Advances in grassland science

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Introduction

Advances in science are based on the development of knowledge, concepts and methodology. Grassland science is an integration of physiology, ecology and chemistry, which operates on the levels of the grassland ecosystem, grassland sward, the plant, the plant organ and the cell. It is a branch of agricultural science that connects herbage plant production with ruminant animal production, management of amenity swards and with nature conservation.

Important knowledge areas in plant physiology related to grassland science are photosynthesis, biochemistry and plant anatomy. Developments in these areas have repercussions for understanding and manipulating the growth of plants, their nutritive value, and the sward-animal interface and fodder conservation.

Before 1950, grassland research in north-western Europe was actively pursued, amongst other in the United Kingdom by the Welsh Plant Breeding Station (Anon., 1970) in Wales since 1919. In Germany, Klapp published the fist edition of the well-known book Wiesen und Weiden in 1934 (Klapp, 1934) and Könekamp (1929) reported on the palatability of grasses in relation to their crude protein content (CP) and vitamin content. In the Netherlands, Ten Rodengate Marissen (1905) published a book on grassland with information about botanical composition of pastures, weeds, feeding value, establishment of grassland, reclamation of heathland, drainage, fertilization, fodder conservation and grazing. Ecological grassland research in the Netherlands was already practised at the turn of the 19th century (Rauwerda (1901–1903), but developed rapidly as a result of the work by De Vries (e.g. 1933) who was stationed at the Government Experimental Station for Crop and Grassland Production in Groningen (established in 1923). Also in North America, grassland research was well developed before 1950, particularly in relation to methodology in rangeland research (e.g. Clements, 1905), grassland ecology (e.g. Clements, 1916; Campbell, 1931; Bauer, 1936) and management of pastures (e.g. Aldous, 1930). In southern Australia, Davies & Trumble (1934) published a paper on methods of temperate grassland research.

Because tropical grassland research was underdeveloped in comparison with that in temperate regions until the middle of the 20th century and with a large input into research and development in northern Australia from the 1950s onward, many major advances in grassland science are related to the tropics. For example, early research on photosynthesis and biological N fixation was carried out solely on temperate plants. New breakthroughs in these areas were achieved in the tropics and subtropics. Australia can lay a valid claim as world pioneer in tropical pasture research (Eyles & Cameron, 1985).

This paper will briefly review a selection of the major advances in grassland science over the last 50 years in tropical and temperate regions related to plant physiology, grassland agronomy, environmental issues related to grassland and methodology of measurements. A more extensive review was published by Humphreys (1997).

Plant physiology

Photosynthesis, C4 versus C3 pathways

One of the main advances in plant physiology in the second half of the 20th century was the discovery and description of the C_4 biochemical pathway of carbon assimilation of sugarcane in Brisbane, Australia (Hatch & Slack, 1966). C_4 plants use both the C_3 (Calvin & Benson, 1948) and C_4 pathways. The first carbon compounds in C_4 plants are 4-carbon malic and aspartic acids instead of the 3-carbon phosphoglyceric acid in C_3 plants. C_4 plants have different cells participating in the C_3 and C_4 pathways. The C_3 pathway is restricted to the bundle sheath cells, whilst the C_4 pathway takes place in the mesophyll cells. The relation with grassland science is that the largest group of C_4 plants is tropical grasses of the subfamilies Panicoideae and Eragrostoideae. C_4 grasses have a higher rate of net photosynthesis both at the individual leaf and at sward level; they lack photorespiration and respond to higher light intensities than C_3 species. Therefore, C_4 grasses grow faster and have higher dry matter productivity than temperate grasses (Ludlow, 1976). Tropical grasses have the ability to produce much more DM than temperate grasses per unit of water loss through transpiration, which is an advantage in drier regions. In addition, there are C_4 grasses (e.g. *Chloris*) that are able to close there stomata to conserve water use in times of water deficiency (Downes, 1970). However, there are also major disadvantages with C_4 grasses that are associated with the differences in biochemistry and leaf anatomy between the two groups. Leaves of C_4 grasses have a lower proportion of easily digestible mesophyll and more of the less digestible epidermis, bundle sheath, sclerenchyma and vascular tissues than C_3 grasses. C_4 grasses also have a higher mean cell wall concentration. As a result, C_4 grasses have a lower digestibility than C_3 grasses grown under the same climatic conditions (Wilson & Hattersley, 1983). However, higher growth temperatures also reduce digestibility of tissues (Deinum, 1966; Minson & McLeod, 1970).

In brief, C_4 grasses (in comparison with C_3 grasses):

- require higher temperatures for growth and have thicker cell walls, less mesophyll, more sclerenchyma and more bundle sheaths and as a result a lower digestibility;

- have a more efficient water use;
- produce more dry matter (DM) per unit of time and area;
- have a greater N efficiency and as a result a lower CP concent;
- have lower water soluble carbohydrate (WSC) reserves.

The C_4 characteristics concerning growth, production, water and N efficiency are favourable, because as a result tropical grasses are able to produce DM under unfavourable conditions. However, the lower WSC and CP concent and lower digestibility are clearly unfavourable for the nutritive value of C_4 forages.

N-fixation by C_4 grasses in association with *Azospirillim* was acclaimed as a potential breakthrough for more sustainable agricultural production (Döbereiner & Pay, 1975), with the prospect of developing biological nitrogen fixation by gramineous crops. However, the estimated rates of N fixation were exaggerated because they had been derived from the acetylene reduction test, which has been abandoned because it is entirely unreliable (Peoples *et al.*, 1989).

Light interception

Photosynthesis is the driving force of plant growth and animal production and is dependent on the area and efficiency of green plant tissue. Early research has concentrated on light interception by leaves as influenced by their shape, distribution and mobility in relation to incoming radiation. De Wit (1965) recognized four types of canopies related to their leaf distribution, ranging from horizontal leaves in planophile canopies to vertical leaves in erectophile canopies. Individual planophile leaves intercept more light than individual erectophile leaves, but the former shade each other more than the latter and therefore a sward of mainly erectophile leaves has a higher rate of photosynthesis than a sward of mostly planophile leaves.

