# THE PLANT ECOLOGY OF SEASONALLY FLOODED AREAS OF THE PONGOLO RIVER FLOODPLAIN, WITH PARTICULAR REFERENCE TO *Cynodon dactylon* (L.) Pers.

## VOLUME 1, TEXT

BY

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*To Beverley, Kirsty and Disa*

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## SUMMARY

The impounding of the waters of the Pongolo river, upstream of its floodplain on the Mocambique coastal plain, may adversely affect the functioning of the floodplain system. A multidisciplinary study of the functioning of the floodplain was initiated to provide a basis for the development of a management strategy for the floodplain.

The study reported in this dissertation considered the flood-dependence and functioning of the vegetation of the seasonally inundated area. The vegetation was mapped and the communities ordinated, according to the Braun-Blanquet technique, in relation to their positions relative to high flood level (HFL) and the level of the water after flood subsidence (i.e. maximum retention level, MRL). Community distribution was shown to be strictly determined by both the height of the floods and by the MRL. It was concluded that periodic floods are essential for the maintenance of the communities.

The *Cynodon dactylon* (L.) Pers. Community, which forms extensive meadows in the zone of periodic inundation, was studied in detail. As the water level receded during winter, productivity was high (up to 23 kg $ha^{-1}$ $d^{-1}$ dry mass) and a palatable sward was produced. This is heavily grazed by domestic stock, but as the soil dries out and water stress becomes significant, production decreases, *C. dactylon* becomes less palatable, and grazing shifts to newly exposed areas. The shift in grazing allows the build up of a large standing crop of both grazeable and ungrazeable (below ground and stolons) material. At the time of inundation by the next floods *c.* 910 kg $ha^{-1}$ of dry mass, *c.* 17 kg $ha^{-1}$ nitrogen and *c.* 2 kg $ha^{-1}$ phosphorus have been removed by grazers. It is concluded that this production, which is flood dependent, forms an important supplement to stock grazing during winter. It is suggested that this source of grazing could be stimulated by irrigation during winter.

*Cynodon dactylon* is shown to decompose rapidly during inundation, losing half of its mass and nutrients in *c*. 28 days. It therefore represents a major energy and nutrient input during the aquatic phase. The extent to which it is grazed during submergence is unknown. The nutrient input is derived ultimately from the soils of the inundated areas and, since nutrients are being removed by both terrestrial grazers and flushing, continued production is reliant upon the annual sediment load reaching the floodplain. Most of the sediment load will now be deposited in the impoundment, and fertilization may be necessary to maintain productivity.

The response of *C. dactylon* to the seasonal fluctuations in water level are used to formulate proposals for water release from the dam. These include proposals for the short-term, i.e. until the demand for irrigation water conflicts with the requirements of the floodplain, and for the long-term, when less water will be available for the floodplain

# CHAPTER 1

## INTRODUCTION

Floodplains are dynamic systems: short- and long-term variations in riverflow create a continuously changing pattern of flooding, silt deposition and erosion, to which floodplain organisms must adapt. Since the floodplain biota includes components which range from aquatic to terrestrial, including those which use the floodplain only during periods of low flow, the interactions are complex. To understand how floodplains function and to be able to predict the impact of various development options on them requires an understanding of how floodplains form and how the floodplain organisms react and interact.

Within the boundary of the Republic of South Africa a number of small floodplain systems are found, however, the only one of notable size is the Pongolo river floodplain (27°S, 32°15'E; with a maximum flooded area of approximately 10 000 ha) situated in Maputaland (Fig. 1.1).

The Maputaland area does not favour human settlement, as water resources are limited (with evaporation exceeding precipitation throughout the year); soils generally are sandy and have a low productivity; Malaria is endemic as was trypanosomyasis until the eradication of the tsetse fly. These factors also account for the fact that Maputaland is probably the least developed area in the Republic of South Africa and there is a complete absence of tarred roads, railways and large towns.

In this remote area the Pongolo river floodplain plays an extremely important role in the subsistence economy of approximately 37% of the population (Heeg and Breen, in press). The annual floods deposit a new layer of silt and irrigate crops during the summer and subsiding water levels allow the development of winter pastures during the dry period.

The Pongolo river floodplain also falls within an area that supports an extension of tropical flora and fauna which, coupled with the highly productive nature of floodplain systems, results in a variety of bird and animal life unique to the area (Heeg and Breen, in press).

Recently the Maputaland area (including the Pongolo river floodplain) has been the subject of investigations into optimal land-use (Thorrington-Smith *et al.*, 1978; Bruton, 1980; Heeg and Breen, in press). These reports concluded that development of the area could best be achieved by promoting agriculture, forestry and tourism.

Tourism has in the past been restricted by the remoteness and inaccessibility of the area as well as limited accommodation. This situation has not changed during recent years. Afforestation has occurred, but has been restricted by the availability and quality of water. The agricultural development of Maputaland has in the past been constrained by lack of water but with the construction during the 1960's of the Pongolapoort Dam immediately above the floodplain, this restriction has been largely overcome. The impounding of the river has serious implications for the floodplain.

Its effect will be twofold i.e. (i) a change in the intensity, duration and timing of floods and (ii) an increase in nutrients contained in runoff and seepage from farming lands. Prior to the construction of the dam, and in proposals for the development of Maputaland, very little attention was paid to the effects that these changes would have on the floodplain. In addition few ecological investigations were conducted which would enable management options to be formulated, so as to maintain the Pongolo river floodplain as a functional unit (Colvin, 1971; Musil, 1972).

In 1974 a research programme was initiated on the Pongolo river floodplain, its main objective being to formulate management proposals for the floodplain based on an understanding of the functioning of the system. Due to the complex nature of floodplain systems this thesis deals with only certain aspects i.e. the occurrence and distribution of the seasonally inundated plant communities; their response to the hydrological regime; and the effects of inundation, exposure and utilization on one of these communities (i.e. the *Cynodon dactylon* (L.) Pers. Community. The thesis also sets out proposals for the management of the vegetation of the seasonally flooded areas of this floodplain.

# CHAPTER 2

## REVIEW OF PERTINENT LITERATURE

## 2.1 Floodplain Geomorphology

### 2.1.1 Floodplain formation

The formation of floodplains is a result of interactions between features of both the river and the area over which it flows.

The river should exhibit fluctuations in flow, so that during low flow periods it is retained within its normal banks, while during high flow periods it is able to overflow the confines of its normal channel and inundate adjacent areas. These fluctuations in flow should be of a regular nature so that the area adjacent to the river is subjected to alternating periods of inundation and exposure.

In addition, changes in river current speed and the volume of its water are important in floodplain formation (Morisawa, 1968; Read and Watson, 1968). A decrease in speed and volume will bring about a decrease in the transporting ability of the river. Material previously held in suspension will be deposited and vertical accretion, resulting in the building up of the floodplain, will occur. A decrease in current speed will occur if there is a decrease in gradient, which results when a river flows from a mountainous area onto a plain or into a still body of water (Morisawa, 1968); when the river flows from one rock type to another (Morisawa, 1968); when the river encounters a downstream obstruction such as the site of a former lake filled with alluvium (Welcomme, 1979a) or when there is an increase in stream length, while the vertical fall remains the same (e.g. as a result of meandering). A decrease in river volume can result from a change in climate (e.g. a decrease in rainfall); increased evaporation when the river flows through arid areas, or when there is an increase in vegetation cover which promotes infiltration and detention of water through storage and vegetative use (Morisawa, 1968).

Vertical accretion is accomplished by inchannel and overbank deposits, which occur during and immediately after floods (Morisawa, 1968). The reason for this is that as the river overflows its banks and spreads out, its velocity decreases and consequently its ability to transport material decreases. Coarse material is deposited near the edge of the river channel and if it remains there, will build up a natural levee. Finer material is carried away from the channel and deposited on adjacent areas (Morisawa, 1968). These deposits provide fertile lands for subsistence agriculture (Welcomme, 1979a).

After the floodplain has been formed by vertical accretion the river meanders over these deposits resulting in lateral migration of floodplain alluvium. This gives rise to a floodplain consisting of features which are predominantly a result of lateral accretion deposits (Morisawa, 1968; Schumm, 1977).

### 2.1.2 Floodplain features

Floodplains have two main features: the river and the alluvial plain. The latter can be further subdivided into :

(1) the levee region which is that area adjacent to the main channel and flooded for the shortest period;

(2) the flats which extend from the levees to the edge of the floodplain.

The development of levees varies considerably from one floodplain system to another. They may be well developed, being only occasionally submerged by the highest of floods (Welcomme, 1979a), while in the case of rivers carrying a very fine silt load they may be absent or tend to diminish in height downstream (Leopold *et al.*, 1964). This differential deposition is important as it results in different soil-types and drainage conditions developing on different parts of the floodplain, which in turn affect the distribution of vegetation.

In addition to differences in levee formation the area between the levees and floodplain margin also shows considerable variation, from systems which have a series of large permanent lakes to those where water remains only temporarily - i.e. the area dries out progressively as floodwaters recede (Welcomme, 1974). These differences are significant, as they provide a range of habitats and therefore allow a wide variety of fauna and flora to develop on a floodplain, which in turn will influence functioning and utilization.

In addition to the above features the meandering nature of a river on a floodplain gives rise to a number of other floodplain features (Leopold *et al.*, 1964; Gregory and Walling, 1973). These include oxbow lakes (the cut off portions of meander bends); point bars (sand bars which form as a result of deposition on the inside of river bends); meander scrolls (due to erosion and deposition as the river migrates laterally downstream); sloughs (formed in cut off meander scroll depressions) and back swamp deposits (fine sediments deposited in slack water between levees and floodplain margins).

Most of these floodplain features can be seen in large systems (e.g. Mississippi, Sacramento and Mekong) whilst in smaller systems they may be difficult to distinguish (Welcomme, 1974), probably because erosion and deposition processes, which are responsible for many floodplain features, occur to a lesser extent in small systems. However, a diversity of floodplain features is encountered on all floodplain systems, which is extremely important in vegetation development, as they create a variety of conditions of substrate and water regime which in turn leads to a mosaic of vegetation types.

## 2.2 Floodplain Hydrology

A major feature which distinguishes floodplains from other aquatic systems is the regular alternation of flood and dry phases (Welcomme, 1974). Flooding can originate from two sources i.e. local rainfall and overspill from the river. Local rainfall can inundate depressions on the floodplain independently of any rise in river level, and this type of flooding has been reported from the Gambia river in north-west Africa (Svenssen, 1933, cited in Welcomme, 1974) and the Kafue river in central Africa (Carey, 1971). However, the majority of floodplains are most frequently inundated by river overspill (Welcomme, 1974, 1979a).

As flow in the river increases a level is reached where water starts flowing out of the main river channel via secondary channels to areas on either side of the levees. When this occurs, shallow basins between the levees and floodplain margins receive flood water. Further increases in flow result in the water level rising until the main river channel is full i.e. bankfull stage (Leopold *et al.*, 1964; Dury, 1970) has been attained. If there is a further increase in water level, the main river channel will no longer be able to contain the volume of water entering the system (Welcomme, 1979a) and water will overspill the banks onto the floodplain. When this occurs many of the water bodies between the levees and the floodplain margin coalesce. Due to the flatness of the floodplain terrain further increase in flow results initially in a lateral expansion of water across the floodplain rather than an increase in depth. This flow across the floodplain is known as 'creeping flow' (Welcomme, 1979a) and it tends to be hampered to some extent by the vegetation on the floodplain. In contrast there is also a strong directional flow, which is usually confined to the main river channel and some of the secondary channels leading from it. These differences in flow influence sediment distribution, as creeping flow is depositional in nature while strong directional flow is erosive in nature (Welcomme, 1979a), and will therefore also influence vegetation distribution.

The alternating periods of inundation and exposure will result in alternating periods of anaerobic and aerobic conditions prevailing in the sediment profile. As the extent and duration of inundation varies considerably across a floodplain, the development of anaerobic conditions in the sediments will show similar variations. The ability of plants to tolerate anaerobic conditions also varies considerably (Crawford, 1978), thus fluctuations in the hydrological regime will determine not only the distribution of vegetation on the floodplain, but will also determine which species are able to inhabit these systems.

## 2.3 Physico-Chemical Conditions

The physico-chemical conditions prevailing on a floodplain will, to some extent, be determined by the characteristics of the water flowing over the floodplain, however, as far as the response of the vegetation of the seasonally inundated areas is concerned, the conditions developing as a result of the alternation in flooding and exposure are of greatest significance.

### 2.3.1 Oxygen levels

Dissolved oxygen levels are extremely important in all aquatic systems (including floodplains), as the amount of oxygen present will determine the quantity and variety of life present in the water column (Beadle, 1974). On floodplain systems, fluctuations in oxygen levels within the sediments are also important in determining the occurrence and distribution of plants, especially in areas where alternating flood and exposure conditions occur.

Dissolved oxygen levels have been reported to be generally lower, in both the river channel and floodplain ponds, during the dry season than during floods (Carey, 1971; Egborge, 1974; Welcomme, 1979a). It has been suggested that these differences are probably due to mixing as a result of greater turbulence during floods and to the aerating action of wind (Welcomme, 1979a). Bonetto (1975) in studies on the Paraná floodplain, found that prior to flooding dissolved oxygen levels were higher in areas without vegetation than in vegetated areas. With the onset of flooding dissolved oxygen levels increased markedly in vegetated areas while at the same time decreasing slightly in areas without vegetation. This change was only maintained for a brief period after which decreases were recorded in both areas as a result of decay of rooted vegetation. However, these decreases were short-lived as dissolved oxygen levels increased and high levels were maintained for the remainder of the flood season. In addition to turbulence during floods, the shallow nature of many floodplain lakes also favours their oxygenation.

It is therefore apparent that dissolved oxygen levels can be expected to fluctuate widely on floodplain systems. As organisms present in the water column are affected by the amount of oxygen present, these fluctuations in dissolved oxygen are likely to influence the occurrence and distribution of these organisms. In the case of seasonally inundated vegetation the situation is slightly different as after floodwaters have subsided, and the sediment has drained, roots of plants growing in these areas are in an aerobic environment. However, following flooding the seasonally inundated sediment becomes water-logged and therefore anaerobic (Beadle, 1974). As different areas of the floodplain are flooded at different times and for varying periods, the development of anaerobic conditions in seasonally inundated areas will vary spatially and temporarily. This in turn will affect the type and distribution of vegetation present, as plants show a wide variation in their ability to tolerate anaerobic conditions (Crawford, 1978).

### 2.3.2 Conductivity and pH

Both these parameters vary considerably between different floodplain systems (Welcomme, 1974) and are determined by factors such as the geology, soil and vegetation types and human activities (farming, urbanization etc.) in the catchment area. It does appear however, that certain changes in pH and conductivity occur in most floodplain systems in response to the flood cycle.

In general pH is lower during the flood season than during the dry season (Tait, 1967; Egborge, 1971; Welcomme, 1979a) probably as a result of the decay of flooded vegetation (Bonetto, 1975) and conductivity is also usually lower during floods (Carey, 1971; Egborge, 1971; Welcomme, 1979a), probably as a result of dilution of lake waters concentrated by evaporation. However exceptions and variations within individual systems are possible. For example pH has been known to increase briefly following flooding (Blanc *et al.*, 1955, cited in Welcomme, 1979a) due to the presence of large amounts of dung on flooded areas, and may fluctuate diurnally in response to photosynthesis (Welcomme, 1979a). Conductivity may increase initially when nutrient-rich soil is inundated (Welcomme, 1979a).

Fluctuations in pH and conductivity of the water are not major factors influencing the floodplain plants directly. Changes in pH of sediments as a result of alternating periods of exposure and inundation, can affect the plants in a number of ways. If a well aerated soil containing nitrates or sulphates becomes waterlogged, both these substances may be reduced

> alkaline

causing a rise in the pH of the soil (Russell, 1961). On the other hand if sulphides are present, as a waterlogged soil dries out they are oxidised and pH decreases (Russell, 1961). Changes in soil pH will affect the growth of plants, mainly through changes in the availability of nutrients (Russell, 1961; Street and Öpik, 1970). Thus the growth and nutrient concentration of plants growing on the seasonally inundated area of a floodplain may change with alternating flood and exposure periods, as these in turn influence sediment pH.

### 2.3.3 Nutrients

There are two main sources of nutrient input to floodplain systems i.e. nutrients dissolved in the water (Welcomme, 1979b) and nutrients adsorbed onto silt (Bayley, 1979; Welcomme, 1979b).

Nutrient concentrations in the water of floodplain systems vary considerably (Sioli, 1964; Johnson, 1967; Bonetto, 1975; Welcomme, 1979a). The reason for this being that in addition to the major factors which determine water chemistry i.e. atmospheric precipitation, nature of the bedrock and evaporation-crystallization processes (Gibbs, 1970), other factors, which vary from one floodplain system to another, also play important roles. The deposition of dung on floodplains, as a result of dry season use by grazers, can contribute significantly to nutrient concentrations in the water (Shepherd, 1976, cited in Welcomme, 1979a). The growth of macrophytes and phytoplankton, as well as human industrial and agricultural activities will also influence nutrient concentrations (Welcomme, 1979a).

The dissolved nutrients will be utilized by phytoplankton, epiphyton and aquatic macrophytes. When these organisms die and start to decay, nutrients contained in them may be incorporated into floodplain sediments including those of the seasonally inundated areas of the floodplain. Thus dissolved nutrient concentrations in the water do not greatly affect vegetation growing in areas subjected to alternating periods of flooding and exposure. Consequently vegetation of the seasonally inundated areas is mainly dependent on nutrients adsorbed onto silt deposited on the floodplain.

During periods of inundation these sediments will become anaerobic (Crawford, 1978), a condition which favours the release of nutrients from the sediment to the overlying water column (Mortimer, 1941, 1942). However, a thin oxidised surface horizon may develop (Gambrell and Patrick, 1978), preventing nutrient movement from sediments to overlying water. Upon exposure these nutrient rich sediments can be utilized by the vegetation of the seasonally inundated areas and nutrients are transferred from sediments to the plants. When these plants are inundated during the subsequent flood, nutrients contained in them are removed by grazers and are released into the water due to leaching and decomposition processes, similar to those occurring in flooded vegetation of lakes (Planter, 1970; Howard-Williams, 1972) and swamps (Howard-Williams and Lenton, 1975). The duration of inundation will largely determine the fate of nutrients released from flooded vegetation. If flow through is maintained they may be exported from the system by floodwaters, rather than utilized within the system.

It therefore appears as if the sediments of the floodplain act as a nutrient sink when new silt is brought down each year. However, despite this reservoir of nutrients and its probable importance, the role of nutrients in floodplain systems, particularly in relation to nutrient pathways and primary production, has largely remained uninvestigated (Welcomme, 1974; Bayley, 1979). In the case of the Pongolo river floodplain the presence of a dam immediately above the floodplain (Chapter 1) will trap silt and the supply to the floodplain will therefore be reduced whilst export may continue.

### 2.4 Floodplain Flora: its importance in the functioning of floodplain systems

There are four main environmental factors which influence the occurrence of aquatic plants i.e. length of the period during which water is present; whether the water is stationary or flowing; the amounts and availability of nutrients, and in the case of submerged plants, the quality and quantity of light penetration (Mitchell, 1978). As floodplains are diverse wetland complexes (Huntley, 1978) various combinations of the above factors can be expected to occur at any one time, resulting in a wide variety of plants occupying floodplain systems (Welcomme, 1979a). These plants include those that are unable to tolerate even relatively short periods of exposure (e.g. submerged and free-floating aquatic macrophytes, phytoplankton and epiphytes) as well as those that are able to tolerate only relatively brief periods of inundation.

### 2.4.1 Submerged and floating plants

#### 2.4.1.1 Phytoplankton

Generally it has been found that phytoplankton density and production tend to be at a maximum during the dry season, decreasing with the onset of flooding (Schmidt, 1970, 1973; Welcomme, 1974, 1979a). These findings contrast with those of Blache (1964, cited in Welcomme, 1974) and the often accepted view that following flooding and the entry into solution of nutrients from inundated dung and vegetation, there are marked increases in phytoplankton. The reasons for lower phytoplankton growth during flooding are probably a decrease in transparency and an increase in velocity, both adversely affecting algal growth (Welcomme, 1979a).

Phytoplankton growth is also higher in floodplain lakes and lagoons than in the river channel (Welcomme, 1979a). This difference is also accompanied by a difference in species composition with blue green algal species (e.g. *Anabeana* and *Lyngbya*) dominant in standing waters whereas river water containes mainly diatoms (e.g. *Melosira*).

Although phytoplankton occur in floodplain systems, their productivity in relation to other primary producers is low (Westlake, 1963; Welcomme, 1979a).

The situation on the Pongolo floodplain is similar to most other floodplain systems, in that there is an increase in phytoplankton numbers during the dry season and populations consist mainly of cyanophyta and *Melosira* (Colvin, 1971). Their productivity is low (Rogers, K.H. unpublished data) as is utilization by fish (Kok, 1978). Thus in the case of the Pongolo floodplain, phytoplankton does not appear to be a major constituent in the functioning of the system.

