and 6.5d). Apart from the reference dykes, however, both fertilized and unfertilized samples show a sudden weight loss half-way through the experiment, when the centrifuge rate had increased to 1200 involutions per minute. This process seems to proceed more rapidly on pastures than on hay meadows, but were not reflected by significant differences between treatments in broken-stick parameters at a depth of 5 to 10 cm (Table 6.4). Only HG- is characterized by a significantly higher

Table 6.5 *Pearson correlation coefficients between parameters of the broken stick model (see Table 6.4 for explanation) and various parameters of soil (mixed samples from a depth of 2-12 cm , shear strength (at 3 and 9 cm), root density at corresponding depths (RL =root length; RW = root weight; SRL = specific root length) and vegetation cover. Correlation coëfficients between these parameters and superficial erosion parameters (soil decline and soil loss at the 4 ls⁻¹ experiment) are also indicated. Values higher than 0.37 (marked with *) indicate a significant correlation within the 5 % confidential limit. Parameters marked with ᵃ are logtransformed. The values of root density, vegetation cover and soil granular composition, used in the calculation, are derived from the results of Chapter 3 and 4.*

Parameters	Erosion spray parameters 4 l s⁻¹		Erosion centrifuge parameters at a depth of 0-5 cm (layer A)				Erosion centrifuge parameters at a depth of 5-10 cm (layer B)			
	Soil decline	Soil loss	b_1A	b_2A	x_cA	y_cA	b_1B	b_2B	x_cB	y_cB
% clay	-0.03	-0.08	- 0.32	0.15	- 0.02	- 0.35	- 0.56*	- 0.41*	0.07	- 0.55*
% loam	-0.04	0.41*	0.04	- 0.19	- 0.30	- 0.13	- 0.48*	- 0.24	- 0.03	- 0.54*
% sand)	-0.04	-0.40*	- 0.03	0.07	0.27	0.14	0.54*	0.33	0.03	0.59*
Liquid limit	0.08	0.01	0.08	- 0.01	0.00	- 0.04	- 0.51*	- 0.27	- 0.17	- 0.48*
Attenberg limit	0.26	-0.03	0.31	- 0.07	0.24	0.28	0.13	0.08	- 0.05	0.15
Plasticity index	-0.1	0.03	- 0.05	0.03	- 0.14	- 0.18	- 0.67*	- 0.33	- 0.17	- 0.65*
RL (layerA and B)	-0.18	-0.52*	- 0.45*	- 0.31	0.09	- 0.42*	- 0.44*	- 0.40*	0.10	- 0.40*
RW (layer A and B)	-0.06	-0.11	- 0.50*	- 0.21	- 0.12	- 0.56*	- 0.56*	- 0.44*	0.25	- 0.47*
SRL(layer A and B)	-0.21	-0.10	0.35	- 0.17	0.29	0.48*	0.25	- 0.04	- 0.19	0.12
shear str. 3/9 cm	-0.03	0.16	- 0.19	0.01	- 0.24	- 0.31	- 0.45*	- 0.25	- 0.03	- 0.51*
Vegetation cover	0.09	-0.49*	- 0.09	- 0.03	0.43*	0.10				

value of x_c compared to G+ (REMLPAIR, p < 0.05), indicating a higher duration of erosion resistance (Figure 6.5b). However, the value of b_2 is quite high in HG-, which means a rather rapid weight loss, once y_c is reached. In spite of a (not significant) lower erosion rate at the beginning of the experiment, i.e. a lower value for b_1 in H- than in H+ (Table 6.4), the unfertilized treatment on hay meadows (H-) demonstrated a more rapid collapse than the fertilized treatment (H+, see Figure 6.5d). In general, the erosion resistance seemed to be lower in the layer 5 to 10 cm than in the layer 0 to 5 cm.

Correlations and regression models

To identify the factors causing the observed differences in erosion resistance (often somewhat lower values of parameter *b1* and *b2* in the unfertilized treatments and the low values obtained for the reference dykes, cf. Table 6.4), correlations were calculated using the broken stick parameters and soil composition, root density, shear strength, the erosion spray parameters soil surface decline and washed material, and vegetation cover. Table 6.6 lists the correlation coefficients of the investigated parameters.

Significant correlations were found between parameters of soil composition and the centrifuge parameters b_1, b_2 and y_c of the B layer (5 to 10 cm, see Table 6.5). Low values for b_1B, indicating a relatively high erosion resistance in the first three hours of the experiment, correlate with high values of percentage clay and loam, and low values of percentage sand, as well as high values of liquid limit and plasticity index. Apparently soil composition is a more determinant factor in erosion resistance at depths of 5 to 10 cm than in the upper layer of 0 to 5 cm, so that a higher erosion resistance could be expected to occur in soils with a larger clay content in the deeper layer.

Root weights and root lengths in the two layers A and B are strongly correlated with each other. They are both negatively correlated with b_1A, y_cA, b_1B and y_cB (Table 6.5)

Table 6.6 *Multiple regression models of the erosion centrifuge parameters b_1, b_2, y_c at depths of 0-5 cm (layer A) and 5-10 cm (layer B) with percentages lutum, loam and sand and root length (m dm^{-3} - root weight (g dm^{-3}) densities and specific root length (SRL m g^{-1}) at corresponding depths, after stepwise selection of variables. R^2-adjusted, coeffients (c) and t-values (d.f.) with significancy (*= t-probability < 0.05; ** t-prob. < 0.01) are given.*

n = 34	y_cA		b_1A		b_2A		y_cB		b_1B		b_2B	
R^2-adjusted	42.5		32.8		15.5		34.5		34.0		21.6	
model parameters	coeff.	t(26)	coeff.	t(26)	coeff.	t(25)	Coeff.	t(24)	coeff.	t(25)	coeff.	t(25)
Constant	12.73	5.15*	0.1004	1.92	142.9	2.64*	-23.9	-1.58	-0.0138	-0.27	-132.6	-1.86
% loam					-2.303	-2.67*					2.23	2.10*
% sand					-1.49	-2.49*	0.396	3.42*	0.0012	2.23*	1.874	2.34*
root length	-0.0114	-4.07**	-0.0001	-3.61*			-0.06	-2.24*	-0.0001	-2.28*	-0.037	-1.59
SRL	0.054	3.55**	0.0002	2.60*			0.0624	2.56*	0.0002	2.69*		

indicating that high root densities result in a higher erosion resistance (lower values for b_1 en y_c) in both layers A and B. In contrast with layer A, the negative correlations between root length and root weight densities and parameter b_2B suggest that root density increases the erosion resistance in the second half of the centrifuge experiment. High specific root length, however, which is indicative for the presence of thin roots, is positively correlated with y_cA, and therefore seems not to favour erosion resistance.

High values of shear strength measured at a depth of 9 cm, correlated with low values of b_1 and y_c, probably because these parameters are strongly correlated with percentage loam as well as root weight (cf. Table 6.3). A low erosion resistance at the beginning of the centrifuge experiment in the upper layer, correlated well with the amount of washed out material (r = 0.45, p < 0.05. The vegetation cover, positively correlated with parameter x_cA, seems to influence the time period before the erosion rate in the centrifuge experiment changes from b_1 to b_2.

Except for the plasticity index in layer B, the variation explained by the different variables is not very large. Multiple regression models, which express the erosion centrifuge parameters as linear combinations of soil composition and root density variables, do not explain large parts of the observed variance either, although significant effects of some parameters were shown (Table 6.6).

No models were found in both layers that had significant variables for x_c. Root length (negative coefficient) and specific root length (positive coefficient) explained the variance of parameters y_c and b_1 in the upper layer of 0-5 cm (layer A) by 42.5 % and 32.8 % respectively, both with a significant effect (p < 0.01, see Table 6.6). A model with root weight alone explained 23 % of the observed variance in both parameters y_c and b_1 , and the figure for root length alone this was 18 %. A model including root length and root weight explained 27 % of the variance, but only root weight had a significant effect.. These results can be interpreted as follows: relatively higher erosion resistance is obtained by greater root lengths but at somewhat low values of specific root length. To prevent erosion roots may not be too thin. The higher (significant) correlation of erosion resistance with root weight as opposed to root length in the model for b_1 and y_c, demonstrate that thick roots appear to reduce erosion more than thin roots. Parameter b_2 in layer A would seem to be influenced by soil composition and not by root density.
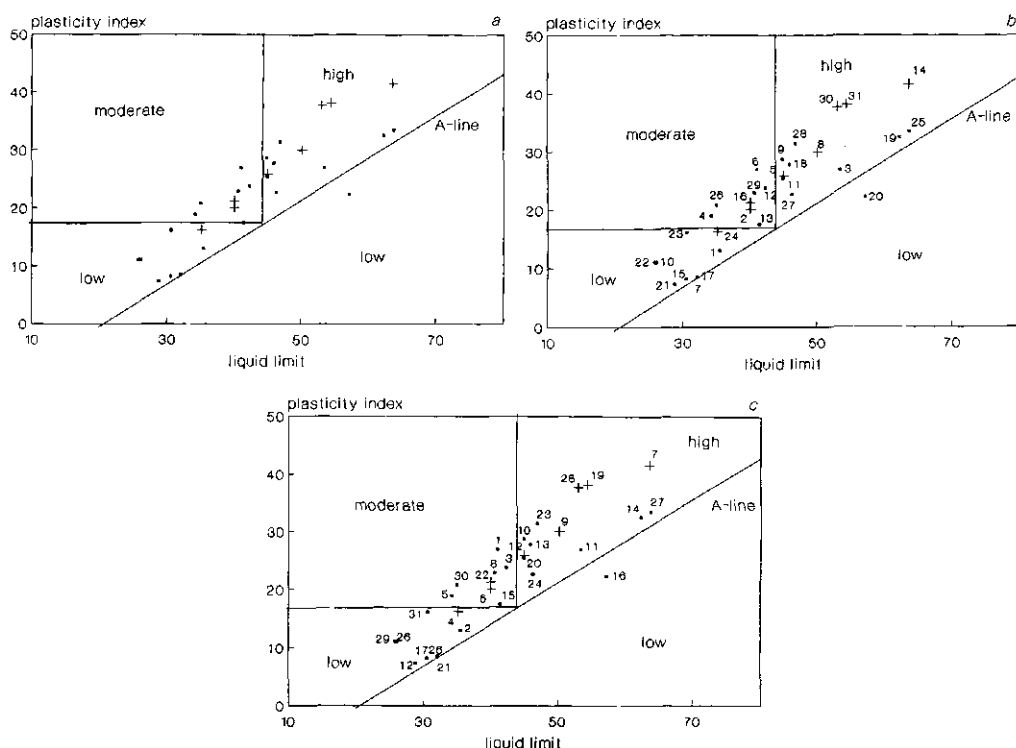
Figure 6.6 *Plasticity diagram of 31 soil samples taken next to the erosion centrifuge samples, based on Atterbergs limits (plasticity index and liquid limit) (a); (b) the same diagram but now with rank-order numbers ranked in order of increasing erosion resistance of the samples and root density (c). Symbols used in diagram: ✶ = % sand < 40; ■ = % sand > 40.*

At a depth of 5-10 cm (layer B) about 34 % of the variation in y_c as well as b_1 was attributable to the sand fraction (significant) in combination with root length and specific root length. Apparently at depths of 5-10 cm both root characteristics and soil composition (partly) determine erosion resistance Parameter b_2 is more influenced by sand and silt content than by root density (Table 6.6). It would appear that in layer B root density together with soil composition influence erosion resistance, whereas in the upper layer root density alone determines erodibility, at least in the beginning of the exposure to water flow.

Classification of samples into three erosion resistance categories, based on soil plasticity index

In Figure 6.6 the 31 soil samples taken along with the erosion centrifuge samples are displayed in a plasticity diagram, in which clay soils are divided into 3 erosion resistance classes, based on Atterbergs limits (plasticity index and liquid limit, cf. Korzilius et al. 1990, Anonymous 1996a). Sand content was not used for the qualification 'low', 'moderate' and 'high' in this diagram. Other symbols, however, were used to indicate the sand content. Because a qualification of 'moderate' and 'high' stipulates a sand content of less than 40%, only 8 samples could be assigned to these categories. These samples came from sites on sea dykes in Zeeland (codes ZB, ZPE, ZH and ZK, see Chapter 2, Table 2.1). A strict application of the criterion 'sand content less than 40%' immediately excludes 75% of the dykes examined from the category 'moderate' and 'good', even though these samples did fit the plasticity index and liquid limit criteria. Table 6.7 gives the erosion category of each sample, listed according to site and treatment. Sand content only differs between sites, whereas erosion category may also vary within the sites, as is demonstrated by differences between treatments in the erosion category of the soil in ZH, ZB, ZPE, ND, G1 and G2 (Table 6.7)

Figure 6.6b and 6.6c show the same plasticity diagram as in Figure 6.6a, but here each sample is placed in order of increasing centrifuge time required for a 15% weight loss from the 0 to 5 cm layer (Figure 6.6b), or increasing root length in this layer (Figure 6.6c). We see here that a low qualification in the plasticity diagram sometimes coincides with high values for centrifuge time(Figure 6.6b; samples 20, 21, 22, 23, 24) and root length (Figure 6.6c; sample numbers 21, 25, 26, 29, 31). Also, samples with a 'high' clay quality according to Figure 6.6a show correspondingly low erosion resistance (short period for 15 % weight loss, samples 5, 3, 8, 9,11, Figure 6.6b) and root density values (samples 7, 9, 10, 11, 12, 13, Figure 6.6c). Apparently a good clay quality does not guarantee a high erosion resistance.

Table 6.7 *Erosion categorie of the samples in different treatments at each site. Symbols used in diagram: * = % sand < 40; 1 = high, 2 = moderate and 3 is low erosion resistance. For explanation of treatments and sites, see Table 6.1.*

site name	code	G+	GG-	HG-	HH-	H+	H-	ref
Friesland	FA	3	3	3	3			
Ossenisse	ZH	3	1	1	3			
Nr. Één - Breskens	ZB	1*	1*	2*	3*			
Hondsbossche Zeewering	NH	3		3	3			
Groningen - Eemshaven 2	G2	1	3	1	1			
Hoedenskerke	ZK	1*					1*	
Perkpolder	ZP					1*	2*	
Den Helder	ND					1	2	
Zwarte polder	ZZD					2	2	
Zandkreekdam	ZZK							3
Oudelandse Zeedijk	ZO							1

6.4 Discussion

Shear strength

The results of this study scarcely confirm the increased soil shear strength as a result of soil reinforcement by roots as was reported in previous studies (Waldron, 1977, Barker 1986, Hewlett *et al.* 1987, Thorne 1990, Rickson & Morgan, 1995). Increased soil cohesion caused by increased root density has been described for soils reinforced by trees (Ziemer 1981, Yen 1987) as well as by grasses (Waldron 1977, Tengbeh 1989). Based on these studies, Rickson & Morgan (1995) stated that the effect of vegetation is best close to the soil surface, where root density is generally highest. Although in our study higher root densities were found at depths of 0 to 15 cm, the shear strength in the upper layers appeared to be lower than in the deeper layers. While significant higher root densities were observed in unfertilized treatments, especially at depths of 5 to 10 cm (see Chapter 4), the shear strength was found to be less in the unfertilized treatments on pastures, compared to the fertilized grazed dykes, whereas no difference in shear strength was found between fertilized and unfertilized hay to meadows. This agrees with the lack of significant correlation between underground biomass and shear strength in salt marshes as reported by Scholand et al. (1991). Moreover, Scholand did find an increased shear strength in grazed areas compared to ungrazed areas, probably due to soil compaction by cattle (Zhang & Horn, 1996). In dyke grassland we found higher values for shear strength on mown dykes than on previously grazed dykes at depths of 9 and 20 cm. These mown dykes, dominated by *Festuca arundinacea* and *Dactilis glomerata* were characterized by the presence of relatively fewer and thicker roots, causing higher tensile strengths than the grazed dykes dominated by *Lolium perenne* and *Festuca rubra* (cf. Lichtenegger 1985), which may explain the increased shear strength. However, the difference can also be attributed to the low sand content of the soils of these mown dykes. Also the shear strength of the shallow rooted *Poo-Lolietum*, mainly occurring on the heavy soils of Zeeland, was significantly greater. As in salt marshes (Scholand et al. 1991), shear strength on sea dyke grassland increased with depth, while root density declined with depth.

These results suggest that the shear strength we measured does not reflect soil cohesion as e result of higher root density. Other factors such as soil grain size, moisture condition, soil compaction and even the lack of roots would seem to be more determining for this parameter. The negative correlation with specific root length and vegetation cover (and positive correlation with open spot size) confirm this suggestion. We have to add, however, that we found a positive correlation with root weight at depths of about 5 to 15 cm. Where many thin roots (high specific root length) are present, e.g. in closed swards, shear strength will be less, because of a fine soil structure due to the intensive root growth and low tensile strength of roots. Thicker roots with higher tensile strength probably enhance shear strength. However, in deeper layers, where only few roots are present, differences in shear strength primarily reflect differences in soil compaction. This agrees with the multiple regression model where 50 % of the variation in shear strength at a depth of 9 cm is explained by loam content ánd root weight, whereas at depths of 3 and 20 cm only loam content has a significant effect.

It is quite possible that shear resistance measured in bare clay soils, characterized by a rather coarse structure of relatively larger aggregates, is much higher than the shear

strength of well-rooted clay soils with a fine grained structure. The erosion of the bare soil however will be higher, due to the flushing away of larger soil particles (Kruse 1994a, 1994b). Well-rooted soils are more erosion-resistant, because of their high porosity and because of the cementation of small aggregates (Kruse 1993). High shear strength would then be related to low erosion resistance.

Except for the negative correlation between erosion rate and shear strength at 9 cm, no clear relation was observed between erosion parameters and shear strength. Also, the relation with root density appeared to be ambiguous. Another confusing factor in measuring shear strength is the influence of moisture conditions, where relatively small differences in moisture content noticeably affected the measured shear strength (Waldron 1977). Consequently, the effect of roots or soil grain size on differences in measured shear strengths is difficult to prove. We conclude that shear strength cannot be used as a reliable parameter for erosion resistance of grass swards on clay.

Wear erosion

The amount of the eroded material resulting from the erosion spray experiments at a flow rate of 2 1 s^{-1}, ranging from 40 to 75 g per 0.25 m^2, agrees with the results of previous experiments on river dyke grassland (Van der Zee 1992) and the sea dyke near Holwerd, Friesland (Sprangers 1993), which showed amounts of eroded material ranging from 25 to 125 g per 0.25 m^2. Furthermore, the soil decline after 30 minutes showering (c. 4 mm hr^{-1}) corresponds with measured erosion rates (3.3 mm hr^{-1}) in the experiments with 1.4 m high waves (Smith 1993). The erosion spray experiment seems to be a reliable small-scale erosion test for the amount of wear erosion. At flow rates of 4 1 s^{-1} more material is washed out compared to the 2 1 s^{-1} experiment, but the soil decline does not differ significantly between the two flow rates. No significant trends in soil decline or washed out material between treatments were observed at a flow rate of 4 1 s^{-1}, although doubling the flow rate from 2 1 s^{-1} to 4 1 s^{-1} affected the fertilized pastures more than the long-term unfertilized meadow. This means that in spite of a somewhat lower vegetation cover species-rich meadows are more resistant against wear erosion at higher flow rates, than species-poor pastures, probably because of a homogeneous distribution of shoots and a high root density in the upper layers.

At both flow rates superficial erosion appeared to depend on the combination of vegetation cover, root density in the upper layer and soil particle size. For grassland types with a low cover and high sand content the erosion spray experiment only confirmed the poor state of the sward, which was already well described by the other parameters. When the vegetation cover was relatively high or the range in soil particle size small, differences in wear erosion between the differently managed grasslands were small and difficult to demonstrate. Moreover, the large variability between sites may also be reason for the lack of significant trends in differences in soil loss between treatments.

Internal erosion and root density

The erosion centrifuge experiments appeared to be more useful in distinguishing between grassland types and treatments. Despite of considerable differences between the sites, the erosion model parameters, calculated on the basis of measurements of accumulated weight loss in the different treatments, revealed some trends in erosion susceptibility. In most

samples there were sudden changes in weight loss during the course of the experiment. The two coeffients (b_1 and b_2) of the model, defined as the slope of the (linear) relation between time period and accumulated weight loss, express the rate of erosion of these two steps.