Watson (1947) introduced the concept of Leaf Area Index (LAI) and Brougham (1958) pioneered research in New Zealand on the relation between LAI and pasture growth. The LAI for maximum light interception depends on pasture species and elevation of the sun. The species effect is caused by the orientation of the leaves. Broad, planophile leaves as in white clover *(Trifolium repens)* intercepted maximum light at a lower LAI (3.5) than perennial ryegrass *(Lolium perenne)* (7.1) with long, slender, more erectophile leaves. In a mixed (50:50) stand the LAI for maximum light interception was intermediate (4.5). The elevation of the sun is important for the penetration of light into the sward. Brougham (1958) also introduced the concept of sward height before and after grazing, which only recently has been revived as a management tool (Hodgson, 1990).

Parsons *et al.* (1983; 1988) shifted the emphasis from pasture growth to utilization as the main criterion in pasture management. There is a dilemma to optimize photosynthesis on the one hand and efficient harvesting of its product on the other. They found that under 'lenient' (LAI 3.0) grazing with sheep gross photosynthetic assimilation was much higher than under a 'hard' (LAI 1.0) grazing, whereas a similar proportion of assimilates was used for respiration and partitioning to non-harvestable parts, mainly roots. However, animal intake was higher in the 'hard' regime, because a far greater proportion of shoot produced was harvested in this than in the 'lenient' regime, leaving a smaller proportion to be lost.

Water-soluble carbohydrates

The water-soluble carbohydrate (WSC) content in grasses is the balance between photosynthesis and respiration and their use for biochemical processes such as the synthesis of proteins, lipids, fats and cell walls. Fructosans and sugars (temperate climates) and starch (tropical climates) are the most important constituents analysed as WSC in grasses; they are mostly stored in the roots and the base of plants. A large research effort has been dedicated to WSC in grassland plants, particularly in relation to the effects of cutting and grazing on photosynthesis and the level of WSC. Alberda (1957) studied the effects of cutting, light intensity and night temperature on tillering, plant growth and WSC level. He found that tiller formation stopped immediately after cutting, but leaf growth continued, although at a much lower rate than in uncut plants. The WSC reserves in the stubble and roots were partly consumed in the formation of new leaves. Because of the diurnal rhythm of photosynthesis WSC levels are lowest early in the morning and increase during the day, to reach their maximum level before the onset of the night. Defoliation generally results in a decrease of WSC reserves. Alberda (1966; 1970) reported that immediately after cutting *Lolium perenne* plants with high WSC levels had twice the rate of respiration and DM production than plants with low WSC levels. This type of more fundamental research led to the assumption that defoliation management of swards should aim at high levels of WSC in roots and crown, which should favour DM production and plant survival (Weinmann, 1952). Humphreys (1997) discredited much of the importance of WSC on pasture growth. He referred to several papers with arguments against the prevailing opinions about the role of WSC. One of these papers was by Blaser *et al.* (1966), who pointed out that high levels of WSC in pasture grasses were a sign of unrealized DM yield potential. This fits in with the generally lower WSC content in tropical compared with temperate grasses, because the former have a greater yielding capacity. The fact that there are few published papers relating pasture management to DM production on the basis of WSC levels is also indicative of little practical importance of the concept. It was further pointed out that other compounds, such as organic acids, hemicellulose, nitrogen compounds (Culvenor *et al.*, 1989), organic N mobilized from roots and stubble and free amino acids (Ourry *et al.*, 1988) are also involved in plant recovery after defoliation. Humpreys (1997) raised the question whether WSC played a more important role in regrowth of grasses in shade on the basis of research by Wong (1993).

Defoliation

The number of research papers on the effects of frequency and height of cutting or grazing on pasture regrowth is very large (Humphreys, 1997). Although cutting experiments have relevance to early germplasm evaluation, for cut-and-carry and green-lot feeding systems they are of no practical significance in grazing systems, which are by far the most used methods of pasture utilization. Infrequent cutting maximizes DM yield, but decreases leafiness, N concentration and nutritive value and increases structural components. Low cutting increases utilization of nutrients but decreases persistence of bunch type grasses. Jones (1967) and Whiteman (1969) found that erect (e.g. *Stylosanthes guianensis*) and trailing tropical legumes (e.g. *Macroptilium atropurpureum, Desmodium intortum,* and *Neonotonia wightii*) are sensitive to height and frequency of cutting and grazing, leading to their rapid disappearance from a sward.

Grassland agronomy

The tropical grassland revolution (Henzell & 'T Mannetje, 1980)

Before the middle of the 20th century grassland research and development were centred in temperate regions, although some exotic germplasm testing with tropical forage plants was taking place in several tropical countries, amongst other in Australia (Eyles & Cameron, 1985) and Hawaii (Hosaka & Ripperton, 1944). However, this was mainly a matter of testing *ad hoc* introductions by agricultural experimental stations, botanical gardens and enterprising farmers; there was no underlying vision, nor was germplasm evaluation supported by other research to study the need for fertilization, inoculation with rhizobial cultures and grazing management.

A well-known British grassland scientist, William Davies (1933) was invited to review and make recommendations about tropical grassland problems in Australia. He lacked knowledge on tropical plant ecology and recommended that temperate species should be tested for use in the tropics and that plant breeding activities should be undertaken to adapt white clover (*Trifolium repens*) to tropical conditions. Some emphasis was given for a while to the testing of temperate species in lowland tropics, but it was soon realized that this was a thankless task. Further hesitations about the use of tropical pasture legumes were caused by European-trained agricultural scientists spreading doubt about the ability of tropical legumes to fix N, because of acid soils, high temperatures and recurring droughts (Masefield, 1952; Appadurai, 1975).