Higher vegetation growing on the floodplain can also influence phytoplankton growth with reduced densities near emergent and floating vegetation, possibly due to the effects of shading (Welcomme, 1979a), and higher values over submerged vegetation (Shepherd, 1976, cited in Welcomme, 1979a).

### 2.4.1.2 Epiphytes

The possible importance of epiphyte production to floodplain systems was mentioned by Welcomme (1979a) who stated that its production may well exceed that of phytoplankton. Although various workers have commented on the abundance of epiphytes in floodplain systems (Carey, 1971; Rzóska, 1974; Welcomme, 1979a), little quantitative data is available (Welcomme, 1979a). Epiphyton requires a substrate on which to grow which should be situated in water where there is sufficient light. Extensive growths of epiphytes have thus been reported on emergent, submerged and floating vegetation (Welcomme, 1979a). Holčik (1979) pointed out that periphyton and perizoon are important for fish production on floodplains, and that while aquatic macrophytes were rarely used by fish, they played an important role in providing a substrate for periphyton and perizoon growth.

In the case of the Pongolo system recent investigations into the role of epiphyton have been undertaken (Rogers, F.E.J., 1981). Results indicate that epiphyton production is higher than that of phytoplankton and that they contribute significantly to the nitrogen budget by nitrogen fixation. From work by Kok (1978) it also appears as if epiphyton are utilized by fish to a greater extent than is phytoplankton. However, epiphyton probably contribute most to invertebrate grazers, particularly snails (Rogers and Breen, in press).

### 2.4.1.3.1 Rooted aquatic macrophytes

These plants are rooted in the substrate and are either completely submerged or produce leaves which float on the surface. They require permanent water and a relatively stable water level (Welcomme, 1979a). Because of these requirements aquatic macrophytes have a restricted distribution on a floodplain (Welcomme, 1979a) and can be expected to be found in those floodplain lakes which have a stable water level, and in areas where there is prolonged flooding. In some cases suitable conditions do not develop and aquatic macrophytes do not occur on a floodplain (Fittkau *et al.*, 1975), while in other cases the onset of floods results in their rapid and almost total disappearance (Bonetto, 1975).

In shallow oligotrophic lakes rooted aquatic macrophytes generally have a higher production than phytoplankton or epiphyton (Westlake, 1963; Wetzel, 1975). This is also true for floodplain systems (Welcomme, 1979a and b). In addition to this higher production, which can be used directly by grazers (Sculthorpe, 1967; Welcomme, 1974, 1979a), these plants provide shelter for fish, support for epizoon and epiphyton (Sculthorpe, 1967) and play a role in nutrient dynamics (Sculthorpe, 1967; Howard-Williams and Lenton, 1975; Rogers and Breen, 1980).

On the Pongolo river floodplain a number of rooted aquatic macrophytes do occur (Musil *et al.*, 1973). The distribution of these plants is influenced mainly by physical factors such as exposure and water depth (Musil *et al.*, 1973), and the plants affect various physico-chemical properties of the water e.g. increasing pH and oxygen levels, while decreasing carbon dioxide levels (Musil *et al.*, 1976). Recently the growth and reproduction of one of these aquatic macrophytes (*Potomogeton crispus* L.) was investigated (Rogers and Breen, 1980). It was found to play an important role in the nutrient dynamics of floodplain lakes, by taking up nutrients from the water and sediment and making them available to higher trophic levels. In addition, it provided an important source of primary production during spring.

### 2.4.1.3.2 Floating aquatic plants

Free floating aquatic plants are present on many floodplain systems (Bonetto, 1975; Fittkau *et al.*, 1975; Smith, 1976; Welcomme, 1979a). Due to their ability to float these plants are not affected by fluctuations in water level encountered on a floodplain to the extent that rooted aquatic macrophytes are (Fittkau *et al.*, 1975). However these plants can be flushed from the system during large floods (Bonetto, 1975) or deposited on floodplain margins when floodwaters recede (e.g. *Eichhornia crassipes* (Mart.) Solms on the Pongolo floodplain, Goodman, personal communication). Some of these plants are highly productive e.g. *E. crassipes* (15 - 44 m.t. dry matter $ha^{-1}$ $yr^{-1}$, Westlake, 1963), but Welcomme (1979a) suggests this high value is exceptional, being due to favourable environmental conditions (i.e. warm nutrient-rich water). Other free floating aquatic plants are possibly not as productive as *E. crassipes*, but do play a role in floodplain systems in that they can be used directly as a food source by fish and birds, as well as providing shelter for young fish (Sculthorpe, 1967).

On the Pongolo floodplain free-floating aquatic plants (e.g. *Azolla pinnata* R. Br. var. africana (Desv.) Bak, *Pistia stratiotes* L.) do occur (Musil *et al.*, 1973; Pooley, 1978) and tend to dominate in protected shallow areas (Musil *et al.*, 1973). These plants have not formed extensive stands, as has occurred in other aquatic systems (Howard-Williams and Junk, 1977; Mitchell, 1978), probably because of a limited number of suitable habitats. These plants do, however, form a food supply for waterfowl and fish on the Pongolo floodplain (Pooley, 1978).

In addition to free-floating plants, floating meadows also develop on floodplain systems (Welcomme, 1979a). These floating meadows are particularly evident on floodplain systems of South America (Junk, 1970, 1973; Howard-Williams and Junk, 1976, 1977) although Sheppe and Osborne (1971) have reported their occurrence on the Kafue floodplain in Zambia. They consist mainly of grasses and are important primary producers (Junk, 1970), providing good living conditions as well as a food source for secondary producers (Junk, 1973). They also play a role in nutrient cycling (Howard-Williams and Junk, 1976, 1977). Floating meadows, of the type described for South American systems do not occur on the Pongolo river floodplain, although grasses such as *Echinochloa pyramidalis* (Lam.) Hitch. & Case. do form small mats on the surface of the water along the lake margins.

### 2.4.2 Plants of the seasonally inundated areas

The vegetation of the seasonally inundated areas of floodplains can be divided into three main types i.e. forest, floodplain meadow and emergent (Welcomme, 1979a).

Floodplain forests may be of two types i.e. lowland forest occupying alluvial plains and gallery or levee forests (Welcomme, 1979a). The former forest type is restricted to rain forest zones, occurring mainly in the Amazon system, (Welcomme, 1979a). The latter type occurs mainly on floodplains located in savanna areas (Bonetto, 1975; Welcomme, 1979a) and occupies the highest lying section of the floodplain i.e. areas subjected to the shortest period of inundation. Although it has been stated that these forests consist of flood-resistant trees (Welcomme, 1979a); that they are long-living structures and therefore would tend to accumulate nutrients (Welcomme, 1979b) and that leaves and fruit from these trees are used by secondary producers (Welcomme, 1979a) - very little work has been undertaken either on factors affecting occurrence and distribution on floodplains, or on the production and role of these forests in the functioning of floodplain systems. They are however subject to human destruction as they often occupy areas favoured for agriculture.

On areas which are regularly subjected to alternating submerged and exposed phases (i.e. slightly lower lying than levees), grasslands ('floodplain meadows') develop as floodwaters subside (Sheppe and Osborne, 1971). Within this grassland zone species such as *C. dactylon*, *Sporobolus robustus* Kunth and *Echinochloa* spp are found in wetter areas (Howard-Williams, 1972). These grasses also differ in their response to flooding. Some species lose most of their photosynthetic tissue, surviving the submerged period by means of stolons and rhizomes. Other species (e.g. *Vossia*, *Echinochloa* and *Oryza*) assume a wet season form (Welcomme, 1979a). With the onset of floods stem length increases rapidly so that the photosynthetic parts of the plants remain above the water level forming 'floating meadows' (see 2.4.1.3.2 - above). These grasslands are used during the dry season by wild game (Sheppe and Osborne, 1971) and by grazing cattle

(Welcomme, 1979b). Grazing may be extremely heavy since in some instances most of the growth of grazing cattle can occur during the period they spend on these grasslands (Sheppe and Osborne, 1971). Apart from this report of heavy grazing, little information is available on the productivity of these grasslands, although Thompson (1976) suggested a value of 10 - 20 t $ha^{-1}$ $yr^{-1}$ would not be an unreasonable estimate.

The third vegetation area is inundated for most of the year. During exceptional years these areas may become exposed but most remain inundated to a depth of up to *c*. 20 cm. Within this area emergent plants such as *Phragmites*, *Typha*, *Scirpus*, *Cyperus*, *Leersia*, *Ipomoea* and *Panicum*, amongst others, are present (Howard-Williams, 1972; Bonetto, 1975; Welcomme, 1979a). In addition to occurring on floodplain systems these plants also occur extensively in swamp systems and in the littoral zones of lakes (Beadle, 1974; Howard-Williams and Lenton, 1975; Mitchell, 1978) and it is in these areas that the plants have been most studied (Beadle, 1974; Howard-Williams and Walker, 1974; Rzóska, 1974; Howard-Williams and Lenton, 1975; Howard-Williams, 1975; Gaudet, 1976, 1977; Howard-Williams, 1979a, b and c). These studies indicate that in both swamp and lake systems emergent vegetation is highly productive and Westlake (1963) regards tropical reedswamps as one of the most highly productive vegetation types. These plants also play an important role in the nutrient dynamics of the systems in which they are found (Howard-Williams and Lenton, 1975; Gaudet, 1976; Mitchell, 1978; Howard-Williams 1979c) and serve as a food source for fish and birds (Sculthorpe, 1967). Although little research has been carried out on the role of emergents on floodplain systems, it is likely that they are as important to these systems as they are to swamp and lake systems.

Although reference has been made to the vegetation of the seasonally inundated areas of the Pongolo river floodplain (Tinley, 1976; Moll, 1977), their distribution, extent and role in the functioning of the system has not been elucidated.

## 2.5 Floodplain Research: Present status and future requirements

Floodplain systems, due to their numerous interacting processes and components, are extremely complex. They are also very specialized and highly productive systems (Thompson, 1976). These production processes are likely to be more complex than other wetland systems (e.g. littoral zones of lakes) due to the dynamic nature and lower predictability of floodplain systems (Bayley, 1979). Because of these complexities and interactions, changes in one functional component of a floodplain system will, to some extent, affect all other components. It can therefore be expected that floodplain systems will be extremely susceptible to disturbances and if these systems are to be maintained as functional units, a thorough understanding of their functioning is necessary. However, from the foregoing discussion it is clear that floodplain systems have been less researched than other aquatic systems and floodplain processes are consequently less well understood (Bayley, 1979).

Floodplains consists of two complementary phases i.e. aquatic and terrestrial, which alternate in dominance (Welcomme, 1979a). During the terrestrial phase vegetation establishes itself on the exposed areas of the floodplain, which is utilized by wildlife and used for grazing cattle (Welcomme, 1979a). During floods material from the previously exposed areas enriches the aquatic environment to the benefit of aquatic organisms (Welcomme, 1979a). Thus the seasonally inundated areas of the floodplain are important to both terrestrial and aquatic organisms, and serve as a link between the aquatic systems of the floodplain (i.e. river and floodplain lakes) and the terrestrial systems of the areas adjoining floodplains. Despite this importance, the seasonally inundated vegetation is the least studied aspect of floodplain systems (see 2.4 above). This need stimulated the research reported here. To achieve this objective it was necessary to : (i) identify the various vegetation types of the seasonally inundated area, (ii) determine their relationship with floodplain features and the hydrological regime, (iii) assess their extent to identify those of greatest importance and (iv) study the dynamics of the important vegetation types to permit formulation of management practices.

# CHAPTER 3

## MATERIALS AND METHODS

## 3.1 Classification and Ordination of the Vegetation

The objective of this section of the study was to identify plant communities, and to ordinate them into a sequence that would indicate which environmental variants were most important in determining their development.

### 3.1.1 Choice of the Braun-Blanquet Method

The Zürich-Montpellier School of vegetation classification is based mainly on the principles expressed by Braun-Blanquet (1932). The Braun-Blanquet method involves the recognition, description and classification of vegetation on the basis of floristic composition (Whittaker, 1962) and is carried out in two distinct phases i.e. sampling and synthesis.

(a) Sampling

Within the study area quadrats are set out in vegetation stands that have been visually assessed to be floristically, structurally and environmentally homogeneous (Werger, 1974). Homogeneity is important as information on one vegetation entity only is required per sample (Werger, 1974). As homogeneity is assessed subjectively it implies a thorough knowledge of the vegetation prior to commencing the survey.

The size of the quadrat used depends on the vegetation type being sampled (Shimwell, 1971) because in the Zürich-Montpellier method a fixed quadrat size or form is not necessary (Werger, 1974). The quadrat size used should result in only one vegetation type being sampled and a typical description of the vegetation type being obtained (Werger, 1974).

At each sampling site a complete list of species present is compiled (Braun-Blanquet, 1932; Shimwell, 1971; Werger, 1974). In some cases (e.g. annuals and geophytes), this is not always possible and permanently recognisable species are emphasised (Werger, 1974). When the species list is complete each species is assigned two numbers; one is an estimate of cover-abundance and the other a sociability index (Shimwell, 1971; Werger, 1974). The cover-abundance value indicates the relative importance of each species, while the sociability index indicates the grouping or clumping of individuals of the same species (Werger, 1974).

Habitat factors are also recorded at each sampling site (Werger, 1974). These factors are selected according to the hypothesis being investigated, and they may include slope, aspect, geological substrate, soil characteristics, water table, as well as biotic influences. Their selection will depend on the purpose and scale of the survey.

A completed site record consisting of the aspects discussed above is known as a relevé. There is no theoretical means to determine the number of relevés required in any survey, but the total set of relevés taken should be an accurate reflection of the vegetation of the study area (Werger, 1974).

(b) Synthesis

After collection the field data is entered into a matrix in which the rows represent species and the columns relevés (Werger, 1974). Relevés and species are rearranged in such a manner that groups of samples (noda) become evident, which are relatively homogeneous and distinct (Whittaker, 1962) as far as species composition is concerned. This arrangement of species on the basis of their presence, allows the recognition of species which are constants or dominants in a nodum (Werger, 1974). Species which are restricted in their occurrence or faithful to one or more noda are termed differential i.e. they differentiate between noda (Werger, 1974) while species occurring exclusively in one nodum, mainly in one nodum and seldom in others, or optimally in one nodum are termed character species. Once the noda have been delineated their relationship with habitat conditions is established. If a nodum which has a definite floristic composition and uniform physiognomy can be related to uniform habitat conditions, it can be regarded as an association which is the basic natural community of the Zürich-Montpellier system (Werger, 1974).

This system of classification, although applied extensively in Europe (Whittaker, 1962; Shimwell, 1971; Werger, 1974) and to a lesser extent in other parts of the world (Shimwell 1971; Werger, 1974), has been criticised. The major criticism has been the subjective nature of the method but Whittaker (1962), in his extensive reivew of the classification of natural communities, concludes a discussion on the subjectivity of this method by stating that no widely used system of classification is inherently less subjective than that of Braun-Blanquet.

The visual assessment of homogeneity has also been criticised (Kershaw, 1973). Werger (1974) discussed this aspect and pointed out that as far as homogeneity is concerned, the human eye, although badly adapted to measurement, readily gives the trained plant sociologist an impression of whether a plant community is homogeneous or not. He also pointed out that no satisfactory method has been proposed which will enable homogeneity to be accurately determined.

Despite criticisms the Braun-Blanquet method has a number of distinct advantages. When completed the final classification contains information on species relations, community types and community - habitat relations which is not conveyed by other classification systems with equal efficiency (Whittaker, 1962). It allows community types to be concisely defined by diagnostic species (Whittaker, 1962). It has been applied to widely different vegetational conditions, and in fact no other system has been as successfully applied to as wide a range of vegetational conditions and research purposes, as has the Braun-Blanquet method (Whittaker, 1962).

Methods and concepts have been standardized which allow the work of different authors to be compared and integrated (Whittaker, 1962; Werger, 1974). The Braun-Blanquet technique also maximises the understanding of the relationship between vegetation and environmental factors for a minimum of time input (Moore *et al.*, 1970; Werger, 1973). These advantages of the Braun-Blanquet method made it particularly suitable for a vegetation survey of the Pongolo floodplain, as information on the communities, their relationship to each other and particularly the flooding pattern, was required. It also enabled comparisons to be made between results of the present study and those of other workers on the basis of community structure, relationships between and development of communities, and the causative factors in community development.

In addition, as the floodplain is seasonally inundated, maximum development of the vegetation of the exposed areas occurs immediately before the onset of flooding. As the occurrence of floods could not be predicted, once the vegetation survey had been started it would have to be completed as rapidly as possible, so as to obtain sufficient relevés from all communities, before flooding.

### 3.1.2 Application of the method

#### 3.1.2.1 Collection of field data

Colour aerial photographs* (scale 1:25 000) were used to demarcate physiognomically distinct vegetational units. Each of these units were then observed in the field, plant collections made and species lists compiled to establish if units had been correctly assigned. Plant nomenclature followed Ross (1972).

Quadrat size was obtained by determining minimal area (Braun-Blanquet, 1932; Mueller-Dombois and Ellenberg, 1974; Werger, 1974). Species lists were compiled from homogeneous stands of the various vegetation types and from the same vegetation types in different areas, by using nested quadrats which increased in size from 1 $m^2$ to 128 $m^2$. The increase in area (x-axis) was plotted against the number of species (y-axis) and the point at which an increase in area did not result in an increase in number of species, was taken to be the minimal area.

The determination of minimal area has often been criticised as it depends on the ratio of the ordinate to the abscissa when species versus area are plotted graphically (Cain, 1938), and because in some cases no

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*Aerial photographs taken by the Department of Land Survey, University of Natal, Durban, and housed in the Department of Botany, University of Natal, Pietermaritzburg.

levelling-off in the number of species occurs as area is increased (Mueller-Dombois and Ellenberg, 1974). In the present study the species-area curve did level-off, probably due to the relatively small number of species occurring on the floodplain. In addition to the use of species-area curve, minimal area was also estimated as the area above which there was no increase in constant species (Werger, 1974), where constant species were those that occurred in 90% of the nested quadrats. Similar results were obtained for both methods which indicated that quadrats of 8 $m^2$ were adequate for all vegetation types except the riverine forest where quadrats of 100 $m^2$ were required. Although quadrat size may be adapted to vegetation type (Werger, 1974) all communities were sampled using 5 x 20 m quadrats. This quadrat size was much larger than required for vegetation types such as *C. dactylon* and *Cyperus fastigiatus* Rottb. but because of the homogeneous nature of the vegetation and the relatively few species present, the larger quadrat size did not prove to be too time consuming or inconvenient.

When quadrats were set out all plant species present (i.e. both annuals and perennials) were recorded and assigned a cover-abundance rating according to the Domin scale (Werger, 1974; Table 3.1). Cover-abundance is a measure of the relative importance of a species in a stand and is based partly on aerial cover and partly on numerical abundance (Braun-Blanquet, 1932; Werger, 1973). All species occurring within a quadrat were also rated on a sociability scale, which indicated the extent of the grouping of individuals of the same species (Werger, 1974; Table 3.2). Within each quadrat the height and percentage cover was also recorded.

In addition, the following site factors were assessed :

(a) Biotic influence: The extent of grazing and trampling, especially by cattle and goats and any burning or cutting of vegetation.

(b) The height of each quadrat in relation to the maximum retention level (MRL) i.e. water level at which contact between lake and river is lost, and high flood level (HFL) i.e. a subjective estimate of the highest level attained by floodwaters during an average year (Breen *et al.*, 1978), was estimated using 1:6000 trigonometrical survey maps (Pongola-Mkuze Irrigation Scheme)* and on site investigation.

(c) Soil samples were collected to a depth of 125 mm, and pH was measured in 1N KCℓ (Jackson, 1958). Clay, silt and sand fractions were estimated by the Bouyoucos hydrometer method (Black, 1965) and soil moisture content by drying samples to a constant mass at 105°C (Black, 1965).

In this study a total of 106 relevés (completed site records of quadrats) were recorded in an area of approximately 8800 ha i.e. a sampling intensity of 1 relevé per 84 ha. Although each vegetation type was sampled, quadrats were not set out in all stands of every vegetation type. In the case of large areas occupied by the same vegetation type, fewer quadrats were used than in the case of a vegetation type occupying a large number of small areas.

### 3.1.2.2 Synthesis of data

Field data were synthesised to facilitate interpretation. A table of cover-abundance values was constructed in which columns represented relevés and rows species. This completed matrix is known as a raw table. The raw table was rearranged by hand so that relevés with similar species composition were grouped together. This was followed by a rearrangement of species so that positively associated species were grouped together. Species and relevés were rearranged a number of times manually, final sorting of the table being done by a computer**. Rearrangement of the table resulted in distinct species - relevé groups emerging, each group being termed a nodum. Some relevés did not fit into a particular nodum. These relevés were retained in the table as it was thought that they may possibly represent a nodum which was undersampled or not recognised (Werger, 1974) and which might be incorporated if more data was obtained

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later. Species occurring in three or less relevés were excluded from the main table to simplify rearrangement (Werger, 1974).