The effects of management on erosion resistance

At a depth of 0 to 5 cm the reference dykes showed a higher erosion resistance (lower erosion rates) than the other treatments. The difference with the fertilized grazed plots was marginally significant (p < 0.07). Erosion rates were also lower in the unfertilized treatments than in the fertilized plots, on both pastures and meadows, but the differences were not significant. At a depth of 5 to 10 cm the same differences were observed between reference dykes, in both unfertilized and fertilized treatments, although erosion rates were generally higher than in the layer 0 to 5 cm. Most samples showed a sudden increased weight loss after 2 to 3 hours (sample collapse), except for the reference dykes. Since soil grain size is constant, these higher erosion resistance of the species-rich meadows at both depths compared to the other treatments can be attributed to their higher root densities (see Chapter 4 and 5). The coexistence of many species, grasses and herbs, as a result of the low nutrient availability, and many other factors influencing both species richness and differences in root morphology, such as spatial heterogeneity in soil macronutrients, mycorrhizal associations (Ozinga et al 1997), and the increased biomass allocation to roots, could account for the increased root density of the vegetation covering the reference dykes. The species-poor fertilized pastures and meadows, on the other hand are characterized by small and shallow-rooting systems, giving lower erosion resistance values.

The somewhat higher erosion resistance of the unfertilized treatments at both depths of 0 to 5 cm and 5 to 10 cm compared to the fertilized plots may be caused by the increased root density in these treatments (see Chapter 4). The haymaking treatment on previous pastures, for example, showed lower (but not significant) erosion rates than the fertilized treatment at a depth of 0 to 5 cm during the centrifuge experiment. Moreover, the time period needed to reach the breaking point of the 'broken stick model' (x_c) was significantly longer (p < 0.05) than the time period to reach this point in the fertilized pasture, which indicates a higher erosion resistance in the unfertilized treatment, given the lower erosion rate (Figure 6.5a). Also, the significant higher value of x_c in the unfertilized treatment HG- (hay-making with grazing) at a depth of 5 to 10 cm compared to the fertilized pasture, indicates a higher erosion resistance. This coincides well with the increased dominance of species as *Festuca rubra*, *Trifolium dubium*, and *Leontodon autumnalis* in these unfertilized treatments (Chapter 3), characterized by dense rooting-patterns compared to *Lolium perenne*, which decreased in these plots. Cessation of fertilization of dyke grasslands in combination with haymaking can bring about a change in botanical composition and consequently root density in a rather short time (3 to 4 years), which favours the erosion resistance. However, the changes in root density induced by the management practices are probably too small to affect the erosion resistance measured in the species-rich meadows, because the duration of the brevity of the treatment

Also, the resistance values of the unfertilized meadow plots were slightly higher than the fertilized plots, which was higher still in the layer at a depth of 0 to 5 cm than in the lower layer of 5 to 10 cm. This could also have been the result of an increased root length density which in this treatment was demonstrated at depth of 3 to 6 cm as well as at 6 to 10 cm (Chapter 4).

The grass-clay complex

The relation between root density and erosion resistance agrees with erosion experiments carried out by Laustrup et al. (1990). They found that damage of grass turf occurred when a critical flow rate of water particles was reached depending on root density. Van Essen (1994) found that the distribution of roots in the soil could probably influence erosion behaviour. Roots can either interconnect aggregates larger than 0.5 mm by penetration, or keep larger aggregates (3 to 5 mm) in place by a dense network, thus influencing internal erosion. Internal transportation of sand and coarse silt-sized particles takes place through a system of larger, millimeter-sized pores, which are considered to be formed by grass roots (Sato & Tokunaga, 1989). Nevertheless, soil properties are as important as root densities. In the multiple regression models of centrifuge erosion rates b_1 and b_2 with soil grain size and root parameters (root length, root weight and specific root length) in our study, only root properties had a significant effect on b_1 in the layer of 0 to 5 cm. This resulted in a low erosion rate when root length density was high, whereas in layer 5 to 10 cm b_1 was influenced by the presence of roots ánd sand content. In both layers the erosion rates of the second half of the experiment (b_2) were significantly influenced by soil grain size only, although the explained variance was rather low (16 to 22 %).

Regarding the higher erosion resistance (lower erosion rates) that were found in the layer at a depth of 0 to 5 cm compared to 5 to 10 cm layer, and the amount of roots present in these layers (respectively c. 50 % and 10 % of the roots in a 50 cm deep soil core, see Chapter 4), these results emphasize how important roots are for soil stability (Barker 1986, Thorne 1990, Dorioz et al. 1993, Kandeler and Murer 1993, Hartge 1994) and for the erosion resistance of the root - soil complex (Kruse 1993, Van Essen, 1994, Anonymous 1998). The difference between the two erosion rates b1 and b2 in the broken stick model, and especially the higher values of b2 at depths of 5 to 10 cm, fits in with the dyke failure model described by Laustrup et al. (1990), where the critical particle velocity of the breaking wave, which initiates damage of the turf, depends on the amount of grass roots. It is possible that internal erosion progresses at a certain speed determined by the root pattern in the soil, until this pattern is disturbed to such an extent that larger soil particles and aggregates are washed away, when the erosion rate will drastically increase, depending on the actual soil particle size.

In the stepwise multiple regression of erosion rate b_1 with root and soil parameters, *root weight* showed the highest (negative) correlation (r^2-adjusted $= 0.23$) in both layers, when one term was allowed in the model. This could indicate that thick roots could do more to reduce erosion than many thin roots. This agrees with studies showing increasing tensile strength with thickness and weight of roots (Lichtenegger 1985, Wu 1995). In the model with two terms, however, *root length* (negative coefficient) in combination with *specific root length* (positive coefficient) showed significant effects on b_1 in both layers with relatively high percentages of explained variance (r^2-adjusted $= 33$ and 34 % respectively). It implies that the presence of many roots but not very thin roots contributes to a high erosion resistance.

The increased porosity and fine soil structure consisting of cemented small aggregates resulting from a strong root growth in the upper clay layers, could hypothetically explain the specific elastic properties of the clay-with-grass layer during severe wave attacks (Kruse 1994a, cf. Anonymous 1998). In this respect soil reinforcement by the tensile strength of thick roots, seems to contribute less to soil stability, than the interaction

between roots and clay, influenced by the root system as a whole including the many thin roots.

Erosion resistance of clay soils

Soil analyses of the investigated sites in this study reveal that the upper layer of most dykes consists of light to heavy sandy clay (Chapter 3). Only 5 out of 31 samples can be classified as "high erosion resistant" according to Atterberg limits (Anonymous 1996a) when the maximum of 40 % sand content is taken into account. The division into erosion categories, however, does not agree with the measured erodibility. Some soil samples classified as "low erosion resistant" have high resistance values in the centrifuge experiment. Otherwise "high resistant" soil samples proved to have low erosion resistance values in the centrifuge experiment. In fact, these soil erosion categories are meant to characterize the erodibility of the 1.0 m width clay layer which is used in the construction of dykes (Anonymous 1998). The clay quality in the upper layer of ca. 0.15 m may deviate, due to chemical and physical processes (forming of aggregates, Anonymous 1996a, 1998). Sometimes a top layer of sandy clay is applied to stimulate the growth of a grass vegetation. Once a well-rooted grass sward has developed in the upper 15 to 20 cm of the dyke, the erosion resistance of this clay root complex appears to be higher than the clay layer underneath (Kruse 1994a, Anonymous 1998). Moreover, when the grass sod is damaged and the upper layer is eroded, the presence of roots at depths of 20 to 50 cm appears to help prevent the erosion of the deeper clay layers (Kruse 1994b).

We suggest that for judging the erodibility of the upper layer of grass-covered dykes other criteria like botanical composition, reflecting root density, and vegetation cover or shoot density must be taken into account in stead of clay quality. The latter seems to be more suitable as an erosion criterion for deeper soil layers. But also then vegetation type could be useful as an indicator for the presence of roots at those depths.

Conclusions

No clear relation was found between shear strength, root density and erosion resistance. The correlation of increased shear strength with high loam content and low root length density suggests that shear strength is merely determined by soil grain size. Since erosion of bare soil appears to be higher than well rooted clay soils, the conclusion is that shear strength cannot be used as a reliable parameter for erosion resistance of grass swards on clay.

Resistance against wear erosion depends on vegetation cover, root density in the upper layer and soil particle size. Erosion spray experiments demonstrated no significant trends in soil loss between management treatments. However, on doubling the flow rate, the sward of the species-rich hay meadows appeared to be less sensitive to wear erosion than unfertilized pastures. Spray experiments seem to be less useful for distinguishing minor differences in erosion resistance between grassland types.

Erosion centrifuge experiments revealed higher resistance values in species-rich meadows, than in fertilized grasslands, which might be the result of higher root densities. Three years following cessation of fertilization a slight increase in erosion resistance was detected in erosion centrifuge experiments. This agrees with the increase in root density and the change in botanical composition when fertilization has been stopped. Resistance

against internal erosion is determined by the combined effects of root density (root length, root weight and root diameter) and soil particle size, probably because of their influence on aggregate stability and porosity, rather than by the soil reinforcement due to the tensile strength of the roots.

To judge the erodibility of grass-covered dykes criteria like botanical composition and vegetation cover (shoot density) should be used in stead of clay quality.

7

Management

Implications for dyke grassland management

7.1 Introduction

As explained in the first chapter of this thesis, for civil engineering purposes, grassland quality is largely determined by the density of the grass sod, which depends on shoot density, root density, and the occurrence of open areas. A well developed root system favours erosion resistance because of its impact on stability and porosity. The interaction of roots and the clay substrate creates a root-clay complex with sufficient specific 'elastic' qualities to absorb the considerable forces generated by waves. Roots favour the formation of a fine granular structure in the soil and supply adhesive substances which bind these fine particles. Where roots have disappeared conduits remain in the soil through which any incoming water will quickly drain, increasing the permeability of the soil. Moreover, a dense root mass prevents larger soil parts from being washed away. The more extensive and varied the rooting structure of the vegetation (Chapter 6), and the more homogeneous the spatial distribution of this well-rooted vegetation (see Chapter 5), the larger the erosion resistance of the grass sward covering the dyke surface.

Both root pattern and spatial heterogeneity of the sward can be influenced by the type of management that is used. Clay quality in and under the sod also determines erosion resistance, but this factor cannot be changed by management. From the results of this study it became clear that the amount of applied fertilizer is a key factor in the development of a closed, densely rooted sward. The roots of unfertilized species-rich, old hay meadows had the highest densities (Chapter 4) and consequently the best erosion resistance (Chapter 6) of all investigated grassland types. Cessation of fertilization in combination with haymaking on previous pastures led to a shift in the dominance of grassland plants in the sward (Chapter 3) and an increased root density (Chapter 4), while the vegetation cover remained the same. It is argued that the increased root density results in an increased allocation of carbon to the roots as well as an increase in species indicative of less nutrient-rich conditions, characterized by other root architecture. Cessation of fertilizer application while continuing grazing, however, showed a change in botanical composition (Chapter 3) but no significant increase in root density, probably as a result of the lack of net N off-take in these plots (Chapter 4).

Avoiding the application of fertilizer is one precondition for the development of erosion-resistant grassland on dykes. Which management needs to be chosen, however, is still unclear. Haymaking produced the best results in our study, but it did not prove that grazing without fertilization will not be as successful as haymaking in creating a

well-rooted sward. On river dykes, species-rich sheep and horse-grazed grasslands were found with relatively high root densities and erosion resistance (Van der Zee, 1992). Also the question of the acceptable extent of grazing at low fertilizer input, needs to be answered. Another important factor is the maintenance of the sward. Stopping the use of fertilizer combined with extensive agricultural use, sometimes results in abandoned swards with a large spatial heterogeneity. Good maintenance measures are needed to assure a spatial homogeneous grass cover. Mowing without removal of cuttings, which is often used by water management authorities, prevents the uncontrolled growth of dyke grasslands, but results in a very open sward with a little erosion resistance .

Apart from maintenance measures from a civil-engineering point of view, the type and intensity of the current dyke grassland management is dependent on the other secondary functions of dykes like agricultural production, recreation (amenity turf) or sometimes ecological functions. It is difficult to give practical guidelines for maintenance and use of dyke grasslands because of the potentially different possible forms of dyke grassland management. In this chapter a discussion is presented of the present dyke grassland use and some practical combination of functions, as well as the official guidelines for testing dyke safety including grass cover that have recently been formulated by the water management authorities (Anonymous 1996a, Anonymous 1998).

7.2 Present dyke grassland use and sod quality

Research and practical experience indicate that intensive agricultural use as well as lack of maintenance result in grassland with insufficient erosion resistance. Heavy use of fertilizer often coincides with a high density of cattle or multiple cuts of hay per year, and results in a species-poor meadow with open patches caused by overgrazing, or a species-poor hay meadow with a very open turf (Figure 7.1a). This practice is used mainly on primary and secondary dykes in the south-western part of the Netherlands. In the meadow *Lolium perenne* is dominant and in the hay meadow *Arrhenatherum elatius*. Use of herbicides against unwanted herbs such as *Cirsium arvense, Stellaria media, Cirsium vulgaris, Urtica dioica, Hordeum murinum* and *Capsella bursa-pastoris* in meadow, and *Heracleum sphondylium, Urtica dioica, Anthriscus sylvestris, Elymus repens* and *Rumex obtusifolius* in hay meadows often results in the opposite of the intended effect. Although these plants seem to disappear, the same species will reappear in the next season in the newly created open areas with a very high soil nutrient content, which makes a new application of herbicides inevitable (Heemsbergen 1994). Especially when grazing is continued during the winter, damage to the sod can be substantial on the slopes of the dyke (sheep-tracks) and concentrated around the feeding and watering sites.

Although mowing without removing the hay cannot be considered 'lack of management', the effect on the grass-sod is identical: when the hay is left on the field, the nutrients in the hay return to the soil within a rather short period of about one to two weeks (Schaffers *et al.* 1998). The increased nutrient content of the soil results in a species-poor vegetation where weeds such as *Heracleum sphondylium* and *Urtica dioica* thrive in the open areas created by suffocation of the vegetation by the hay litter. Although this management type was common practice by public works and water management authorities for maintaining dyke grasslands and road verges, nowadays there is noticeable policy change towards haymaking without fertilizer use.

Pasture   **Hayfield**

herbicides	**a. Heavily fertilized**	herbicides
overgrazing	$(75-150 \text{ kg N ha}^{-1} \text{ yr}^{-1})$	mowing 2 - 3 times with
open spots		(or unfert. without) hay removal
weeds		very open turf
low root density		low root density
very few species		very few species

periodically grazed	**b. Moderately fertilized**	1 -2 times mowing
closed turf	$(50-75 \text{ kg N ha}^{-1} \text{ y}^{-1})$	closed turf / tussocks
many thin roots in top layer		thick roots
species poor		species poor

| periodically grazed | **c. Unfertilized** | 1 time mowing |
closed turf		closed turf
thick and thin roots		thick and thin roots
species rich		deep roots
		species rich

Figure 7.1   *Above- and belowground grass sward structure as influenced by management intensities.*

A less intensive agricultural use of dyke grassland can be found in the Dutch provinces Friesland and Groningen, where 75 to 100 kg of nitrogen per hectare per year is used to fertilize dyke grassland. Plots of dyke are periodically grazed and the remaining

biomass is mown and removed. The resulting grassland has a high shoot density and a high root density with many thin roots in the top layer from 0 to 5 cm (Figure 7.1b), with a higher erosion resistance than heavily fertilized grassland plots as indicated in the erosion centrifuge experiment. The upper layer was more resistant to erosion than the next lower layer (5 to 10 cm), probably because the alternating periods of grazing and non-grazing might have caused proliferation of roots in the upper layer into a dense sward. The intensive grazing and soil compaction by sheep (cf. Zhang & Horn 1996) together with the (light) fertilization could be responsible for the presence of mainly thin roots in the upper layer. Apart from *Lolium perenne* the grasses *Festuca rubra* and *Poa trivialis* as well as some herbs (*Geranium molle*, *Bellis perennis* and *Cerastium fontanum*) occur in these grasslands, but the total number of species is low.

When a relatively low application of fertilizer is combined with haymaking a closed vegetation develops, which is poor in herbs and mainly consists of *Arrhenatherum elatius*, *Poa pratensis* and tussocks of *Festuca arundinacea*, and is characterized by a dominance of thick roots. This type of management is used on dykes along the Oosterschelde and Westerschelde in the south-western part of the Netherlands, although heavily fertilized hay meadows also occur on these dykes. With lawn management (7 - 8 times mowing per year, sometimes combined with a low level of fertilization) the mown biomass is not removed, but the frequent mowing result in a low production. The quality of the grass-sod is comparable to those of the periodically grazed and moderately fertilized Frysian dykes. This type of management is often used near buildings, houses and recreation spots.

No fertilizer is applied in the most extensive form of dyke grassland management, and depending on the production the grassland is grazed or mowed once or twice (Figure 7.1c). The resulting vegetation is varied and contains many grass and herb species. The unfertilized species-rich pastures are located on river dykes. Also, species-rich hay meadow occur more frequently on river dykes (cf. Sykora & Liebrand 1987, Van der Zee, 1992), but are sometimes also found on sea dykes (Sprangers *et al.* 1991). In general the vegetation on these dykes is mature and stable. Both this study and the research on river dykes (Van der Zee, 1992) has shown that the dense and uniformly distributed root mass of these grassland types result in a high erosion resistance. Table 7.1 summarizes the different management types, categorized by the amount of fertilizer that is applied, with resulting erosion resistance levels, vegetation types, (agronomic) usefulness and required maintenance measures.

7.3 Guidelines for dyke grassland management

The guideline that both grazing with sheep and fertilization are essential for grasslands on primary dykes with optimal erosion resisting properties (Jonker & Brummel 1958, Huisman 1976, Bouwsema 1978, Minderhoud 1989) can no longer be upheld. Based on this study as well as practical experience we can state that *no (or the restricted) application of fertilizer* and *proper management and maintenance over longer periods* are the main prerequisites for a high sod quality. Current grassland management on dykes is dependent on several factors such as potential for agricultural grassland use; position of the dyke in the landscape; local circumstances and recreational use; financial possibilities for alternatives; and legal claims of grassland use by farmers. Therefore, management types are needed, that fulfil the necessary civil engineering preconditions, but also are compatible

Table 7.1 *Management, root characteristics, cover, erodibility, vegetation type, use and maintenance of dyke grasslands at different N input.*

N-input (kg ha⁻¹y⁻¹)	management	root characteristics	cover	Erosion resistance	vegetation type	dyke grassland use/problems	maintenance (by wat. auth.)
0	haymaking 1-2 cuttings	many thick and thin roots in 0-20 cm soil	> 70 %	good	species-rich Arrhenatheret um	feed quality hay; high botanical value	removal of cuttings, dumping ? mole control
	sheep grazing (periodically or continuously)	thick and thin roots in 0-15 cm (?) soil	> 85 %	high	species-rich Lolio-Cynosuretum	8 sheep/ha; grazing area?, winter grazing ? high botanical value	regular mowing, dragging, extra cutting mole control
	mowing 7-8 x (lawn management)	thin roots in 0-5 cm	> 85 %	moderate	species poor Lolio-Cynosuretum	nearby housing, recreation spot	frequently mowing
	mulching 2 x	few thick roots	< 60 %	very low	spec. poor Arrh.	-	easy and cheap maintenance
50 -75	sheep grazing (in periods)	thin roots in 0-5 cm	> 85 %	moderate	species -poor Lolio-Cynosuretum	12 sheep/ha, grazing area? winter grazing ?	regular mowing, dragging, extra cutting mole control
75-100	grazing (continuously)	few thin roots in upper layer	> 85 %	low	Poo-Lolietum	16 sheep/ha	-
	haymaking	few thick roots	< 60 %	very low	sp. poor Arr	2 cuttings of good quality	-

with one of the other forms of dyke grassland use, to form an optimal combination of functions.