It was not until all efforts were concentrated on tropical grassland species that progress was made. The new approach received great impetus with the arrival in Queensland of Dr. J. Griffiths Davies in 1952 as Associate Chief of the CSIRO Division of Plant Industry to head the Plant and Soils Laboratory in Brisbane, which became the CSIRO Division of Tropical Pastures in 1959 and went through several name changes since then (Division of Tropical Crops and Pastures, Tropical Agronomy and Tropical Agriculture, Sustainable Ecosystems).

Shaw & Bryan (1976) have published on concepts and methods of tropical pasture research. The philosophy on which tropical pasture improvement research and development was based can be summarized as follows (Davies & Shaw, 1963; Shaw & Bryan, 1976):

- unimproved native pastures are deficient in productivity because of the nature of the pasture species, which have evolved strategies to survive under conditions of low nutrient levels and/or unreliable erratic rainfall in which high productivity is not an ecological advantage; the species develop rapidly after the first rains following the cooler dry season during which the species are dormant and come to flower within weeks after the start of regrowth; they have low DM yields, low CP concen-

trations and low digestibility;
- the best ways to overcome these problems are to replace the native species by productive and persistent grasses and legumes, or by oversowing a legume into the existing native pasture; where necessary and economically feasible nutrient deficiencies should be overcome by the use of non-nitrogen fertilizer or species should be used that have lower nutrient requirements;
- pasture management should aim to optimize animal production and maximize persistence of the pasture species;
- pasture research for development is expensive and should be restricted to regions of adequate rainfall (i.e., above 650 mm per annum with a growing period of no less than 5 months) to make it potentially profitable.

The research activities used to achieve these goals were:
- an integrated approach to pasture improvement in the sense that research was not aimed at a particular narrow aspect of grassland science, but at the whole production system, consisting of the complex of soil, plants, animals, their interactions with each other and with the environment, as influenced by management (fertilization, grazing, cutting) in relation to DM production, botanical composition, nutritive value and animal production;
- plant introduction for an improved germplasm base from East Africa (grasses) and South America (legumes) with regional on-farm evaluation studies to test for adaptability to climate and soils;
- studies of N-fixing bacteria for efficient nodulation and N fixation of legumes;
- plant nutrition studies on mineral deficiencies and to develop fertilizer recommendations;
- phytochemistry to study plant toxicity of introduced species;
- plant physiology to study growth and the effects of stress;
- plant genetics to study breeding systems and carry out plant breeding to improve pest and disease resistance;
- animal nutrition to test nutritive value;
- pasture agronomy and ecology for pasture and grazing management.

This approach was in sharp contrast to that adopted in southern Africa in which native pasture management studies (grazing, spelling, burning) were undertaken to bring about desired changes in botanical composition (Scott, 1947). Although this has led to some improvement in forage utilization, very few results on animal production were published. Furthermore, the South African approach was strongly influenced by the concept that the climax or sub-climax vegetation suitable for grazing of the veld should be maintained.

The Australian approach to research and development of tropical pastures has had its impact on pasture development in northern Australia, tropical America, South East Asia and the Pacific Islands. Since 1961 some 70 grass and legume cultivars were released in northern Australia (Eyles & Cameron, 1985). Many of the early cultivars required fertilizer inputs, had major deficiencies in terms of grazing intolerance, lack of persistence and susceptibility to pests and diseases, which were not present at cultivar release, e.g. anthracnose (*Colletotrichum gloeosporioides*) on *Stylosanthes* spp.; rust

(*Uromyces appendiculatus*) on *Macroptilium atropurpureum* cv. Siratro; and psyllid (*Heteropsylla cubana*) on *Leucaena leucocephala.*

However, susceptible cultivars were replaced by cultivars with the desired properties. Cultivars are now available of *Stylosanthes* spp. tolerant of anthracnose (Cameron *et al.*, 1993) that can grow on soil with low P status and low pH, a rust tolerant cultivar of *Macroptilium atropurpureum* (Bray, 1988) and cultivars of *Arachis pintoi, Vigna parkeri, Chamaecrista rotundifolia* and *Desmodium ovalifolium* that can tolerate heavy grazing (Cameron *et al.*, 1989). The psyllid epidemic that caused leaf losses in *Leucaena leucocephala* has been curtailed by predators that have increased as a result of the epidemic (Oka & Bahagiawati, 1988). However, the severe psyllid damage reported in other countries in the Pacific region has not occurred in northern Australia (Anon., 1986). Psyllid resistance has been found in other *Leucaena* species and plant-breeding work has led to the development of psyllid tolerant genotypes (Bray & Woodroff, 1988). The original problem with mimosine poisoning in ruminants has been overcome in 1986 by transferring DHP (3-hydroxy-4(1H)-pyridone, a poisonous breakdown product of mimosine) degrading rumen bacteria from Hawaii to Australia (Jones & Megarrity, 1986) and has since been spread to other parts of the tropics. *Leucaena leucocephala* has the longest record of persistence of tropical legumes with a half-life of 23 years measured in a long-term experiment in Queensland started in 1959 (Jones & Bunch, 1995).

Without effective and persistent legumes the amount of N available for forage production is limited to 8–10 t DM ha^{-1} $year^{-1}$, with a CP content of less than 7%. With an effective legume DM yields and CP levels can be doubled ('T Mannetje, 1997). Tropical pasture legumes came into general use only after 1960. Although tropical legumes have a great potential for animal production and N fixation, the rate of adoption of tropical legume technology is still small in non-industrialized tropical countries, due to socio-economic reasons ('T Mannetje, 1997). There is reasonable adoption of the new technology in tropical Australia and parts of South East Asia and Latin America. However many countries have such a low development status, particularly on common lands in Africa, that more pressing socio-economic problems, related to land tenure, infrastructure and social justice, need to be solved before large-scale development and application of new technologies will be possible. Nevertheless, there are many reports in the literature of small-scale legume use in African countries, particularly in crop-livestock systems (e.g. Muhr *et al.*, 1998).