Within each nodum character and differential species were recognised (see 3.1.1 above).

Once the noda had been established they were compared with the habitat conditions to determine if floristic variation correspond with environmental variation. The floristic composition of noda were also compared in the field with vegetation types they were supposed to represent. A nodum which was found to have a definite floristic composition, uniform physiognomy and to occupy a uniform habitat, was regarded as a plant community (Werger, 1974). The sociability index was not included in the phytosociological table but was used to assist in describing the communities.

To test the importance of flooding as a determinant in community development the plant communities were arranged in the phytosociological table according to their response to flooding, i.e. from those showing a close affinity to MRL to those more closely associated with HFL. Communities were thus ordinated along an environmental gradient.

## 3.2 Functioning of the *Cynodon dactylon* Community

*C. dactylon* was observed to form extensive, almost pure communities in zones of periodic flooding (Plate 5.4). These areas are exposed during the winter months when they are utilized as a source of grazing for domestic stock, principally cattle. During the summer months the *C. dactylon* community is inundated resulting in a transfer of energy and nutrients from the terrestrial to the aquatic phase of the floodplain system.

This investigation was undertaken to determine the importance of *C. dactylon* meadows to terrestrial and aquatic phases of the floodplain system and the effects of exposure period and grazing on crop growth rate (C) and on nutrient content of *C. dactylon*. These latter estimates aided the formulation of a flooding programme for management.

### 3.2.1 Measurement of standing crop and amount removed by grazing

Standing crop and amount removed through grazing by livestock (mainly cattle) were determined using techniques similar to those described by Brown (1954) and Milner and Hughes (1968). Although insects and soil invertebrates are important herbivores in most terrestrial ecosystems (Caldwell, 1975), only grazing by livestock was considered in the present study.

The grazeable fraction, comprising the erect shoot system from approximately 3 mm above the ground, and the ungrazeable fraction, consisting of horizontal stems, rhizomes and roots, between 3 mm above ground level and depth of 125 mm, were sampled.

Grazeable fraction was sampled from within 0,25 mm$^2$ circular quadrats. Quadrats of this size proved to be the most satisfactory for the level of accuracy required (i.e. dry mass of samples from both grazed and ungrazed areas had a S.E. of less than 10% of the mean), and for the time taken to harvest material. Similar sized quadrats have been used on grassland studies, although they were not always circular in shape (Milner and Hughes, 1968). However, Coleman (1959) and Van Dyne *et al.*, (1963) showed that a circular shaped quadrat is most suitable for sampling grassland vegetation types. The combined effects of exposure and grazing were determined by comparison of the grazed area with an area in a permanent exclosure. This consisted of an area 18 x 18 m, enclosed by 50 mm wire mesh to a height of 1,75 m.

In addition to the permanent exclosure, moveable exclosures were used to determine the amount removed by grazers, i.e. the difference between the standing crop in the grazed area at the start of each interval and that inside the moveable exclosures. Each moveable exclosure was 0,5 m high, completely enclosed in 50 mm mesh, and had a base area of 1 x 3 m. Five adjoining 25 x 25 m areas were demarcated along the north-east shore of Namanini lake (Fig. 3.1), whilst the *C. dactylon* was still inundated with shallow water. The permanent exclosure was positioned in one area and the remaining four were divided into quarters. The first samples were taken immediately the water receded from the demarcated areas. Within the permanent exclosure a 3 m wide border was excluded from sampling and 20 random samples were taken from within the 144 m² area at approximately 25 day intervals on seven occasions. One quarter of each demarcated area was sampled by five quadrats on each occasion and no quarter was sampled more than twice. The moveable exclosures were placed in the same area, and numbers varied between three and five depending on disturbance by local inhabitants. Three samples were taken within each exclosure after each time interval and they were relocated at approximately 25 day intervals.

Harvested material was placed in polythene bags, sealed and returned to the laboratory for drying (forced draught oven at 60°C) before being massed.

Ungrazeable material was determined from two 100 m diameter soil cores, taken from each 0.25 m² area, after grazeable fraction material had been clipped, combined and placed in polythene bags which were then sealed for removal to the laboratory.

Soil was removed by the floatation method of McKell *et al.*, (1961). Material thoroughly, but carefully, washed in distilled water before being dried at 60°C and massed. The separation of living and dead roots has always been difficult (Milner and Hughes, 1968; Böhm, 1979) various techniques such as staining (Milner and Hughes, 1968), floatation (Böhm, 1979) and measuring differences in electrical conductivity (Greenham and Cole, 1949) have been tried, but none has proved satisfactory (Milner and Hughes, 1968; Böhm, 1979). Böhm (1979) states that a combined assessment of root colour, the elasticity of the roots, and the presence of cortex and lateral roots can help to distinguish between living and dead roots. However he also pointed out that in practice this is difficult and errors are often great. In the present study no attempt has therefore been made to separate living and dead material of the ungrazeable fraction. In the case of the grazeable fraction little dead material was observed and because of this no separation into living and dead fractions was carried out.

### 3.2.2 Calculation of mean crop growth rate

Crop growth rate (C) can be defined as the instantaneous rate of dry matter production per unit area of land (Hunt, 1978). It is used as a simple and important index of agricultural productivity. Although C is an instantaneous value, being the product of the instantaneous values of the unit leaf rate (ULR = net assimilation rate) and leaf area index (LAI) the mean C($\bar{C}$) can be obtained without determining ULR or LAI by using the following formula :

$$\bar{C} = \frac{1}{P} \cdot \frac{2^W - 1^W}{2^T - 2^T} \quad \text{(after Hunt, 1978).}$$

Where $1^W$ and $2^W$ are the dry weights of the crop harvested from equal, but separate, areas of ground (P) at times $1^T$ and $2^T$. If $1^W$ and $2^W$ are each expressed per unit quantity of P, as is the case in the present study, then the calculation of $\bar{C}$ becomes simplified to :

$$\bar{C} = \frac{2^W - 1^W}{2^T - 1^T}$$

According to Hunt (1978), $\bar{C}$ in this form becomes an absolute growth rate i.e. a difference in size divided by a difference in time.

### 3.2.3 Measurement of nutrient content

Changes in nutrient content of both the grazeable and ungrazeable fractions of *C. dactylon*, from within the permanent and moveable exclosures as well as in the grazed area were determined. After material had been dried and massed (see 3.2.1), the entire sample was ground and subsamples taken for chemical analyses (i.e. N, P, K, Na, Ca and Mg).

(a) Nitrogen:

The Kjeldahl method of Humphries (1956) was used. This involved digestion of plant material with sulphuric acid followed by steam distillation into boric acid, which was titrated with hydrochloric acid, using a mixed Methyl red - Bromocresol green indicator.

(b) Phosphorus, K, Na, Ca and Mg :

Sub-samples of 0.1 g were ashed at 490°C and taken up in acid (hydrochloric and nitric; Humphries, 1956). This solution was used for both cation determinations using an atomic absorption spectrophotometer and for phosphorus using the Vanado-molybdate method (Jackson, 1958).

### 3.2.4 Integration of processes taking place on the floodplain

As the water level dropped both the area available for grazing and the time differential between the first and recently exposed areas increased. Thus standing crop and grazing varied spatially and temporarily and integration of the data derived from sampling one area with time, was necessary to elucidate the significance of these processes to the system as a whole. The area of *C. dactylon* exposed during each time interval was determined by a combination of survey and planimetry, since during a particular interval half the area exposed was considered to have been exposed for the full period of that interval. During the second interval of exposure one half of the area was considered as being exposed to conditions prevailing during the first, whereas the second half was experiencing the conditions of the second interval. This procedure for integration is represented diagrammatically in Fig. 3.2. Processes for which this integration was used were: changes in biomass and amounts of nutrients of the grazeable and ungrazeable fractions of *C. dactylon* in both grazed and ungrazed areas, as well as biomass and amount of nutrients removed by grazing.

### 3.2.5 Determination of water status

#### 3.2.5.1 Soil moisture content

Soil samples for moisture determinations were collected from the areas where *C. dactylon* was being harvested (see 3.2.1). They were taken to a depth of 125 mm using a 100 mm diameter core sampler, placed in polythene bags, sealed and returned to the laboratory. Each sample was thoroughly mixed before the removal of three sub-samples which were massed before being dried in a forced draught oven at 105°C to constant mass. Loss of mass was determined by difference and percentage moisture content calculated on a dry mass basis.

### 3.2.5 Measurement of soil matric potential

Soil matric potential was measured using the pressure plate technique (Richards, 1949; Kramer, 1969).

Undisturbed soil samples were collected in circular tins (750 mm in diameter and 250 mm high) with lids on both ends, by first carefully clearing the soil surface of plant material and loose soil and then pressing the tin, with one lid removed, into the soil until the top was level with the surrounding soil. The tin was carefully dug out and excess soil on the undersurfaces removed with a hacksaw blade. The bottom lid was then replaced and the edges of the tins sealed with masking tape. To determine matric potential both lids were removed and samples placed on a porous ceramic plate, in a pressure chamber and allowed to stand in excess water for approximately 24 hours. The pressure chamber was then closed and pressure applied (see below). Samples were left to equilibrate for 10 days. Water content was then determined by drying samples to a 'constant' mass at 105°C.

In this study the matric potential used to plot the moisture characteristics curve were as follows: -30; -100; and -1500 kPa (for practical purposes regarded as permanent wilting point; Slatyer, 1967; Kramer, 1969), the mean value of eight determinations being used. The moisture content at -10 kPa (for practical purposes regarded as field capacity; Marshall, 1959) was not measured, but an estimate was obtained by extrapolation from the moisture characteristic curve. The moisture characteristic curve was used to obtain an indication of the availability of soil water for plant growth i.e. 'the amount of water retained in a soil between field capacity and the permanent wilting percentage' (Slatyer, 1967).

### 3.2.5.3 Measurement of xylem pressure potential

Xylem pressure potentials (Ritchie and Hinckley, 1975) of *C. dactylon* shoots (*c.* 5 cm in length) were determined using the pressure chamber system as described in detail by Waring and Cleary (1967). Two modifications were used; firstly the cover design of Millar and Hansen (1975) was used so that the cut end of the shoot was clearly visible with only 1 - 2 mm of stem protruding from the rubber bung; and secondly a rubber bung which had been slit from the centre to the circumference was used in place of a bung with its centre perforated with a hole. This was to prevent the *C. dactylon* shoots, which had a very small diameter, from being forced through the hole in the bung when pressure was applied.

A x10 magnifying glass was used to observe xylem sap exudation from the protruding end of the stem.

Xylem pressure potential was measured four times per day (Table 3.3) at approximately 25 day intervals on seven occasions. On each occasion the early morning measurement i.e. between 05h00 and 06h00 were always taken before sunrise ('predawn'). Measurements were made in both grazed and ungrazed areas and sufficient samples were taken to obtain a S.E. of less than 10% of the mean.

### 3.2.5.4 Measurement of vapour pressure deficit

Air temperature and relative humidity were measured using a wet and dry-bulb whirling hygrometer, at the same time as xylem pressure potential measurements were made. Temperature and relative humidity results were used to calculate vapour pressure deficit using the following relationship :

$$e_d = e_a \times \frac{RH}{100} \qquad \text{(after Schulze, 1974)}$$

where $e_d$ = actual vapour pressure

$e_a$ = saturated vapour pressure (calculated from values in Oosting, 1956)

RH = Relative humidity

### 3.2.6 Measurement of decomposition rates

With the onset of summer floods the extensive 'marginal meadows' of *C. dactylon* which develop and are grazed during the winter, become inundated. Judging by what remains after re-exposure, a substantial part must either have decomposed or been grazed during submergence.

Rates of decomposition and nutrient release were measured *in situ* using both living and dried material. Dry material has been used for the measurement of decomposition rates (Boyd, 1970; Godshalk and Wetzel, 1978a; Howard-Williams and Davies, 1979), however it was thought that this would result in errors due to the effects of drying. In addition, the situation on the floodplain is that living *C. dactylon* is inundated. It was therefore decided to investigate decomposition rates of living and dried *C. dactylon* material.

Material was collected by clipping randomly placed quadrats 3 mm above the substrate. Approximately 25 g of material (accurately massed) was placed in 20 x 30 cm nylon bags (Boyd, 1970; Howard-Williams and Davies, 1979; Danell and Sjöberg, 1979) having a 2 mm mesh size. Where fresh material was used, bags were placed in the lake immediately while additional material, collected at the same time, was first dried at 60°C before being located adjacent to bags containing fresh material.

Bags were weighted so that they rested on the substrate. Unfortunately persistent interference by local inhabitants prevented extension of the experiment beyond 40 days. Four bags from each treatment were sampled at approximately five day intervals.

Inundated material was sampled in the field using a van Veen grab. It was not possible to sample quantitatively with this technique and thus only changes in concentration were followed during submersion.

Plant material was rinsed with distilled water, dried at 105°C (Hunter, 1976) and ground. Ground samples were analysed for nitrogen, phosphorus , K, Na, Ca and Mg as described above (see 3.2.3).

# CHAPTER 4

## DESCRIPTION OF THE STUDY AREA

### 4.1 Location

The Pongolo river has its origin in the Wakkerstroom area of the south-eastern Transvaal (Fig. 1.1), some 2200 m above mean sea level (a.m.s.l.). The river flows almost due east for approximately 340 km through a 7830 km² catchment until it reaches the Lebombo mountains. Here it is deflected to the south, for about 8 km, before turning eastwards again and passing through a narrow gorge between the Lebombo and Ubombo mountain ranges (Fig. 1.1), at a altitude of 75 m a.m.s.l. Thus from its source to the site of the Pongolapoort Dam, the Pongolo river has a mean gradient of 1:160.

On emerging from the Pongolapoort gorge the river flows in a north-easterly direction, across the Makatini flats, which form part of the Maputaland coastal plain, and joins the Usutu river at the South African-Mocambique border (Fig. 1.1). Here it is 20 m a.m.s.l. This section of the Pongolo river therefore has a mean gradient of 1:3000 and it is on this relatively flat low-lying area that the Pongolo river floodplain is developed (27°S; 28°E, Fig. 4.1).

The floodplain is approximately 60 km long and 0.8 km wide and covers 10 416 ha (Welcomme, 1974; Fig. 4.1), of which 8800 ha are flooded regularly (i.e. the area from Mzinyeni lake in the south to the confluence with the Usutu river; Fig. 4.1). It is this area only that is considered in the present study. The area studied comprised the part occupied by the Tembe-Thonga people between Mzinyeni lake and Ndumu Game Reserve (Fig. 4.1), an area which is subjected to considerable human exploitation (Krige, 1971), as well as the section of floodplain within Ndumu Game Reserve (Fig. 4.1) which has been conserved since 1959 (Scotcher, 1974).

## 4.2 Geology and Geomorphology

The entire coastal plain of north-eastern Natal consists of sediments of the Cretaceous System which are overlain in places by relatively thin tertiary and recent deposits (Fig. 4.2). Both are of marine origin (du Preez, 1967). The cretaceous deposits can be divided into two types : the Lower Cretaceous beds (conglomerate) and the Upper Cretaceous beds (clayey sandstone). The Lower Cretaceous deposit flanks the western fringe of the Pongolo floodplain, while the Upper Cretaceous deposit forms a north-south belt, which straddles the Pongolo river (Fig. 4.3). Tertiary and recent sands of marine origin are found to the east of the Pongolo floodplain (Fig. 4.3). Thus the Pongolo floodplain is situated mainly on the Upper Cretaceous deposits. Seepage waters from these deposits are highly mineralised (du Preez, 1967), and seepage water that enters the Pongolo river or any of the floodplain lakes may increase total dissolved solid levels and cause some lakes (e.g. Mhlolo and Nyamithi) to be saline (Heeg *et al.*, 1978).

As the entire Maputaland plain is covered by material of marine origin it must at some stage have been below sea level. In fact during the Pliocene Period the Pongolo river entered the sea where it leaves the Pongolapoort gorge (King, 1972). Following this period (i.e. during the Pleistocene Period) sea level fluctuated, although there was a general regression in an easterly direction (Hobday, 1979). This resulted in a series of north-south dune ridges developing in the vicinity of the contemporary shore. It was one of these contemporary shoreline dunes that formed a barrier to the eastward flow of the Pongolo river, deflecting it to its present northerly course across the Makatini flats. The relatively flat nature of this area resulted in reduced river flow and the deposition of large amounts of its sediment load, which has given rise to the alluvial soils of the floodplain (Fig. 4.2).

## 4.3 Climate

The Maputaland coastal plain falls within the climatic region described by Schulze (1965) as 'warm to hot, humid, sub-tropical'. Summers

(October - March) are hot with mean monthly temperatures between 23°C and 27°C and mean monthly maxima usually above 30°C (Table 4.1). Winters (April - September) are moderate with mean monthly temperatures between 16°C and 22°C (Table 4.1).

The mean annual rainfall from a number of stations in the vicinity of the floodplain (Table 4.2) varies from 485 mm (Mzinyeni lake) to 642 mm (Otobotini) with an overall average of 574 mm. Rainfall is markedly seasonal and at the Makatini Agricultural Research Station more than 70% occurs during summer (October - March; Table 4.1).

The mean annual rainfall for the two stations on the floodplain (Mzinyeni and Mamfene) is 519 mm, which is slightly less than the mean of 596 mm for the higher-lying stations in the vicinity (i.e. Pongolapoort Dam, Makatini Research Station, Ndumu, Ndumu Game Reserve and Otobotini; Table 4.2) and considerably less than that received on the adjacent Lebombo mountains (i.e. 850 mm at Ingwavuma; Heeg and Breen, in press). Little of this rainfall on the Lebombo mountains finds its way directly to the floodplain (Heeg and Breen, in press) as only four lakes (Mayazela, Mfongozi, Mzinyeni and Ntunte) have feeder streams originating in the mountains (Fig. 4.1). In addition four lakes (Nhlanjane, Mhlolo, Maleni and Nyamthi) have short feeder streams which drain small catchments, situated on the high-lying area of the Maputaland coastal plain, off the Pongolo floodplain. Although local rainfall has little influence on the flooding of the Pongolo floodplain, it is important in maintaining grazing areas adjacent to the floodplain, which are utilized by cattle of the local inhabitants during summer.

Floodwaters originate in the Pongolo river catchment west of the Lebombo mountains. This catchment has a mean annual rainfall of 864 mm, of which 692 mm (80%) falls during the period October to March and flooding is therefore predominantly a summer phenomenon (Heeg and Breen, in press).

The floodplain is frost free. Heavy dew and dense morning mists are common during the dry winter (Scotcher, 1974) and may serve as important sources of moisture for plants.

The evaporation rate in the vicinity of the floodplain, as measured at the Makatini Agricultural Research Station, is high (2388 mm per annum; Table 4.1) and exceeds precipitation in all months (Fig. 4.4). This high evaporation rate, especially during summer, is probably a result of the high temperatures and the high wind run (Table 4.1; Fig. 4.5). In addition to its effect on evaporation, wind also affects the turbulence and turbidity of the lakes. This in turn adversely affects the growth of phytoplankton, epiphytes and rooted aquatic macrophytes. It may also cause erosion particularly on sandy areas, and prevent the establishment of terrestrial vegetation.

## 4.4 Hydrology

### 4.4.1 Hydrology prior to the construction of the Pongolapoort Dam

Although flooding of the Pongolo river floodplain is dependent on rainfall in the catchment to the west of the Lebombo mountains (see section 4.3), the degree of flooding is dependent on three parameters :

(i) volume of water delivered to the floodplain;
(ii) rate of flow;
(iii) duration of high flow;

data for these parameters are available from a gauging station (No. W4M06), above the floodplain (Fig. 1.1), for the period 1929 - 1976 (Department of Water Affairs*). During this 47 year period annual flow in the Pongolo river averaged 1082 x $10^6$ $m^3$ fluctuating between a minimum of 309 x $10^6$ $m^3$ (1930/1) and a maximum of 3295 x $10^6$ $m^3$ (1938/9).

Monthly records for the 1929 - 1976 period, in a statistically correct-corrected form (Fig. 4.6; Heeg and Breen, in press) show that 70% of the total flow occurred during the period November to March, with the greatest volume (17.5%) during February. Lowest flow occurred during the period June to September (approximately 10.5% of the total) and although floods have been recorded during this period they are infrequent.