No fertilizer application

No or low fertilizer input has three effects: (1) the increase of erosion resistance as a result of increased root density, (2) a less intensive (agricultural) grassland use, with a diminished chance of disturbance (e.g. by overgrazing), and (3) the increase of species diversity. The high erosion resistance of old hay meadows proves the benefit of this management rule. The old unfertilized pastures covering the Wadden sea dykes in the Netherlands and Germany in 1920-40 as well as the dyke grasslands of the south-western Delta area, appeared to possess also a relatively high erosion resistance (De Vries 1956), Edelman 1958, Thierry 1958). However, species diversity was relatively low in the northern area (Anonymous 1942, De Vries 1958).

What does happen when the management practice is changed and fertilization is discontinued? This research shows that the shift from fertilized grazing to unfertilized haymaking after four years results in an improved root density and erosion resistance, while shoot density is unaffected. The question is often raised as to whether some fertilization is required in the long term. This is not the case, because a different type of vegetation will develop with species characterized by a lower aboveground (and a higher belowground production, see Chapter 5), and a more efficient use of nutrients in the soil (Chapter 4).

Grazing or haymaking

With regard to the primary function of the dyke grassland, i.e. preventing erosion by wave action, this study shows that the best results are obtained with the management type 'unfertilized haymaking'. This does not mean that all sheep should be taken off the dykes immediately, but the outcome does indicate that unfertilized haymaking could be a useful alternative to the types of dyke grassland management that are currently causing problems. An additional aspect is the increase in natural quality in the long term by the increased species richness and the establishment of rare species. This agrees with the plans for a more environmentally-sound management of river beds and dykes. Such plans are at the moment being developed within the framework of the Nature Policy Plan (1990). A natural vegetation of riversides and dykes supports the plans for a 'Main Ecological Infrastructure' and the establishment of a 'network of green pathway's' in productive agricultural landscapes.

In the initial phase after converting management from grazing to haymaking without fertilization, the grassland should be mown at least twice a year to reduce the nutrient content of the soil. In the longer term when the release of nutrients from the soil has reached a lower level, the grassland can be mown once a year (mid-July). A side-effect of changing from a fertilized to an unfertilized situation can be an increased growth of *Cirsium arvense*. This weed should be mown just before inflorescence.

When 'grazing without fertilization' it is important to know how farming practices can be adapted to the reduced production, and whether sheep farmers' practice of grazing sheep on low productive dykes, really pays off. In Friesland at present, a reduced application of fertilizer has been shown to be feasible, maintaining an acceptable profit for sheep farmers. A good production can be combined with a low nitrogen gift at a fertilizer application of approximately 60 kg N ha^{-1} y^{-1} and a careful selection of grazing intervals depending on weather conditions. The procedure used for grazing is important. It is better to graze a small section of dyke with a large number of animals for a short period of time than to let a few animals graze on a large area continuously. In this respect the 'Frysian system' performs best: periodical grazing of relatively small parcels of land with 35 to 40 ewes and lambs per hectare, which is about 15 ewes per hectare on an annual base. This system has been applied successfully for years while the use of fertilizer has been steadily reduced. It results in a good, erosion resistant grass sod, with particularly many (thin) roots in the top 0 to 5 cm soil layer, but a relatively low species richness.

It is advised to use the 'Frysian system' (periodically grazing of small parcels) at a zero fertilizer application. De Boer & Sprangers (1994) have calculated whether a reasonable yield can be obtained when fertilization is reduced or completely stopped. It was shown that at 0 kg N ha^{-1} y^{-1} the same net return (*f*730,- per ha) can be achieved as in the current situation with 75 kg N ha^{-1} y^{-1} (*f*1225 - *f*500 lease costs), on the condition that no costs of tenancy have to be paid, and a large area can be grazed. At a minimum herd size of 200 ewes and a production of 4 ton dw ha^{-1} y^{-1} an area of 24 ha is required, giving an average density of 8 animals per ha. Similar to the current situation the animals need extra feeding and additional grazing areas. The earnings at a fertilizer gift of 150 kg N ha^{-1} y^{-1} are *f*1071.

Maintenance

Extensive management should not lead to mismanagement. Abandonment, and not carrying out the necessary maintenance measures, usually results in irregular growth of a bushy sward, composed of tussocks. For improving and maintaining grassland quality (in terms of erosion resistance) maintenance rules must be obeyed (cf. Bakker, 1988). Part of these rules are based on years of experience with managing grassland dykes in the northern part of the Netherlands (Jonker & Brummel 1958), some of which have resisted several spring tides prior to dyke reinforcements.

Grazing should be supplemented by regular mowing of the unpalatable herbs left after grazing, and by levelling the soil surface in order to retain a uniform grassland vegetation. In the province Groningen this is done by superficially spreading out clay soil with a (dung) spreading machine on the Wadden Sea dykes. Very extensive grazing is often recommended for the management of natural areas because it leads to a differentiation of the vegetation. For this same reason it is not appropriate for dyke grasslands. When combined with the grazing of neighbouring salt marshes, dykes should not be grazed in the winter months, while in the summer period regular mowing or one hay-cut could be necessary when biomass production on the dykes is high. Whereas in the Netherlands, dykes are usually managed separately from marshes, on German and Danish dykes along the Wadden Sea, combined grazing of salt marsh and dyke by sheep is common practice (Dijkema 1983 , Sprangers & Muijs, 1997). However, fertilization of the dykes often takes place and high sheep densities (10 sheep/ha) are common. Under such conditions lowering the grazing intensity to 1.5 sheep/ha and cessation of grazing was found to increase species diversity (Kiehl *et al.* 1996

For both grazing and mowing grassland vegetation ought to be low (at most 10 cm) at the onset of winter. Taller grass plants will recline after a while resulting in a tussock-like structure. Depending on the amount of regrowth in the autumn an extra event of mowing may be required. Given the low production of the grassland and the wet soil in winter, dykes should not be grazed during the period November - March. After haymaking it is advisable to remove the cuttings within a period of two weeks to prevent the leaking of nutrients to the soil (Schaffers *et al.* 1998). Cuttings must be removed at all times, even in wet periods when haymaking is difficult, to prevent enrichment of the soil.

Hay meadows with tall vegetation in particular may encourage high densities of mice, which by their burrowing can cause considerable damage to the turf, locally undermining areas of a few square meters. Moles are usually actively controlled by gas cartridges or traps. Although fewer mole hills there were counted on unfertilized river dykes than on fertilized dykes (Van der Zee, 1992), and the density of mole hills was also less in the unfertilized treatment areas on sea dykes, moles can still exhibit considerable activity depending on moisture and nutrient conditions of the neighbouring land. For a good sod quality a continued control of moles is required.

Grazing requires a considerable effort to maintain the grassland and to check the implementation of the right type of grassland management (for civil-technical purposes). In Friesland and Groningen an important element in sheep grazing there is that the organization responsible for the dykes applies the fertilizer, performs all maintenance tasks, and determines the periods for grazing. In Zeeland these activities are done by the tenant farmers resulting in a less organized manner, more dependent on individual farming

practices. Except for the dykes that are properly maintained by the farmers, haymaking is a useful alternative giving more control over grassland management.

The good quality of older grasslands in the northern part of the Netherlands, and of the old hay meadows in the south-western area, which have been subject to identical management practices over a long period of time, indicates the is importance of perpetuate the correct form of grassland management.

7.4 Testing dyke grassland civil-technical quality

In 1996 The Technical Advisory Committee for public Waterworks (TAW) published guidelines for judging the safety of dykes and dyke rings in the Netherlands (Anonymous 1996b). The publication is a tryout version, in order to prepare final guidelines that can be confirmed in a later phase. The guidelines serve as an instrument assisting waterboard authorities in the Netherlands to comply with the legal demands for dyke safety that require to be checked every five years. They provide criteria for judging the safety of a dyke, given the actual calculated load (duration and height of waves) and a statistic probability of dyke failure of 1:4000. Different sets of criteria are formulated for every construction feature of a dyke, like height, slope, stone cover, clay layer, grass turf. For the grass cover the following criteria apply: macrohomogeneity, vegetation cover, number of species or the number of erosion indicator species, root density, and clay quality in the grass sod.

The procedure for evaluating the dyke safety is twofold and as follows: after a pre-selection of dyke sections based on height and frequencies of waves and experience of previous dyke failure, the grass cover is tested by a *simple method* based on a global judgement of *macrohomogeneity* (number of open spots, relief and number of mole hills in a dyke section), *management, slope* and *clay quality*. If the outcome of the test is negative a *detailed testing method* is used, based on *macrohomogeneity, vegetation cover* (measured with a point quadrat method, cf Chapter 3), *number of plant species or the number of erosion indicator species, clay quality in the sod* (measured by hand or with a laboratory method) and *root density* (laboratory). Although the criteria *clay under the grass sod* and *slope stability* are also mentioned, these criteria can be regarded as stability criteria which are not directly influenced by the type and management of the sward.

Vegetation cover, data on plant species and root density are included in the detailed test, but they contribute only slightly to the outcome of the test. For example, where macrohomogeneity is insufficient, these parameters are neglected, and judgement of the sod solely concentrates on clay quality in the sod, a parameter which cannot be used as a reliable indicator of sward erodibility, as we have demonstrated in Chapter 6. Moreover, a grass sward with a low root density, vegetation cover, botanical diversity, and macrohomogeneity will not be rejected if the clay quality in the sod is adequate. The results of this study clearly revealed that this type of sward had a low erosion resistance in spite of its adequate clay quality. In a recent publication of the Technical Advisory Committee on Water defences (TAW, Anonymous 1998), the ambiguity of the importance of clay quality in the upper layer to erosion resistance was discussed, and more emphasis was put on the grass sward itself.

Another example is the judgement of vegetation cover or contribution of botanical composition. High cover swards will be judged as 'good', without examining the root density. This step is questionable: fertilized swards with a high cover may be very poorly

rooted as is the case with the *Poo-Lolietum* grassland type. Also the number of species (more or less than 15 for the rejection of a sward) or number of erodibility indicators that are used in the detailed method are ambiguous criteria. In swards with a low erosion resistance, more than 15 species can easily occur.

The results of this study clearly demonstrate that measured cover, botanical composition, and root density are correlated with the erodibility of the grass cover on dykes. The botanical composition can also provide information about the status quo of the sward, in order to help decide which management type is appropriate or which maintenance measurements are needed. We therefore strongly urge that in the detailed method the following are treated as equally contributing criteria: *botanical composition* (species groups), *vegetation cover* (in terms of shoot density) and *root density*, which can be determined by a hand method, and not the clay quality in the sod. Recently a method has been worked out to determine both root density by hand and the erodibility of the sward with these criteria (cf. Sprangers & Arp, 1998).

References

Anonymous (1984). *Erosiebestendigheid van gras op dijktaluds. Verslag modelonderzoek in 1982 en 1983 uitgevoerd in de stroomgoot te Lith.* Grondmechanica Delft rapport CO-265412/15; Waterloopkundig Laboratorium rapport M 1930 voor COW, RWS/DWW, Delft, 28 pp.

Anonymous (1987). *In situ erosiesproeiproeven.* Rapport Rijkswaterstaat, Dienst Weg en Waterbouwkunde, Delft.

Anonymous (1990a). *Impacts of sea level rise on Dutch society, a description of the ISOS case study for the Netherlands.* Nota GW-AO- 90.016 Rijkswaterstaat, Dienst Getijdewateren; rapport H750 Delft Hydraulics, Delft.

Anonymous (1990b). *Nature Policy Plan.* Ministry of Agriculture, Nature Conservation and Fisheries, 's Gravenhage.

Anonymous (1992). *Botanisch basisregister.* Centraal Bureau voor de Statistiek, Voorburg.

Anonymous (1994a). *Handreiking constructief ontwerpen.* Rapport Technische Adviescommissie voor de Waterkeringen, Rijkswaterstaat, Dienst Weg en Waterbouwkunde, Delft.

Anonymous (1994b). *Handreiking inventarisatie en waardering LNCaspecten.* Rapport Technische Adviescommissie voor de Waterkeringen, Rijkswaterstaat, Dienst Weg en Waterbouwkunde, Delft.

Anonymous (1994c). *Erosiecentrifugeproeven met boormonsters van zeedijken.* Rapport Grondmechanica Delft, RWS/DWW, Delft.

Anonymous (1995a). *Nature across motorways.* Compiled by Nieuwland Advies for the DirectorateGeneral for Public Works and Water Management (RWS), Road and Hydraulic Engineering Division (DWW), Delft.

Anonymous (1995b). *Voorlopige analyse hoogwaterperiode januarifebruari 1995.* DWWrapport AK-R95.048, Rijkswaterstaat, Dienst Wegen Waterbouwkunde, Delft.

Anonymous (1995c). *Under pressure.* Report of the Technical Advisory Committee for public Waterworks (TAW), DirectorateGeneral for Public Works and Water Management (RWS), Road and Hydraulic Engineering Division (DWW), Delft.

Anonymous (1995d). *Veiliger de winter in? beoordeling van de rivierdijken voor het winterseizoen 1995-1996.* Rapport WD-WW-95352, Rijkswaterstaat, Dienst Wegen Waterbouwkunde, Delft.

Anonymous (1996a). *Technisch Rapport klei voor dijken.* Rapport Technische Adviescommissie voor de Waterkeringen, Rijkswaterstaat, Dienst Wegen Waterbouwkunde, Delft.

Anonymous (1996b). *Leidraad Toetsen op Veiligheid.* Technische Adviescommissie voor de Waterkeringen, Rijkswaterstaat, Dienst Wegen Waterbouwkunde, Delft.

Anonymous (1998). *Technisch rapport Erosiebestendigheid van Grasland als Dijkbekleding.* Technische Adviescommissie voor de Waterkeringen, Rijkswaterstaat, Dienst Wegen Waterbouwkunde, Delft.

Atwell, B.J. (1993). Response of roots to mechanical impedance. *Environmental and Experimental Botany,* vol. 33, No. 1, 27-40.

Bakker, J.P. (1987). Restoration of species-rich grassland after a period of fertilizer application. *Disturbance in Grasslands* (ed. by J. van Andel, J. Bakker & R.W. Snaydon), pp. 185-200, Junk Publishers, Dordrecht.

Bakker, J.P. (1989). *Nature management by grazing and cutting.* Diss. Kluwer, Dordrecht.

Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M. & Thompson, K. (1996). Seed banks and seed dispersal: important topics in restoration ecology. *Acta Bot. Neerl.,* 45, 461-490.

Bakker, N. (1988). *Beheer en onderhoud van zee en slaperdijken*. Waterschap Ommelanderzeedijk, Onderdendam, The Netherlands.

Barker, D.H. (1986). Enhancement of slope stability by vegatation. *Ground Engineering*, April 1986, 11-15.

Barkman, J.J., Doing, H., Segal, S. (1964). Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. *Acta Bot. Neerl.* **13**: 394-419.

Bekker, R.M., Schaminée, J.H.J., Bakker, J.P. & Thompson, K. (1998). Seed bank characteristics of Dutch plant communities. *Acta Bot. Neerl.,* **47**, 1527.

Bell, G. & Lechowicz M.J. (1994). Spatial heterogeneity at small scales and how plants respond to it. *Exploitation of environmental heterogeneity by plants* (ed. by M.M. Caldwell & R.W. Pearcy), pp. 391-414, Academic press, London.

Belcher, J.W., Keddy, P.A., & Twolan-Strutt, L. (1995). Root and shoot competition intensity along a soil depth gradient. *Journal of Ecology*, **83**, 673-682.

Bengtsson, J., Fagerström, T., & Rydin, H. (1994).Competition and coexistence in plant communities. *Trends in Ecology and Evolution*, **9**, 246-250.

Bencough, A.G., & Mullins, C.E. (1991). Penetrometer resistance, root penetration and root elongation rate in two sandy loam soils. *Plant and Soil* **131**, 59-66.

Berendse, F. (1982). Competition between plant populations with different rooting depths. *Oecologia*, **53**, 50-55.

Berendse, F. (1990). Organic matter accumulation and nitrogen mineralisation during secondary succession in heathland ecosystems. *Journal of Ecology* , **78**, 413-427.

Berendse, F. (1993). Ecosystem Stability, Competition and Nutrient Cycling. *Biodiversity and Ecosystem function of biodiversity* (ed. by E.D. Schulze and H.A. Mooney), *Ecological Studies*, **99**, pp. 409-431, Springer Verlag, Heidelberg.

Berendse F. (1994). Competition between plant populations at low and high nutrient supply. *Oikos*, **71**, 253-260.

Berendse, F., & Elberse, W.Th. (1989). Competition and nutrient losses from the plant. *Causes and consequences of variation in growth rate and productivity of higher plants.* (ed. by H. Lambers, M.L. Cambridge, H. Konings, T.L. Pons), pp. 269-284, SPB Academic publishing, the Hague.

Berendse, F. & Elberse, W.Th. (1990). Competition an nutrient availability in heathland and grassland ecosystems. *Perspectives on Plant Competition* (ed. by J.B. Grace & D. Tilman), pp. 94-116, Academic Press, New York..

Berendse, F. , de Kroon, H. & Braakhekke, W.G. (1998). Acquisition, use and loss of nutrients. *Handbook of Functional Plant Ecology* (ed. by F.I. Pugnaire), in press, Marcel dekker Inc., New York.

Berendse, F., Oomes, M.J.M., Altena, H.J. & Elberse, W.Th. (1992). Experiments on the restoration of speciesrich meadows in The Netherlands. *Biological Conservation*, **62**, 59-65.

Berendse, F., Oomes, M.J.M., Altena, H.J., & De Visser, W. (1994). A comparative study of nitrogen flows in two similar meadows affected by different ground water levels. *Journal of Applied Ecology*, **31**, 40-48.

Berendse F., Aerts, R. & Bobbink, R. (1993). Atmospheric nitrogen deposition and its impact yon terrestrial ecosystems.*Landscape Ecology of a Stressed Environment* (ed. by C. Vos and P. Opdam), pp.104-118, Chapman & Hall, London.

Bland, W.L. & Mesarch, M.A. (1990). Counting error in the line-intercept method of measuring root length. *Plant and Soil* **125**, 155-157.

Boer, J. de & Sprangers, J.T.C.M. (1994). *Mogelijkheden voor extensieve schapenhouderij op dijken - een modelmatige benadering met het schapenstapelmodel van het PR.* Intern rapport Proefstation voor de Rundveehouderij, Schapenhouderij en Paardenhouderij, Lelystad en Landbouwuniversiteit Wageningen, 16 pp.

Boot, R.G.A. (1990). *Plant growth as affected by nitrogen sypply; effects on morphology and physiology of species from contrasting habitats.* PhD.Thesis. Department of Plant Ecology and Evolutionary Biology, University of Utrecht, Utrecht, 92 pp.

Boot, R.G.A. & Mensink, M. (1991). The influence of nitrogen availability on growth parameters of fast- and slow-growing grasses. *Plant root growth, an ecological perspective* (ed. by D. Atkinson), pp. 161-170, Blackwell, Oxford.

Bouwsema, P. (1978). *De Emmapolder in de eerste 30 jaar na aanleg.* Rapport Rijkswaterstaat, Baflo.

Brouwer, R. (1962). Nutritive influences on the distribution of dry matter in the plant. *Netherlands Journal of Agricultural Science* **10**, 399-408.

Brouwer, R. (1983). Functional equilibrium: sense or nonsense? *Neth. J. Agric. Sci.*, **31**, 335-348.

Bullock, J.M., Clear Hill, B., Dale, M.P. & Silvertown, J. (1994). An experimental study of the effects of sheep grazing on vegetation change in a species poor grassland and the role of seedling recruitment into gaps. *Journal of Applied Ecology* **31**, 493-507.

Caldwell, M.M. (1994). Exploiting Nutrients in Fertile Soil Microsites. *Exploiting of Environmental Heterogeneity by plants* (ed. by M.M. Caldwell & R.W. Pearcy), pp.325-347, Academic Press, London.

Caldwell, M.M., Richards, J.H. & Beyschlag, W. (1991). Hydraulic lift: ecological implications of water efflux from roots. *Plant Root Growth an ecological perspective* (ed. by D. Atkinson), pp. 423-436, spec. publ. British Ecological Society, nr 10, Blackwell Scientific Publishers, London.

Chapin F.S. (1980) The mineral nutrition of wild plants. *Annual Review of ecology and systematics* **11**, 233-260.

Chaneton, E.J., & Facelli, J.M. (1991). Disturbance effects of plant community diversity: spatial scalees and dominance hierarchies. *Vegetatio*, **93**, 143-155.