Intensive grassland production in north-western Europe

Grassland production improvement research and practice have received special emphasis in north-western Europe immediately after the World War II when there were food shortages and widespread poverty in rural areas. Intensive dairy production systems using high levels of N fertilizer and imported feed concentrates were developed in Western Europe after Word War II and remained the dominant form of dairy production until the 1980s. Grassland research aiming at higher production levels was stimulated by government funded developments, such as regional and infrastructural improvements and extension services. Production per cow, per ha and per unit of labour were rising continuously. The increased output of dairy products was subsidized and farmers had no concerns about markets or environmental consequences (Wilkins, 2000). The successes of scientific research, extension and farming, supported by guaranteed prices for products and subsidies to farmers, were phenomenal and total dairy and meat production increased to such an extent that Western Europe changed from a net importer to a net exporter of animal products. The production of cows' milk in Western Europe, for example, increased from about 90 Mt in 1950 to about 170 Mt in 1980. However, since the introduction of the European Community (EC) milk quota system in 1984, milk production declined again to about 165 Mt in 1990 (Anon., 1962; 1981; 1991). The EC and national policies regarding pricing of agricultural products and subsidies were maintained even after production greatly exceeded the demand of European and export markets for the ever-increasing amounts of agricultural products. Eventually, the EC was no longer prepared to accept the very high costs associated with this. Furthermore, the efficiency of N in these intensive production systems was very low (ca. 16%). This led to unacceptable emissions of NH_3 (volatilization), NO_3 (leaching) and N_2O (denitrification and nitrification) (Van Der Meer & Wedin, 1990).

Improvement of temperate grass and legume cultivars

Plant breeding and selection have played an important role in temperate grassland production improvement. Before the 1960s newly seeded grassland consisted of several grass species plus white clover. However, since that time seed mixtures have become simpler and even monospecific, consisting solely of one or two cultivars of perennial ryegrass. With a management regime of high N applications and intermittent grazing and cutting for conservation, multispecific swards have tended to become near pure swards of perennial ryegrass. Perennial ryegrass, Italian ryegrass (*L. multiflorum*) and hybrid ryegrass (*L. perenne* x *L. multiflorum*) comprise over 90% of the grasses sown in north-western Europe (Humphreys & Theodorou, 2001). Tetraploid ryegrasses were developed in the early 1960s and at the time produced 8–15% higher yielding ryegrass cultivars (Feuerstein & Paul, 1993) with higher digestibility, intake (Alder, 1964), palatability and WSC (Harkess 1966/1967), milk production (Castle & Watson, 1971) and rust resistance. Van Wijk & Reheul (1991) calculated that DM yield of perennial ryegrass cultivars had increased by 0.5% per annum over the previous 25 years in Western Europe. Well-managed swards of recently bred perennial ryegrass cultivars can produce 15 t ha^{-1} during a 6 months grazing season whilst the latest cultivars can produce up to 25 t ha^{-1} (Humphreys & Theodorou, 2001), coming close to the maximum DM yields of perennial ryegrass in temperate regions of 29 t ha^{-1} (Cooper, 1969). The United Kingdom, the Netherlands, Denmark and Belgium are the most active in forage species breeding. The Institute of Grassland and Environmental Research (IGER) in the UK has succeeded in breeding perennial ryegrass cultivars with higher DM yields, higher WSC contents, higher digestibility and better N use efficiency (Humphreys & Theodorou, 2001). Cultivars with 10–15% higher WSC gave increased milk yields with reduced urine-N levels (Miller *et al.*, 1999).

One of the latest developments in grass breeding by IGER has been the discovery of indefinite greenness on senescing leaves of *Festuca pratensis*. This is due to a gene that prevents the breakdown of chlorophyll, which has been transferred to the genus *Lolium* (Thomas *et al.*, 1999) and eventually led to the development of the cultivar AberNile used in amenity grasslands. The stay-green property has also been used in maize and *Sorghum* (Robson *et al.*, 2001).

For many years white clover (*Trifolium repens*) improvement had been stagnant. However, with increased pressure to reduce N fertilizer use, the demand for more resistant white clover cultivars led to more plant breeding with this species. The UK has been most successful in developing cultivars with better compatibility with grasses, improved spring growth and winter hardiness, whilst tolerating moderate levels of N fertilizer (Humphreys & Theodorou, 2001).

Plant breeding for improved forage quality is faced with the problem of a relatively low heritability (30%) of quality traits and in some cases improved quality has led to reduced DM yield. Reduced lignification and modified lignin composition responsible for increased forage quality in some species has led to reduced insect and disease resistance mechanisms (Casler, 1997).

Techniques for genetic manipulation of forages have been developed and transgenic cultivars have been obtained by direct gene transfer to protoplasts, microprojectile bombardment, and *Agrobacterium*-mediated transformation (Spangenberg *et al.*, 1997).

Competition between pasture species

Competition between pasture species for light, nutrients and water determines botanical composition of permanent pastures. The level of competition is dependent on the species and environmental factors and their interactions. Competition also occurs where one species excludes other ones by the release of toxic compounds (allelopathy). Several tropical grasses have been shown to possess allelopathic properties at the expense of other species (Takahashi *et al.*, 1985; Chou, 1989).

The main contributions to a better understanding of competition among pasture plant species were made by De Wit (1960), Donald (1963) and Harper (1977; 1978). De Wit developed a mathematical model to quantify competition in two-component mixtures through time. This model analyses the results of pot or field experiments involving two species planted in a replacement series, in which plant density is held constant, but the proportions of the two species are varied. It is an empirical approach, which involves no fundamental assumptions or expectations. According to the approach of De Wit plants compete for 'space' without specifying which factors are involved. However, Hall (1974a) proposed a method to identify factors involved in the competition. The De Wit model has been applied particularly on problems of competition for nutrients in the Netherlands (e.g. Van Den Bergh & Elberse, 1962; De Wit & Van Den Bergh, 1965) and in Australia (Hall, 1971; 1974a; 1974b).

Donald (1963) on the other hand emphasized the importance of identifying the factors being competed for by using divided pots and by varying plant densities or nutrient levels. With the divided-pot technique it was possible to separate above and below-ground competition, but it had the disadvantage that plants growing in undivided pots had twice the volume of soil than those growing on either side of a pot divider despite the equal plant densities in all cases.