The summer flooding is characterised by several floods of relatively short duration (Heeg and Breen, in press), which may be grouped into

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two peak periods of flooding (i.e. during December and to a greater extent during February; Fig. 4.6). Summer rains start during September and October (Fig. 4.4) and during this period infiltration is greatest because of the dry period that precedes the rain, and therefore floods are small (Fig. 4.6). As the rainy season progresses the ground becomes more saturated, infiltration rate decreases and consequently the rainfall during December results in higher runoff and hence greater floods (Fig. 4.6). The continuing rains during January further increase the ground water content and hence runoff, thus during the peak rainfall period in February (Fig. 4.4) flooding is at a maximum (Fig. 4.6).

during

Using data obtained during a 43 year period, the long term average number of days that the daily average flow is equalled or exceeded has been calculated (Phélines *et al.*, 1972; Table 4.3). Relating this to the flow rates at which lakes are flooded (Table 4.4), the average number of days that the major lakes of the floodplain will receive floodwater can be estimated (Table 4.4). In addition, the diversity of lakes comprising the floodplain system becomes obvious from those that are flooded relatively easily (e.g. Mzinyeni, Bumbe, Ngodo and Namanini) to those that are only flooded occasionally (e.g. Shalala and Pongolwane).

### 4.4.2 Hydrology after construction of the Pongolapoort Dam

The Pongolapoort Dam first affected flow in the Pongolo river when the construction openings in the dam wall were closed in March 1970 (Phélines *et al.*, 1972).

The long term average number of days that daily average flow was equalled or exceeded, before and after construction of the Pongolapoort Dam (Tables 4.3 and 4.5), indicate that conditions on the floodplain between 1972 - 1976 were wetter than average prior to the construction of the dam. In fact during this period (1972 - 1976) floodplain lakes received water for up to four times longer than would have been the case in a year indicated by the average long term means (Table 4.4).

These wetter conditions could be due to a number of interacting factors (e.g. amount and duration of rainfall, time of year during which rain fell, duration of dry periods). Thus the wetter conditions on the floodplain after impoundment cannot be ascribed to the presence of the dam only. However, the presence of the dam did result in changes in the flow rate of the Pongolo river during the period 1974 - 1976 (Fig. 4.7). Unlike the river, which shows rapid and marked changes in flow, discharge from the dam was steady for extended periods which were followed by rapid changes in flow. The short duration floods, which occurred prior to the construction of the Pongolapoort Dam, were replaced by floods of long duration.

### 4.4.3 Hydrology between the Pongolapoort Dam and Mocambique

Eighty-eight percent of the mean annual runoff from the entire Pongolo river catchment area (i.e. from source to the confluence with Usutu river) originates west of the Pongolapoort Dam (Pitman and Weiss, 1979). Of the remaining 12% (approximately 150 x $10^6$ $m^3$) the Ingwavuma river contributes approximately 110 x $10^6$ $m^3$. Thus if the Ingwavuma river flooded at the same time as the Pongolo river, it would probably contribute to the flooding of lakes in the vicinity of its confluence with the Pongolo (i.e. Mandlankuzi and Namanini; Fig. 4.1; Pitman and Weiss, 1979). The remaining 40 x $10^6$ $m^3$ adds little to the flow of the Pongolo river (Pitman and Weiss, 1979) and therefore will have little influence on the flooding of the system.

The mean annual runoff from the Usutu river catchment (Fig. 1.1) is approximately twice that of the Pongolo river (Pitman and Weiss, 1979). Thus when in flood the Usutu river has the effect of damming up the flow of the Pongolo thereby causing flooding by the Pongolo river at flow rates that would not normally result in flooding. This effect is limited to the lower reaches of the Pongolo river floodplain, particularly Nyamithi lake (Pitman and Weiss, 1979).

## 4.5 Inhabitants

The Maputaland coastal plain is inhabited by Tembe-Thonga people (Krige, 1971). Their distribution in this area is not uniform, probably because of available freshwater. They occupy three separate areas : adjacent to the Pongolo river, the Mozi swamp and the coastal region. There is very little movement of people between these zones, particularly those living along the Pongolo river who may move their home frequently in the vicinity of the floodplain, but seldom move to the Mozi swamp or coastal areas. They have little, if any, social contact with the people of these areas (Krige, 1971). The population associated with the floodplain was given as 25 926 in January 1976 (Kwazulu Department of Health*) i.e. 27% of the total population of Maputaland. Heeg and Breen (in press) have estimated that 19% of the male population were employed outside Maputaland in 1976. If remunerative employment were available in Maputaland these people would have remained in the area and the population in January (1976) would have been *c.* 39 519 (Heeg and Breen, in press).

The main activities of the Tembe-Thonga people that live in the vicinity of the floodplain, are subsistence agriculture, food-gathering and fishing.

Cattle were not kept by many people in the past, probably due to the prevalence of trypanosomyasis but with the eradication of the tsetse fly, cattle numbers have increased and stock sales are now held regularly. The demand for winter (dry season) grazing on the floodplain has therefor also increased and consequently the marginal meadows of the floodplain system have assumed a greater importance as a grazing source. In addition, during winter, areas off the floodplain are dry and little grazing is available although some browsing may take place.

The main crops on the floodplain are maize, sweet-potatoes, groundnuts, sugarcane, pumpkins, tomatoes and cabbages. Planting of crops takes place after flooding, on river banks, adjacent flat areas and along the water's edge of lakes that form after flooding. As these lakes dry up,

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cultivated areas are extended and if the lakes dry up completely the entire dry bed may be under cultivation (Krige, 1971). Areas adjacent to the floodplain are also cultivated and this practice appears to be increasing, probably due to increasing population size and hence the need for more food. Disruption of the flood pattern may therefore alter the method and extent of cultivation of the floodplain. Dam has disrupted altering flood rate.

Fish are also an important source of protein, but few people are regularly involved in fishing using nets and basket traps. For the majority of people along the floodplain fishing is seasonal. The method used being isifonyo fishing (Krige, 1971) which takes place in the numerous lakes and shallow water bodies that form after flooding. Very little fishing is done in the Pongolo river itself (Krige, 1971).

In addition to the above activities the gathering of some indigenous plants for food is evident particularly on and adjacent to the floodplain (Krige, 1971). On the floodplain the corms of *Nymphaea* spp and the fruits of *Trapa natans* L. var. bispinosa (Roxb.) Makino are important in the diet of the people for many months of the year. Some plants found adjacent to the floodplain (e.g. *Strychnos madagascariensis* Poir, *Landolphia kirkii* Dyer. and *Vangueria infausta* Burch.) are also utilized for food.

The Tembe-Thonga people living along the Pongolo river are thus dependent on the floodplain, its regular flooding cycle and its resources for their livelihood.

### 4.6 Vegetation

Acocks (1975) described the veld types of the Maputaland area as coastal forest, thornveld and bushveld. He designated the vegetation, in its original state, as forest and scrub-forest.

Tinley (1976) described areas flanking the Pongolo river floodplain as *Acacia* tree and bush vegetation in the south, with *Terminalia* and mixed woodland in the north. Patches of sand forest were scattered on either side of the floodplain.

More recently Moll (1977) described the vegetation of the coastal plain in more detail, classifying it into 11 basic types. These vary from dune and swamp forest along the coast and the Kosi Bay area, to coastal grassland and palmveld between the coast and Mozi swamp, to various bushveld types which flank the floodplain. Small scattered patches of sand forest and thicket are also found along the floodplain margin. However, little remains of the natural vegetation outside Ndumu Game Reserve.

No detailed ecological investigation of the Maputaland coastal plain vegetation (including the floodplain), has been undertaken. This is a significant omission as Maputaland forms part of a transitional area where tropical conditions give way to subtropical. It also forms part of a migration route for terrestrial vegetation by which tropical species have moved southwards into South Africa, and Breen (1979) states that a number of terrestrial species have either their northern or southern limits in Zululand and Southern Mocambique. Aquatic species are more cosmopolitan in occurrence than terrestrial species. The role of the Maputaland coastal plain as a migratory route and transitional zone is therefore less important to aquatic vegetation. However aquatic plants are important on the Pongolo floodplain as they are the primary producers on which all higher trophic levels depend.

The coastal plain of Zululand, including the Pongolo river floodplain, is thus an area of considerable botanical interest. It is also an area in which the local people are largely dependent upon subsistence agriculture and hence on the maintenance of their natural environment. The Pongolapoort impoundment has disrupted and may continue to disrupt this system unless its requirements are defined and can be incorporated into future management policy.

# CHAPTER 5

## THE PLANT COMMUNITIES

### 5.1 Results

Six communities have been recognised and they may be grouped according to their relative periods of exposure and inundation : (1) The communities (two) of high-lying areas, which are only inundated for short periods; (2) those (three) of low-lying gently sloping areas, which only become exposed as water approaches and drops below MRL, i.e. those having the longest submergence and shortest period of exposure; and (3) the community which occupies the intermediate areas, where the slope is slightly steeper so that water drains off fairly rapidly thereby preventing the development of the communities typical of the low-lying areas.

### 5.1.1 Communities of the high-lying areas (Fig. 5.1)

Two communities may be recognised : The *Ficus sycomorus* L. - *Rauvolfia caffra* Sond. Community with two sub-communities, occupying 406 ha, which is restricted to levees on either side of the main river channel, and the *Acacia xanthophloea* Benth. - *Dyschoriste depressa* Nees Community, 128 ha in extent, which is confined to narrow bands along the margin of the floodplain (Fig. 5.2; Plate 5.1).

### 5.1.1.1 The *Ficus sycomorus - Rauvolfia caffra* Community

This community forms a distinct vegetational unit. Since most of the species present do not occur in any other community, they may be regarded as character or differential species (Table 5.1). They include *F. sycomorus*, *R. caffra*, *Trichilia emetica* Vahl, *Entada spicata* (E. Mey.), *Syzygium guineense* (Willd.) DC., *Adina microcephala* (Del.) Hiern, *Allophylus decipiens* (Sond.) Radlk., *Kraussia floribunda* Harv. and *Monanthotaxis caffra* (Sond.) Verdc.

Outside the Ndumu Game Reserve (relevés 67, 65, 96, 81, 80, 87, 83 and 104, Table 5.2), the community usually comprises only two strata : a tall tree straum (12 - 15 m), formed principally by *R. caffra*, *F. sycomorus* and *T. emetica* with cover of 60 - 80%, and a 2 - 3 m shrub stratum of *A. decipiens*, *Grewia caffra* Meisn., *M. caffra*, *Ficus capreifolia* Del., *S. guineense* and *A. microcephala* with cover of 10 - 20%. Within the reserve a further two strata comprised of shade tolerant species are evident (relevés 73, 72, 68, 69, 70, 71 and 74), the taller (0.75 - 1.25 m, cover 15 - 20%) of *Dicliptera heterostegia* Pres ex Nees, non Chev. and *Setaria chevalieri* Stapf ex Stapf & C.E. Hubb. whilst in some relevés (81, 87) the grass *Oplismenus hirtellus* (L.) Beauv. forms a low stratum (0.1 - 0.25 m) with cover not exceeding 10%. The tendency for these two strata to be developed within the Reserve reflects the agricultural disturbance on the levees outside the Reserve.

Two sub-communities are recognisable :

#### 5.1.1.1.1 The *Ficus sycomorus - Eriochloa meyeriana* (Nees) Pilg. Sub-community

This develops where the impact of agriculture is severe. Because of clearing, the upper stratum (8 - 10 m, cover 40%) is only occasionally present (relevés 90, 93, 91, 49, 48, Table 5.2), and the middle (shrub) and lower (herb) strata are poorly developed. The second stratum of *D. heterostegia*, *M. caffra*, *K. floribunda* and *S. chevalieri* is 0.75 - 1,25 m tall with slightly higher cover (15%) compared with the *F. sycomorus - R. caffra* Community. The lower stratum (0.1 - 0.25 m, cover 15 - 60%) contains a number of species which are found in other communities eg. *Sida alba* L., *E. meyeriana* and *Commelina africana* L. In moister areas, *E. pyramidalis* forms quite dense mats (relevés 49, 48). The presence of opportunist species such as *S. alba* and *C. africana*, and the extent (2142 ha) and distribution of this sub-community (Plate 5.1) suggest that it results from disturbance. It is thus present along the levees and between the old and present river course north and east of Mzinyeni and south of Pongolwani lakes, sites which are favoured for agriculture and where, under undisturbed conditions, the *F. sycomorus - R. caffra* Community would normally be present.

### 5.1.1.1.2 The *Ficus sycomorus* - *Acacia xanthophloea* Sub-community

This sub-community has very restricted distribution (10 ha, Fig. 5.1) and is represented by only two small stands (relevés 86, 85, 58, Table 5.2).

Four strata are present, the upper (8 - 10 m, cover 40 - 50%) is comprised of *F. sycomorus*, *A. xanthophloea* and two climbers, *Ipomoea digitata* L. and *Jasminum fluminense* Vell. The 2 - 4 m shrub stratum, dominated by, *F. capreifolia* and *G. caffra* but also containing *A. xanthophloea* has relatively low cover (10 - 20%). A third stratum of approximately 0.75 m comprising mainly *K. floribunda*, *Mimosa pigra* L. and young *A. xanthophloea* is present with cover not exceeding 30%. The lowest stratum (0.4 m) is characterised by both the greatest species diversity and, at times, the highest cover. Dominant species are *D. depressa*, *Cissampelos mucronata* A. Rich., *Eriochloa parvispiculata* C.E. Hubb, *Cardiospermum halicacabum* L., *Hemarthria altissima* (Poir.) Stapf & C.E. Hubb, *E. meyeriana* and *E. pyramidalis*.

Two sites where this sub-community has developed, to the south-west of Khangazini and west of Mengu lakes (Fig. 5.1), are areas where the river levees and the margin of the floodplain are close together. Such a situation would facilitate an intergrading of the *F. sycomorus* - *R. caffra* and the *A. xanthophloea* - *D. depressa* Communities. This sub-community is therefore regarded as transitional.

### 5.1.1.2 The *Acacia xanthophloea* - *Dyschoriste depressa* Community (Plate 5.2)

*A. xanthophloea* and *D. depressa* are confined to this community and the *F. sycomorus* - *A. xanthophloea* Sub-community, and they may therefore be regarded as either character or differential species (Table 5.1; relevés 99, 18, 53, 23, 16, 11, 13, 15, 17, 45, 102, 30, 26, 32, 36, 100, 43, 98 and 75). A striking feature of this community is that it is formed of two strata only, the tree stratum being comprised entirely of *A. xanthophloea* (8 - 12 m, cover 20 - 50%). The second stratum is made up of low-growing (0.15 - 0.45 m) herbs with sparse cover (usually 7 - 10%). *D. depressa* is the most prominent, others being *S. alba*, *Heliotropium ovalifolium* Forsk., *H. indicum*, *C. dactylon*, *Ambrosia artemisiifolia* L. and *C. halicacabum*. These latter species tend to be widely distributed and have low cover-abundance values (r or +). Many may be regarded as opportunists, reflecting the unstable conditions brought about by flooding and grazing. In some areas outside the relevés investigated, a few well established *F. sycomorus* are present. These stands are, however, not considered typical. It does however, serve to indicate the close relationships between this community and the *F. sycomorus* - *R. caffra* Community.

### 5.1.1.3 Interrelationships

Both communities of the high-lying areas develop on widely varying soils, usually slightly acidic (pH 4 - 6.6) and with extremely variable clay (9 - 68%), silt (3 - 49%) and sand (16 - 62%) fractions. This suggests that some other factor(s) predominate in determining their distribution. Because of topographical variation along the floodplain, different lakes at MRL have different elevations with respect to both the river level and HFL. This has a striking influence on the vegetation, those communities intolerant of flooding being closely related to HFL, whereas those communities which are more hygrophilous and more tolerant of flooding have a distribution which is closely related to MRL irrespective of its height relative to HFL. Fig. 5.3a reveals that although the distribution of both communities is relative to height below HFL, and thus to the period of inundation whilst the river is in flood, the *F. sycomorus* - *R. caffra* Community is the more sensitive to flooding in that it develops on the highest areas. Clearly, however, distribution of the community is not only determined by period of inundation because it is absent from areas around the margin of the floodplain, even where they may have an almost identical flooding regime to that of the levees. It seems likely that seasonal availability of soil moisture acts in conjunction with inundation, because proximity to the river would prevent the development of the very dry conditions which arise along the edge of the floodplain during the dry winter months (see Chapter 8). The seasonally drier conditions along the margin of the floodplain eliminates *R. caffra* and other hygrophilous woody species, while the presence of occasional *F. sycomorus* suggests that it may be somewhat more tolerant. Although more favourable soil moisture conditions might be found at lower elevations along the floodplain margin, development of the woody component is prevented by the longer period of inundation. The combination of these factors is probably responsible for the distinct separation of the *F. sycomorus* - *R. caffra* and *A. xanthophloea* - *D. depressa* Communities.

The *A. xanthophloea* - *D. depressa* Community tends to develop in slightly lower-lying areas than the *F. sycomorus* - *R. caffra* Community, but above MRL (Fig. 5.2). It is therefore, inundated only whilst the Pongolo river is in flood, and the period of inundation is greater than that experienced by the *F. sycomorus* - *R. caffra* Community.

### 5.1.2 The Communities of the low-lying areas

Three communities were recognised (Table 5.2). The *Phragmites australis* (Cav.) Trin ex Steud. and the *Phragmites mauritianus* Kunth Communities together occupy an area of *c.* 234 ha, most of which (65%) is in the Ndumu Game Reserve. The *Cyperus fastigiatus* Rottb. - *E. pyramidalis* Community is one of the largest, covering *c.* 2471 ha, with particularly extensive stands occurring west of Tete and Nsimbi lakes and in the Ndumu Game Reserve (Fig. 5.1; Plate 5.3).

#### 5.1.2.1 The *Phragmites australis* Community

This community is dominated by *P. australis*, which may be regarded as the character/differential species (Table 5.1). Under protection in the Ndumu Game Reserve (relevés 76 and 77, Table 5.2), it forms dense stands growing to a height of 2.0 - 3.0 m with high cover-abundance values and few other species (relevés 76 and 77). Where its vitality is reduced by cutting and burning (relevés 92, 94 and 95), invasion by other species, principally *E. pyramidalis* and *Eriochloa meyeriana* (Nees) Pilg. which form a stratum between 0.3 and 0.45 m, occurs.

### 5.1.2.2 The *Phragmites mauritianus* Community

*P. mauritianus* is the dominant and differential species (Table 5.1), growing to a height of 1.5 to 3.5 m and forming dense stands with high cover-abundance values (Table 5.2). It is usually associated with *E. pyramidalis* and *Alternanthera sessilis* (L.) DC., although other species are also found in this community (e.g. *E. meyeriana*, *S. alba* and *C. dactylon*), particularly outside the Ndumu Game Reserve. Only one relevé (64) was, however, examined within the Reserve. Where present, these species form a low-growing stratum (0.15 - 0.4 m) with low cover-abundance values.

### 5.1.2.3 The *Cyperus fastigiatus - Echinochloa pyramidalis* Community

*C. fastigiatus* and *E. pyramidalis* were differential species (Table 5.1) for this community (Table 5.2) and when they have high cover-abundance values (relevés 59 and 105), few other species are present. Where cover-abundance of the differential species is lower, opportunist species (e.g. *Glinus lotoides* L., *Heliotropum indicum* L. and *C. halicacabum*) are more common. Three strata may be recognised, an upper comprising mainly *C. fastigiatus* (1 - 2 m; cover 20 - 80%), intermediate (0.3 - 0.4; cover 15 - 80%) dominated by *E. pyramidalis* and a layer formed by prostrate species such as *C. dactylon* and *Polygonum aviculare* L. (0.1 - 0.15 m; cover 5 - 20%).

### 5.1.2.4 Interrelationships

The three communities of the low-lying areas all develop on acidic soils pH 3.3 to 6.4 of rather variable texture (Table 5.2). It seems possible that the *P. australis* Community develops on soils which are more sandy (27 - 73%) than those of the *P. mauritianus* and *C. fastigiatus - E. pyramidalis* Communities (10 - 57%).

The development of all three communities is closely associated with MRL (Fig. 5.3b). This suggests that it is not so much inundation as the presence of a more stable water supply that controls the position of these communities. The *Phragmites* Communities tend to occupy the lower positions, particularly *P. australis* which favour swampy areas as opposed to those dominated by *P. mauritianus* which show preference for sites where there is water movement e.g. river banks. The *C. fastigiatus* - *E. pyramidalis* Community develops only on flat and gently sloping, draining areas adjacent to lakes, and in depressions which remain wet for most of the dry season (Fig. 5.2).

The *C. fastigiatus* - *E. pyramidalis* Community shows marked affinities with the *Phragmites* Communities through the extension of the distribution of *E. pyramidalis* into these semi-aquatic habitats, and with the *C. dactylon* and *A. xanthophloea* - *D. depressa* Communities because of the presence of *C. fastigiatus* in these higher-lying areas. The degree to which these rather broad distributional patterns reflect the distribution under natural and undisturbed conditions is debatable because reduction in the cover of the *Phragmites* Communities might favour intrusion of *E. pyramidalis* whereas grazing of *C. fastigiatus* seems to favour an increase in the *C. dactylon* component. Where both differential species are grazed, particularly in the areas west of Sivunguvungu and to the south and south-west of Khangazini lakes, their cover-abundance values are lower and a wider variety of species is present (relevé 46, 38 and 39, Table 5.2).