Coppin, N.J. & Richards, I.G. (1990). *Use of Vegetation in Civil Engineering.* Construction Industry Research and Information Association (CIRIA), Butterworths, London, 292 pp.

Coppin, N. & Stiles, R. (1995). Ecological principles for vegetation establishment and maintenance. *Slope Stabilisation and Erosion Control a Bioengineering Approach* (ed. by R.P.C. Morgan & R.J. Rickson), pp.59-94, E & F N Spon, Chapman & Hall, Cambridge.

Cui, M. & Caldwell, M.M. (1996). Facilitation of plant phosphate acquisition by arbuscular mycorrhizas from enriched soil patches. I. Roots and hyphae exploiting the same soil volume. *New Phytologist*, **133**, 453-460.

De Kroon, H. & Hutchings, M.J. (1995). Morphological plasticity in clonal plants the foraging concept reconsidered. *Journal of Ecology*, **83**, 143-152.

De Leeuw, J., Olff, H. & Bakker, J.P. (1990). Year-to-year variation in peak aboveground biomass of six saltmarsh Angiosperm communities as related to rainfall deficit and inundation frequency. *Aquatic Botany*, **36**,139-151.

De Vries, D.M. (1956). Verslag van de excursie, gemaakt met de werkgroep 'Grasmat op dijken' naar de westkust van Sleeswijk-Holstein van 13 to 17 juni 1955. *Gestencilde mededelingen*, Centraal Instituut voor landbouwkundig onderzoek, Jaargang 1956 nr.21, Wageningen.

De Vries, D.M. (1958). Botanische samenstelling en dichtheid van de grasmat op de dijken in Nederland. *Grasmat op dijken.* Rapport van de werkgroep, pp. 26-58, Kon. Inst. v. Ingenieurs & Kon. Gen. v. Landbouwwetenschappen, Den Haag, Wageningen.

Dickinson, N.M., & Polwart, A. (1982). The effect of mowing regime on an amenity grassland ecosystem: above- and below-ground components. *Journal of Applied Ecology*, **19**, 569-577.

Dirven, J.G.P., & K. Wind, De beworteling van enige grassoorten bij verschillende bodemvruchtbaarheid. *Stikstof*, **95/96**, 354-359.

Dijkema, K, & Wolff, W.J. (eds.) (1983). *Flora and vegetation of the Wadden Sea islands and coastal areas. Report 9 of the Wadden Sea Working Group*, Leiden, 413 pp.

Dorioz, J.M., Robert, M & Chenu (1993) The role of roots, fungi and bacteria on clay particle organization. An experimental approach. *Geoderma*, **56**, 179 -194.

Dumortier, M. (1991). Belowground dynamics in a wet grassland ecosystem. *Plant Root Growth an ecological perspective* (ed. by D. Atkinson), pp. 301-310, spec. publ. British Ecological Society, nr 10, Blackwell Scientific Publishers, London.

Edelman, T. (1958). Aanvalsfactoren waaraan een grasmat blootstaat. *Grasmat op dijken*. Rapport van de werkgroep, pp. 12-25, Kon. Inst. v. Ingenieurs & Kon. Gen. v. Landbouwwetenschappen, Den Haag, Wageningen.

Elberse, W. Th., Van den Bergh, J.P., & Dirven, J.G.P. (1983). Effects of use and mineral supply on the botanical composition and yield of old grassland on heavy-clay soil. *Neth. J. agric. Sci.* **31**, 63-88.

Elberse, W.Th., & Berendse, F. (1993). A comparative study of the growth and morphology of eight grass species from habitats with different nutrient availabilities. *Functional Ecology*, **7**, 223-229.

Ellenberg, H. (1978). *Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht*. 2. Eugen Ulmer, Stuttgart.

Ericsson, T. 1995 Growth and shoot:root ratio of seedlings in relation to nutrient availability. *Plant and Soil* **168/169**: 205-214.

Essen, H.M. Van (1994). *Experiments on internal erosion of grass sods from dikes*. Delft Geotechnics Report CO329370/17, Delft

Fiala, K. (1993). Underground biomass in meadow stands. *Structure and Functioning of Seminatural meadows* (ed. by M. Rychnovská), pp. 133-151, Czechoslovak Academy of Sciences, Academia, Prague.

Fiala, K. & Studeny, V. (1988). Cutting and fertilization effect on the root system in several grassland stands. II. Vertical distribution of root biomass and changes in the carbohydrate content. *Ekologia* (CSSR) **7**(1): 27-42.

Fitter, A.H. (1987). An architectural approach to the comparative ecology of plant root systems. *New Phytol.*, **106**, 61-77.

Fitter, A.H. (1994). Architecture and biomass allocation as components of the plastic response of root systems to soil heterogeneity. *Exploiting of Environmental Heterogeneity by plants* (ed. by M.M. Caldwell & R.W. Pearcy), 305-323, Academic Press, London.

Fliervoet L.M. (1984). *Canopy structure of Dutch grasslands*. Thesis, University of Utrecht, Utrecht.

Fliervoet, L.M. (1992). *Aanleg en beheer van grasland op rivierdijken*. Rapport. Unie van Waterschappen en Adviesgroep Vegetatiebeheer, IKC-NBLF, Wageningen, 63 pp.

Glinsky, J., & Lipiec, J. (1993). *Soil Physical Conditions and Plant Roots*. CRC Press. Florida.

Goss, M.J. (1991). Consequences of the activity of roots on soil. *Plant Root Growth an ecological perspective* (ed. by D. Atkinson), spec. publ. British Ecological Society, nr 10, pp. 171-186, Blackwell Scientific Publishers, Oxford.

Gough, M.W., & Marrs, R.H. (1989). A Comparison of Soil Fertility between Semi-natural and Agricultural Plant communities: Implications for the Creation of Species-rich grassland on Abandoned Agricultural Land. *Biological Conservation*, **51**, 83-96.

Grime J.P. & Lloyd, P.S. (1973). *An ecological atlas of grassland plants*. Edward Arnold, London.

Grime, J.P. (1979). *Plant strategies and vegetation processes.* John Wiley and Sons, Chichester.

Grime, J.P., Mackey, J.M.L., Hillier, S.H., & Read, D.J. (1987). Floristic diversity in a model system using experimental microcosms. *Nature,* vol. 328, 420-422.

Grime, J.P., Campbell, B.D., Mackey, J.M.L. & Crick, J.C. (1991). Root plasticity, nitrogen capture and competitive ability. *Plant Root Growth, an ecological perspective* (ed. by D. Atkinson), pp. 381-398, spec. publ. British Ecological Society, nr 10, Blackwell publ., London.

Grime, J.P. (1994) Role of plasticy in exploiting environmental heterogeneity. *Exploiting of Environmental Heterogeneity by plants* (ed. by M.M. Caldwell & R.W. Pearcy), pp. 1-19, Academic Press, London.

Gross, K.L., Pregitzer, K.S., & Burton, A.J. (1995). Spatial variation in nitrogen availability in three successsional plant communities. *Journal of Ecology,* 83, 357-367.

Hartge, K.H. (1994). Soil Structure, its Development and its implications for Properties and Processes in Soils – a synopsis based on recent research in Germany. *Z. Pflanzenernähr. Bodenk.,* 157, 159-164.

Hrabe, F. & Halva, E. (1993). Exploitation and management of grassland in the BohemianMoravian Uplands. *Structure and function of seminatural meadows* (ed. by M. Rychnovská), pp.323-340, Czechoslowak Academy of Sciences, Academia, Prague.

Heemsbergen, H. (1994). Mag het iets minder zijn ? – Gebruik van bestrijdingsmiddelen in beheers- en reservaatsgebieden. IKC-NBLF-rapport nr. 2, Ministerie van Landbouw, Natuurbeheer en Visserij, Utrecht.

Hermy, M. & De Blust, G., eds. (1997). *Punten en lijnen in het Landschap.* Schuyt & co., Haarlem, 336 pp.

Hewlett, H.W.M., Boorman, L.A. & Bramley, M.E. (1987). *Design of reinforced grass waterways.* Construction Industry Research and Information Association, Report 116, London.

Hill, M.O. (1979a). *DECORANA - a FORTRAN program detrended correspondence analysis and reciprocal averaging.* Ecology and Systematics, Cornell University, Ithaca, New York.

Hill, M.O. (1979b). *TWINSPAN, a FORTRAN program for arranging multivariate data in an ordered two way table by classification of the individuals and attributes.* Ecology and Systematics, Cornell University, Ithaca, New York.

Hill, M.O., & Gauch, H.G. (1980) Detrended correspondence analysis, an improved ordination technique. *Vegetatio,* 42, 47-58.

Hill, M.O., Evans, D.F., & Bell, S.A. (1992). Long-term effects of excluding sheep from hill pastures in North Wales. *Journal of Ecology,* 80, 1-13.

Hook, P.B., Lauenroth, W.K. & Burke, I.C. (1994). Spatial patterns of roots in a semiarid grassland: abundance of canopy openings and rgeneration gaps. *Journal of Ecology* 82, 485-494.

Hornung, M. (1990). Measurement of Nutrient Losses resulting from Soil Erosion. *Nutrient Cycling in terrestrial Ecosystems* (ed. by A.F. Harrison and P. Ineson), pp.80-102, Elsevier Applied Science, London.

Houba, V.J.G., Van der Lee, J.J., Novozamsky, J., Walinga, I.(1989). *Soil and Plant Analysis, part 5: Soil Analysis Procedures.* Dpt. of Soil Science and Plant Nutrition, Agricultural University, Wageningen.

Hrabe, F. & Halva, E. (1993). Exploitation and management of grassland in the BohemianMoravian Uplands. *Structure and Functioning of Seminatural meadows* (ed. by M. Rychnovská), pp. 323-339, Czechoslovak Academy of Sciences, Academia Praha.

Huisman, P.J. (1976). Onderhoud van grasmat op dijken. *Flevobericht,* nr. 120.

Hutchings, N.J. (1991). A model of a grass sward continuously grazed to a constant mean height. *Ecological Modelling,* 59, 73-91.

Jackson, R.B., & Caldwell M.M. (1993). Geostatistical patterns of soil heterogeneity around individual perennial plants. *Journal of Ecology*, **81**, 683-692.

Jackson, R.B., & Caldwell M.M. (1996). Integrating resource heterogeneity and plant plasticity: modelling nitrate and phosphate uptake in a patchy soil environment. *Journal of ecology*, **84**, 891-903.

Johanson, J.C.P. (1990). *Bath, dimensionering van de bekleding*. DWW-notitie WB-AN-90.123, Rijkswaterstaat, Dienst Weg en Waterbouwkunde, Delft, 20 pp.

Jongman, R.H.G., ter Braak, C.J.F., Van Tongeren O.F.R. (eds.) (1987). *Data analysis in community and landscape ecology*. Pudoc Wageningen, 299 pp.

Jonker, J.J. & Prummel, B. (1958). Onderhoud van de grasmat. *Grasmat op dijken*. Rapport van de werkgroep, 81-86., Kon. Inst. v. Ingenieurs & Kon. Gen. v. Landbouwwetenschappen, Den Haag, Wageningen.

Kandeler, E & Murer, E (1993). Aggregate stability and soil microbial processes in a soil with different cultivation. *Geoderma*, 56, 503-513.

Keddy, P. (1991). Plant competition and resources in old fields. *Tree*, vol. 6, no.8, 235-237.

Kent, M. & Coker, P. (1992). *Vegetation description and analysis a practical approach*. Belhaven Press, London, 363 pp.

Kiehl, K., Eischeid, I., Gettner, S.,Walter J. & Klotzli, F. (1996). Impact of different sheep grazing intensities on salt marsh vegetation in northern Germany. Int. Symp. on Community ecology and conservation Biology. *Journal of vegetation Science*. 7:1, 99-106.

Kleijn, D. 1997. *Species richness and weed abundance in the vegetation of arable field boundaries*. PhDthesis, Wageningen Agricultural University, Wageningen, 177 pp.

Kmoch, H.G. (1952). Ueber den Umfang und einige Gesetzmässigkeiten der Wurzelmassenbildung unter Grasnarben. *Z. Acker Plflanzenb*. 95, 363-380.

Knight, D (1989). Nice work for a worm. *New Scientist* 8 july 1989, 55- 59.

Koerselman, W., & Meuleman, A. F.M. (1996). The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *Applied Ecology*, 33, 1441-1450.

Korzilius, E.P.E. (1990). *Validatie keuringseisen klei voor bekleding van dijkenmet grasbedekking*. Rapport CO307280/10, Grondmechanica Delft, 75 pp.

Kopecky, K. & Hejný, S. (1974). A new approach to the classification of anthropogenic plant communites. *Vegetatio* **29**, 17-20.

Kopecky, K. & Hejný, S.(1978). Die Anwendung einer deduktiven Methode syntaxonomischer Klassifikation bei der Bearbeitung der strassenbegleitenden Pflanzengeselschaften Nordostböhmens.*Vegetatio* **36** (1), 43-51.

Koster, A. (1991). Spoorwegen, toevluchtsoord voor plant dier. Uitgeverij KNNV, 236 pp.

Kruijne, A.A., De Vries, D.M., Mooi, H. (1967). *Bijdrage tot de ecologie van de nederlandse graslandplanten*. Pudoc, Wageningen, 65 pp.

Kruse, G.A.M. (1993) *Opbouw en erosie van graszode op dijken*. Grondmechanica Delft rapport CO307282/18 voor Rijkswaterstaat, Dienst Wegen Waterbouwkunde, Delft

Kruse, G.A.M. (1994a). *Meetverslag grastaludproeven*. Grondmechanica Delft, rapport CO-334430/17 voor RWS/DWW, Delft.

Kruse, G.A.M. (1994b). *Eerste analyse van Deltagootproeven op een grastalud*. Grondmechanica Delft, rapport CO-334430/25 voor Rijkswaterstaat, Dienst Wegen Waterbouwkunde RWS/DWW, Delft.

Kutschera, L. & Lichtenegger, E. (1982). *Wurzelatlas mitteleuropäischer Grünlandpflanzen. I. Monocotyledonae*. Gustav Fischer Verlag, Stuttgart.

Lambers, H., Chapin, F.S., & Pons, T.L. (1998). *Plant Physiological Ecology*. Springer Verlag, Berlin, 540 pp.

Larcher, W. (1983). Physiological Plant Ecology. Translated and revised from the German edition (publ. 1973 by Eugen Ulmer), SpringerVerlag, Berlin.

Laustrup, C., Madsen, T.H., Jensen, J. & Poulsen, L. (1990). Dike failure calculation model based on in situ tests. *22nd International Conference on Coastal Engineering*, paper no. 176: 351-352.

Lichtenegger, E. (1985). Die Ausbildung der Wurzelsysteme krautiger Pflanzen und deren Eignung für die Böschungssicherung auf verschiedenen Standorten. *Ingenieurbiologie. Wurzelwerk und Standsicherheit von Böschungen und Hängen*. (ed. by K. Boeminghaus, K. Limpert & W. Pflug), pp.63-92, Sepia Verlag, Aachen.

Lush W.M. & Rogers, M.E. (1992). Cutting height and the biomass and tiller density of *Lolium perenne* amenity turfs. *Journal of Applied Ecology*, **29**, 611-618.

Lynch, J.M. (1990). Some consequences of microbial rhizosphere competence for plant and soil. *The Rhizosphere. Wiley Series in ecological and applied microbiology* (ed. by J.M. Lynch) pp. 135, John Wiley & Sons, Chichester.

Maarel, E. van der (1979). Transformation of coverabundance values in phytosociology and its effects on community similarity. *Vegetatio* **39** (2): 97-114.

Mamolos, A.P., Elisseou, G.K., & Veresoglou, D.S. (1995). Depths of root activity of coexisting grassland species in relation to N and P additions, measured using non radioactive tracers. *Journal of Ecology*, **83**, 643-652.

Margadant W.D., H. During (1982). *Beknopte flora van de Nederlandse blad en levermossen*. W.J. Thieme & Cie, Zutphen.

Marschner, H. (1995). *Mineral Nutrition of Higher Plants*, 2nd edn., Academic Press, San Diego.

Matthew, C., Xia, J.K., CHU, A.C.P., Mackay, A.D. & Hodgson, J. (1991). Relationship bewteen root production and tiller appearance rates in perennial ryegrass (*Lolium perenne* L.). *Plant Root Growth, an ecological perspective* (ed. by D. Atkinson), pp. 281-309, spec. publ. British Ecological Society, nr 10, Blackwell publ., London.

Mcconnaughay K.D.M. & Bazzaz, F.A. (1992). The occupation and fragmentation of space: consequences of neighbouring roots. *Functional Ecology* **6**, 704-710.

McMichael, B.L., & Quisenberry, J.E. (1993). The impact of the soil environment on the growth of root systems. *Environmental and Experimental Botany*, vol. **33**, No.1, 53-61.

Mennema, J., Quene-Boterenbrood, A.J., & Plate, C.L. (1985, red.). *Atlas van de Nederlandse Flora 2. Zeldzame an vrij zeldzame planten*. Bohn, Scheltema & Holkema, Utrecht, 349 pp.

Meijden, R. van der (1990). Heukels' Flora van Nederland. WoltersNoordhoff, Groningen, 662 pp.

Miles, J. (1987). Soil variation caused by plants: a mechanism of floristic change in grassland? *Disturbance in grasslands* (ed. by J. van Andel, J.P. Bakker & R.W. Snaydon), pp. 37-49, Junk, Publ., Den Haag.

Miller, R.E., Verhoef, J.M., & Fowler, N.L. (1995). Spatial heterogeneity in eight central Texas grasslands. *Journal of Ecology*, **83**, 919-928.

Minderhoud, J.W. (1989). Aanleg en onderhoud van de grasmat op water kerende dijken. *Handboek grasveldkunde en grasveldbeheer* (ed. by J.W. Minderhoud, M. Hoogerkamp & J.G.C. van Dam), pp. 168-179, Pudoc Wageningen.

Morecroft, M.D., Sellers, E.K., & Lee, J.A. (1994). An experimental investigation into the efrfects of atmospheric nitrogen deposition on two semi-natural grasslands. *Journal of ecology*, **82** , 475-483.

Morgan, R.P.C. & Rickson, R.J. (1995). Water erosion control. *Slope Stabilisation and Erosion Control a Bioengineering Approach* (ed. by R.P.C. Morgan & R.J. Rickson), pp. 133-190, E & F N Spon, Chapman & Hall, Cambridge.

Mountford, J.O., Lakhani, K.H., & Kirkham, F.W. (1993). Fertilizer effects on grassland composition. *Journal of Applied Ecology*, 30, 321-332.

MuellerDombois, D & Ellenberg, H. (1974). *Aims and methods of vegetation ecology*. John Wiley and Sons, London: 547 pp.

Muijs, J.A. (1996). *Scheurvorming in de kleibekleding van het binnentalud van de Balgzanddijk mogelijke oorzaken en remedies*. Nota WD-WW-96052, Rijkswaterstaat, Dienst Weg en Waterbouwkunde, Delft, 29 pp.

Neuteboom J.H., Lantinga, E.A. & Van Loo, E.N. (1992). The use of frequency estimates in studying sward structure. *Grass and Forage Science*. Volume 47, 358-365.

Newman, E.I. (1966). A method for estimating total length of root in a sample. *J. Appl. Ecol.* 3: 139-145.

Norusis, M.J. (1986). *SPSS/PC+: SPSS for the IBM PC/XT/AT*. SPSS inc., Chicago, Illinois.

Oberdorfer, E. (1983). *Süddeutsche Pflanzengesellschaften. Teil III.* G. Fischer Verlag, Stuttgart.

Olff, H., Van Andel, J. & Bakker, J.P. (1990). Biomass and shoot/rootallocation of five species from a grassland succession series at different combinations of light and nutrient supply. *Functional Ecology*, 4: 193-200.

Olff, H. & Bakker, J.P. (1991). Longterm dynamics of standing crop andspecies composition after the cessation of fertilizer application to mown grassland. *Journal of Applied Ecology*, 28: 1040-1052.

Olff, H., Berendse, F. & De Visser, W. (1994a). Changes in nitrogen mineralisation , tissue nutrient concentrations and biomass compartmentation after cessation of fertilizer application to mown grassland. *Journal of Ecology*, 82: 611-620.