Another approach to study interference between pasture plants in established swards based on population dynamics studies (Hay *et al.*, 2000) was developed by Harper (1977; 1978). Harper's theorem was that fitness for a species to survive depends on the number of descendants that species leave compared with its neighbours, not on maximizing physiological functions.

A comprehensive review of competition theory and methods of study was published by Wilson (1978).

Nutritive value

Research on the nutritive value of forages has concentrated on digestibility and intake since the 1960s. Limiting factors to the nutritive value of forages, particularly grasses are:

- high cell wall content causing low digestibility and resistance to passage from the rumen, which in turn reduces voluntary intake (Wilson, 1985).
- relatively high protein breakdown in the rumen resulting in low protein absorption, often caused by a high protein:energy ratio of the feed, resulting in reduced N use efficiency and increased N emission, causing environmental damage (Van Vuuren & Meys, 1987; Valk, 1994).

Research on digestibility of the cell wall has been carried out since the 1980s, with special attention to research on grass leaf anatomy and cell wall mass and structure (Engels, 1989; Wilson, 1994; Deinum, 1994). The digestion of the walls of sclerenchyma, bundle sheath and xylem cells is lower in tissues grown at the higher temperatures, especially for leaf, which was correlated with an increase in lignin concentration (Wilson *et al.*, 1991). Apart from absolute digestibility, the rate of digestion is equally important at the high levels of digestibility found in perennial ryegrass pastures. However, doubts have been raised over the significance of further increases in organic matter digestibility of grass of already high digestibility, as is the case in much of Western Europe. Nevertheless, this research is highly relevant to digestibility and intake of tropical forages, which are much lower than those of temperate species.

Although forage from intensively managed grasslands is generally of high nutritive value, with high digestibility and CP level, DM intake is still limited for high producing dairy cattle. There is no single factor or simple combination of factors that can be held responsible (Van Vuuren, 1994; Beever & Reynolds, 1994).

Tropical legumes contain generally high CP, minerals and trace element contents, with the exception of Na. Intake of tropical legumes is higher than that of grasses because rumen retention is shorter. Coarse stems are usually rejected and some legumes are unpalatable in spring. The main effect of legumes in mixed grass-legume pastures, apart from N fixation, is improvement of feed quality, as grasses have high growth rates, combined with low digestibility and low CP concents (Wilson, 1994).

It had been suggested that water stress, frequently occurring in the seasonally dry tropics and subtropics leads to low digestibility (French, 1957). This has been disproved (Wilson, 1982). Actually, moderate water stress delays leaf ageing and stem development, leading to a slower decline in digestibility and CP concent (Wilson, 1984). 'T Mannetje (1982) found that grazing animals had substantially higher liveweight gains in dry years with still adequate pasture growth to satisfy animal intake requirements than in wet years.

Forage conservation

Silage making has largely replaced hay making in Western Europe after about 1950. This can be attributed to mechanization and a better understanding of silage fermentation. The most important factors affecting fermentation were established as WSC content and buffering capacity. The desired process is for lactic acid bacteria to ferment WSC to lactic acid and to a lesser extent acetic acid, which reduces the pH to between 4 and 5, thereby inhibiting spoilage micro-organisms and conserving the forage. A high sugar content in the forage and anaerobic conditions in the silo favour this process. Spoilage can occur with high numbers of clostridia in the silo causing a clostridial fermentation, which turns lactic into butyric acid and gives the silage a pH of over 5. Low DM silages and aerobic conditions favour butyric acid fermentation. Many of these spoilage organisms do not only decrease the feed value of the silage, but also have a detrimental effect on animal health and/or milk quality, which can cause 'late blowing' in hard cheeses (Oude Elferink *et al.*, 2000).

Whereas before about 1960 nearly all silage in Western Europe was made from freshly cut grass, later grass was first left to dry in the field to a DM percentage of 25–45%. Bosma (1991) refined the wilting process by regular tedding and conditioning of the swath so that grass could be ensiled within 24 hours after cutting. Wilted grass has a higher osmotic value of the cell contents inhibiting clostridia, and the practice of wilting has solved the major environmental problem of effluents (Woolford, 1978). When the DM content is too high (ca. 60%) it becomes difficult to compress the material and to expel the air.

The use of additives has improved silage quality, particularly at high moisture contents of the grass. Additives are used to either improve or inhibit fermentation, to inhibit aerobic spoilage or to act as nutrients or absorbents (Oude Elferink *et al.*, 2000, Mühlbach, 2000).

In Western Europe the most common forages that are ensiled are grasses and legumes, maize and cereals (whole crop silage). Present research is concentrated on fermentation processes, especially on the use of inoculants and on the improvement of aerobic stability, which is important after opening the silage stacks for feeding. However, the use of individually wrapped bales contributes to reduced problems in this respect.

Silage making in the tropics is not common practice, but can be very profitable depending on type of farm system and on the climate ('T Mannetje, 2000a). For a start, feed conservation is generally only a proposition for intensive farm systems, such as milk production for a liquid milk market (Cowan, 2000) and for smallholders to ensure feed availability during short periods of feed limitation (Wong, 2000). In tropical countries anything that has feeding value is ensiled, depending on availability and quality, including grasses, legumes, fodder crops, crop residues, oil palm fronds, poultry litter and tomato pomace ('T Mannetje, 2000a). Tropical grasses (C_4) have a relatively high concentration of cell wall contents and a too low a level of fermentable carbohydrates for good silage making (Catchpoole & Henzell, 1971) compared with temperate (C_3) grasses, with the exception of *Sorghum* spp. and maize. Therefore, to ensure a good fermentation and high quality silage of tropical grasses it is necessary to add 5–10% of sugar, for which molasses is most commonly used. However, average storage temperatures in tropical climates are too high (> 30°C) for ideal fermentation conditions. In addition, tropical grasses tend to be stemmy, making it difficult to compact the material to exclude air. Chopping the material before ensiling is therefore recommended.