### 5.1.3 The Community of the intermediate areas

Only one community, the *C. dactylon* Community, has been recognised, covering 171 ha of the floodplain. It is generally found on gently sloping areas which become exposed gradually as the floodwaters recede (Table 5.2, Plate 5.2). The soils vary from acidic (pH 4.5) to almost neutral (pH 6.8) with very variable texture, clay 29 - 73%, silt 6 - 36% and sand 11 - 63%. *C. dactylon* is extremely tolerant of extended periods of dry conditions following exposure, and of submergence. Not surprisingly, therefore, the distribution of the *C. dactylon* Community does not show marked relationships with either height above MRL or below HFL (Fig. 5.3a and b). It thus extends from below MRL to above HFL (Fig. 5.2). *C. dactylon* may be found in all the communities, particularly where disturbance has occurred.

#### 5.1.3.1 The *Cynodon dactylon* Community (Plate 5.4)

*C. dactylon*, the differential species (Table 5.1) for this community, forms dense, almost pure, stands of considerable extent around some lakes (e.g. Namanini-Bumbe 42 ha, east of Mthikeni and Nsimbi 27 ha). It forms a single stratum (0.2 m) with up to 90% cover where conditions are most favourable (relevés 5, 8 and 10, Table 5.2). Elsewhere, where cover is reduced (relevés 27 and 28), and grazing more intense, the height may be less (0.05 m) and the weeds (*A. artemisiifolia*, *Conyza bonariensis* (L.) Cronquist and *P. aviculare*) become more prominent. These species form an ill-defined stratum of 0.2 - 0.3 m in height.

### 5.1.3.2 Interrelationships

The close relationships of the *C. dactylon* Community with other communities on the floodplain are emphasised not only by the distribution of *C. dactylon*, but also by the five relevés (56, 21, 19, 35 and 20) which form a nodum of indeterminate rank between the *C. dactylon* and *C. fastigiatus* - *E. pyramidalis* Communities.

It seems probable that this community would normally develop in areas where the inundation period was too long for the woody communities and where it became too dry for the communities characteristic of the low-lying areas (Plate 5.2). Since it presently extends into areas which clearly show relics of other communities it must be concluded that disturbance has increased the extent of this community. At the lower levels it is principally by replacement of *C. fastigiatus*, which is adversely affected by grazing and trampling and at higher levels by clearing, which reduces competition and allows more direct illumination, both of which favour *C. dactylon*.

### 5.1.4 Relevés of undetermined affinity

Six relevés (50, 12, 47, 41, 60 and 62) did not appear to fit satisfactorily into the communities outlined above. Although they could have been allocated to specific communities, thereby improving the information on total floristics, the affinity did not, in our opinion, justify this action. They are included in the table because an advantage of the Braun-Blanquet method is that new relevé data may continuously be added thereby facilitating recognition of communities which may not be presently recognisable (Werger, 1973).

## 5.2 Discussion

The studies by Tinley in 1958 (published in 1976) are the earliest reports on the Pongolo river floodplain vegetation. He recognised two formations, the Riparian Forest, which included the disturbed and undisturbed vegetation of the levees and high-lying margins of the floodplain, and the Aquatic and Marginal Pan vegetation. This broad classification, which does not take into account the observed marked influence of the flooding regime, does not agree well with the community distinctions drawn up in this study.

More recently De Moor *et al.* (1977) and Pooley (1978) have reported on the vegetation within the Ndumu Game Reserve (Fig. 4.1). Only a portion of this Reserve includes the floodplain of the Pongolo river. De Moor *et al.* (1977) using the system of Fosberg (1967), recognised six formations (Table 5.3) of which five correspond well with those recognised in this study. The microphyllous deciduous shrub savanna is however, difficult to relate to our communities because it includes species such as *Sesbania sesban* (L.) Merrill, *E. pyramidalis* and *P. australis* which appear to exhibit markedly different responses to inundation and it therefore probably forms a transition between 'forest and grasses' as has been suggested by Pooley (1978). Neither De Moor *et al.* (1977) nor Pooley (1978) have, however, attempted to relate the plant communities to flooding regimes.

Werger (1974) has suggested that in areas exposed to extreme conditions, emphasis should be placed on permanently recognisable species in phytosociological analysis. This concept was applied to the floodplain vegetation because particularly above MRL, where both inundation and exposure have to be tolerated, conditions may be considered to be extreme. It reduces the number of species from 64 to 25, but does not alter the definitions of the communities (Table 5.4).

None of the communities recognised on the Pongolo river floodplain are unique. They have been recorded from widely separated areas on the African continent, on floodplains and areas of fluctuating water levels.

*P. australis* and *P. mauritianus* both have a world-wide distribution (Clayton, 1967; Fernandes *et al.*, 1971), although *P. mauritianus* tends to be more tropical and is frequently encountered in swampy and seasonally flooded areas (Gordon-Gray and Ward, 1971; Howard-Williams and Walker, 1974; Rzóska, 1974). The distinction in ecological preference between *P. australis*, which favours standing water and *P. mauritianus* which prefers moving water, supports the observations of Gordon-Gray and Ward (1971). Howard-Williams and Walker (1974) reported similar environmental conditions in stands of *P. mauritianus* in Lake Chilwa, although it was also present in alkaline swamps. In other parts of Central Africa, Vesey-Fitzgerald (1963) recorded *Phragmites* in Riverine Grasslands and 'lakes' where it formed dense stands on silt banks, sand bars and in lagoons. He did not record it from 'Pans' or 'alkaline swamps and flats', but this may, in the former instance, reflect the fact that the pans being investigated were shallow depressions which normally dried up during the dry season. They are clearly different from those of the Pongolo system. Vesey-Fitzgerald did not record the specific names of *Phragmites* and from the distribution (Clayton, 1967; Fernandes *et al.*, 1971) it seem likely that although both *P. australis* and *P. mauritianus* could have been present, *P. mauritianus* would be the more common.

*C. fastigiatus* is widespread in the province of Natal in South Africa (Ross, 1972), but has not been recorded in tropical areas (Vesey-Fitzgerald, 1955, 1963; Dean, 1967; Cook, 1968; Howard-Williams and Walker, 1974; Imevbore and Bakare, 1974; Rzóska, 1974). Ross (1972) claims that *C. fastigiatus* is closely allied to the more tropical *Cyperus auricomus* Sieber ex Spreng., which is also placed with *C. digitatus* Roxb. subsp. *auricomus* by Kükenthal (in Ross, 1972). Howard-Williams and Walker (1974) reported *C. digitatus* from relatively acidic soils (pH below 6.0) in their neutral to acidic marsh vegetation type. These conditions are similar to those in which *C. fastigiatus* is found on the Pongolo system.

Unlike *C. fastigiatus*, *E. pyramidalis* is widespread in wet areas where it is often associated with a variety of other species (Vesey-Fitzgerald, 1955, 1963; Dean, 1967; Cook, 1968; Imevbore and Bakare, 1974; Howard-Williams and Walker, 1974). The description of its growth in floodplain grassland by Vesey-Fitzgerald (1963) aptly describes its behaviour in the Pongolo system : 'Growth starts at the onset of the rains but the stature depends on the extent of flooding. Under optimum conditions the previous season's accumulation of rough rots away in the water and the new growth is very vigorous'. Although *E. pyramidalis* is grazed by hippopotamuses (Scotcher *et al.*, 1978), the numbers of hippopotamuses outside the Ndumu Game Reserve on the Pongolo floodplain are small and they do not exert a marked effect. However, as soon as the floods recede and the marshy areas become dry enough for cattle, both *E. pyramidalis* and *C. fastigiatus* are grazed. As in tropical areas, even when drying out and being grazed, node shoots remain green until quite late in the season. In areas where grazing is particularly heavy and where drainage is slightly more rapid following the floods, *E. pyramidalis* may form a mosaic with *C. dactylon* as has been observed by Vesey-Fitzgerald (1955) and Dean (1967).

The development of *C. dactylon* communities under conditions of fluctuating water levels is well documented, both as pure stands (Lea and van V. Webb, 1939; Vesey-Fitzgerald, 1955; Dean, 1967; Greenway and Vesey-Fitzgerald, 1969) and in association with other species (Lea and Van V. Webb, 1939; Burnett, 1951; Anderson and Herlocker, 1973; Howard-Williams and Walker, 1974). These short-grass lawns develop on a wide range of soils from acid to alkaline in areas where prolonged flooding is not experienced. Dean (1967) noted that *C. dactylon* was easily killed by flooding. On the Pongolo, it regularly tolerates periods of submergence of up to 150 days, apparently without too much detrimental effect.

During summer the *C. dactylon* around the lakes may be inundated thereby becoming an integral part of the aquatic system. Even if it is not completely inundated the substrate is generally too wet for access by cattle and goats. Thus it is only during the drier parts of the year that these lawns become accessible to terrestrially based grazers, for which it provides a valuable source of pasturage.

The distribution of *A. xanthophloea* tropical and sub-tropical river courses and in damp depressions is well documented (Greenway and Vesey-Fitzgerald, 1969; Anderson and Herlocker, 1973). Vesey-Fitzgerald (1974) concluded that the cyclic and seral status of groves of *A. xanthophloea* were substantially influenced by drainage conditions. A consequence of this is that trees along the lake-shore may succumb during periods of high lake levels (Greenway and Vesey-Fitzgerald, 1969) a situation which was observed on the Pongolo floodplain particularly in the vicinity of Mzinyeni lake (Fig. 4.1; Plate 5.2) during the unnaturally extended floods caused by discharge of water from the Pongolapoort Dam since its construction.

*Ficus sycomorus* occurs throughout Africa along river courses, swampy areas and even arid areas where the water table is high (Palmer and Pitman, 1972). Site preference seems to be for those areas where drainage is quite good and yet water is freely available, because the best stands on both the Pongolo floodplain (in the Ndumu Game Reserve) and in Lake Manyara National Park (Greenway and Vesey-Fitzgerald, 1969) are along the tops of the river banks and levees.

## 5.3 Conclusions and future research priorities

This study has illustrated the importance of the flooding regime in the development of the plant communities of the Pongolo river floodplain. As a result, changes in the pattern of flooding, both of frequency and, more importantly, of duration of inundation and exposure, can be expected to exert a profound effect on the communities as has been observed elsewhere (Dean, 1967; Attwell, 1970; Townsend, 1975). On the Pongolo river floodplain the response of the vegetation to changes in the flooding regime could be established by repeating the Braun-Blanquet survey under different conditions to those prevailing during present study, or by establishing permanent transects on the floodplain.

With the very sandy nature of the soils of the floodplain particularly of the levees and around the lakes, destruction of vegetation, resulting either directly from changes in the flooding pattern or indirectly as a result of allowing cultivation and grazing in areas which were formerly too wet, could increase erosion thereby having a profound impact on the floodplain system as a whole. These effects would also become evident if changes were monitored by means of permanent transects.

# CHAPTER 6

## CROP GROWTH RATE OF *Cynodon dactylon* IN RESPONSE TO EXPOSURE AND GRAZING

### 6.1 Results

### 6.1.1 Crop growth rate in the absence of grazing

### 6.1.1.1 Grazeable fraction :

As floodwaters recede the remains of *C. dactylon* become exposed. They consist of short (5 - 7 cm) erect shoots devoid of leaves, which may or may not be living. The standing crop was usually low *c.* 195 kg ha$^{-1}$ (Fig. 6.1b). Under the very wet conditions following exposure (0 - 25 days, Fig. 8.3) relative growth rate (RGR) was rapid (0.045 g g$^{-1}$, Fig. 6.1a), resulting in a 118% increase in standing crop but, due to the small initial standing crop, mean crop growth rate ($\bar{C}$) was only 9.2 kg ha$^{-1}$ d$^{-1}$ (Fig. 6.1a). Maximum RGR was attained between 25 and 51 days after exposure (Fig. 6.1a) and although this rate was only 9% higher than that during the first 25 days, because of the greater standing crop at the start of this period, it had a marked effect on both the size of the grazeable fraction (Fig. 6.1b) and $\bar{C}$, which increased by 154% to its maximum (23.4 kg ha$^{-1}$ d$^{-1}$, Fig. 6.1a). Relative growth rate declined rapidly after 51 days as soil moisture decreased (Fig. 8.3), and remained low for the rest of the exposure period (Fig. 6.1a). Although $\bar{C}$ also declined after 51 days (Fig. 6.1a), the decrease was not as marked as for RGR, because of the gradually increasing standing crop (Fig. 6.1b). During the 161 day exposure period the grazeable fraction increased from 195 to 1840 kg ha$^{-1}$ and its contribution to the total standing crop from 6% to 17%.

### 6.1.1.2 Ungrazeable fraction

The RGR of the ungrazeable fraction was highest during the first interval of exposure (0.019 g g$^{-1}$ d$^{-1}$, Fig. 6.1c) decreasing slightly during the second (0.016 g g$^{-1}$ d$^{-1}$) and third (0.013 g g$^{-1}$ d$^{-1}$) intervals.

Between 0 - 51 days it was less than half that of the grazeable fraction, probably reflecting the increasing development of the grazeable fraction. Because of the much larger standing crop of ungrazeable material at exposure, $\bar{C}$ was more than twice that of the grazeable fraction during the first 76 days of exposure (Fig. 6.1a and c), despite the considerably lower RGR of the ungrazeable fraction.

A marked decrease in RGR occurred between 76 - 98 days. This was about 50% greater than that recorded for the grazeable fraction, possibly implying that the ungrazeable fraction was more susceptible to increasing moisture stress than the grazeable fraction. The decrease also effected a sharp decrease in $\bar{C}$ (Fig. 6.1c) so that ungrazeable fraction standing crop only increased by 1.6% (115 kg ha$^{-1}$, Fig. 6.1b) during the 76 - 98 day period. After 98 days RGR and $\bar{C}$ increased sharply before decreasing again during the final 30 days of exposure. These changes in RGR and $\bar{C}$ between 98 and 161 days are difficult to explain and may reflect effects of a number of interacting factors including decreasing soil moisture, movement of storage reserves and the possible utilization of material by small grazers (e.g. insects) and soil organisms.

After an exposure period of 161 days ungrazeable fraction standing crop had increased almost three fold to 9030 kg ha$^{-1}$ (Fig. 6.1b), compared with the nine fold increase in grazeable fraction standing crop.

### 6.1.2 Crop growth rate in the presence of grazing

#### 6.1.2.1 Grazeable fraction

During the first 25 days very little grazing took place and standing crop inside (ungrazed area) and outside (grazed area) the exclosures were similar. Despite this both RGR and $\bar{C}$ were *c.* 20% lower in the grazed area than the ungrazed area (Fig. 6.2). This suggests that conditions within the exclosure were more favourable for growth. Why this should be the case is not clear. Grazing pressure was heavy during the 25 - 51 day interval (Fig. 6.3), and 98% of the production was removed. As expected, it adversely affected growth during the subsequent interval (i.e. 51 - 76 day days). Both RGR and $\bar{C}$ decreased by 98% (Fig. 6.2a). The consequence of this decline and continued grazing was that during the 51 - 76 day period grazing exceeded $\bar{C}$ and the standing crop declined (Fig. 6.2b). This overgrazing together with continuing exposure of new areas effected a shift in grazing pressure further down the slope, to a more recently exposed lush growth. A period of recovery was therefore possible between 76 and 98 days during which only 38% of the production was removed. This recovery was reflected in a marked increase in RGR (45 fold) and $\bar{C}$ (54 fold). Both these parameters attained their maximum in the grazed area during this period (Fig. 6.2a), and resulted in an increased standing crop (Fig. 6.2b).

During the final 63 days of exposure both RGR and $\bar{C}$ declined, while grazing pressure increased initially (64% of production being removed between 78 - 131 days) and then decreased (43% production being removed between 131 and 161 days). These factors interacted to bring about a steady increase in standing crop so that after 161 days standing crop in the grazed area (825 kg ha$^{-1}$, Fig. 6.2b) was 45% of that in the ungrazed area. The total removed by grazing (914 kg ha$^{-1}$) amounted to 50% of the ungrazed area standing crop and virtually accounted for the difference in standing crop between the grazed and ungrazed areas after a 161 day exposure period.

### 6.1.2.2 Ungrazeable fraction

Initially (0 - 25 days) both RGR and $\bar{C}$ were slightly lower in the grazed than the ungrazed area despite the fact that very little, if any, grazing had occurred. However, during the following period (25 - 51 days) both RGR (0.022 g g$^{-1}$ d$^{-1}$) and $\bar{C}$ (79.3 kg ha$^{-1}$ d$^{-1}$) increased to a maximum in the grazed area, exceeding the corresponding values in the ungrazed area by about 30%. This occurred in spite of heavy grazing, and implies that initially grazing and/or trampling may have had a stimulating effect on production of the ungrazeable fraction. However, the effects of grazing were most evident during the following period (51 - 76 days) when RGR and $\bar{C}$ were reduced considerably (Fig. 6.2c) to approximately 45% of the corresponding values within the exclosure.

The decrease in $\bar{C}$ and RGR continued until 131 days, both these parameters being at first (76 - 98 days) greater in the ungrazed area but then as exposure period increased (98 - 131 days) higher values were recorded in the grazed area. During the final 30 days of exposure RGR and $\bar{C}$ increased despite the removal of grazeable material during this period, albeit at a reduced rate (Fig. 6.3). A grazing effect or the transfer of reserves within the plant, together with the effect of the first summer rains which fell during this period might explain this increase which was not evident in the ungrazed area.

Despite the marked influence of grazing, the ungrazeable fraction standing crop in the absence of grazing, was only *c.* 5% more than in the grazed area after 161 days.

## 6.2 Discussion

The growth of grass plants is a response to the interaction of a number of environmental factors. These factors include soil water, soil temperature, physical conditions of the soil, light intensity, day length, defoliation (grazing) and mineral nutrition (Troughton, 1957; Barnard, 1964; Spedding, 1971). Once the grass has become established its growth is determined by the seasonal cycle of environmental growth factors. The rate of growth at any particular time will however depend on the relative intensity of the various growth influencing factors and will probably be controlled by the factor exerting a dominating influence (Troughton, 1957). In the case of *C. dactylon* on the Pongolo floodplain the seasonal cycle is one of inundation (during summer floods) and exposure when floods recede (winter). The main factors influencing growth are therefore likely to be : the effects of increasing exposure period (i.e. the development of an aerobic soil profile and subsequently of moisture stress); defoliation (i.e. the effects of grazing) which become evident when floodwaters recede; and waterlogging, with associated anaerobic conditions and light limitation when inundation occurs.

Cooper (1975) has shown that there is a change in the rate of production (which can be equated to $\bar{C}$ in the present study) of *C. dactylon* with a change in latitude, from 63 kg $ha^{-1}$ $d^{-1}$ at latitude 36° to 87 kg $ha^{-1}$ $d^{-1}$ at latitude 31°.

The Pongolo floodplain is situated at approximately 27°S latitude and thus a value of *c*. 93 kg $ha^{-1}$ $d^{-1}$ could be expected. In the present study a maximum value of 23.4 kg $ha^{-1}$ $d^{-1}$ was obtained 25 - 51 days after exposure. This was considerably lower than the expected value (*c*. 93 kg $ha^{-1}$ $d^{-1}$). However, under South African conditions, a rate of production of 7.0 kg $ha^{-1}$ $d^{-1}$ for unfertilized *C. dactylon* pastures has been reported (Meredith, 1955). When heavily fertilized, a newly established pasture attained a production rate of 39.8 kg $ha^{-1}$ $d^{-1}$ within 120 days of planting. The fact that the maximum value on the Pongolo floodplain was 3 to 4 times higher than results from an unfertilized area, suggests that the annual flooding may have some fertilizing effect. The peak $\bar{C}$ on the floodplain was short-lived and occurred between 25 - 51 days after exposure. It was followed by a period of decreasing RGR and $\bar{C}$ i.e. after 51 days, conditions on the floodplain became less favourable for *C. dactylon* growth.

Strugnell and Pigott (1978) have shown a linear relationship between dry matter production and rainfall in grasslands of Uganda. Although it was not possible to correlate rainfall and $\bar{C}$ at Namanini lake, it is evident that the lack of rainfall during the first 136 days (Table 8.1), was a major factor reducing $\bar{C}$ (Chapter 8). The marked increase during the last 25 days was associated with 51.5 mm of rain which fell in the vicinity of Namanini lake between 136 and 161 days after exposure (Natal Parks, Game and Fish Preservation Board)*.