Olff, H., Pegtel, D.M., Van Groenendael, J.M., Bakker, J.P. (1994b). Germination strategies during grassland succession. *Journal of Ecology* 82: 69-77.

Oomes, M.J.M. (1990). Changes in dry matter and nutrient yields during the restoration of speciesrich grasslands. *Journal of Vegetation Science* 1: 333-338.

Oomes, M.J.M. & Mooi, H. (1985). The effect of management on succession and production of formerly agricultural grassland after stopping fertilization. *Sukzession auf Grünlandbrachen* (ed. by K.B. Schreiber), pp. 59-67, Symp. I.V.V., Münstersche Geographische Arbeiten, Paderborn.

Oomes, M.J.M. & Altena, H.J. (1987). Drogestof-produktie en mineralenoogst bij verschralend beheer. *De Levende Natuur* 88 (6): 248-253.

Oomes, M.J.M., Olff H., Altena H.J. (1996). Effects of vegetation management and raising the water table on nutrient dynamics and vegetation change in a wet grassland. *Journal of applied Ecology* 33: 576-588.

Ozinga, W.A., Van Andel, J., & McDonnell-Alexander, M.P. (1997). Nutritional soil heterogeneity and mycorrhiza as determinants of plant species diversity. *Acta Botanica Neerlandica*, 46 (3), 237-254.

Passioura, J.B. (1991). Soil Structure and Plant Growth. Aust. J. Soil Res., 29, 717-728.

Pegtel, D.M. (1987). Soil fertility and the composition of semi-natural grassland. *Disturbance in grasslands* (ed. by J. van Andel, J. Bakker & R.W. Snaydon), pp.51-66, Junk Publishers, Dordrecht.

Perfect, E., Kay, B.D., Van Loon, W.K.P., Sheard, R.W., Pojasok,T. (1990). Factors influencing soil structural stability within a growing season. *Soil Science Soc. Am. J.*, 54: 173-179.

Robertson, G.P. & Gross, K.L. (1994). Assessing the Heterogeneity of Belowground Resources: Quantifying Pattern and Scale. *Exploitation of environmental heterogeneity by plants* (ed. by M.M. Caldwell & R.W. Pearcy), pp. 237-253, Academic press, New York.

Rorison, H.I. (1987). Mineral nutrition in time and space. *New Phytologist* **106** (Suppl.), 79-92

Rozenzweig, M.L.(1995). *Species Diversity in Space and Time.* Cambridge University Press, Cambridge.

Ruitenberg, G.H., Wopereis, F.A., & Oenema, O. (1991). *Berekende optimale stikstofbemesting voor grasland als functie van grondsoort.* Rapport 173, NMI, DLO-SC, Haren, Wageningen.

Ryser, P., & Lambers, H. (1995). Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. *Plant and Soil,* **170,** 251-265.

Sato, K., & Tokunaga, K. (1989). Studies on the macrophores structure of grassland's soil. *XVI International Grassland Congress,* Nice.

Sattelmacher, W., Gerendas, J., Thoms, K., Brück, H., & Bagdady, N.H. (1993). Interaction between root growth and mineral nutrition. *Environmental and experimental Botany,* Vol. **33,** nr.1, 63-73.

Schaffers, A.P. (1991). *DENDRO; programma voor het maken van dendrogrammen.* Vakgroep VPO, Landbouwuniversiteit, Wageningen.

Schaffers, A.P., Vesseur, M.C., & Sykora, K.V. (1997). Short term nutrient losses from cuttings of roadside vegetation; effects of a delayed removal of cuttings on nutrient balance. *Journal of Applied Ecology* **35,**349-364.

Schaminée, J.H.J., Stortelder, A.H.F., & Weeda, E.J. (1995). *De Vegetatie van Nederland,* deel 1, Opulus Press, Uppsala.

Schiechtl, H.M. (1985). Pflanzen als Mittel zur Bodenstabilisierung. *Ingenieurbiologie. Wurzelwerk und Standsicherheit von Böschungen und Hängen* (ed. by K. Boeminghaus, K. Limpert & W. Pflug), pp. 50-62, Sepia Verlag Aachen..

Schippers, P., & Olff, H. (1998). Biomass partioning, architecture and plasticity of herbaceous species in relation to their position in an old field succession. *Oecologia* (submitted).

Scholand, M., Austenfeld, F.A. & Von Willert, D.J. (1991). Underground biomass and its influence on soil shear strenght in a grazed and ungrazed german coastal marsh.. *Plant Root Growth, an ecological perspective* (ed. by D. Atkinson), pp. 281-309, spec. publ. British Ecological Society, nr 10, Blackwell publ., London.

Schreven, A.C. (1947). *De begroeiing van de zeedijken aan de noordkust van Groningen.* Rijkswaterstaat, Directie Landaanwinning Landaanwinningswerken in Friesland en Groningen, Baflo.

Schubert, R. (1991). Root research in natural ecosystems. *Plant roots and their environment* (ed. by B.L. McMichael and H. Persson), pp. 344-365.

Seijffert, J.J.W. & Philipse, L.A. (1990). Resistance of grassmat to waveattack. PIANC, 2 pp.

Sibma, L. & Ennik, G.C. (1988). Ontwikkeling en groei van productiegras onder Nederlandse omstandigheden. Pudoc Wageningen, 53 pp.

Silvertown, J., Lines, C.E.M., Dale, M.P. (1994). Spatial competition between grasses – rates of mutual invasion between four species and the interaction with grazing. *Journal of Ecology,* **82,** 31-38.

Smit A.L., Sprangers, J., Sablik, J.P.W. & Groenwold, J. (1994). Automated rootlength measurement with a 3DHighresolution scanner and image analysis. *Plant and Soil* **158:** 145-149.

Smith, G.M., (1993). *Grasdijken; Graserosie, reststerkte en golfoverslag.* Concept meetverslag grootschalig modelonderzoek, H1565, Waterloopkundig Laboratorium, Delft, 153 pp.

Smith, R.S. & Rushton, S.P. (1994). The effects of grazing management on the vegetation of mesotrophic (meadow) grassland in Northern England. *Journal of Applied Ecology* **31:** 13-24.

Sokal, R.S. & Rohlf, F.J. (1995) *Biometry: the Principles and Practice of Statistics in Biological Research,* 3rd edn. W.H. Freeman and Company, New York

Sprangers, J.T.C.M. (1989). *Vegetatie van Nederlandse zeedijken; plantengemeenschappen in relatie tot standplaatsfactoren.* Vakgroep Vegetatiekunde, Plantenoecologie en Onkruidkunde, Landbouwuniversiteit Wageningen, voor DWW/Rijkswaterstaat, Delft, 119 pp.

Sprangers, J.T.C.M. (1991). *Vegetatie en erosiebestendigheid van zeedijken in relatie tot beheer.* Voortgangsrapport1, intern rapport Vakgroep Terrestrische Ecologie & Natuurbeheer, Landbouwuniversiteit Wageningen, voor DWW/Rijkswaterstaat, Delft, 46 pp.

Sprangers, J.T.C.M. (1992). Vegetatie, zodestructuur en worteldichtheid van graszoden voor golfbelastingsproeven in de Deltagoot. *Grasdijken; graserosie, reststerkte en golfoverslag* (ed. by G.M. Smith), appendix III, Rapport Waterloopkundig Laboratorium voor DWW/RWS, Delft.

Sprangers, J.T.C.M. (1993). *Erosie sproeiproef op een dijk bij Holwerd.* Intern rapport RWS/DWW, Delft, 15 pp.

Sprangers, J.T.C.M. (1994). Grasland als dijkbekleding. M. Vroom, *Samenvatting van lezingen Kust en oeverdag 1993.*(ed. by M Vroom), pp. 60-66, Werkdocument RIKZ/AB94.601, Rijksinstituut voor Kust en Zee, Rijkswaterstaat, Haren..

Sprangers, J.T.C.M., Fliervoet, L.M. & Sýkora, K.V. (1991). Botanische en civieltechnische aspecten van zeedijkvegetaties. *Landinrichting* 1991/31 nr.5: 2-10.

Sprangers, J.T.C.M., & Muijs, J.A.. (1997). *Groene zeedijken in Noord-Duitsland en Denemarken- verslag van een studiereis 3-7 juni 1991.* Rapport DWW/Rijkswaterstaat, Delft.

Sprangers, J.T.C.M., & Raemakers, I. (1998). *Erosiebestendigheid van zeedijkgrasland - effecten van extensief beheer na een periode van 7 jaar.* Rapport DWW/Rijkswaterstaat, Landbouwuniversiteit, Wageningen.

Sprangers, J.T.C.M., & Arp, W. A. (1998). *Syllabus cursus kwaliteitsherkenning dijkgrasland.* Rapport IBN-DLO, Wageningen (in prep).

Strykstra, R.J., Bekker, R.M., & Bakker, J.P. (1998) Assesment of dispersule availability:its practicle use in restoration management. *Acta Botanica Neerlandica* **47**, 45-56

Stark, J.M. (1994). Causes of soil nutrient heterogeneity at different scales. *Exploitation of environmental heterogeneity by plants* (ed. by M.M. Caldwell & R.W. Pearcy), 255-284, Academic press, New York.

Steur, G.G.L., Locher, W.P. & De Bakker, H. (1987). *Veldboekje Bodemkunde.* Stichting voor Bodemkunde, Wageningen.

Styczen, M.E. & Morgan, R.P.C. (1995). Engineering properties of vegetation. *Slope Stabilisation and Erosion Control a Bioengineering Approach* (ed. by R.P.C. Morgan & R.J. Rickson), pp. 558, E & F N Spon, Chapman & Hall, Cambridge.

Sýkora, K.V., 1983. *The LolioPotentillion anserinae R. Tüxen 1947 in the northern part of the Atlantic Domain.* Thesis, Stichting Studentenpers Nijmegen.

Sýkora, K.V. & Liebrand, C.I.J.M. (1987). *Natuurtechnische en civieltechnische aspecten van rivierdijkvegetaties.* Vakgroep Vegetatiekunde, Plantenoecologie en Onkruidkunde, Landbouwuniversiteit Wageningen, Ponsen & Looijen, Wageningen, 194 pp.

Sýkora, K.V. & Liebrand, C.I.J.M. (1988). Revegetation of river dikes and techniques for encouragement of species-rich grassland. *Aspects of Applied Biology* **16**: 9-18.

Sýkora, K.V., Van der Krogt, G, Rademakers, J. (1990). Vegetation change on embankments in the southwestern part of the Netherlands under the influence of different management practices (in particular sheep grazing). *Biological Conservation* **52**, pp. 49-81.

Sýkora, K.V., De Nijs, L., & Pelsma, T.A.H.M. (1993). *Plantengemeenschappen van Nederlandse wegbermen.* Uitgeverij KNNV, Utrecht.

Sýkora, K.V., Schaminée, J.H.J., & Weeda , E.J. (1996) Plantaginetea majoris. *De vegetatie van Nederland, deel 3* (ed. by J.H.J. Schaminée, A.H.F. Stortelder, & E.J. Weeda), 13-46, Opulus Press, Uppsala.

Sykora, K.V. & Westhoff, V.W. (1979). Droge stroomdalgraslanden langs de Maas en Niers (with English summary). *Gorteria* 9, nr. 10, pp. 334-341.

Tennant, D. (1975). A test of a modified line intersect method of estimatingroot length. *Journal of Ecology 63*, pp. 995-1001.

Tengbeh, G.T. (1989). *The effect of grass cover on bank erosion.* Thesis, Silsoe College, Cranfield Institute of technology.

Ter Braak, C.J.F. (1987). *CANOCO a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal component analysis and redundancy analysis (version 2.1).* Agricultural Mathematics Group, Wageningen, 95 pp.

Thierry, J.W. (1958). Algemene beschouwingen. *Grasmat op dijken.* Rapport van de werkgroep, pp. 511, Kon. Inst. v. Ingenieurs & Kon. Gen. v. Landbouwwetenschappen, Den Haag, Wageningen.

Thórallsdóttir, T.E. (1990a). The dynamics of a grassland community: a simultaneous investigation of spatial and temporal heterogeneity at various scales. *Journal of Ecology,* **78**, 884-908.

Thórallsdóttir, T.E. (1990b). The dynamics of five grasses and white clover in a simulated mosaic sward. *Journal of Ecology,* **78**, 909-923.

Thorne, C.R. (1990). Effects of Vegetation on Riverbank Erosion and Stability. *Vegetation and Erosion* (ed. by J.B. Thornes), 125-144, John Wiley & Sons, Chichester, UK.

Throughton, A. (1981). Lenght of life of grass roots. *Grass and Forage Science* 36, 117-120.

Tilman, D. (1982). *Resource competition and community structure.* Princeton University Press, Princeton.

Tilman, D. (1986). Resources, competition, and the dynamics of plant communities. *Plant Ecology* (ed. by. M.J. Crawley), pp. 51-75, Blackwell, Oxford.

Tilman, D. (1988). *Plant strategies and the dynamics and structure of plant communities.* Princeton University Press, Princeton.

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology,* **75**, 2-16.

Tilman, D. (1997). Mechanisms of plant competition. *Plant Ecology,* 2nd Edition (ed. by M.J. Crawley), pp. 239-261, Blackwell, Oxford.

Tuzinkevich, A.V., & Frisman, Ye.Ya. (1990). Dissipative structures and patchiness in spatial distribution of plants. *Ecological Modelling,* **52**, 207-223.

Van der Werff, A. (1993). *Fast- and slow-growing monocots; the effects of N-supply on respiration, photosynthesis and optimization of carbon and nitrogen allocation.* Thesis. Utrecht University, Utrecht.

Van Noordwijk, M, Johan F., & De Jager, A. (1985). Sampling schemes for estimating root density distribution in cropped fields. *Netherlands Journal of Asgricultural Science,* **33**, 241-262.

Van Noordwijk, M., & De Willegen, P. (1987). Agricultural conceptsof roots: from morphogenetic to functional equilibrium between root and shoot growth. *Netherlands Journal of Agricultural Science* **35**, 487-496.

Verheij, H.J., Meijer, D.G., Kruse, G.A.M., Smith, G.M. & Vesseur, M. (1995). *Onderzoek naar de sterkte van graszoden van rivierdijken.* Rapport Q1878, Waterloopkundig Laboratorium, DWW/RWS, Delft, 218 pp.

Waldron, L.J. (1977). The shear resistance of rootpermeated homogeneous and stratified soil. *Soil Science,* **132**, 427-35.

Walinga I, Van Vark, W.G., Houba, V.J.G., Van der Lee, J.J. (1989). *Soil and Plant Analysis, part 7: Plant Analysis Procedures.* Dpt. of Soil Science and Plant Nutrition, Agricultural University, Wageningen., 239 pp.

Werger, M.J.A., 1974. The place of the ZürichMontpellier method in vegetation science. *Folia Geobot. Phytotax., Praha,* 9: 99-109.

Westhoff V. & Van der Maarel, E. (1973). The BraunBlanquet Approach. *Handbook of Vegetation Science* (ed. by R.H. Whittaker), pp. 619-726, Junk, Publ, Den Haag.

Westhoff V. & Den Held, J.J. (1975). *Plantengemeenschappen in Nederland.* Thieme, Zutphen, 324 pp.

Wilkins, R.J., Hopkins, A., Kirkham, F.W., Sargent, C., Mountford, O., Dinn, C., Gilbey, J. (1989). Effects of changes in fertilizer use on the composition and productivity of permanent grassland in relation to agricultural production and floristic diversity. *XVI International Grassland Congress,* Nice, 101-102.

Wilson, S.D., & Tilman, D. (1991a). Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community. *Oecologia,* 88, 61-71.

Wilson, S.D., & Tilman, D. (1991b). Components of plant competition along an experimental gradient of nitrogen availability. *Ecology,* 72 (3), 1050-1065.

Wilson, E.J., Wells, T.C.E., & Sparks, T.H. (1995). Are calcareous grasslands in the UK under threat from nitrogen deposition? – an experimental determination of critical load. *Journal of Ecology,* 83, 823-832.

Wu, T.H. (1995). Slope stabilisation. *Slope Stabilisation and Erosion Control a Bioengineering Approach* (ed. by R.P.C. Morgan & R.J. Rickson), pp. 221-264, E & F N Spon, Chapman & Hall, Cambridge.

Yen, C.P. (1987). Tree root patterns and erosion control. *Proceedings of the International Workshop on Soil Erosion and Its Countermeasures* (ed. by S. Jantawat), pp. 92-111, Soil and Water Conservation Society of Thailand, Bangkok.

Zee, F.F. van der (1992). *Botanische samenstelling, oecologie en erosiebestendigheid van rivierdijkvegetaties.* Landbouwuniversiteit Wageningen, in opdracht van DWW/Rijkswaterstaat, 271 pp.

Zhang, H.Q. & Horn, R. (1996). Effect of sheepgrazing on the soil physical properties of a coastal salt marsh (II): soil strength. *Zeitschrift für Kulturtechnik und Landentwicklung* 37, 5: 214-220.

Ziemer, R.R. (1981). Roots and stability of forested slopes. *Int. Assoc. Hydrol. Sci.,* Pub. No. 132, 343-361.

Zuidhoff, A.C., Schaminée, J.H.J., & Van 't Veer, R. (1996). Molinio-Arrhenatheretea. *De vegetatie van Nederland, deel 3: plantengemeenschappen van graslanden, zomen en droge heiden* (ed. by J.H.J. Schaminée, A.H.F. Stortelder, & E.J. Weeda), pp.13-46, Opulus Press, Uppsala.

Zonderwijk, P. (1979). *De bonte berm.* Zomer & Keuning Boeken bv., Ede.

Summary

In the Netherlands, in addition to the width and height of the dyke body itself, renewed measures for reconstruction and maintenance of dykes have stressed the importance to the safeguarding of the dyke, of the grass cover's protection of the clay-layer against erosion.

From an inventory of different aspects of dyke grassland erodibility and the construction of the grass-clay complex (Chapter 1), it became clear that roots and the configuration of the root system hold the key to the specific erosion resistance properties of grasslands on clay dykes. Roots have a considerable influence on soil stability as well as soil porosity. They contribute to the formation of small aggregates in clay soils and supply adhesive substances which bind these particles, resulting in a fine structured and stable soil. Conduits remain where roots die off, increasing the total pore volume and thus the permeability of the soil, which enables rapid draining of incoming water from wave attack or overtopping. A high porosity and fine structure of cemented particles ensures that only relatively small amounts of soil material will be washed away, while a dense root network prevents larger soil particles to flush away.

Management of the grass sward has a great impact on the quality of erosion resistance, because of its influence on vegetation cover and root density. Sheep grazing or frequent cutting usually results in a closed sward but also reduces the amount of root growth. Haymaking on the other hand, leads to deeper root growth at the cost of shoot density. When fertilizer is applied on pastures or when cuttings are not removed, root densities are low, and overgrazing or suffocation results in large open spots. Previous studies on dyke grasslands revealed that, in contrast with species-poor, heavily fertilized and intensively grazed pastures or fertilized hayfields, the species-rich vegetation types (unfertilized pasture or hay meadow) have a dense root system and a relatively high erosion resistance.

In Chapter 1 the relation between management, vegetation type, root density and erodibility is reviewed in detail, with the emphasis on the increase of root density by lowering the nutrient level in soils. This review brings us to the main question of this thesis: *is it possible to enhance root density and erosion resistance of dyke grassland by cessation of fertilization combined with a less intensive grazing or cutting regime?* To answer this question, an experiment was set up on dykes along the Dutch coast (Chapter 2) to analyse the effects of cessation of fertilization and different management types on: botanical composition and vegetation cover (Chapter 3); above- and belowground biomass and the amount of nutrients in plant and soil(Chapter 4); and erosion resistance (Chapter 6). Seasonal variability and spatial patterns in vegetation cover and root density have also been analysed (Chapter 5), and practical implications of the results discussed (Chapter 7).

Experiment

In January 1991 14 locations were selected on grazed dykes for four treatments on each location: continuing grazing with the use of fertilizer; two periods grazing without fertilizer

application; haymaking followed by grazing without fertilizer use; and haymaking (two cuts) without fertilizer application. On mown dykes 9 locations were selected for two treatments: haymaking with and without fertilizer application. Species-rich hay meadows that had not been fertilized for at least 20 years were treated as references.