Grassland and the environment

The aim of grassland production should be to combine efficient production with care for nature and the environment, although it will not be possible to carry out production without any negative environmental effects. Grassland vegetation in general provides a cover and thus protection against soil erosion.

Extensively managed rangelands have generally less harmful environmental effects than intensively managed pastures. Rangelands also act as watersheds and as habitats for wild fauna and flora.

Globally, grasslands (including rangelands) play a major role in the so-called greenhouse effect. The greenhouse gases are carbon dioxide (CO_2), which contributes 49%, methane (CH_4) 18%, chlorofluorocarbons (CFC's) 14%, nitrous oxides 6% and others 13%. Three of the greenhouse gases, CO_2, CH_4 and nitrous oxides (mainly N_2O) have relevance to grasslands. Grasslands play a positive, i.e., beneficial, role in the storage of C, but a negative role because of the emission of CH_4, mainly by grazing ruminants, whilst the role of extensively used rangelands in relation to the release of N_2O is negligible, because of the low levels of N in the rangelands ecosystems. The role of grasslands in the storage of C and in the emission of CH_4 will be briefly discussed.

Carbon emissions and sequestration

The global carbon (C) balance is being disturbed, because there is a rapid increase in CO_2 emissions to the atmosphere as a result of burning of fossil fuels and removal and burning of vegetation. The process that counteracts the accumulation of CO_2 in the atmosphere is photosynthesis, by which green terrestrial and aqueous plants assimilate CO_2 from the atmosphere. The atmosphere is estimated to contain 730 gigatonnes (10^9, Gt) C and the annual assimilation by photosynthesis was estimated at 120 Gt C. The earth's plant cover is estimated to contain 563 Gt C and the soil 1515 Gt. In addition, the ocean holds 39,000 Gt C, of which 725 Gt in surface layers (De Groot, 1990). The main stores of C on earth are the oceans, forests, grasslands and rangelands, with little difference between forests on the one hand and grasslands plus rangelands on the other (Goudriaan, 1990; Minami *et al.*, 1993). Most of the C stored by grasslands can be attributed to soil organic matter.

Grasslands also release CO_2 to the atmosphere as a result of respiration, burning and the fermentation of feed in the rumen. Although burning of grassland is a common practice in the seasonally dry tropics, the total amount of C released by burning is only of the order of 4–7 Gt year^{-1}, which is previously stored C and compensated for by photosynthesis of the regrowth (Goudriaan, 1990; Minami *et al.*, 1993). Furthermore, if the material would not be destroyed by fire, most of it would decompose within a year, releasing the same amount of C to the atmosphere (Hall & Scurlock, 1991). In a study covering the whole continent of Australia over a period of 18 years Graetz (2002) concluded that for a full year, the CO_2 emissions from grassland and clearing fires are dwarfed by the uptake as a result of regrowth. Over the year, the grassland fire CO_2 emission is just 5% of the continental uptake flux of 5.97 Gt CO_2, which is recovered by regrowth in less than 1 year. Repeated burning of savannas increases the C content of the soil because every year a fraction of the burned wood is turned into the very stable charcoal (Minami *et al.*, 1993).

The amount of C accumulation in the soil depends on the Net Primary Production (NPP) (DM growth minus respiration) of the vegetation. C_4 grasses have a greater NPP than C_3 grasses and legumes. Therefore, net C sequestration by grassland will be higher in the tropical than the temperate zones. Long & Jones (1992) estimated that tropical grasslands alone store 26% of the total terrestrial carbon, tropical forest 19%.

Van Den Pol-Van Dasselaar & Lantinga (1995) studied C fluxes in permanent grasslands in the Netherlands and concluded that the amount of soil organic C accumulation would be highest at low to moderate application levels of N (6000–7000 kg C ha^{-1} year^{-1}) and higher under grazing than cutting. Vleeshouwers & Verhagen (2002) calculated regional estimates of net C sequestration by different land-management practices in Europe. They concluded that the average C flux on grasslands during 2008–2012 would be 0.15 t C ha^{-1} year^{-1} compared with –84 t C ha^{-1} year^{-1} for arable land. Average C flux for the conversion of cropland to grassland would be 1.5 t C ha^{-1} year^{-1}.

Large areas of rainforest have been cleared in Central and South America and South East Asia. This land is used for plantation agriculture, arable cropping and grasslands. Clearing of rainforest destroys the above-ground C accumulated in the standing timber and when the land is used for arable cropping there is a greater net loss of C from the soil than when the land is used for pastures (Detwiler, 1986). However, the soil C dynamics under pasture depend on the type of grassland vegetation.

The introduction of improved grasses and legumes to rangelands will improve production and also increase the C sequestration potential compared to the native savannas. In the llanos of Colombia, Fisher *et al.* (1994) measured C storage of 237 t ha^{-1} under a 6-years-old *Andropogon gayanus-Stylosanthes capitata* pasture, with about half of it in the 40–100 cm deep soil layer, compared with 186 t ha^{-1} under unimproved savanna. At another site, the soil under unimproved savanna held 197 t C per ha, that under *Brachiaria humidicola* alone 223 t ha^{-1} and under *B. humidicola–Arachis pintoi* 268 t ha^{-1}. Comparable levels of C sequestration have been measured by Ayarza *et al.* (1987), Fisher *et al.* (1995; 1997; 1998), Tarré *et al.* (2001) and Boddey *et al.* (2002). The deposition of carbon at depth can be explained by the massive root systems and deep-rootedness of tropical grasses, which often extends to more than 1 m (Ayarza *et al.*, 1993; Fisher *et al.*, 1994).