Few data are available on the underground mass of *C. dactylon*, although Cooper (1975) states that due to its extensive root and rhizome system it may reach 14 000 kg $ha^{-1}$, which is about 35% higher than underground biomass in the present study. This probably reflects the method of sampling in this study where the *C. dactylon* was divided into grazeable and ungrazeable fractions, the latter included some above ground horizontal rhizomes and stolons and therefore may not be strictly equated with the

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underground biomass referred to by Cooper (1975). Another possible cause of this discrepancy is that below ground biomass reaches a maximum value during the first year or two after establishment and then declines as has been reported by Holt and Lancaster (1968). This could account for the fact that under South African conditions values between 3313 - 6130 kg ha$^{-1}$ (i.e. similar to those obtained in the present study) have been reported (Weinmann and Goldsmith, 1948 in Troughton, 1957) from a 7 year old sward. The *C. dactylon* meadows have been present on the Pongolo floodplain for a number of years and this, together with the effects of periodic submergence (Chapter 9) and developing water stress during exposure (Chapter 8), could account for values lower than those of Cooper (1975).

The marked decreases in $\bar{C}$ in the 76 - 98 and 131 - 161 days intervals are difficult to explain. The former could be due to developing water stress, relieved after 98 days by the effects of heavy early morning mists (Chapter 8). Since flowering also occurred during this period it could explain the decreased root biomass (Strugnell and Pigott, 1978). Stuckey (1941) reported evidence which suggested that growth of new roots almost ceased at the time of flowering and that disintegration of roots produced during the previous season could also be occurring, resulting in small increases in root biomass. It is possible that this happened to *C. dactylon* between 76 - 98 days after exposure. The decrease of the ungrazeable fraction RGR and standing crop (Fig. 6.1b and c) could be due to the decomposition of the previous seasons growth, which had not decomposed earlier due to the anaerobic conditions prevailing in the soil profile, but as conditions became aerobic with drying there was some decomposition. An increase in decomposition can also occur as a result of the irrigating effect of rainfall following drought (Troughton, 1957), this situation was evident on the floodplain as little rain fell during the first 131 days of exposure while during the final 30 days (131 - 161 day period) over 50 mm were recorded (Table 8.1). The reduction could also possibly be due to a below ground grazing effect. Decomposition and below ground grazing seem to be the most likely explanations for this decrease, as a transfer of material from the ungrazeable to grazeable fraction could not account for the reduced ungrazeable fraction during the final 30 days of exposure, as there was no marked increase in grazeable fraction $\bar{C}$ or standing crop during this period.

The response of grasses to heavy and light grazing are variable and depend not only on the amount removed, but also on the intensity of other factors such as temperature, light intensity and available nitrogen (Barnard, 1964). Heavy and continual grazing will inevitably reduce production (Troughton, 1957; Barnard, 1964). Light to moderate grazing could bring about improved growth conditions, resulting in increased production (Troughton, 1957; Barnard, 1964; Roberts, 1967; Kumar and Joshi, 1972). Thus there will be an optimum stocking density (which can be related to grazing), at which primary production will be at a maximum (Vickery, 1972). This varies with area and time because of changing soil moisture. The factors which most influence a change in grazing pressure are probably overgrazing and possibly, to a lesser extent, unpalatability.

The movement of grazers across the floodplain in response to decreasing water level is probably similar to migration on the Serengeti Plains in response to rainfall (Bell, 1972), and appears to be extremely important as it prevents the removal of grass to the extent that regeneration may be detrimentally affected. *C. dactylon* is thus able to recover after heavy grazing and thus maintain its viability throughout the summer inundation period. It is also likely that there was migration between Namanini and adjacent lakes (e.g. Ngodo and Bumbe, Fig. 4.1) where rate of exposure and therefore the condition of the *C. dactylon* pastures at any particular time differed.

A marked increase in grazing as the rate of increase in exposure of new *C. dactylon* decreased, was not evident. This could have several explanations : there was a large area to graze; the grazers were more uniformly distributed across the floodplain; or because of a movement of grazers on a wider scale e.g. from one lake margin to another. However, since local custom controls grazing and cattle do not move extensively over the floodplain, it seems most likely that floodplain grazing was supplemental to grazing off the floodplain.

Grazing reduced the standing crop of the ungrazeable fraction. This was particularly evident during the 98 - 161 day period when standing crop values in the grazed area were markedly lower than in the ungrazed area. It also reduced the contribution of the grazeable fraction to the total standing crop by about 50% after 161 days, showing that grazing had a greater effect on the grazeable than ungrazeable fraction. This conflicts with the statement by Troughton (1957) that following defoliation growth of the whole plant is reduced, the decrease in root growth being greater than that of the shoots. However, Vickery (1972) showed that the changes in underground biomass were influenced by stocking density but seasonal effects also played an important role. It may therefore be that in the present study the effects of grazing on the ungrazeable fraction only became evident once other conditions (e.g. soil moisture) become unfavourable.

## 6.3 Implications for the floodplain

Increase in total standing crop around Namanini lake was largely the result of an increase in the ungrazeable fraction. The initial rate of increase was slow (1042,7 kg $d^{-1}$ during the 0 - 25 day period) and was probably due to the small initial standing crop. This was followed by a rapid increase in standing crop (1553,2 kg $d^{-1}$; Fig. 6.4) until 98 days when the rate again decreased (555.7 kg $d^{-1}$) until flooding at 161 days. The slower rate during the final 63 days of exposure probably reflects a a combination of a lower rate of area exposure and increasing water stress.

Although the grazeable fraction standing crop never exceeded 25% of the total mass, it is extremely important in the functioning of the system because it serves both as a source of grazing following exposure and as an input into the aquatic system following flooding (Chapter 9).

The total amount removed by grazers increased linearly with increasing area exposed (Fig. 6.5a) and after 161 days (136 day grazing period) 15 790 kg had been removed. This removal would be able to support 15 animals for the entire 136 day grazing period (assuming a full grown mass of 300 kg and a daily intake of 2.5% of body mass - Bransby, personal communication). The peak period of removal (150 kg $d^{-1}$, 51 - 76 day period) would give a stocking rate of 1 - 2 animals $ha^{-1}$. This is high for unfertilized natural grazing under South African conditions (Bransby, personal communication). However on occasions up to 300 head of cattle were on the *C. dactylon* areas around Namanini lake alone. It is obvious therefore that the *C. dactylon* meadows would not be able to support the large herds of cattle in the vicinity of the floodplain, especially in view of the fact that increasing population size will result in an increase in stock numbers. *C. dactylon* is therefore more likely to be serving as supplement to grazing and browsing off the floodplain. Its importance may be considerable however, as *C. dactylon* is a grass with a particularly high protein content (Meredith, 1955). The grasses off the floodplain during winter, when *C. dactylon* becomes exposed, can be expected to have a protein content of about 2% (Meredith, 1955). At the same time the nitrogen content of *C. dactylon* on the floodplain was between 1 - 3% (Chapter 7) of dry mass i.e. a protein content of 6% - 18%.

In addition to removal by grazing there must be a loss to the aquatic phase, as there is a decrease in standing crop of both grazeable and ungrazeable fractions following inundation. This loss will depend on the stage of growth when inundation occurs, period of inundation and rate of decomposition of the inundated material. Detailed consideration is given to these aspects as well as the actual transfer of material and nutrients to the aquatic phase in Chapter 9.

The above discussion on increase in standing crop and amount removed by grazing applies to Namanini lake, however the *C. dactylon* area around this lake is approximately $\frac{1}{8}$ of the total *C. dactylon* on the floodplain. Assuming similar conditions to those at Namanini lake for the entire floodplain, a 161 day period would result in 121 x $10^3$ kg being removed by grazers (this would support 118 head of cattle for the entire 136 day grazing period).

As grazers only come onto the floodplain for a few hours every day, most of their time is spent off the floodplain. Thus the amount of material grazed can be considered as a net export from the system. This would have to be balanced by an input to the system, which could be brought about by animals such as hippopotamuses or by silt deposition by the Pongolo river during floods.

## 6.4 Conclusions and future research priorities

Production of *C. dactylon* compares favourably with what would be expected from unfertilized grasslands under South African conditions. However, $\bar{C}$ was found to decrease with increasing exposure, and as conditions also became drier with exposure, it is likely that available moisture could become a limiting factor for *C. dactylon* growth. An autecological study on *C. dactylon* which included its response to different amounts of available moisture, could assist in determining at what stage water becomes limiting to *C. dactylon* growth and the extent to which irrigation of *C. dactylon* meadows during the exposure period could increase production.

The *C. dactylon* meadows serve as an important supplement to grazing material found off the floodplain. In addition the potential amount of material that can be transferred from the terrestrial to the aquatic phase of the Pongolo floodplain system via the inundated *C. dactylon* meadows is considerable (Chapter 9). Grazers and the aquatic phase would benefit from an increase in *C. dactylon* production which might result from irrigation of the floodplain (see above) or fertilization of *C. dactylon* areas (Chapter 7). Conversely they would be adversely affected by a reduction in flooding frequency.

The effect of grazing depends on its intensity : heavy grazing reduces growth while light to moderate grazing tends to stimulate growth. Under heavy grazing standing crop and $\bar{C}$ are greatly reduced so that if the area exposed did not increase after 76 days, the limited area of floodplain exposed would become overgrazed resulting in a decrease in both the amount that could be removed by grazers and the potential input to the aquatic phase. However, although some information on the effects of grazing on *C. dactylon* was obtained in the present study, more detailed studies on the carrying capacity of *C. dactylon* meadows, particularly under irrigated and fertilized conditions, would supply information enabling management options to be formulated.

The conclusions as to the effects of exposure and grazing on *C. dactylon* were determined from conditions prevailing on the floodplain during the study period. The response of *C. dactylon* under other hydrological conditions (i.e. different periods and rates of exposure) should also be investigated, as with the construction of the Pongolapoort Dam and the possible use of stored water for crop irrigation, changes in the hydrological regime will occur.

# CHAPTER 7

## NUTRIENT STATUS OF *Cynodon dactylon* IN RESPONSE TO EXPOSURE AND GRAZING

### 7.1 Results

### 7.1.1 Changes in nutrient concentration during exposure and grazing

### 7.1.1.1 Grazeable fraction

With increasing period of exposure the pattern of change in concentration of all nutrients studied was similar under grazed and ungrazed conditions. The differences in content which did occur were often significant (Fig. 7.1). During the first 25 days nitrogen and phosphorus concentrations were significantly lower in the grazed areas whilst sodium concentration was higher in the grazed area, despite the fact that no grazing could be measured during this period (Fig. 7.1a, b and e). Although it is possible that these differences may reflect between site differences independent of grazing, it is interesting that, with the exception of sodium, higher values in the grazed area were consistently evident after 25 days, grazed areas having higher concentrations than ungrazed areas.

Nitrogen concentration (Fig. 7.1a) rose sharply during the first 25 days (from *c.* 2.3% to *c.* 3.1% of dry mass) and then decreased, the rate of decrease becoming slower as exposure period increased (Fig. 7.1a), attaining values of *c.* 1.1% and 0.9% of dry mass in grazed and ungrazed areas respectively, 131 days after exposure. During the final 30 days of exposure, concentrations in both grazed and ungrazed areas increased slightly, possibly as a result of rain during this period (Table 8.1), so that after 161 days concentrations in grazed and ungrazed areas were *c.* 1.2% and *c.* 1.0% of dry mass respectively.

Potassium (Fig. 7.1c) and magnesium (Fig. 7.1d) concentrations showed similar trends to those of nitrogen. Slight differences being that initial and final increases shown by potassium were more pronounced than those of nitrogen, while magnesium concentration continued to decrease during the final 30 days of exposure. Magnesium concentration was always lower in the grazed area, while potassium concentration was lower at first (0 - 76 days) in the grazed area but after 76 days it was higher in the grazed than ungrazed area. Over the 161 day exposure period potassium concentrations were between 0.4% and 1.4% of dry mass (Fig. 7.1c), while magnesium concentrations were much lower i.e. between 0.12% and 0.36% of dry mass (Fig. 7.1d).

Phosphorus concentration (Fig. 7.1b) decreased steadily during the first 131 days of exposure (i.e. from *c*. 0.38% to *c*. 0.18% of dry mass), the rate of decrease declining with increasing exposure period. During the final 30 days, concentration remained constant in both grazed (*c*. 0.19% of dry mass) and ungrazed (*c*. 0.15% of dry mass) areas. With the exception of the 25 day value, concentrations were significantly higher in the grazed area.

Sodium concentration (Fig. 7.1e) increased sharply during the first 25 days (0.17% to *c*. 0.5% of dry mass) and then more slowly until 98 days (*c*. 0.7% of dry mass). Between 98 and 161 days concentrations in both grazed and ungrazed areas decreased to *c*. 0.3% of dry mass. Except during the period 51 - 98 days, sodium concentration was higher in the grazed area.

Calcium concentration (Fig. 7.1f) increased initially (0 - 25 days) from 0.05% to *c*. 0.07% of dry mass. After 25 days concentrations fluctuated slightly and, although there was no consistent change, the trend was for values to decrease, so that after 161 days concentration in both grazed and ungrazed areas were slightly lower (i.e. *c*. 0.03% of dry mass) than at exposure. Calcium concentration was higher in the grazed area between 51 and 98 days, but 25 and 131 days after exposure concentration in grazed areas were lower than those of the ungrazed area.

#### 7.1.1.2 Ungrazeable fraction

Although patterns of change in nutrient concentration of the ungrazeable fraction were similar under grazed and ungrazed conditions (Fig. 7.2), they were markedly different from those of the grazeable fraction. Significant differences brought about by grazing occurred less frequently than those noted in the grazeable fraction, suggesting that grazing had a smaller influence on the concentration of nutrients in the ungrazeable than the grazeable fraction.

Nitrogen and magnesium concentrations were fairly constant during the initial 76 days of exposure (*c*. 0.9% and 0.17% of dry mass respectively), but fluctuated, particularly in the ungrazed areas, during the remaining 63 days. Initial and final concentrations of both nutrients were similar (Fig. 7.2a and d). Nitrogen concentrations were higher in the grazed area between 51 and 98 days, while the reverse was true during the initial and final periods of exposure. Magnesium concentrations were slightly lower in the grazed area during the first 51 days of exposure but during the remainder of the exposure period they were higher in the grazed than ungrazed area.

Phosphorus concentration decreased sharply during the first 25 days of exposure (i.e. 0.19% to *c*. 0.13% of dry mass), then increased gradually until 98 days (to *c*. 0.15% of dry mass) before decreasing slightly (Fig. 7.2b). With the exception of the first 25 days, they were higher in the grazed than the ungrazed area although these differences tended not to be significant.

Calcium concentration decreased slightly at first (0 - 25 days) from 0.07% to *c*. 0.06% of dry mass, and then more rapidly attaining a value of *c*. 0.035% of dry mass 51 days after exposure. Between 51 and 131 days concentrations fluctuated before increasing sharply during the final 30 days of exposure to *c*. 0.09% and *c*. 0.07% of dry mass in grazed and ungrazed areas respectively (Fig. 7.2f). Thus in the grazed area, concentration was higher after 161 days than at exposure. Concentrations in the grazed area were lower than those of the ungrazed area between 51 and 76 days after exposure only. Concentrations in the ungrazed area were similar at exposure and after 161 days.

Potassium concentration increased initially (0 - 25 days) from 0.34% to *c.* 0.38% of dry mass, more so in the grazed area, then decreased slowly but steadily in the grazed area until 161 days (to *c.* 0.3% of dry mass). In the ungrazed area concentrations continued to increase slowly between 25 and 98 days, and then decreased (Fig. 7.2c). This resulted in the situation where between 76 and 131 days potassium concentrations were significantly lower in the grazed than the ungrazed area, and both areas contained only marginally lower potassium concentration after 161 days than they did at exposure.

Sodium concentration initially (0 - 25 days) increased sharply from 0.12% to *c.* 0.17% of dry mass, then more slowly (25 - 98 days) before decreasing during the final 63 days of exposure (Fig. 7.2e), so that initial and final concentrations for the 161 day exposure period were the same (i.e. *c.* 0.12% of dry mass). With the exception of 131 days after exposure, sodium concentration tended to be greater in the grazed than the ungrazed area.

### 7.1.2 Removal of nutrients by grazers from the area around Namanini lake

The pattern of nutrient removal is determined by changes in : the area exposed, in the amount of *C. dactylon* removed by grazing, and in the concentration of the nutrients. When these are integrated, it is evident that the pattern of removal of all nutrients was similar, the amounts removed increasing steadily with increasing exposure period (Fig. 7.3). Amounts removed and rates of removal differed for each nutrient.

Nitrogen was removed in the largest amount : 3.36 kg ha$^{-1}$ removed after 51 days (Fig. 7.3a) which increased to 16.4 kg ha$^{-1}$ after 161 days. Calcium was removed in the smallest amounts (Fig. 7.3b) : 0.09 kg ha$^{-1}$ removed after 51 days increasing to 0.50 kg ha$^{-1}$ after 161 days. Removal of P, K, Na and Mg increased consistently from the 25 - 51 day period (P : 0.34 kg ha$^{-1}$; K : 1.44 kg ha$^{-1}$; Na : 0.81 kg ha$^{-1}$ and Mg : 0.38 kg ha$^{-1}$; Fig. 7.3) so that after 161 days, total amounts removed were : P : 1.88 kg ha$^{-1}$; K : 6.78 kg ha$^{-1}$; Na : 4.72 kg ha$^{-1}$ and Mg : 1.95 kg ha$^{-1}$.

The rates of removal of all nutrients were greatest during the period 51 - 98 days, after which removal rates tended to be low and constant (Table 7.1).

### 7.1.3 Nutrients contained in the standing crop of *C. dactylon* around Namanini lake

Throughout the 161 day exposure period most of the nutrient standing crop was present in the ungrazeable fraction (Fig. 7.4a to f). The pattern of change in total nutrient standing crop therefore followed closely that of the ungrazeable fraction (Fig. 7.4). The total standing crop of calcium in the plants increased initially (25 - 51 days), stabilized (51 - 76 days) and then increased steadily during the remaining 85 days of exposure. In all other nutrients studied, total standing crop increased rapidly during the first 98 days of exposure (Fig. 7.4). Between 98 and 161 days slower rates of increase were recorded for nitrogen, phosphorus and magnesium. Sodium increased until 131 days then decreased, while potassium showed a slight but steady decrease after 98 days.

Nitrogen was present in the greatest amount, increasing from *c.* 26 kg ha$^{-1}$ after the initial exposure period (0 - 25 days; Fig. 7.4a), to *c.* 80 kg ha$^{-1}$ after 161 days, while calcium was the nutrient present in the smallest quantities (*c.* 1.5 kg ha$^{-1}$ after 25 days increasing to *c.* 4.7 kg ha$^{-1}$ after 161 days; Fig. 7.4f). Throughout the exposure period nutrient standing stocks were N > K > Na > Mg > P > Ca, although in the case of the grazeable fraction P > Mg during the 76 - 161 day period.

## 7.2 Discussion

The uptake of nutrients by plants, and therefore the concentration of these nutrients in the plant, is determined by factors external to the plant e.g. temperature, light, pH, external concentration, interaction between ions; as well as inherent factors e.g. internal concentration, growth rate and surface to volume ratio of absorbing organs (Sutcliffe, 1962). This results in plant material containing a large number of mineral constituents each showing a range of concentrations (Sutcliffe and Baker, 1974) which are influenced by both internal and external factors. They are therefore expected to differ from one species to another as well as within a single species, as environmental conditions change.

### 7.2.1 Effects of exposure on nutrients concentration

In grasses, differences in nutrient concentration between species (Clark *et al.*, 1980), as well as differences within a single species due to seasonal (Troughton, 1957) and environmental differences (Ramakrishnan and Kumar, 1971; Ramakrishnan and Gupta, 1973), have been observed. Seasonal changes in nutrient concentration follow a general pattern in that during spring and summer (i.e. a period of active growth) nutrient concentrations tend to decrease in the root material and increase in the shoot material, while during autumn and winter the reverse is the case (Troughton, 1957).

In the present study these seasonal fluctuations in nutrient concentrations were not evident. In addition changes in nutrient concentration could not be related to changes in growth, as the greatest increase in growth occurred between 25 - 51 days (Chapter 6; Fig. 6.1a), whereas nutrient concentration tended to decline after 25 days. They do, however, follow closely changes in the water status of *C. dactylon*. This aspect is discussed in some detail in Chapter 8 where it becomes evident that the trend is for nutrient concentrations to increase under favourable moisture conditions, and decrease under unfavourable moisture conditions.

Sodium concentration in the grazeable fraction did not follow the same trend as K, Mg and Ca : it increased in concentration until 98 days, after which there was a decrease until 161 days. Ramakrishnan and Krishan (1973) found that in some populations of *C. dactylon*, an increasing content in the soil resulted in an initial increase in sodium content of shoot material; but with further increases in soil sodium, sodium in the plant tissue decreased. A similar effect could occur on the Pongolo river floodplain as much of the area is underlain by cretaceous marine deposits (Van Wyk, 1963; du Preez, 1967). It has also been shown that as the dry season progresses (i.e. period of exposure increases) there is an increase in salinity of ground water (Heeg *et al.*, 1978).