In March 1994, data on vegetation cover and root density were collected from plots in the different treatments at all sites, and erosion spray experiments were carried out. Samples were taken at the same time for erosion centrifuge experiments. In the summer of 1994 the botanical composition in the plots was described and soil samples were taken together with data of the above and belowground biomass. The aboveground biomass was also determined for the preceding years. Seasonal variability in above- and belowground production was analysed on the basis of six-weekly measurements in 1992 in fertilized pastures and on reference dykes. Data on spatial variation were collected in 1993. The experiment continued until the summer of 1997, and data were collected in 1995 and 1997.

Botanical composition and vegetation cover.

The vegetation of the investigated dyke grasslands (Chapter 3) can be described as relatively species poor (8 to18 species per 25 m²), although some sporadic species-rich grasslands were located (25 to 34 species per 25 m²). Nine plant communities were distinguished. Three communities were assigned to variants of the *Lolio-Cynosuretum cristati* and a related trunk community, and one to the *Poo-Lolietum*, while five communities were described as variants and subassociations of the *Arrhenatheretum elatioris* and trunk communities characterized by species of the *Arrhenatheretalia*. Although the variance in species composition was primarily determined by the difference in study sites and linked habitat factors (soil texture, exposure to sunlight and salt spray), multivariate analysis of species cover and environmental factors revealed a small but significant effect of cessation of fertilizer application in combination with grazing or haymaking.

Cessation of fertilizer application produced a slight increase of species numbers (from 13 to 16 species per 25 m² in unfertilized treatments on grazed dykes and 14 to 17 species on mown dykes), and a strong decline in cover /abundance of *Lolium perenne* and an increased abundance of species indicative of less nutrient-rich conditions like *Festuca rubra* and *Trifolium dubium*. Furthermore, the proportion of herbs in the grass sward was observed to have increased. The question remains as to whether this rather rapid response to the change in regime, compared to other experiments, is an effect of the poor moisture conditions of dyke grasslands, resulting in a direct, drastic lowering of nutrient availability when fertilization has stopped.

The observed vegetation change after fertilization cessation combined with haymaking, which also on sea dykes can be considered as the result of the interaction between the changed nutrient availability and vegetation structure, did not adversely affect the sward density. The somewhat lower cover of the vegetation in the species-rich hay meadows is compensated by a high shoot density, indicating a diffuse distribution of shoots over the surface and the presence of small open spots. This means that apart from vegetation cover (cut back to 2 cm above ground level) shoot density must also be taken into account when judging the sward quality from a civil engineering point of view.

Above and belowground biomass

The rather rapid decline observed in aboveground biomass production 3-4 years after stopping fertilization (from 9-10 tonnes dry matter to 7 t ha^{-1}y^{-1}) followed by a further decline up to 5-6 t ha^{-1}y^{-1} after 7 years, complies with the results of a restoration experiment of species-rich meadows on clay and peat soils. Shifting from grazing to haymaking, without the use of fertilizer, results in the most rapid fall in productivity from 9 to 5 t ha^{-1}y^{-1} after 7 years, reaching a level that is favourable for the development of species-rich grassland. The peak biomass (July) is higher on sun exposed slopes, whereas regrowth (July - October)on these slopes is lower compared to slopes that receive a smaller amount of sunlight. In agreement with the decrease in production a decline in availability of mineral nitrogen was measured. The total soil N pool in unfertilized treatments, however, did not change when compared to the fertilized plots, although there seems to be a small net N off-take according to our calculations, especially in the mown treatments. In spite of low P concentrations in shoots of the species-rich old meadows, the low N/P ratio indicates that productivity is N limited in these grasslands.

Cessation of fertilization resulted in an increase of root length and root weight in the mown treatments on both pastures and hay meadows. This extension of the root system at the cost of aboveground plant parts was expressed by a lower shoot/root ratio in the unfertilized mown treatment on former pastures. The species-rich old hay meadows were characterized by a relatively high root length and root weight and a low shoot/root ratio; the maximum difference between these meadows and the species-poor fertilized pastures was detected at a depth of 3-15 cm. The latter demonstrated a sharp decline of root length density compared with a less steep decline in the species-rich meadows. In the unfertilized mown treatments the vertical distribution of roots shows similarities to that of the old meadows. Pastures exhibited relatively high values for specific root length (SRL, thin roots) and low total root weights, whereas low SRL values and high root weights (thick roots) were found in hayfields. The species-rich hay meadows, however, had high SRL values and high total root weights. The reactions of grassland plants and root growth in response to the decline in N availability and the different management types (grazing or haymaking) together with their morphological consequences are discussed.

Temporal and spatial variation

Seasonal variation in root characteristics, which can affect the erodibility of dyke grasslands, was investigated in fertilized pastures and unfertilized old hayfields (Chapter 5). Maximum aboveground biomass was reached in May-June in the fertilized pasture and in July in the hay meadow; both achieving maximum regrowth was reached in September. In agreement with the results given in Chapter 4 the investment in belowground biomass was much larger in the unfertilized hayfield than in the fertilized pasture. No significant fluctuation in root mass was measured during the year in both grassland types, so that variation in shoot/root ratio is similar to the variation in aboveground biomass. In the fertilized pasture the seasonal fluctuation in root length took place in the top 3 cm of the soil, where the increase of the predominantly fine roots paralleled the aboveground growth, with peaks in July and September. In the unfertilized hay meadow, where we measured higher root lengths at depths of 3-20 cm than in the fertilized pasture, the variation in root length occurred below this upper layer (from 3 to 40 cm).

The spatial variation in floristic diversity, vegetation cover and root weight density was studied (Chapter 5) in three grasslands belonging to the *Arrhenatheretum elatioris brizetosum* (old unfertilized hayfield), *Lolio-Cynosuretum cristati* (lightly fertilized pasture) and *Poo-Lolietum* (heavily fertilized pasture). The first two types exhibited a more mosaic pattern of floristic composition compared to the spatial floristic homogeneity of the *Poo-Lolietum*. The last-mentioned had a large spatial variation in the size of open spots, and in root growth. The high root weights in the *Arrhenatheretum* showed less spatial variation. Also, the *Lolio-Cynosuretum* had a more homogeneous spatial distribution of roots. Apparently, aboveground floristic homogeneity is not necessarily correlated with a small variation in root density. Within each grassland type, patterns in horizontal distribution of roots were not detected, and there was little variation in the vertical distribution of roots. However, in agreement with previous results (Chapter 4), in the unfertilized hay meadow, root mass declined less steeply with depth than in the other communities.

Erodibility

The erosion resistance of the dyke grassland sites was investigated by measuring three different parameters (Chapter 6): the *shear strength* at different depths of the rooted soil layer, the soil loss in erosion spray experiments (*wear erosion*), and the percentage weight loss of samples tested in an erosion centrifuge device (*internal erosion*).

Our observations revealed that the shear strength of soils with high root densities was low, while the shear strength of soils with a high percentage of loam, low vegetation cover, low root length densities or few but relatively thick roots, was high. These results suggest that shear strength does not reflect soil cohesion due to a higher root density. Moreover, no correlation was found between erosion parameters and shear strength. We concluded that shear strength can not be used as a reliable parameter for erosion resistance of grass swards on clay.

The erosion spray experiment did not reveal any significant trend in soil decline or washed out material between the different treatments. Only at higher flow rates did the species-rich hay meadows appear to be more resistant against wear erosion than species-poor pastures. It would seem that differences in wear erosion between differently managed dyke grasslands were difficult to demonstrate, because of the relatively high vegetation cover and the small range in soil particle size.

Most samples demonstrated a sudden increase in weight loss rate during the course of the centrifuge experiment. This was probably due to the roots in the soil which prevents erosion of soil particles until they are damaged to such an extent that the erosion rate is determined by soil properties only. Both erosion rates were lower in the 0-5 cm samples, whereas in the 5-10 cm samples erosion proceeded more rapidly reaching a sample collapse in most cases. Multiple regression of erosion parameters and soil and root characteristics revealed that at a depth of 0-5 cm, with the largest amount of roots, the erosion rate in the first half of the experiment (before the sudden change) was determined mainly by root density, whereas at a depth of 5-10 cm both root density and sand content influenced the rate of weight loss. In the second half of the experiment the erosion rate in both layers was influenced mainly by sand and loam content. Resistance against internal erosion is determined by the combined effects of root density and soil particle size, probably because of the influence of roots on aggregate stability and porosity. Regarding

the root length - root weight ratio, this type of soil reinforcement seems to result more from the root system as a whole, including many thin roots, than the tensile strength of the roots.

Species-rich hay meadows show higher resistance values than fertilized grasslands, which can be attributed to their higher root densities. Cessation of fertilization led to a slight increase in erosion resistance after three years. This agrees with the increase in root density and the change in botanical composition of plots were fertilization has stopped.

To judge the erodibility of grass swards on clay dykes, it is proposed to use botanical composition (reflecting root density), and shoot density (reflecting surface quality) as reliable criteria rather than clay quality of the upper layer.

Management

Both rooting pattern and spatial heterogeneity of the vegetation, being the main factors determining erosion resistance of dyke grassland, can be influenced by the type of management. The main prerequisites for a high sod quality appears to be: *the avoidance of fertilizer application* and *continuity of management and maintenance* over longer periods The unfertilized old hay meadows proved to have the highest erosion resistance and root densities. It is argued that unfertilized meadows maintained by sheep-grazing, will also have a high erosion resistance, while the agricultural earnings do not seem to differ much from those of fertilized pastures. However, fertilizer can be applied at a maximum of 50 kg N $ha^{-1}y^{-1}$ in combination with grazing, without substantial loss of sod quality, but complete stopping of fertilization gives even better results.

To improve and maintain grassland quality in terms of erosion resistance, management rules consist of: regular mowing and dragging when grazing; allowing a maximum vegetation height of 10 cm at the onset of winter; removal of cuttings after one week; active control of mole activity; and the continuity of management. It is concluded that for judging the erodibility of dyke grasslands more emphasis should be put on botanical composition, vegetation cover and root density rather than on clay quality in the sod, which is an important factor in present erodibility tests.

Samenvatting

In Nederland wordt bij nieuwe maatregelen voor verbetering en onderhoud van dijken om de veiligheid te vergroten, niet alleen rekening gehouden met de breedte en hoogte van het dijklichaam zelf, maar ook met de kwaliteit en het beheer van het dijkgrasland. De begroeiing van de dijk geeft immers een erosiebestendige bescherming aan de onderliggende kleilaag. Hoofdstuk 1 geeft een overzicht van de diverse aspecten van erosiebestendigheid van dijkgrasland en van de opbouw van het gras-klei complex. Hieruit blijkt dat vooral de wortels en de architectuur van het wortelpakket bepalend zijn voor de specifieke erosiewerende eigenschappen van grasdijken. Wortels hebben een grote invloed op de stabiliteit en porositeit van de bodem. Zij dragen bij aan de vorming van kleine klei-aggregaten en leveren kitstoffen waarmee de fijne deeltjes aan elkaar zijn gehecht. Het resultaat is een stabiele bodem met een fijne structuur. Waar wortels afsterven blijven poriën achter, waardoor het porievolume en dus de doorlatendheid van de bodem toenemen en instromend water, bijvoorbeeld door de werking van golfklappen of overslag, snel weg kan. Een dicht wortelnet voorkomt uitspoeling van de grotere bodemdeeltjes.

Het graslandbeheer heeft een duidelijk effect op bedekking van de vegetatie en op de worteldichtheid en heeft daardoor een grote invloed op de erosiebestendigheid. Beweiding met schapen of frequent maaien (gazonbeheer) leidt doorgaans tot een dichte zode, maar een beperkte wortelgroei. Hooien daarentegen levert vaak een diepere doorworteling, maar dit gaat wel ten koste van de plantdichtheid. Wanneer weiland wordt bemest of wanneer maaisel niet wordt afgevoerd, is de worteldichtheid laag en leidt overbeweiding of verstikking tot grote open plekken. Uit eerder onderzoek blijkt dat - in tegenstelling tot soortenarm, zwaar bemest en intensief beweid grasland of bemest hooiland - de soortenrijke vegetatietypen (onbemest weiland of hooiland) een uitgebreid wortelstelsel hebben en een relatief hoge erosiebestendigheid.

Een uitgebreide verkenning van de relatie tussen beheer, vegetatietype, worteldichtheid en erosiegevoeligheid (hoofdstuk 1) leidt tot de centrale vraag van het uitgevoerde onderzoek: *Nemen worteldichtheid en erosiebestendigheid van dijkgrasland toe, na beëindiging van de bemesting en aanpassing van het beweidings- of maairegiem?* In 1991 is een experiment gestart op dijken langs de Nederlandse kust (hoofdstuk 2). Hierbij werd onderzocht wat het effect is van beëindiging van bemesting en verschillend beheer op de botanische samenstelling en bedekking van de vegetatie (hoofdstuk 3), de boven- en ondergrondse biomassa-productie en chemische samenstelling van bodem en plantenweefsel (hoofdstuk 4), en de erosiebestendigheid (hoofdstuk 6). Bovendien werden de seizoensvariatie in worteldichtheid en de ruimtelijke variatie in bedekking en wortelgewicht geanalyseerd (hoofdstuk 5). Tot slot zijn in hoofdstuk 7, op basis van de onderzoeksresultaten, richtlijnen besproken voor dijkgraslandbeheer.

Experiment

In 1991 zijn op beweide dijken 14 locaties geselecteerd met op elke locatie vier behandelingen: continueren van beweiding en bemesting; twee perioden beweiden zonder bemesting; hooien met nabeweiding zonder bemesting; en alleen hooien (twee sneden) zonder bemesting. Op gehooide dijken zijn 9 locaties gekozen waarop twee behandelingen werden uitgevoerd: hooien (2 sneden) mét en zonder gebruik van kunstmest. Soortenrijk hooiland op dijken dat de afgelopen 20 jaar niet is bemest geldt als referentie.

In maart 1994 zijn in de verschillende behandelingen de bedekking van de vegetatie en de worteldichtheid gemeten, en zijn erosie-sproeiproeven uitgevoerd. Ook zijn boormonsters genomen voor de erosiecentrifugeproef en is de afschuifweerstand gemeten. In de zomer van 1994 is de botanische samenstelling in de proefvakken opgenomen, zijn bodemmonsters verzameld en is de boven- en ondergrondse biomassa bepaald. De bovengrondse biomassa is ook in voorgaande jaren bemonsterd. De seizoensvariatie in boven- en ondergrondse productie is geanalyseerd op basis van metingen die om de zes weken zijn uitgevoerd vanaf februari 1992 tot februari 1993 in bemest weiland en op referentiedijken. In voorjaar en zomer van 1993 zijn gegevens verzameld met betrekking tot ruimtelijke variatie. Na 1994 is het experiment voortgezet tot 1997 en zijn gegevens verzameld in 1995 en 1997. Enkele daarvan (bovengrondse biomassa en chemische samenstelling van bodem en plant) worden in dit proefschrift besproken.

Vegetatie

De vegetatie van de onderzochte dijkgraslanden is relatief soortenarm (8-18 soorten per 25 m²), hoewel op sommige plekken soortenrijk grasland is aangetroffen (25-34 soorten per 25 m²). Negen gemeenschappen zijn onderscheiden. Twee ervan behoren tot varianten van het *Lolio-Cynosuretum cristati*, een gemeenschap behoort tot het *Poo-Lolietum* (onlangs in de literatuur omschreven als de rompgemeenschap *Poa trivialis-Lolium perenne-[Plantaginetea majoris, Cynosurion cristati]*) en één is benoemd als de rompgemeenschap *Festuca rubra-Cirsium arvense-[Molinio-Arrhenatheretea/Plantaginetalia]*. De overige vijf gemeenschappen zijn omschreven als varianten en subassociaties van het *Arrhenatheretum elatioris* en rompgemeenschappen van de *Arrhenatheretalia*. Hoewel de variatie in soortensamenstelling voor een groot deel wordt bepaald door verschillen in habitatfactoren tussen de locaties (bodemsamenstelling, expositie en invloed van inwaaiend zout water), werd met een multivariate analyse van soortensamenstelling en omgevingsfactoren, een significant effect van bemesting in combinatie met beheer worden aangetoond. Beëindiging van de bemesting leidde tot een lichte toename van het aantal soorten (van 13 naar 16 en van 14 naar 17 soorten per 25 m² in de onbemeste vakken van respectievelijk begraasde en gehooide dijken), een relatief sterke afname in bedekking van *Lolium perenne* en een toename van soorten van minder voedselrijke omstandigheden. Ook het aandeel kruiden in de grasmat nam toe. Mogelijk kan deze relatief snelle response op het veranderde beheer in vergelijking met andere experimenten worden verklaard door de slechte vochthuishouding van dijkgraslanden, waardoor direct een aanzienlijke verlaging van de nutriëntenbeschikbaarheid optreedt na beëindiging van de bemesting.

De successie na stoppen van de kunstmestgift, die ook op zeedijken kan worden opgevat als het resultaat van de interactie tussen veranderde nutriëntenbeschikbaarheid en vegetatiestructuur, leidde niet tot een afname van de bedekking van de vegetatie (gemeten

na knippen tot op een hoogte van 2 cm). In het soortenrijke hooiland kan de bedekking op 2 cm relatief laag zijn, terwijl de plantdichtheid relatief hoog is door een gelijkmatige verdeling van spruiten over het oppervlak. Dit betekent waarschijnlijk dat naast de bedekking van de vegetatie (op 2 cm hoogte) ook plantdichtheid van belang is voor de civieltechnische beoordeling van de zodekwaliteit

Boven- en ondergrondse biomassa

De bovengrondse biomassa blijkt in 3-4 jaar na het beëindigen van de mestgift snel af te nemen van 9-10 ton droge stof naar 7 ton ha^{-1}jr^{-1}, gevolgd door een verdere daling tot 5-6 ton ha^{-1}jr^{-1} na 7 jaar. Dit stemt overeen met resultaten van een experiment gericht op het herstel van soortenrijk grasland op klei-op-veen gronden. De overgang van beweiden met kunstmest naar hooien zonder bemesting, leidt tot de snelste daling in productie (van 9 naar 5 ton ha^{-1}jr^{-1} na 7 jaar) tot op het niveau dat gunstig is voor de ontwikkeling van soortenrijk grasland. De piekproductie (juli) is hoger op de zuidelijk geëxponeerde hellingen, terwijl de hergroei (oktober) hier lager is dan op de taluds die minder zonlicht ontvangen.

In overeenstemming met de productieafname werd na het stoppen van de bemesting, in de bodem een lagere hoeveelheid beschikbaar mineraal N gemeten. De totale hoeveelheid N in de bodem was echter niet lager in vergelijking met de bemeste vakken, hoewel op basis van de berekende N-balans een kleine netto afname van de totale hoeveelheid bodem N kan worden verwacht, vooral in de gehooide variant. Ondanks lage P concentraties in planten van de soortenrijke oude graslanden, duidt de N/P-ratio op een limitatie van N in deze graslanden.

Beëindiging van de kunstmestgift resulteerde in een toename van wortellengte en wortelgewicht in de gehooide varianten op zowel voorheen beweide als gehooide dijken. Deze uitbreiding van het wortelstelsel ten koste van bovengrondse plantendelen, kwam tot uitdrukking in een lagere spruit-wortelverhouding in de onbemeste gehooide variant op de voorheen beweide dijken. In de soortenrijke hooilanden is een relatief grote wortellengte en een hoog wortelgewicht gemeten, en een lage spruit-wortelverhouding. Het grootste verschil in worteldichtheid met het soortenarm bemest weiland manifesteerde zich op een diepte van 3-15 cm. Het bemeste soortenarme type vertoonde een scherpe daling van de worteldichtheid met de diepte, terwijl deze in het soortenrijke hooiland veel geleidelijker afnam. In de onbemeste gehooide varianten is de verticale verdeling van wortels verschoven in de richting van de verdeling zoals waargenomen in het soortenrijke hooiland. Weilanden en soortenrijke hooilanden werden gekenmerkt door een hoge specifieke wortellengte (SWL), hetgeen duidt op aanwezigheid van dunne wortels, terwijl de lage SWL in (soortenarm) hooiland wijst op aanwezigheid van dikke wortels. In de soortenrijke hooilanden werd een hoge SWL gemeten. De verschillende reacties van de wortelgroei van graslandplanten op een afname in N-beschikbaarheid en de verschillende typen beheer (beweiden of hooien), zijn besproken.