Forest destruction is carried out for arable cropping and for grassland establishment. Arable land stores little C in the soil in contrast to grasslands (Detwiler, 1986). Ibrahim (1994) measured 47 t C per ha in the top 10 cm of soil under grazed *B. brizantha-A. pintoi* pastures, which had been established 3 years previously, in the Atlantic Zone of Costa Rica. This amount of soil C was comparable with that found under the original rainforest. Therefore, forest destruction, although deplorable for many reasons, does not necessarily lead to total C storage loss when the land is sown to grassland. The permanent destruction of rangelands by cultivation and desertification, however, is usually irreversible and therefore a significant addition to C releases from terrestrial sources.

Methane emissions

As a contributor to greenhouse gas emissions, methane is second only to carbon dioxide. CH_4 is 4 to 6 times more thermogenic than CO_2. CH_4 emissions to the atmosphere arise largely from anaerobic ecosystems and human activities such as natural wetlands (20%), paddy rice fields (20%), fermentative digestion systems of ruminants and other herbivorous mammals that possess a hindgut fermentation system (15–22%), oceans, lakes, biomass burning, natural gas, coal mining and rubbish tips (Moss, 1993; Howden *et al.*, 1994). In rangelands CH_4 is produced by wild and domesticated grazing animals and by a proportion of the faecal materials decomposing anaerobically (Leng, 1993). Rumen micro-organisms ferment the rangeland feed to volatile fatty acids with CH_4 and CO_2 as by-products (Moss, 1993). A proportionally larger part of the metabolizable energy intake of ruminants is transformed into CH_4 from poor quality feed (15–18%), such as that produced by rangelands and many crop residues in the tropics, compared with high quality feed (7%) such as perennial ryegrass (*Lolium perenne*) (Goossensen & Meeuwissen, 1990; Leng, 1993). Therefore, it is not only important to improve grasslands in the tropics for higher feed production, but as a side effect there will be less CH_4 emitted per unit of feed intake. According to Howden *et al.* (1994) globally, ruminant livestock produce about 80 Mt of CH_4 annually, accounting for about 22% of global CH_4 emissions from human-related activities. An adult cow may be a very small source by itself, emitting only 80–120 kg of CH_4, but with about 1.2 billion large ruminants in the world, ruminants are one of the largest CH_4 sources.

Nitrogen emissions

All grazed grassland systems contribute to N emissions to the atmosphere (NH_3 from animal excreta and N_2O from denitrification) and to the ground water (NO_3 leaching from fertilizers, urine and dung spots and slurry). However, since the size of N flows in extensively grazed rangelands will be small, rangelands can be taken as not to contribute significantly to N emissions. However, intensively managed temperate pastures contributed heavily to environmentally harmful emissions of N (and P) (Van Der Meer, 2001).

Measures to reduce nitrogen emissions

Research since about 1980 started to look for alternative fertilization regimes and organic manure management with reduced emissions. 'T Mannetje (1983) initiated research in the Netherlands to assess the optimum rate of N fertilizer in long-term grazing experiments instead of in annual cutting trials as had been the practice till that time and N flows and losses were monitored in the same experiments (Van Der Meer, 1991). A group of scientists from various research institutes in the Netherlands measured NH_3 volatilization (Bussink, 1992), NO_3 leaching (Steenvoorden *et al.*, 1986) and denitrification (Corré *et al.*, 1990). However, the amount of N immobilized in soil organic and microbial biomass remains a largely unknown factor (Hassink & Neeteson, 1991).

Means to reduce N losses from grasslands are to reduce N fertilization and to improve N efficiency in the production system. Deenen (1994) found in the Netherlands that herbage yields under grazing did not respond to applied N over 250 kg ha^{-1} $year^{-1}$, whilst in the 1980s a standard recommendation of 400 kg N ha^{-1} $year^{-1}$ (fertilizer plus organic manure) was still in force ('T Mannetje, 1994).

Another way to reduce immediate N losses from ruminant production systems is to remove animals from pasture and resort to year-round day and night housing, but more realistically, overnight housing during the growing season will reduce the time at pasture and therefore the losses caused by the deposition of excreta considerably. However, care must then be taken to dispose of the slurry in environment-friendly ways. If, in addition to removing the animals from pasture, they are fed a low protein high energy diet (e.g. maize silage or beet pulp) whilst indoors, the energy:protein ratio in the feed will be improved, leading to reduced NH_3 volatilization and increased N efficiency, without a reduction in milk yield (Van Vuuren & Meys, 1987; Valk, 1994).

There are also major problems associated with volatilization of NH_3 from slurry (Pain *et al.*, 1989). This occurs from the floor of the housing, from the storage tanks and when slurry is applied to the field. Losses from NH_3 volatilization, NO_3 leaching and denitrification can be reduced by slurry treatment with nitrification inhibitors and acid (Pain *et al.*, 1994). However, these measures have not been implemented to any extent and in the case of acidification there are serious problems with corrosion of the equipment. The method of field application also has a big influence on the extent of NH_3 volatilization. Huijsmans *et al.* (2001) found that surface spreading resulted in volatilization of 77% of the total ammoniacal N, compared with 20% for narrow-band application and only 6% for shallow injection.

Scholefield *et al.* (1988) reported that renewing grassland by cultivation and reseeding caused severe N losses by leaching and denitrification and that seasonal N fertilizer timing alone had large effects on levels of potentially leachable soil-N.

Mean annual surpluses (input – output + immobilization) of 175 specialized dairy farms in the Netherlands decreased from 468 kg N ha^{-1} and 32 kg P ha^{-1} over the period 1983–1986 to 358 kg N ha^{-1} and 23 kg P ha^{-1} in 1997–1998 (Van Der Meer, 2001). This decrease may have been partly effected by the introduction of the milk quota system in 1984 by the EU and of the Mineral Accounting System (MINAS) (Van Den Brandt & Smits, 1998) in the Netherlands in 1997, which forced farmers to reduce N surpluses to set maximum levels at the peril of paying fines. In addition, between 1987 and 1996 the Dutch Government introduced measures to reduce organic manure application in terms of amounts applied per ha and time of application (only in the growing season). Slurry application has to be done by low-emission techniques such as injection (Van Der Meer, 2001).