The ungrazeable fraction nutrient concentration (with the exception of sodium) in the absence of grazing did not show the same pattern of change that was evident in the grazeable fraction. The pattern of change of sodium concentration was the same in grazeable and ungrazeable fraction, probably due to effects of soil sodium (see above). The situation described by Troughton (1957), whereby the nutrient concentrations in the ungrazeable fraction showed opposite trends to those observed in the shoot fraction was also not evident.

This is not altogether surprising as Weinmann (1947) did not find any evidence of seasonal variations in concentrations of nitrogen, phosphorus or potassium in the roots or rhizomes of *C. dactylon* grown under South African conditions. Troughton (1957), while admitting that the reason for this absence of fluctuation in concentration was not clear, suggested that it could be due to the ability of *C. dactylon* to withstand adverse conditions in hot climates and to its large food reserve in the rhizomes.

### 7.2.2 Effects of grazing on nutrient concentration

Differences in concentration (expressed as a % of dry mass), between grazed and ungrazed areas, were evident in both grazeable and ungrazeable fractions.

Decreases in both nitrogen and phosphorus concentrations (expressed as % dry mass) in *C. dactylon* tissue, as noted in this study for the grazeable fraction, have been shown to occur with an increase in plant density (Ramakrishnan and Kumar, 1971). Due to the removal of material by grazers, the density of *C. dactylon* in grazed areas can be expected to be lower than in ungrazed areas, which would account for the observed differences in nitrogen and phosphorus. In addition to the effect of grazing on plant density, it has been suggested that an increase in grazing intensity can result in an increase in nitrogen and phosphorus uptake (Parton and Risser, 1979). If this does occur, nitrogen and phosphorus concentrations can be expected to be higher in grazed than ungrazed areas, as was the case on the Pongolo floodplain.

Unlike nitrogen and phosphorus concentration in the grazeable fraction of *C. dactylon*, potassium concentration in the grazed area only exceeded that of the ungrazed area after 78 days. This slower response by potassium to differences in plant density is also evident in the results of Ramakrishnan and Kumar (1971).

Calcium is relatively immobile in plants (Nason and McElroy, 1963; Bieleski, 1973) and may be present in higher concentrations in older than in younger leaves (Meyer *et al.*, 1960). In an ungrazed area the ratio of older leaves to younger will be greater than in a grazed area, resulting in a higher calcium concentration in the ungrazed area. This may account for the situation between the commencement of grazing and 98 days after exposure, but does not explain that between 98 and 131 days after exposure, when calcium concentration in the ungrazed area increased sharply (Fig. 7.1f). This increase is difficult to explain in view of the relative immobility of calcium in plants. A possible explanation is that as calcium is transported in the xylem system of plants (Biddulph *et al.*, 1959; Weatherley, 1969) and the accumulation of calcium is dependent on the total volume of the transpirational stream (Biddulph *et al.*, 1959), an increase in transpiration could result in an increase in calcium accumulation. After an exposure period of 98 days base-P had decreased and vapour pressure deficit was high (Chapter 8), thus a high transpiration rate could be expected at least during part of the day. It is possible that these high transpiration rates contribute to the increase in calcium concentration of *C. dactylon*, particularly in the ungrazed area. A similar increase in calcium concentration in the grazed area would also be expected but the effect of grazing in reducing calcium concentration (see above) to some extent counteracted the apparent accumulation of calcium during periods when transpiration rate was high. Thus calcium concentration remained unchanged between 98 and 131 days (Fig. 7.1f).

Magnesium concentrations in the grazeable fraction were consistently higher in the ungrazed area. As magnesium is the only mineral element present in the chlorophyll molecules, a large proportion of magnesium present in plants is contained in chlorophyll containing organs (Meyer *et al.*, 1960). The proportionately greater amount of green tissue in ungrazed plants could therefore account for their higher magnesium content. Another possible explanation for higher magnesium concentrations in the ungrazed area is that magnesium accumulates in structures such as seeds (Zimmerman, 1947; Meyer *et al.*, 1960), and in the case of grasses the infloresence can be removed by grazing. This will result in a lower seed content in grazed areas and hence a lower magnesium concentration in *C. dactylon* from a grazed area.

In the case of sodium no consistent differences were found between grazed and ungrazed areas, possibly because of the overriding effect of soil sodium on sodium concentrations in plants (see 7.2 above).

Growth habit may play a significant part in showing up trends in nutrient concentrations in grazed areas. This is because when plants have an erect habit most of the photosynthetic fraction is removed by grazing, whereas when the habit is prostrate a smaller part can be removed by grazers (Troughton, 1957). Weinmann (1947) suggested that it was the prostrate growth habit of *C. dactylon* that accounted for the lack of correlation between available carbohydrates in roots and rhizomes and increasing severity of defoliation. Since grazing alters the growth habit which in turn influences nutrient concentration, the interactions are particularly complex.

### 7.2.3 Comparison of nutrient concentrations in *C. dactylon* on the floodplain with that in other areas

Despite the fluctuations in concentration of nutrients in *C. dactylon* the dominance order was always K > Mg > Ca which was the same as that reported by Ramakrishnan and Kumar (1971). They were, however, present in lower concentrations in the present study than had been reported previously (Ramakrishnan and Singh, 1966; Ramakrishnan and Kumar, 1971;

Ramakrishnan and Gupta, 1973; Ramakrishnan and Krishan, 1973). Potassium was present at about half previously reported concentrations, while sodium, calcium and magnesium concentrations were about 10 times lower than reported values. Most of these studies were carried out on plants grown in the laboratory and supplied with a nutrient solution, thus ensuring more favourable growth conditions. Ramakrishnan and Gupta (1973) noted that as the amount of nutrient supplied to *C. dactylon* was increased, the concentration in the plant tissue increased. From this it may be implied that the concentrations of K, Mg and Ca in *C. dactylon* on the floodplain are limited by the amounts available in the floodplain soils.

Nitrogen and phosphorus concentrations in the present study were similar to previously reported values (Ramakrishnan and Kumar, 1976) and it may be assumed that they are in adequate supply. However, should a decrease in supply occur consequent upon continued removal of nutrients by grazers, without replenishment by silt deposition during floods, then production would be markedly reduced. However, since atmospheric nitrogen fixation may be significant in flooded soils (Gambrell and Patrick, 1978), phosphorus may be of greatest significance in controlling production.

### 7.2.4 The effect of nutrient removal by grazing on the standing stock of nutrients

The *C. dactylon* standing crop consisted mainly of ungrazeable material (Fig. 6.2b), and changes in the nutrient standing stock of all nutrients followed closely changes in the nutrient standing stock of the ungrazeable fraction. The initial rapid nutrient increases (0 - 98 days) were due mainly to increases in the standing crop of ungrazeable material while the slower rates of increase (98 - 161 days) in nutrient standing stock (and slight decreases for K and Na) were due to a combination of decreasing nutrient concentration (especially for K and Na) and a slower increase in the standing crop of ungrazeable material.

The grazeable fraction nutrient standing stocks were far lower than in the ungrazeable fraction, mainly as a result of removal by grazing cattle. Nitrogen was present in the largest amount (between *c.* 6.4 and 9.5 kg $ha^{-1}$), while calcium was present in the smallest amount (between *c.* 0.16 kg $ha^{-1}$ and *c.* 0.03 kg $ha^{-1}$). Changes in pattern of nutrient standing stocks were, however, different from those found in the ungrazeable fraction.

The initial increase in grazeable fraction standing stocks were due to the combined effects of the initial exposure of a large area (Table 9.3) and high nutrient concentrations prevailing at the time (Fig. 7.1), as well as an absence of grazing during the 0 - 25 day period. Removal of nutrients by grazers from the area around Namanini occurred after 25 days exposure, the rate of removal increasing to a maximum between 51 and 76 days (Table 7.1). At this stage nitrogen was being removed at the greatest rate (i.e. 0.197 kg $ha^{-1}$ $d^{-1}$, Table 7.1), and calcium at the slowest rate (i.e. 0.006 kg $ha^{-1}$ $d^{-1}$, Table 7.1). This increased rate of removal occurred at the same time as a decrease in nutrient concentrations in areas exposed for longer than 25 days, resulting in nutrient standing stocks decreasing (Fig. 7.4). Between 76 - 98 days rates of removal declined and then remained virtually unchanged (Table 7.1). This unchanged removal rate after 98 days occurred at the same time as nutrients concentrations either declined at a slower rate (Fig. 7.1) or increased slightly (e.g. N and P, Fig. 7.1). The combined effect of these factors resulted in slight increases in nutrient standing stocks (Fig. 7.4). The only nutrient which did not show the above trends was sodium, the reason probably being due to the effects of an increase in soil sodium as the dry season progressed (see page 72).

## 7.3 Implications for the Floodplain

The area occupied by *C. dactylon* at Namanini lake is approximately $\frac{1}{8}$ of the total *C. dactylon* area on the floodplain. Assuming conditions prevailing at Namanini lake (i.e. period of exposure, rate of exposure, effects of exposure and grazing) were the same for all *C. dactylon* areas on the floodplain, the nutrient standing stocks, as well as the amounts of nutrients and protein (i.e. nitrogen x 6.25) removed by grazers from the *C. dactylon* areas of the entire floodplain, were calculated (Table 7.2 and 7.3). The nutrient standing stocks on the floodplain are considerable as can be seen when considering nitrogen (the nutrient with largest standing stock) and calcium (the nutrient with the smallest standing stock). Nitrogen increased from 2356 kg after 25 days exposure to 14 298 kg after 161 days exposure, whereas during the same period calcium increased from 140 kg to 842 kg. The greater proportion of these were contained in the ungrazeable fraction i.e. after 25 days grazeable fraction nutrients contributed between 10% and 25% to the total whereas after 161 days their contribution had decreased to between 6% and 16% of the total. This lower contribution by the grazeable fraction as exposure period increased being due largely to the amounts of nutrients removed by grazers (Table 7.3). The importance of this removal by cattle becomes apparent when considering the fact that during the exposure period grazing areas off the floodplain are in a poor condition (Chapter 4, page 39), while at the same time the amount of protein removed by grazers from the floodplain (Table 7.3) increased from 2813 kg (after a 51 day exposure period) to 16 194 kg (after a 161 day exposure period).

Grazers which utilize the *C. dactylon* areas of the floodplain do so for only part of the day, the remainder of the day and the night are spent off the floodplain. Thus it can be expected that there will be an export of nutrients, in the form of urine and dung, from the floodplain to adjacent areas. This export will have to be balanced by an input if a decrease in floodplain production is to be avoided. Nutrient input to floodplain systems occurs as nutrients adsorbed to silt, or as dissolved nutrients (Welcomme, 1979b). In the case of the Pongolo floodplain, dissolved nutrient levels (especially nitrate nitrogen and orthophosphate) are low (Musil, 1972), thus the main input is from silt. As the Pongolapoort Dam has been built immediately above the floodplain, the amount of silt reaching the floodplain could decrease, thereby detrimentally affecting the floodplain.

In addition to the grazeable fraction being a source of nutrients to grazers during exposure period, upon inundation both the grazeable and ungrazeable fractions of *C. dactylon* contribute nutrients to the aquatic phase of the floodplain system (Chapter 9). As nutrient standing stocks change as exposure period increases, the amounts of nutrients that could be incorporated into the aquatic phase also change, this aspect is discussed in detail in Chapter 9.

## 7.4 Conclusions and Future Research Priorities

The concentration of nutrients in the grazeable fraction of *C. dactylon* was affected to a greater extent by a decrease in soil moisture, as a result of increasing period of exposure (which tended to decrease nutrient concentrations), than by the effects of grazing. Nutrient concentration changes in the ungrazeable fraction were small compared to those of the grazeable fraction and could not be related to exposure period, the effects of grazing or changes in the grazeable fraction. It has been suggested that the prostrate growth habit of *C. dactylon* can account for this lack of marked change in nutrient concentrations. To determine if this is the case an autecological study of *C. dactylon* under controlled conditions would be necessary.

The *C. dactylon* nutrient standing stocks were high and large amounts of nutrients were contributed to grazers during exposure and to the aquatic phase during inundation. However, the concentrations of nutrients in *C. dactylon* were lower than previously reported values. The reasons for this were not always clear and a detailed investigation into the soil nutrient status of floodplain soils, and the effects of flooding and decreasing soil moisture content on nutrient availability, could assist in explaining these low concentrations.

The fact that nutrient concentrations were low suggests that if nutrients were supplied to actively growing *C. dactylon* on the floodplain, nutrient concentration (and hence standing stocks and nutrient contributions to both grazers and the aquatic phase) could be increased. The effects of adding nutrients to *C. dactylon* areas (fertilization) should therefore be investigated. Such experiments could supply information on the possibility of increasing the nutrient and protein content of *C. dactylon* which could influence the productivity of both the aquatic and terrestrial phases of the system. Effects of fertilizer application on species composition would also become evident. An understanding of the effects of an increased nutrient supply to *C. dactylon* areas would be extremely important in determining future management options for the floodplain, as the use of water from the Pongolo river to irrigate crop lands adjacent to the floodplain is being considered (see Chapter 4). Runoff from these lands is likely to contain higher concentrations of nutrients than are at present found in the waters of the Pongolo systems.

Present utilization by grazers appears to result in an export of nutrients from the floodplain system; this could be confirmed by determining the time spend by grazers on the floodplain. In addition the role of silt as the major source of nutrient input to the floodplain should also be investigated. This aspect is of particular importance as the Pongolapoort Dam will trap silt, thus reducing amounts reaching the floodplain.

Investigations into the effects of different rates of nutrient removal and lengths of exposure periods on nutrient concentrations of *C. dactylon*, would also assist in determining future management options involving an artificial flooding programme.

# CHAPTER 8

## WATER STRESS AS A FACTOR INFLUENCING GROWTH OF *Cynodon dactylon*

## 8.1 Results

### 8.1.1 Precipitation

Rainfall, fog and mist data were obtained from Ndumu Game Reserve*. This recording station (447/565) is situated on a small hill approximately 1 km west of the floodplain. The presence of fog or mist at the station and in the surrounding area was recorded by a subjective index of its intensity (i.e. light, medium and heavy). When fog or mist was recorded as being 'nearby', it implies that it was present only on the surrounding low-lying areas (including the floodplain) but not at the recording station; when fog or mist was present at the station, it was also present on the floodplain. Thus although the data for fog and mist are somewhat subjective, they do give an indication of both frequency of occurrence and intensity of mist on the floodplain *c.* 8 km to the north of Namanini lake.

The weather station at Ndumu** (447/446), from which only rainfall data were available, is situated on the low-lying Maputaland coastal plain approximately 5 km north-west of Namanini lake. This station is slightly closer to the study area than station 447/565.

Rainfall data for the two stations (Table 8.1) indicate that only 7.3 mm of rain fell at Ndumu Game Reserve (station 447/565) while no rain was recorded at Ndumu (station 447/446) during the first 143 days after exposure. During the next 12 days good rains fell in both Ndumu Game Reserve (47 mm) and Ndumu (51 mm). In Ndumu Game Reserve these were augmented by a further 3.6 mm during the final 6 days of the study. Mist and fog were recorded on 40 days during the study period. Heavy

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mists, which occurred on a few days, persisted until 11h00 or 12h00 at Namanini lake. On most occasions however, mist had lifted by 08h00.

### 8.1.2 Vapour pressure deficit (VPD)

Diurnal changes in VPD were measured on five occasions, at approximately 25 day intervals, between 51 and 161 days after exposure (Fig. 8.1). Although these were single day measurements, they are considered to represent the general trend in VPD because so little rain was recorded during the study period, particularly during the initial 143 days (Table 8.1). During the 51 - 98 day period maximum values (which always occurred at 12h00) increased from 1.17 kPa to 1.6 kPa, and minimum values (which occurred at night) from 0 kPa to 0.3 kPa (Fig. 8.1). At 131 days after exposure VPD had decreased sharply, a maximum value of 0.67 kPa (at 12h00) and a minimum value of 0.1 kPa (at 18h00) being recorded. On this occasion light rain was falling at Namanini lake. During the final 30 days of exposure, despite approximately 50 mm of rain being recorded (Table 8.1), VPD increased markedly during the day (a maximum of 2.05 kPa being recorded at 12h00; Fig. 8.1). The minimum value however, decreased slightly to 0.08 kPa (06h00; Fig. 8.1). The general trend during the 161 day exposure period was for VPD to increase. Values recorded during the day (12h00 and 18h00) doubled during the exposure period while night values (24h00), although being lower than day values, showed a 3 to 4 fold increase.

### 8.1.3 Soil characteristics : field capacity (FC) and permanent wilting Point (PWP)

During the first 10 days of exposure, soil moisture content exceeded the FC value of 45% (i.e. a matric potential of -10 kPa; Fig. 8.2) and decreased slightly during the next 18 days (Fig. 8.3). However, between 28 and 73 days soil moisture decreased markedly from 43% to 27% (Fig. 8.3), some 20% below the PWP % at -1500 kPa (i.e. 34% moisture content, Fig. 8.2), which was attained 51 days after exposure. After 73 days soil moisture continued to decrease, although at a slower rate (Fig. 8.3) until 101 days, when the lowest value for the entire 161 day study period was recorded (i.e. 25%, Fig. 8.3). During the final 60 days of exposure soil moisture did increase slightly (Fig. 8.3) although it remained below that at PWP (i.e. < 34%).

### 8.1.4 Xylem pressure potential (P)

The diurnal pattern of P, with lowest values (most negative) occurring during the day and late afternoon and highest values (least negative) occurring during the night and early morning, was the same for grazed and ungrazed areas throughout the 161 day exposure period (Fig. 8.4). However, despite the similar pattern, after 51 days significant differences (at the 95% level) were recorded between grazed and ungrazed areas (Fig. 8.4). At these times P was generally more negative in the grazed area (Fig. 8.4).

The results for base-P showed two marked decreases i.e. after 98 days (*c.* -800 kPa) and 161 days (*c.* -700 kPa; Fig. 8.5). *C. dactylon* was thus experiencing increased water stress during the period 76 - 98 days and again between 131 - 161 days. At these times base-P tended to be lower in grazed areas. This decrease in base-P illustrates that the plants were not able to reinstate favourable conditions by uptake of water from the soil at night. At this time soil moisture was below PWP (i.e. a matric potential < -1500 kPa). In the case of minimum P ($P^{min}$), values were relatively high (*c.* -900 kPa; Fig. 8.5) initially, but decreased to *c.* -1950 kPa after 98 days of exposure. This was followed by a period (98 - 131 days) during which $P^{min}$ became less negative, before again decreasing, attaining a minimum value of *c.* -2250 kPa 161 days after exposure. Thus $P^{min}$ values indicate that *C. dactylon* was subjected to increasing water stress conditions during the day as exposure period increased, and that stress was relieved partially after 131 days. They also show that $P^{min}$ was considerably more negative than the -1500 kPa PWP.

## 8.2 Discussion

### 8.2.1 Effects of exposure on water stress

Despite the very wet soil conditions prevailing immediately following subsidence of floodwaters (Fig. 8.3) transpirational water loss by *C. dactylon* exceeded uptake during the day, causing P to become increasingly negative. The freely available soil moisture allowed reinstatement of a favourable water status during the night, as shown by a marked increase in P (i.e. P became less negative) and the fact that base-P was high (slightly negative, Fig. 8.5). The magnitude of the water stress conditions evident during the day was unexpected as soil water potential was high. However, water stress symptoms in plants subjected to flooding has been reported (Kramer, 1969; Sojka and Stolzy, 1980) where they have been ascribed to a decreased oxygen availability to the roots (Mees and Weatherley, 1957; Sojka *et al.*, 1975; Sojka and Stolzy, 1980). This can result in an increased root resistance to water absorption (Kramer, 1969) which reduces the rate of replacement of water lost by transpiration (Sojka and Stolzy, 1980). Provided transpirational loss did not decrease, P would become more negative, as was observed in the present study. Sojka and Stolzy (1980) have pointed out however, that the root-resistance hypothesis does not explain all cases of water stress development under anaerobic conditions. They suggest that either the production of physiologically active chemicals (e.g. ethylene), or a change in the potassium content of guard cells could play a role in the development of water stress conditions as a result of anaerobiosis. In *C. dactylon*, root and shoot development is initiated under waterlogged conditions. Without a shoot system, oxygen diffusion to the developing roots must be small if it occurs at all, and it seems probable that anaerobic metabolism provides the energy for the first flush of growth. It would be interesting to know if carbohydrate reserves in stolons and rhizomes, coupled with the metabolic control of malic enzyme to prevent ethanol production, as occurs in plants found in flooded or aquatic environments (Crawford, 1978), provide for the initial energy demand, particularly since *C. dactylon* is typically terrestrial and not aquatic. In addition, to fully understand the effects of changes in soil aeration on plant growth, *in situ* studies are required (Sojka *et al.*, 1975) but due to the difficulties involved, studies of this nature do not appear to have been undertaken.