Temporele en ruimtelijke variatie

De seizoensvariatie in worteldichtheid, die van belang kan zijn voor de erosiebestendigheid van dijkgrasland, is onderzocht in bemest weiland en langdurig onbemest hooiland. In het bemest weiland werd de maximale bovengrondse groei bereikt in mei-juni, en in het onbemeste hooiland in juli. Beide typen hadden een maximale hergroei in september. In

overeenstemming met de resultaten van hoofdstuk 4 investeert het onbemeste hooiland veel meer in ondergrondse biomassa dan het bemeste weiland. In beide graslandtypen werd echter geen significante verandering in wortelgewicht gedurende het jaar gemeten, zodat de variatie in spruit-wortelverhouding overeenstemt met de variatie in bovengrondse biomassaproductie. In het bemeste weiland werden tijdens het seizoen belangrijke veranderingen in wortellengte gemeten in de bovenlaag van 0-3 cm, met een toename van overwegend fijne wortels in juli en september, volgend op de bovengrondse groei. In het onbemeste hooiland, dat op een diepte van 3-20 cm altijd een grotere wortellengte heeft dan het bemeste weiland, werden aanzienlijke veranderingen in wortellengte gedurende het seizoen gemeten op een diepte van 3-40 cm.

De ruimtelijke variatie in floristische diversiteit , bedekking van de vegetatie en worteldichtheid (gewicht) is onderzocht in drie graslandtypen behorende tot het *Arrhenatheretum elatioris brizetosum* (oud onbemest hooiland), het *Lolio-Cynosuretum cristati* (licht bemest weiland) en het *Poo-Lolietum* (zwaar bemest weiland). De ruimtelijke variatie in floristische samenstelling van de eerste twee typen vertoont een mozaïek patroon, in vergelijking met het in floristisch opzicht homogene *Poo-Lolietum*. Dit type vertoonde wel een grote ruimtelijke variatie in de grootte van open plekken en het wortelgewicht, terwijl de hogere wortelgewichten in het *Arrhenatheretum* en ook het *Lolio-Cynosuretum* ruimtelijk minder varieerden. Kennelijk is een ruimtelijk homogene floristische samenstelling niet *per se* gecorreleerd met een lage variatie in worteldichtheid. Binnen een type werden geen patronen gevonden in de horizontale verdeling van wortels, en ook de ruimtelijke verschillen in het verticale wortelverloop binnen een vegetatietype waren klein. Wel bleek ook hier, in overeenstemming met eerdere resultaten, in het onbemeste hooiland de afname in wortelmassa met de diepte minder abrupt te zijn dan in de andere gemeenschappen.

Erosie

De erosiebestendigheid van het dijkgrasland op de diverse locaties is onderzocht met behulp van drie parameters (hoofdstuk 6): de *afschuifweerstand* gemeten op verschillende diepten van het doorworteld profiel, de bodemafname en hoeveelheid uitgespoelde grond in erosiesproeiproeven *(slijterosie)* en het percentage gewichtsverlies van boormonsters in een erosiecentrifuge-proef (*interne erosie*).

In bodems met hoge worteldichtheden bleek de afschuifweerstand laag te zijn , terwijl een hoge afschuifweerstand werd gemeten in bodems met een lage bedekking van de vegetatie, een lage worteldichtheid (maar relatief dikke wortels) of een hoge siltfractie. Afschuifweerstandsmetingen zijn blijkbaar niet indicatief voor de stabiliteit van de bodem als gevolg van de inwerking van wortels op klei. Ook werd geen correlatie gevonden met andere erosieparameters. De afschuifweerstand kan daarom niet worden gebruikt als een betrouwbare parameter voor de erosiebestendigheid van dijkgrasland.

In de erosiesproeiproeven is geen duidelijke significante trend gevonden in bodemafname of hoeveelheid uitgespoeld materiaal van de verschillende beheersvormen. Alleen bij een hogere stroomsnelheid bleek het soortenrijke hooiland meer weerstand te bieden tegen oppervlakte-erosie dan het soortenarme weidetype. Het schijnt dat door de relatief hoge bedekkingen en kleine verschillen in granulaire samenstelling van de bodem, verschillen in slijterosie tussen de verschillend beheerde dijkgraslanden klein zijn.

De interne erosie van veel monsters wordt gekenmerkt door een plotselinge toename van de erosiesnelheid (gewichtsverlies) gedurende de loop van het experiment. Dit wordt waarschijnlijk veroorzaakt door de beworteling van de bodem, waardoor de erosie van bodemdeeltjes wordt geremd totdat de wortels zover beschadigd zijn dat de erosiesnelheid alleen wordt bepaald door bodemeigenschappen. In het algemeen waren beide erosiesnelheden (voor en na de plotselinge verandering) lager in de monsters van 0-5 cm, terwijl in de monsters gestoken op een diepte van 5-10 cm de erosie sterker was en in de meeste gevallen leidde tot het bezwijken van het monster. Op een diepte van 0-5 cm, waar de grootste hoeveelheid wortels voorkomt, werd de erosiesnelheid in de eerste helft van het experiment hoofdzakelijk bepaald door de worteldichtheid, terwijl deze op een diepte van 5-10 cm werd beïnvloed door de worteldichtheid én het zandgehalte. In de tweede helft (na de plotselinge verandering) was de erosiesnelheid in beide lagen vooral afhankelijk van zand- en siltgehalte. De interne erosieweerstand wordt dus bepaald door het gecombineerde effect van worteldichtheid en granulaire samenstelling van de bodem. Het is mogelijk dat deze bodemversterking eerder het resultaat is van het effect van het gehele wortelpakket op bodemstabiliteit en porositeit, dan van de trekkracht van de wortels.

Soortenrijk hooiland wordt gekenmerkt door hogere waarden van de erosieweerstand dan bemeste graslanden, waarschijnlijk als gevolg van de hogere worteldichtheid. In sommige onbemeste vakken is na drie jaar de erosieweerstand iets hoger dan in de bemeste graslanden. Dit is in overeenstemming met de hogere worteldichtheid en de verandering in botanische samenstelling in deze vakken. Voorgesteld wordt om als criteria voor de beoordeling van de erosiebestendigheid van dijkgrasland, *botanische samenstelling* (indicatief voor de worteldichtheid) en *plantdichtheid* (indicatief voor de bedekking) te hanteren en niet de kleikwaliteit in de bovenlaag van de bodem.

Beheer

Zowel de mate van doorworteling als de ruimtelijke variatie in bedekking van de vegetatie, de twee belangrijkste factoren voor de erosiebestendigheid van dijkgrasland, kunnen worden beïnvloed door het type graslandbeheer. Geen bemesting en continuïteit in beheer en onderhoud zijn de belangrijkste randvoorwaarden voor een hoge kwaliteit van de graszode. De langdurig onbemeste hooilanden hebben inderdaad de hoogste worteldichtheid en erosiebestendigheid. Onbemeste schapenweiden hebben mogelijk ook een hoge erosiebestendigheid, terwijl het verschil in agrarische opbrengst ten opzichte van bemest weiland niet zo groot lijkt te zijn. Een maximale mestgift van 50 kg N ha^{-1}jr^{-1} in combinatie met weiden is mogelijk zonder dat de zode sterk aan kwaliteit verliest, maar aanbevolen wordt geen bemesting toe te passen.

Voor verbetering en handhaving van een erosiebestendige grasmat, is een aantal onderhoudsmaatregelen geformuleerd, zoals het maaien van slecht afgegraasde stukken en het gebruik van de weidesleep bij beweiding, het handhaven van een maximum vegetatiehoogte van 10 cm aan het begin van het winterseizoen, het afvoeren van maaisel binnen 1 tot maximaal 2 weken, actieve bestrijding van mollen en continuïteit van het beheer. Bij de beoordeling van de erosiebestendigheid van dijkgrasland, moet meer de nadruk worden gelegd op botanische samenstelling, bedekking en worteldichtheid, in tegenstelling tot de huidige toets, die *de facto* vooral gebaseerd blijkt te zijn op de kleikwaliteit in en onder de zode.

Appendix I

Phytosociological table

Species are grouped into syntaxonomical elements according to their syntaxonomical status (Westhoff & Den Held 1975, Ellenberg 1978, Oberdorfer, 1990). I-V: species present in respectively 2-20 % (I), 21-40 % (II), 41-60 % (III), 61-80 % (IV), 81-100 % (V) of the relevés of each community, + = present in one percent of the relevés. Superscripts denote the average frequency/abundance of a species in the relevés of a community, according to the ordinal Braun-Blanquet scale (cf. Barkman et al. 1964, Van der Maarel 1979): 1 = one individual present (poorly developed), 2 = one well developed individual or 2-20 individuals, 3 = 20-50 individuals, 4 = high frequency (> 50 individuals), but low cover (< 5 %), 5 = cover 5-12.5 %, 6 = cover 12.5-25 %, 7 = cover 25-50 %, 8 = cover 50-75 %, 9 = cover 75-100 %.

Community (number)	2	1	3	4	6	7	5	8	9
Community (code)	LR	LG	LF	PL	AF	AC	AH	A0	AB
Number of relevés	27	57	55	66	9	36	7	23	11
Av. species number	18.2	13.5	18.3	12.4	12.0	13.4	7.9	24.7	34.4
Standard deviation	3.6	2.4	4.5	3.4	3.5	4.3	4.4	5.8	5.8

Molinio-Arrhenatheretea

Species	LR	LG	LF	PL	AF	AC	AH	A0	AB
Anthoxanthum odoratum	-	-	-	-	-	-	-	$+^1$	IV^5
Festuca rubra	IV^6	IV^6	V^6	IV^5	II^5	IV^5	-	V^5	V^5
Cerastium fontanum ssp. font.	V^3	V^3	IV^3	IV^3	II^2	III^2	-	IV^2	V^2
Poa pratensis	IV^4	IV^4	IV^4	III^4	II^4	IV^4	II^4	V^5	V^4
Poa trivialis	V^5	V^6	IV^5	V^5	IV^5	V^5	-	IV^4	IV^3
Medicago lupulina	I^3	I^3	II^3	$+^2$	-	-	-	-	II^3
Symphytum officinale	-	-	I^4	-	I^2	I^2	-	I^3	-
Cardamine pratensis	-	$+^2$	-	-	-	-	I^5	-	-
Rhytidiadelphus squarrosus	-	-	$+^4$	-	-	-	-	$+^4$	-
Holcus lanatus	II^4	-	II^4	$+^4$	-	I^4	-	II^4	IV^4
Plantago lanceolata	III^3	I^2	II^3	$+^2$	II^3	I^3	II^2	IV^3	V^4
Prunella vulgaris	-	-	$+^2$	-	I^2	-	-	I^2	I^2
Rumex acetosa	I^3	$+^2$	$+^2$	-	-	-	-	I^2	III^2
Trifolium pratense	$+^3$	$+^6$	III^4	$+^2$	I^2	$+^3$	-	III^4	III^4
Vicia cracca	-	-	-	$+^3$	-	$+^4$	-	-	-
Centaurea jacea	-	-	-	-	-	-	-	-	III^4
Rhinanthus angustifolius	-	-	-	-	-	-	-	-	I^2
Polygonum bistorta	-	-	$+^2$	-	-	-	-	-	-

Arrhenatherion elatioris

Species	LR	LG	LF	PL	AF	AC	AH	A0	AB
Alopecurus pratensis	-	-	-	-	-	$+^5$	III^4	$+^3$	-
Bellis perennis	V^4	IV^4	IV^4	I^2	III^3	II^2	-	V^3	III^2
Leucanthemum vulgare	-	-	-	-	-	-	-	-	III^3

Dactylis glomerata	IV^4	$+^2$	II^3	IV^5	V^5	V^5	V^4	V^5	V^4
Festuca pratensis	-	-	-	I^4	-	I^3	-	III^5	I^3
Heracleum sphondylium	-	-	$+^2$	-	-	I^3	III^3	$+^2$	II^3
Lathyrus pratensis	-	-	$+^3$	-	-	I^3	-	II^5	-
Ranunculus acris	I^2	$+^1$	I^2	-	II^2	$+^2$	I^2	II^3	-
Trifolium dubium	V^6	IV^4	III^4	II^4	I^7	III^3	-	V^5	V^3
Allium vineale	-	-	$+^2$	-	-	I^2	I^3	III^2	V^3
Hypochaeris radicata	I^2	$+^1$	I^3	-	-	-	-	I^3	II^2
Achillea millefolium	IV^3	II^3	II^3	I^2	I^3	$+^3$	-	III^2	V^3
Crepis capillaris	I^2	I^2	II^2	I^2	II^2	I^2	-	IV^2	II^2
Agrostis capillaris	I^4	I^4	I^5	$+^3$	-	-	-	$+^3$	II^4
Lotus corniculatus ssp. corn.	I^3	$+^2$	I^2	-	-	-	-	$+^2$	II^4
Luzula campestris	-	-	-	-	-	-	-	-	II^4
Senecio jacobaea ssp. jac.	$+^1$	$+^1$	I^2	$+^1$	I^2	-	-	-	II^2

Arrhenatheretum elatioris

Arrhenatherum elatius	-	-	$+^3$	I^4	III^6	IV^6	V^6	IV^6	IV^6
Daucus carota	$+^2$	-	I^3	-	-	I^2	-	IV^3	V^3
Pastinaca sativa	-	-	$+^5$	-	-	-	-	-	II^2
Trisetum flavescens	I^4	-	$+^3$	-	-	$+^3$	-	II^3	III^4
Tragopogon pratensis subs	-	-	-	-	-	-	-	I^2	II^2
Anthriscus sylvestris	-	-	-	-	-	I^2	-	$+^2$	-

Diff towards Lolio-Cynosuretum:

Heracleum sphondylium	-	-	$+^2$	-	-	I^3	III^3	$+^2$	II^3
Anthriscus sylvestris	-	-	-	-	-	I^2	-	$+^2$	-
Symphytum officinale	-	-	I^4	-	I^2	I^2	-	I^3	-
Euphorbia esula	-	-	-	-	-	-	-	-	I^3

Subassociation group A inops:

Heracleum sphondylium	-	-	$+^2$	-	-	I^3	III^3	$+^2$	II^3
Anthriscus sylvestris	-	-	-	-	-	I^2	-	$+^2$	-
Ranunculus repens	-	II^3	III^3	I^2	II^2	$+^2$	I^2	I^2	-
Glechoma hederacea	-	-	I^3	$+^2$	III^3	I^2	III^2	I^2	I^3
Alopecurus pratensis	-	-	-	-	-	$+^5$	III^4	$+^3$	-

Subassociation group B (differential species):

Senecio erucifolius	-	-	-	$+^2$	-	I^2	-	III^2	III^3
Ranunculus bulbosus	III^2	I^2	$+^2$	I^2	-	I^3	-	II^3	V^3
Senecio jacobaea ssp. jac.	$+^1$	$+^1$	I^2	$+^1$	I^2	-	-	-	II^2
Trisetum flavescens	I^4	-	$+^3$	-	-	$+^3$	-	II^3	III^4

picriditosum

Pastinaca sativa	-	-	$+^5$	-	-	-	-	-	II^2
Agrimonia eupatoria	-	-	-	-	-	-	-	I^2	I^3
Picris species	-	-	-	-	-	$+^1$	-	$+^2$	-

brizetosum

Briza media	-	-	-	-	-	-	-	-	II^5
Carex flacca	-	-	-	-	-	-	-	I^2	II^3
Anthoxanthum odoratum	-	-	-	-	-	-	-	$+^1$	IV^5
Hypochaeris radicata	I^2	$+^1$	I^3	-	-	-	-	I^3	II^2
Hieracium pilosella	-	-	-	-	-	-	-	-	I^4
Crepis capillaris	I^2	I^2	II^2	I^2	II^2	I^2	-	IV^2	II^2
Agrostis capillaris	I^4	I^4	I^5	$+^3$	-	-	-	$+^3$	II^4
Bromus hordeaceus ssp. hord.	V^5	V^5	III^5	V^4	III^3	III^3	-	IV^3	V^3

Lolio-Cynosuretum

	1	2	3	4	5	6	7	8	9
Cynosurus cristatus	III⁴	IV⁵	+⁴	-	-	+²	-	I³	II³
Phleum pratense ssp. prat.	I⁴	I³	I³	+³	-	-	-	-	-
Lolium perenne	V⁶	V⁶	V⁶	V⁷	V⁴	I³	I³	II³	III⁴
Trifolium repens	III⁴	IV⁵	V⁴	I²	I⁴	I³	-	+³	-
Leontodon saxatilis	I³	I²	II³	-	-	-	-	+³	I²

diff. towards Arrhenatheretum:

	1	2	3	4	5	6	7	8	9
Leontodon autumnalis	-	I²	II²	-	-	-	-	+³	-
Hordeum secalinum	I³	+²	-	I³	-	-	-	-	I³

Subassociation group A:

	1	2	3	4	5	6	7	8	9
Anthoxanthum odoratum	-	-	-	-	-	-	-	+¹	IV⁵
Luzula campestris	-	-	-	-	-	-	-	-	II⁴
Holcus lanatus	II⁴	-	II⁴	+⁴	-	I⁴	-	II⁴	IV⁴
Festuca rubra	IV⁶	IV⁶	V⁶	IV⁵	II⁵	IV⁵	-	V⁵	V⁵
Briza media	-	-	-	-	-	-	-	-	II⁵
Agrostis capillaris	I⁴	I⁴	I⁵	+³	-	-	-	+³	II⁴

luzuletosum campestris

	1	2	3	4	5	6	7	8	9
Festuca rubra	IV⁶	IV⁶	V⁶	IV⁵	II⁵	IV⁵	-	V⁵	V⁵
Luzula campestris	-	-	-	-	-	-	-	-	II⁴
Lotus corniculatus ssp. Corn .	I³	+²	I²	-	-	-	-	+²	II⁴
Trifolium dubium	V⁶	IV⁴	III⁴	II⁴	I⁷	III³	-	V⁵	V³
Hypochaeris radicata	I²	+¹	I³	-	-	-	-	I³	II²

Subassociation group B:

	1	2	3	4	5	6	7	8	9
Agrostis stolonifera	IV⁵	III⁵	IV⁵	III⁵	III⁵	I⁴	-	I³	III⁴
Carex spicata	-	-	I²	-	-	-	-	-	-
Potentilla reptans	I²	-	I²	-	-	-	-	+²	IV⁴
Dactylis glomerata	IV⁴	+²	II³	IV⁵	V⁵	V⁵	V⁴	V⁵	V⁴
Trisetum flavescens	I⁴	-	+³	-	-	+³	-	II³	III⁴
Cirsium arvense	I³	I²	IV³	II²	I²	III²	I²	I³	I²

juncetosum gerardii

	1	2	3	4	5	6	7	8	9
Juncus gerardi	-	-	+⁴	-	-	-	-	-	-
Trifolium fragiferum	-	-	+²	-	-	-	-	-	-

plantaginetosum mediae

	1	2	3	4	5	6	7	8	9
Ranunculus bulbosus	III²	I²	+²	I²	-	I³	-	II³	V³
Medicago lupulina	I³	I³	II³	+²	-	-	-	-	II³
Cirsium vulgare	I²	I²	I²	I²	-	I²	-	+¹	IV²

ononidetosum

	1	2	3	4	5	6	7	8	9
Ranunculus bulbosus	III²	I²	+²	I²	-	I³	-	II³	V³
Medicago lupulina	I³	I³	II³	+²	-	-	-	-	II³
Cirsium vulgare	I²	I²	I²	I²	-	I²	-	+¹	IV²
Eryngium campestre	-	-	-	-	-	-	-	-	IV⁴
Ononis repens ssp. spinosa	I³	-	+²	-	-	-	-	-	III³
Convolvulus arvensis	-	-	+³	-	-	I³	-	+²	I³
Verbena officinalis	-	-	-	-	-	-	-	I²	-

Origanetalia vulgaris/Trifolion medii

	1	2	3	4	5	6	7	8	9
Lathyrus nissolia	-	-	-	-	-	+³	-	II³	-

Origanum vulgare	-	-	-	-	-	-	-	II^4	-
Orobanche lutea	-	-	-	-	-	-	-	I^2	-
Senecio erucifolius	-	-	-	$+^2$	-	I^2	-	III^2	III^3
Agrimonia eupatoria	-	-	-	-	-	-	-	I^2	I^3