These measures all lead to reduced organic and inorganic N fertilization. However, a good nutrient status of pastures is important for adequate DM yields, botanical composition and nutritive value. Highly valued grasses such as perennial ryegrass require a good soil fertility status in order to persist (Korevaar, 1986; Wind *et al.*, 1994).

Methodology of measurements

Over the last 50 years development of methods has greatly benefited grassland research. A recent review of grassland research methodology was published by 'T Mannetje & Jones (2000). New methods apply particularly to the areas of nutritive value, the estimation of botanical composition and forage yield, assessment of rangeland condition and remote sensing.

Nutritive value

In vitro digestibility analysis (Tilley & Terry, 1963) has made a great contribution to the estimation of *in vivo* digestibility of forages. Large numbers of samples can be analysed in a relatively short time giving accurate estimates, provided standard samples with known *in vivo* digestibility are included. The method uses rumen fluid obtained from rumen-fistulated animals, but more recently cellulase has been used successfully instead of rumen fluid (Adesogan *et al.*, 2000). Another method to estimate *in vivo* digestibility is the gas production technique of Menke *et al.* (1979), which simulates the fermentation of forages. The main advantage of this technique is that it mimics the fermentation process in the rumen (Adesogan *et al.*, 2000). It is also possible to use rumen-fistulated animals to measure *in situ* rumen degradability by hanging forage-filled polyester bags in the rumen *(in sacco)*. By weighing the material before and after inclusion inside the rumen digestion can simply be calculated (Adesogan *et al.*, 2000).

Near-infrared reflectance spectroscopy (NIRS) has been adapted to predict the nutritive value of forage samples. It relies on a regression analysis between NIRS spectral data and laboratory or *in vivo* values of nutritive indices. It produces fast, reliable quantitative and qualitative information on the nutritive value of forages (Adesogan *et al.*, 2000).

Botanical composition and forage yield

Traditional methods for measuring botanical composition by weight and DM yield relied nearly entirely on cutting quadrats and hand sorting, drying and weighing the cut material (Brown, 1954). Because of the time and effort required sample numbers were often inadequate for accurate estimates of botanical composition. The Dry-Weight-Rank method developed by 'T Mannetje & Haydock (1963), modified by Jones & Hargreaves (1979), is non-destructive, accurate and fast for estimating the proportion by dry weight of the different species in a sward. It relies on determining which species or component of the vegetation within a quadrat takes first, which second and which third place in terms of DM. By multiplying the number of quadrats in which a species of component occupies first, second or third place with empirically derived constants an accurate estimate of the botanical composition is obtained (Whalley & Hardy, 2000).

For estimating DM yield the Comparative Yield Method of Haydock & Shaw (1975) was developed. The procedure is based on selecting standards covering the range of DM yield usually on a 1 (lowest) to 5 (highest) scale. The area is then sampled using many quadrats with yields visually estimated to 0.1 units on the same 1–5 scale. The standards are cut and the material weighed to obtain a calibration curve. The mean DM yield of an area is then derived by regression of the estimates. The Comparative Yield Method has been widely used, particularly in combination with the Dry-Weight-Rank method in the computer programme BOTANAL (Tothill *et al.*, 1992). The combination has proved to be accurate, rapid and effective in dealing with large experimental areas, but also with small plots or exclosures ('T Mannetje, 2000b).

DM yield of a sward is related to height and density of the vegetation. These can be integrated using a round or square disc of light metal or foam plastic of a given weight that can slide along a central rod, which is lowered or dropped from a fixed height onto the sward. A calibration curve of height on DM yield has to be constructed to arrive at the mean DM yield ('T Mannetje, 2000b).

Assessing rangeland condition

An important new concept in rangeland management and condition assessment was the development of the 'State-and-Transition' model by Westoby *et al.* (1989), which replaced the Clementsian (Clements, 1916) successional model to evaluate range condition (Dyksterhuis, 1949). According to the successional model all possible states of vegetation from degraded to excellent fit onto a continuous linear scale and the actual condition of the rangeland is its position along this continuum. Trend of rangeland condition is a movement along this line as a result of grazing intensity and long-term weather conditions.

According to Westoby *et al.* (1989) the dynamics of rangelands are better described in terms of discrete 'states' between which rangeland condition can move by means of 'transitions', which are driven by management (grazing, fire, fertilization) and long-term weather conditions.

Advantages of the 'State-and-Transition' model, which has been adopted very widely, are that with ecological knowledge management can manipulate change from one state to another, provided the condition of the rangeland has not reached an irreversible state, e.g. when an originally perennial vegetation has been replaced by annuals as a result of overgrazing and when soil seed reserves of perennial species have been exhausted, or when overgrazing has reached the stage of severe erosion with the topsoil removed. This model can also be used by land managers to better understand the management of their pastures to assist them to move towards a more sustainable production system.

Remote sensing

Radiation reflectance measurements for vegetation studies received great impetus when the resource satellite Landsat was launched in 1972. The reflectance spectra depend on the wavelength and the surface characteristics of the reflected subject. The application of remote sensing to grassland research is in canopy reflectance, which is affected by the reflectance properties of the subject and the Leaf Area Index (LAI) (Roderick *et al.*, 2000). Thus it is usable for qualitative features of the landscape and to estimate DM yield of not fully closed canopies (LAI < 1), which applies to most rangelands in dry climates (Pickup *et al.*, 1994). Tappan *et al.* (1992) monitored seasonal growing conditions of Sahelian and Sudanian rangelands and compared long-term productivity between types of rangelands.

Conclusion

Grasslands play a pivotal role in the development of sustainable agriculture all over the world. Their productivity, persistence and nutritive value are important for food production, the protection of the soil, nature conservation and the storage of carbon. These aspects are in need of continued research for development and adoption of new technology consisting of better cultivars showing superior properties in productivity, persistence and nutritive value for animal production. A better understanding of processes of adoption, production, ecology and the utilization of resources (nutrients, energy) will also contribute to the development of more sustainable grassland systems both for production and for protection of nature and the environment.

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