Koelerio-Corynephoretea + Festuco-Brometea (differential species)

Galium verum	$+^2$	-	$+^2$	-	-	-	-	-	IV^4
Ranunculus bulbosus	III^2	I^2	$+^2$	I^2	-	I^3	-	II^3	V^3
Hieracium pilosella	-	-	-	-	-	-	-	-	I^4
Koeleria macrantha	$+^2$	-	-	-	-	-	-	-	I^4
Avenula pubescens	-	-	-	-	-	-	-	-	III^5
Arenaria serpyllifolia	$+^3$	$+^1$	-	$+^1$	-	-	-	-	I^1
Festuca ovina	-	-	-	-	-	-	-	-	I^5

Koelerio-Corynephoretea + Festuco-Brometea

Potentilla argentea	-	-	-	-	-	-	-	-	I^2
Trifolium arvense	-	-	$+^2$	-	-	-	-	-	
Myosotis stricta	-	-	$+^2$	-	-	-	-	-	$-^2$
Taraxacum tortilobum	$+^2$	-	-	-	-	-	-	-	$-^2$
Trifolium campestre	-	-	I^2	$+^2$	-	-	-	-	II^3
Vicia lathyroides	-	-	-	-	-	-	-	-	I^1
Carex arenaria	-	-	-	-	-	-	-	-	I^1
Hypericum perforatum	-	-	-	$+^2$	-	-	-	$+^3$	I^2
Rumex acetosella	-	-	$+^5$	-	-	-	-	-	I^2
Vicia sativa sp nigra	$+^2$	-	I^2	-	-	II^2	-	III^3	V^3
Ceratodon purpureus	-	-	-	$+^3$	-	-	-	-	-

Mesobromion (Brometalia)

Ononis repens ssp. spinosa	I^3	-	$+^2$	-	-	-	-	-	III^3
Arabis hirsuta	-	-	-	$+^2$	-	I^3	-	-	-

Medicagini-Avenetum pubescentis

Ononis repens ssp. spinosa	I^3	-	$+^2$	-	-	-	-	-	III^3
Bromus inermis	-	-	-	-	-	-	-	-	I^3
Eryngium campestre	-	-	-	-	-	-	-	-	IV^4

Plantaginetalia majoris/Lolio-Plantaginion

Lolium perenne	V^6	V^6	V^6	V^7	V^4	I^3	I^3	II^3	III^4
Poa annua	I^2	II^3	I^3	I^3	-	$+^3$	-	-	-
Plantago major	-	$+^2$	I^2	$+^2$	-	-	-	-	-
Tussilago farfara	-	-	$+^2$	-	-	-	-	-	-
Carex distans	-	-	$+^2$	-	-	-	-	-	-
Carex hirta	-	-	I^3	-	-	-	-	-	-
Elymus repens	III^4	I^3	V^4	IV^5	V^6	III^7	V^7	IV^4	III^3
Leontodon autumnalis	-	I^2	II^2	-	-	-	-	$+^3$	-
Lotus corniculatus ssp. corn.	-	-	$+^5$	-	-	-	-	-	I^5
Potentilla anserina	-	-	-	-	-	-	$+^2$	-	-
Pulicaria dysenterica	-	-	-	-	-	$+^2$	-	I^3	-
Ranunculus repens	-	II^3	III^3	I^2	II^2	$+^2$	I^2	I^2	-
Rumex crispus	I^2	$+^2$	II^2	$+^2$	-	II^2	I^2	$+^2$	-
Trifolium fragiferum	-	-	$+^2$	-	-	-	-	-	-
Festuca arundinacea	$+^3$	-	$+^6$	I^4	V^5	III^6	-	IV^5	I^3
Lysimachia nummularia	-	-	-	-	-	$+^1$	-	-	-
Rorippa sylvestris	-	-	I^3	$+^2$	-	-	-	-	-

Poo-Lolietum

Lolium perenne	V^6	V^6	V^6	V^7	V^4	I^3	I^3	II^3	III^4
Taraxacum species	V^3	IV^3	V^3	IV^3	V^3	III^2	I^2	V^3	II^2
Poa pratensis	IV^4	IV^4	IV^4	III^4	II^4	IV^4	II^4	V^5	V^4
Poa trivialis	V^5	V^6	IV^5	V^5	IV^5	V^5	-	IV^4	IV^3
Ranunculus repens	-	II^3	III^3	I^2	II^2	$+^2$	I^2	I^2	-
Trifolium repens	III^4	IV^5	V^4	I^2	I^4	I^3	-	$+^3$	-
Plantago major	-	$+^2$	I^2	$+^2$	-	-	-	-	-

Artemisietea

Dipsacus fullonum	-	-	-	-	-	-	-	I^2	-
Cirsium vulgare	I^2	I^2	I^2	I^2-	-	I^2	-	$+^1$	IV^2
Cirsium arvense	I^3	I^2	IV^3	II^2	I^2	III^2	I^2	I^3	I^2
Lamium album	-	-	-	-	-	-	I^2	-	-
Verbena officinalis	-	-	-	-	-	-	-	I^2	-
Urtica dioica	-	-	-	-	-	I^2	III^2	$+^3$	-
Calystegia sepium	-	-	-	-	I^6	-	-	-	I^3
Glechoma hederacea	-	-	I^3	$+^2$	III^3	I^2	III^2	I^2	I^3
Sonchus arvensis	-	-	$+^2$	I^2	-	I^2	-	$+^2$	-
Lathyrus tuberosus	-	-	-	-	-	-	-	I^4	-
Carex spicata	-	-	I^2	-	-	-	-	-	-
Phragmites australis	-	-	-	-	-	-	II^5	$+^3$	-
Elymus athericus	-	-	-	$+^3$	-	I^5	-	$+^2$	-

Chenopodietea

Chenopodium album	-	-	-	$+^1$	-	-	-	-	-
Senecio vulgaris	-	-	$+^2$	-	-	-	-	-	-
Sonchus oleraceus	-	-	-	$+^2$	-	-	-	I^3	-
Stellaria media	I^3	$+^1$	$+^2$	II^2	-	I^2	I^1	$+^3$	I^3

(Eu-)Polygono-Chenopodion

Anagallis arvensis	-	-	$+^2$	-	-	-	-	-	-
Geranium dissectum	II^2	I^2	I^2	II^2	II^2	II^2	-	IV^2	IV^2
Polygonum persicaria	-	-	$+^3$	-	-	-	-	-	-
Sonchus asper	I^2	-	I^2	II^2	-	I^2	-	I^2	I^2
Veronica persica	-	-	-	-	-	-	-	$+^1$	-
Echinochloa crus-galli	-	-	-	-	-	-	-	-	-
Erodium cicutarium	$+^2$	-	I^4	$+^6$	-	-	-	-	-
Lamium purpureum	-	-	-	-	-	$+^2$	-	-	-

Sisymbrietalia
Sisymbrion

Erigeron canadensis	-	-	-	$+^2$	-	-	-	$+^2$	-
Cardaria draba	-	-	-	$+^5$	-	I^3	-	-	-
Sisymbrium officinale	-	-	-	-	-	$+^2$	-	-	-
Hordeum murinum	II^3	I^2	I^2	II^4	-	-	-	-	-
Allium vineale	-	-	$+^2$	-	-	I^2	I^3	III^2	V^3
Convolvulus arvensis	-	-	$+^3$	-	-	I^3	-	$+^2$	I^3

Polygono-Coronopion

Capsella bursa-pastoris	I^2	-	I^3	I^3	-	I^3	-	-	-
Polygonum aviculare	-	-	$+^2$	$+^2$	-	-	-	-	-
Sagina procumbens	-	I^3	I^3	-	-	-	-	-	-
Pohlia species	-	-	$+^3$	-	-	-	-	-	-

Helminthion echioidis

Medicago arabica	I^3	-	$+^5$	I^3	-	I^5	-	I^4	III^4
Picris echioides	-	-	$+^2$	-	-	-	-	-	-
Torilis nodosa	-	I^2	I^2	$+^3$	-	-	-	-	-

Secalietea

Species	1	2	3	4	5	6	7	8	9
Valerianella locusta	-	-	-	-	-	-	-	-	I^2
Vicia hirsuta	-	-	-	-	-	-	-	$+^3$	I^2
Vicia tetrasperma ssp. tetrasp.-	-	-	-	-	I^2	-	$+^2$	-	
Matricaria recutita	-	-	$+^2$	I^2	-	$+^2$	-	-	-
Myosotis arvensis	-	-	-	-	-	-	-	-	III^3
Sherardia arvensis	-	$+^3$	$+^3$	-	-	-	-	-	-

Other species

Species	1	2	3	4	5	6	7	8	9
Atriplex patula	-	-	-	$+^2$	-	-	-	-	-
Cardamine hirsuta	$+^1$	-	-	-	-	$+^1$	-	$+^1$	-
Cerastium glomeratum	I^4	$+^2$	$+^3$	I^3	-	I^3	-	II^2	-
Crepis vesicaria	-	-	-	-	-	-	-	-	I^3
Equisetum arvense	$+^2$	-	$+^2$	-	-	I^2	-	II^3	II^3
Geranium molle	II^2	V^3	III^3	II^3	I^3	-	-	$+^2$	I^2
Lolium multiflorum	-	-	-	-	-	I^5	-	I^6	-
Prunus serotina	-	-	$+^2$	-	-	-	-	-	-
Rubus caesius	-	-	-	-	-	-	-	II^2	I^2
Veronica arvensis	III^3	II^3	II^2	II^2	-	I^2	-	I^1	I^2
Veronica chamaedrys	-	-	-	-	-	-	-	-	I^2
Phleum prat sp bertolonii	-	$+^2$	-	-	-	-	-	-	-
Rubus fruticosus	-	-	-	-	-	-	-	-	I^2
Beta vulgaris	-	-	-	$+^2$	-	-	-	-	-
Ranunculus ficaria	-	-	-	-	-	-	-	$+^1$	-
Barbula unguiculata	-	$+^2$	-	I^3	-	I^4	-	I^3	-
Brachythecium albicans	$+^3$	-	$+^3$	$+^3$	-	-	-	$+^3$	-
Brachythecium rutabulum	IV^5	IV^5	II^4	II^5	II^5	III^6	I^4	V^5	I^6
Bryum rubens	-	-	-	$+^4$	-	$+^3$	-	I^3	-
Calliorganella cuspidata	-	-	-	$+^5$	-	$+^7$	-	-	-
Eurhynchium hians	-	-	$+^3$	-	-	$+^4$	-	I^4	-
Eurhynchium praelongum	$+^5$	-	I^4	I^4	II^4	II^5	-	III^5	-
Fissidens species	-	-	$+^2$	-	-	-	III^4	$+^4$	-
Hypnum cupressiforme	-	-	-	$+^3$	-	-	-	-	-
Hypnum lacunosum	-	-	-	-	-	-	-	-	I^8
Mnium species	-	-	-	-	-	-	-	-	I^2
Phascum cuspidatum	$+^3$	-	-	-	-	-	-	-	-
Plagiomnium affine	-	-	-	-	-	-	-	-	I^2
Pottia truncata var. major	$+^3$	-	$+^3$	-	-	-	-	-	-
Pseudoscleropodium purum	$+^4$	-	-	-	-	$+^5$	-	-	II^6
Festulolium (x-) species	-	-	-	$+^2$	-	-	-	-	-
Matricaria species	-	-	-	$+^2$	-	-	-	-	-
Rumex species	-	-	$+^2$	-	-	-	-	-	-
Veronica species	-	-	$+^1$	-	-	-	-	-	-
Cochlearia danica	-	-	$+^3$	-	-	-	-	-	-
Alopecurus bulbosus	-	-	$+^3$	-	-	-	-	-	-
Polygonum amphibium	-	-	$+^2$	-	II^2	-	II^2	-	-
Matricaria maritima	-	-	I^2	-	-	$+^2$	-	-	-
Crataegus monogyna	-	-	$+^1$	-	-	-	-	-	I^1
Prunus spinosa	-	-	-	-	-	-	-	-	I^1
Hieracium umbellatum	-	-	-	-	-	-	-	-	I^2
Fraxinus excelsior	-	-	-	-	-	-	-	$+^1$	-

Appendix II

Erosion centrifuge parameter values

Parameter values of the erosion centrifuge experiment in different treatments at all investigated sites. See chapter 6 and chapter 2 for legends of treatments and site codes. The parameters *b1A*, *b2A*, *b1B* and *b2B* represent the linear coefficients of the first (*b1*) and second (*b2*) curve of the broken stick model, described by $y = y_c + (x < x_c) * b_1 * (x - x_c) + (x > x_c) * b_2 * (x - x_c)$, which is calculated on the basis of measurents of weight loss (*y*) with time (*x*) in the erosion centrifuge experiment with samples of depths of 0-5 (A) and 5-10 (B) cm. The coordinates of the 'breaking point' are x_c and y_c in both layers A and B. The values of r^2-adjusted (r^2-adjA/ r^2-adjB) are given as well. Measurements of some samples with very low weight losses during the experiment do not correspond well with the brocken-stick model.

unr	Code	b1A	b2A	ycA	xcA	r2adjA	b1B	b2B	ycB	xcB	r2adjB
1	G1I	0.09935	0.0285	12.33	124.0	0.9927	0.05002	3.1075	10.38	183.3	0.9649
3	G1HH	0.01813	0.0055	4.70	233.8	0.9563	0.04826	0.4926	13.54	294.0	0.9767
9	G2I	0.00508	0.0591	0.31	123.3	0.9793	0.02361	0.2298	3.95	128.7	0.9661
11	G2HH	0.11417	0.0479	31.21	262.8	0.9822	0.04081	0.1363	6.51	115.6	0.9858
13	G2HW	0.03096	0.0089	7.91	233.2	0.9695	0.05828	0.0250	16.60	252.6	0.9795
15	G2WW	0.03835	0.0182	9.39	230.9	0.9726	0.06128	0.0096	13.29	175.8	0.9582
28	FAI	0.05252	0.0133	13.77	212.7	0.9475	0.08876	3.4726	16.15	185.5	0.9909
30	FAHH	0.07076	0.0169	20.13	266.1	0.9661	0.15799	4.7181	29.01	175.0	0.9652
32	FAHW	0.04440	0.0152	11.98	223.8	0.9456	0.08198	6.7959	16.68	206.6	0.9812
34	FAWW	0.03608	0.0069	10.11	261.7	0.9541	0.10640	0.8537	30.47	300.0	0.9810
46	NHI	0.01441	0.0247	4.57	112.4	0.8596	0.09278	0.2658	16.68	140.2	0.9843
48	NHHH	0.04267	0.1157	3.52	103.0	0.9690	0.07696	1.4962	12.50	137.8	0.9878
50	NHHW	0.00895	0.0308	2.16	50.0	0.9122	0.08110	0.5933	24.47	300.0	0.9739
92	ZHIb	0.40010	0.3713	20.95	50.0	0.9034	0.26880	1.4192	39.68	131.9	0.9801
94	ZHHH	0.05857	0.0262	19.06	230.6	0.9405	0.03158	0.1392	7.37	186.1	0.9481
96	ZHHW	0.06637	0.0891	14.56	149.6	0.9628	0.07063	8.3071	12.34	228.9	0.9718
98	ZHWW	0.05215	0.0712	6.06	80.4	0.9669	0.12376	3.4615	18.39	147.2	0.9978
100	ZBI	0.06643	0.0208	14.95	164.5	0.9167	0.01187	0.1805	0.00	63.6	0.9185
103	ZBHHbu	0.01478	0.0344	0.80	50.0	0.8626	0.00253	0.0000	0.00	300.0	-0.1383
104	ZBHW	0.11244	0.0408	27.03	218.6	0.9816	0.09967	0.9315	16.88	156.3	0.9789
106	ZBWW	0.10097	0.0169	9.46	67.0	0.6851	0.01052	0.0902	0.00	133.2	0.8915
112	DHHI	0.04210	0.0177	10.07	190.4	0.9441	0.05653	0.0239	17.18	252.6	0.9683
114	DHHE	0.00000	0.0126	1.50	136.3	0.9599	0.04078	0.0284	3.38	50.0	0.9036
124	ZOhe	0.00000	0.0050	2.36	105.6	-0.0233	0.00883	0.0077	0.00	83.0	0.1914
125	ZZKhe	0.01430	0.0000	6.25	300.0	0.6336	0.02814	0.0070	4.49	188.8	0.9060
139	ZKHI	0.01126	0.0000	0.00	300.0	-2.1821	0.00552	0.0000	0.00	300.0	-1.6460
142	ZKHE	0.00000	0.0000	0.68	66.5	-0.0909	0.00000	0.0081	1.72	227.8	0.1469
148	ZPEHI	0.04653	0.1520	10.25	164.8	0.9847	0.07671	0.1940	8.44	117.4	0.9691
150	ZPEHE	0.02114	0.0689	4.49	135.2	0.9595	0.00000	0.3553	1.85	210.6	0.7616
160	ZZDHE	0.03813	8.9865	12.03	229.6	0.9942	0.07567	0.0439	20.24	250.0	0.9792
162	ZZDHI	0.08554	0.0216	18.78	214.2	0.9854	0.00000	0.0202	0.58	52.2	0.8594

Curriculum vitae

Hans Sprangers is geboren op 15 mei 1952 in Ulvenhout, waar hij opgroeide en de lagere school bezocht. In 1970 behaalde hij het diploma gymnasium-β aan het Titus Brandsma Lyceum in Oss. Aansluitend begon hij zijn studie biologie aan de Katholieke Universiteit Nijmegen.

Na het kandidaatsexamen B4 (biologie met scheikunde) in mei 1974, volgde hij een doctoraalprogramma met een bijvakstudie aan de afdeling chemische cytologie en farmacologie (*dopamine-turnover in het striatum van rattehersenen*), en een bijvakstudie aan de afdeling toegepaste landschapsecologie van de VU (*een economisch-ecologisch model van de Nederlandse landbouw*). De hoofdvakstudie aan de afdeling Geobotanie omvatte twee onderwerpen: een plantensociologisch onderzoek naar *syntaxonomie en synecologie van duingraslanden langs de kust van Bretagne* en een onderzoek naar *plantensociologische samenstelling en structuur van droge kustbossen in oost-India*. In december 1978 behaalde hij met lof het doctoraal examen.

Vervolgens was hij tot juni 1980 werkzaam bij de Dorschkamp, rijksinstituut voor onderzoek in de bos- en landschapsbouw, en betrokken bij het project *landschapecologische relaties in Nederland*. Na een korte tijd als muzikant te hebben gewerkt, begon hij in 1982 in het onderwijs. Twee pilotprojecten interactief computerondersteund onderwijs volgden (*CGO-microscopische anatomie* bij de medische faculteit KUN, en *CGO- bloedgroepenserologie* bij de Hogeschool Arnhem Nijmegen); daarna was hij docent biologie aan de scholengemeenschap Isendoorn in Zutphen van october 1986 tot januari 1991.

Al tijdens de onderwijsbaan kreeg zijn belangstelling voor de vegetatiekunde en wetenschap een nieuwe impuls. Hij raakte betrokken bij het COAL-project en verrichtte als vegetatiekundige in dienst van het CABO in 1987 en 1988 onderzoek naar de *ecologische effecten van aangepaste landbouw*. Hierna begon hij in de zomer van 1988 in opdracht van de Technische Adviescommissie voor de Waterkeringen, Rijkswaterstaat, bij de vakgroep Vegetatiekunde, Plantenoecologie en Onkruidkunde, LUW, een vooronderzoek naar *de vegetatie van Nederlandse zeedijken*. Deze studie die in 1989 werd afgerond vormde het begin van het langer lopende zeedijkenproject, gericht op *effecten van beheer op erosiebestendigheid*, uitgevoerd in de periode 1991-1997, weer in opdracht van Rijkswaterstaat bij de vakgroep VPO/TON. De resultaten van dit onderzoek zijn grotendeels vastgelegd in dit proefschift.

Op 15 september 1997 is hij in dienst getreden bij het DLO-instituut voor Bos en Natuuronderzoek, waar hij werkt aan het entameren en uitvoeren van onderzoek op het gebied van integraal landschapsbeheer en multifunctionaliteit van de groene ruimte.