After 51 days, soil moisture approached the -1500 kPa PWP level (Fig. 8.3). Water stress conditions could therefore be expected to result from the unavailability of soil moisture, rather than from the effects of anaerobic conditions. The extent of water stress conditions in *C. dactylon* at this time is evident from the $P^{min}$ value of *c.* -1300 kPa measured at 12h00 (Fig. 8.4). Despite this, base-P remained high (Fig. 8.5) indicating that at night the plants were still able to make up any daytime water deficit (Ritchie and Hinckley, 1975). Clearly, therefore, either PWP does not occur at a matric potential of -1500 kPa or, more probably, the -1500 kPa PWP level does not represent the PWP for *C. dactylon*. There is evidence in the literature to suggest that plants vary in their PWP, ranging from -1000 kPa to -2000 kPa (Slatyer, 1967; Kramer, 1969). A value of -1500 kPa is therefore to be used only as a guide to PWP. In addition, *C. dactylon* has been reported to be a drought resistant plant (Weinmann, 1955) and it is likely that PWP for *C. dactylon* may be closer to -2000 kPa than -1500 kPa. This is supported by the fact that base-P decreased to -2250 kPa (Fig. 8.5), which was considerably more negative than the -1500 kPa PWP. However, it cannot be assumed that soil moisture is the only source of water available to plants : the occurrence of mist (Table 8.1) could also account for *C. dactylon* growing at a soil moisture content less than the -1500 kPa PWP level, if it acted as a source of moisture.

The effects of mist, fog and dew can be either indirect in that VPD (or atmospheric evaporation demand; AED) and hence potential transpiration are reduced (Slatyer, 1960), or direct in that moisture is taken up. Water may condense on the plant and be taken up directly through stomata (Bornman *et al.*, 1973) or flow down the stem to the soil providing moisture for uptake by plant roots (Went, 1955; Shure and Lewis, 1973). Went (1955) noted that for fog and mist to be effective as sources of moisture for plants, there must be air movement past the condensing surface and this surface should be small and narrow, so as to minimise deflection of droplets of water carried in the air. The later requirement, in particular, is satisfied by *C. dactylon* as these plants have thin stems and narrow leaves. Air movement, particularly during the second half of winter when the occurrence of mist is important to *C. dactylon*, can be expected as wind run was at a maximum during this period (Table 4.1).

The amount of water obtained by plants from mist can be considerable : Gindel (1965) stated that annual precipitation from mist in some parts of the world exceeds that of rainfall by a factor of 10, i.e. in the deserts of Chile and Peru annual precipitation from mist may be 300 - 400 mm while actual rainfall does not exceed 40 mm. On the Pongolo river floodplain this is probably considerably less but, perhaps none the less significant since it occurs during the dry period.

Further evidence supporting the idea that the -1500 kPa PWP level does not apply to *C. dactylon* and that this plant is able to utilize atmospheric moisture, is that base-P did not become significantly more negative until 47 days after the -1500 kPa PWP level had been attained, and after a reduction in frequency of occurrence of mist (i.e. between 76 and 100 days; Table 8.1). It is likely that at this stage (98 days after exposure) as a result of the decreasing soil water content, roots would experience increasing difficulty in obtaining water. Under these conditions the water potential of the leaves would increase, maintaining the gradient between leaves and roots (Denmead and Shaw, 1962) and reducing the turgor pressure of leaf cells. Stomata close, due to this reduced turgor pressure, bringing about a decline in transpiration rate (Denmead and Shaw, 1962). If this occurred in *C. dactylon*, water loss would decrease at a time when there was a decrease in soil moisture and an increase in AED.

Base-P increased significantly 131 days after exposure (Fig. 8.5) indicating more favourable moisture conditions. In part this was due to decreased AED, it was also due to uptake of water from the light rain falling while sampling was being carried out. The rain was insufficient to raise the soil moisture content above PWP (i.e. -1500 kPa level) but, as the -1500 kPa index of PWP may not be low enough to represent PWP for *C. dactylon*, uptake from the soil could also occur. In addition, the amount of moisture obtained from fog, mist and light rain may have wet the upper layer of soil only (i.e. in the vicinity of the extensive stolon and rhizome systems of *C. dactylon*). Stone (1963), in his review of the ecological importance of dew, pointed out that plants are able to absorb water from the part of the soil which is adequately supplied and translocate it to roots growing in dry soil. It is probable, therefore, that small amounts of water (mist and light rain) can be utilized by *C. dactylon* even though they are insufficient to significantly increase soil water content. This emphasises the importance of precise estimation of mist interception and precipitation in situations of this type.

During the period 131 to 161 days AED increased and was accompanied by a significant decrease in base-P, indicating that plants were experiencing considerable difficulty in obtaining water. This is confirmed by the change in the shape of the diurnal curve for P which, instead of forming a distinct peak at about noon, levelled off during the afternoon (Fig. 8.4), indicating that soil moisture was becoming limiting (Ritchie and Hinckley, 1975). As the plants were still living, the PWP for *C. dactylon* had clearly not been reached and PWP for *C. dactylon* must be considerably lower than -1500 kPa.

### 8.2.2 Effects of water stress on growth and nutrient content

In the present study, *C. dactylon* grazeable fraction and ungrazeable fraction in the ungrazed area showed an increase in $\bar{C}$ during the first 51 days of exposure (Fig. 6.1, Chapter 6). This coincided with a period of high soil moisture content, the soil matric potential being between FC and PWP. The initial increase in $\bar{C}$ is not surprising, as it has been pointed out (Singh *et al.*, 1980) that during the early stages of growth limited amounts of moisture are required. The same may apply to nutrient uptake during the first 10 days (when soil moisture exceeds FC) because although it is adversely affected by anaerobic conditions in the root zone (Sojka *et al.*, 1975; Gambrell and Patrick, 1978), relatively small amounts are required. Clearly, when the duration of the waterlogged period associated with growth is short (*c.* 10 days), the adverse effect does not appear to be too marked. In the present study the period between successive samples was too long to establish if this did occur. Between 10 and 51 days, soil moisture content was between FC and PWP and the rhizosphere would have been better aerated while the plant had access to the soil water. As water stress increased (51 - 76 days after exposure), ungrazeable fraction growth rate stabilized while grazeable fraction growth rate decreased (Fig. 6.1). During the following 22 days (76 - 98 day period), water stress increased markedly. This had the effect of further decreasing grazeable fraction growth rate, while at the same time dramatically reducing ungrazeable fraction growth rate. These effects on growth were to be expected as an increase in water stress is known to reduce plant growth (Slatyer, 1967; Kramer, 1969). Hsiao (1973) pointed out that the reduction in growth can be brought about by reduced turgor pressure, which plays a critical role in cell growth. Thus water stress, not severe enough to close stomata and inhibit photosynthesis, can readily reduce leaf area development (Hsiao *et al.*, 1976). This could explain the observation in the present study that the initial development of water stress had a greater effect on the grazeable fraction than on the ungrazeable fraction growth. Wardlaw (1969) found that with increased water stress there was a decrease in extension growth of roots and shoots in *Lolium temulentum* L. and when this did occur, roots appeared to be more sensitive to water stress than shoots. Similar findings were reported by Viets (1972) and Gales (1979), while Kramer (1969) pointed out that as soil moisture approaches PWP there is probably little or no root growth. These observations could account for the constant $\bar{C}$ between 25 and 76 days and the marked decrease in ungrazeable fraction growth rate between 76 and 98 days, as water stress increased. In addition to reduced root and shoot elongation, continued water stress results in reduced photosynthesis (Crafts, 1968; Wardlaw, 1969; Viets, 1972; El-Sharkawy and Hesketh, 1964; Boyer, 1976), reducing production of the entire plant. After 98 days there was a period of reduced water stress (131 days) followed by a period of increased water stress. These changes were also reflected in growth. The ungrazeable fraction, possibly because it is more sensitive to moisture stress than grazeable fraction (Wardlaw, 1969; Viets, 1972), showed a marked increase in growth rate during the 98 - 131 day period, but then decreased sharply (131 - 161 day period) as water stress again increased (Fig. 8.4). The response of the grazeable fraction was slower and growth rate continued to decrease until 131 days, although at a reduced rate. During the final 30 days of exposure there was a slight increase in growth rate possibly in response to the favourable moisture conditions that occurred 131 days and between 143 - 145 days after exposure (Table 8.1).

In addition to affecting growth, water stress could also alter the nutrient status of *C. dactylon*. Increasing water deficit can reduce the availability of nutrients to plants (Crafts, 1968; Viets, 1972). Low and Piper (1960) showed that the uptake of phosphorus, in particular, was reduced when water stress increased. In addition to the availability of nutrients, the nutrient levels in plants can change, and according to Viets (1972) if mineral nutrient concentrations in the plants decline with increasing water stress (as was the tendency in the present study for grazeable fraction material after 25 days exposure; see Chapter 7) then nutrient availability has been affected to a greater extent than growth. The change in nitrogen concentration is anomalous, as with increasing water stress nitrogen concentration in the plant would be expected to increase (Naylor, 1972). However, according to Viets (1972), if the availability of soil moisture decreases, nitrogen levels in the plant could decrease. A reduction in nutrient concentrations in plants can also occur if, as soil moisture decreases, water is obtained from a zone other than that where nutrients are present (Viets, 1972). This could happen on the floodplain when *C. dactylon* obtains its moisture from the atmosphere or perhaps the surface layer of soil, as a result of heavy early morning mists.

Nutrient concentrations in the ungrazeable fraction fluctuated but did not follow the same pattern as ungrazeable fraction growth rate, and in fact, concentrations at exposure and after 161 days were similar (see Chapter 7). This could be due to the fact that much of the ungrazeable system of *C. dactylon* consists of rhizomes and stolons which act as storage organs. Increasing water stress could result in a translocation of nutrients to these storage organs. This would off-set any concentration changes that may occur in the ungrazeable fraction due to water stress, resulting in the apparent relative stability of ungrazeable fraction nutrient concentrations.

As moisture stress adversely affects growth and nutrient content of *C. dactylon* the irrigation of *C. dactylon* meadows to increase both production and nutrient content could be considered. The irrigation of crops to prevent the undesirable effects of moisture stress is well known (Russell, 1961). In the case of crop plants, it was found that the amount of water required to prevent moisture stress developing differed according to the stage of growth (Mallett and De Jager, 1971; De Bruyn and De Jager, 1978). Thus studies have concentrated on determining at what stage water stress can be expected to occur, when plants are most sensitive to water stress and what amount of water would be required to prevent water stress developing. To achieve this, measurement of moisture stress and changes in yield must be conducted over relatively short periods (e.g. 2 - 5 days; De Bruyn and De Jager, 1978). Thus with results from the present study it is not possible to determine when irrigation of *C. dactylon* should occur, or the amount of water that should be applied to prevent water stress conditions developing. There is little doubt, however, that application of water after 51 days would improve yield.

### 8.2.3 Effects of grazing on water stress

Although the above discussion has considered the effects of water stress on ungrazed *C. dactylon*, so as to exclude the effects of changes as a result of grazing, the situation on the floodplain is such that exposed *C. dactylon* is subjected to varying intensities of grazing (see Chapter 6). The diurnal pattern of P in grazed and ungrazed areas was similar throughout the 161 day exposure period. Despite the similarity, grazed area values for P were generally more negative, in some cases significantly so (at the 95% level, Fig. 8.4), than those of the ungrazed areas.

This indicates that the grazed area was subjected to a greater degree of water stress than the ungrazed area. Possible explanations for this are either that the removal of *C. dactylon* material by grazing allows the plant to lose more water, but since the difference between grazed and ungrazed only became significant after grazing had peaked, this effect may not be important; or grazing reduces the ability of the plant to utilize mist as a source of moisture, as the size of a plant and the presence of narrow leaves determine the extent to which mist (and fog) can be utilized (Went, 1955). It would therefore be expected that following heavy grazing significant difference in P between grazed and ungrazed areas would occur. Conversely, following light grazing P values should be similar in both areas. This, however, was not always the case, as can be seen when grazing pressure was at a maximum (25 - 51 day period, Fig. 6.3), yet after 51 days no significant difference in P between grazed and ungrazed areas were recorded (Fig. 8.4). The most probable reason for this is that $\bar{C}$ was high during the 25 - 51 day period (Fig. 6.2) and compensated for material removed. During the 51 - 76 day period grazing pressure decreased sharply (Fig. 6.3) yet significant differences in P between grazed and ungrazed areas occurred (Fig. 8.3). Again $\bar{C}$ could have influenced these results as it decreased to its lowest value in the grazed area during the 161 day exposure period (Fig. 6.2). To test these possibilities would therefore require an estimation of P at much shorter intervals, perhaps at 2 day intervals.

Thus in the grazed area a number of factors, in addition to soil and atmospheric conditions (e.g. amount of *C. dactylon* removed; crop growth rate), interact to influence P, generally making it slightly more negative than in the ungrazed area.

## 8.3 Implications for the Floodplain

The *C. dactylon* Community occupies an intermediate area on the floodplain (see Chapter 5). Some communities (i.e. *Phragmites* and *Cyperus fastigiatus - Echinochloa pyramidalis*) prefer wetter conditions while others (i.e. *Ficus sycomorus - Rauvolfia caffra* and *Acacia xanthophloea - Dyschoriste depressa*) prefer drier conditions than those favoured by *C. dactylon* (Chapter 5). Thus all communities will not be affected to the same degree by an extended period of exposure. The communities occupying low-lying areas and favouring wet conditions are likely to be more sensitive to low soil moisture content than those that normally occupy the higher-lying drier areas of the floodplain. This could explain the recent deterioration of the well developed *Cyperus fastigiatus - Echinochloa pyramidalis* Community in the vicinity of Tete lake (Plate 5.3; Chapter 5), probably as a result of increased moisture stress due to longer intervals between floods which have occurred since the construction of the Pongolapoort Dam (Fig. 4.7). Others, particularly those growing on the levees, may have roots growing to the watertable, and thus not really experience water shortage even during long periods between floods. Although the *C. dactylon* Community, which occupies an intermediate position on the floodplain (Chapter 5), may be less stable relative to other communities because water stress reduces $\bar{C}$ and nutrient content, it is important in the functioning of the system. Water stress affects the quantity and quality of material available to grazers during winter, and the input of material and nutrients to the aquatic system when these meadows are flooded. Regular flooding of these meadows is essential for the maintenance of floodplain productivity.

## 8.4 Conclusions and Future Research Priorities

During a 161 day exposure period *C. dactylon* was subjected to varying degress of water stress despite some relief from mist, fog and rain. The effects of water stress were to reduce $\bar{C}$ and nutrient content.

The extent to which moisture stress develops, and therefore influences *C. dactylon* growth and nutrient content, depends on the period of exposure and the amount of precipitation (rain, fog and mist) occurring during the exposure period. However, although fog and mist have been identified as supplying moisture to *C. dactylon*, a more detailed study as to the amount of precipitation that occurs on the floodplain as a result of mist and fog, as well as its significance to *C. dactylon*, should be undertaken

The period of exposure during the present study (161 days) was slightly shorter than the average exposure period at Namanini lake since the construction of the Pongolapoort Dam (i.e. 177 days; Table 4.5). Once the stored water is used for irrigation purposes, the amount available for the floodplain can be expected to decrease, and the exposure period will increase. Thus *C. dactylon* and other floodplain communities can be expected to be subjected to a greater degree of water stress than was the case during the present study. To prevent water stress developing in *C. dactylon* and to increase production for exploitation, irrigation of *C. dactylon* meadows could be undertaken. However, before this can be undertaken more frequent measurements of P, soil moisture content and changes in production and nutrient concentration will be required. In addition, the soil moisture content at which PWP for *C. dactylon* occurs should also be determined. This will enable the period during which *C. dactylon* is susceptible to moisture stress (and thus requiring irrigation) to be identified.

# CHAPTER 9

## DECOMPOSITION OF *Cynodon dactylon*

### 9.1 Results

### 9.1.1 Pattern and rate of loss of organic and mineral fractions from harvested *C. dactylon* material

The decomposition of fresh and dried material displayed a distinct diphasic pattern of decay (Fig. 9.1a and b) which, taken over the entire experimental period, can also be described by an exponential model of the type $y = \underline{ae^{bx}}$ ($r^2 = 0.98$; $p = 0.001$ for fresh and dried material).

During the initial phase, fresh material decomposed more slowly (1.7% $d^{-1}$) than dried material (2.1% $d^{-1}$), but in both the slower phase only became evident when the dry mass had been reduced by *c.* 50%. The latter phase therefore developed after 18 days in dried and 28 days in fresh material.

Loss of mineral ash was also diphasic with the rates of loss being similar in both fresh and dried material. The second phase became evident after *c.* 22 days (Fig. 9.1a and b).

Decay of fresh and dried material was distinctly linear during the first phase and changed rather abruptly to the second phase which, considering the limitation of the data available, appears also to be linear.

### 9.1.2 Patterns and rates of loss of nutrients from harvested *C. dactylon* material

Loss of all nutrients (N, P, Ca, Mg, Na and K) from both fresh and dried material followed an exponential pattern. Nitrogen and phosphorus were lost more rapidly and in greater amounts from dried than from fresh material and, at least initially, nitrogen was lost more slowly than phosphorus (Fig. 9.2b and d). In fresh material *c.* 20% of the nitrogen and phosphorus were lost within 4 days, whereas in dried material more phosphorus (40%) and less nitrogen (8%) were lost. After 21 days 40% of the nitrogen and phosphorus had been lost from fresh material whilst 60% and 70% were lost from the dried samples. After 21 days, losses from fresh and dried material were small.

Drying appeared to change the pattern of release of magnesium (Fig. 9.2a and c). In fresh material release was very slow initially and increased gradually, whereas in dried samples loss started rapidly and then became slower. After 30 days loss from fresh and dried material was 30% and 45% respectively.

Loss of calcium, potassium and sodium from both treatments proceeded at similar initial rates but slowed down more rapidly in the dried than in the fresh material (Fig. 9.2a and c). Thus the fresh lost 10% more of their calcium, magnesium, sodium and potassium than dried samples.

### 9.1.3 Changes in nutrient content of the inundated above-ground fraction of *C. dactylon*

The chemical composition of the *C. dactylon* standing crop showed marked changes during submersion (Table 9.1). All nutrients and the ash component decreased initially, phosphorus particularly rapidly. Very small changes were evident in potassium and magnesium. With the exception of sodium and calcium, which declined in concentration throughout the period, all nutrient concentrations had, after 120 days submergence, increased to levels above those at the start of inundation. The ash-free component did not vary significantly.

## 9.2 Discussion

An exponential pattern of decay of aquatic macrophytes has been demonstrated frequently (Jewell, 1971; Novak *et al.*, 1975; Petersen and Cummins, 1974; Twilley, 1976). Howard-Williams and Davies (1979) have, however, suggested that in *Potamogeton pectinatus* L. the exponential pattern should simply be regarded as a convenient form of describing the decay process because physical leaching during the early stages causes a significant deviation from this pattern. Leaching might be expected to occur more rapidly from dried material in which membranes and organelles have been disrupted. The more rapid loss of nitrogen, phosphorus and magnesium from dried *C. dactylon* support this observation, although, rather surprisingly, the initial loss rates of sodium and potassium were not influenced by drying and the results suggest that losses may even have been retarded.

If drying increases leaching then it would tend to enhance the diphasic pattern of decay which has been observed (Howard-Williams and Junk, 1976; Mason and Bryant, 1975; Howard-Williams and Howard-Williams, 1978; Odum and Heywood, 1978). Rogers and Breen (in press) have shown that in *P. crispus* loss from fresh material is not diphasic whereas it is from dried material. In *C. dactylon*, however, decay was distinctly diphasic despite the use of fresh material. It has been suggested that this pattern may result from differential rates of decomposition of different fractions (Boyd, 1970, 1971; Kaushik and Hynes, 1971; Planter, 1970; Visser, 1964; Wetzel and Manny, 1972). Since the diphasic pattern seems to be particularly well developed in emergent and floating macrophytes (Boyd, 1970, 1971; Howard-Williams and Howard-Williams, 1978; Howard-Williams and Junk, 1976; Mason and Bryant, 1975) it is probably partly related to the greater development of supporting and conducting tissue in these species (Howard-Williams and Junk, 1977; Polisini and Boyd, 1972). *C. dactylon* falls into this category, having wiry erect shoots bearing rather softer leaves. After a period of inundation, when the water recedes, all that remains of the above-ground standing crop are the erect shoots, devoid of leaves and shoot tips. The rapid loss of the softer components (principally the leaves), followed by the slower decay of the stems, would result in a diphasic pattern despite leaching. In such a situation decay may even be expected to have three phases during inundation : leaching, loss from easily decayed components and loss from resistant components (Godshalk and Wetzel, 1978b and d).

Howard-Williams and Davies (1979) have compared the decomposition rates of different species on the basis of the time taken for the initial mass to be reduced to 50% ($T_{\frac{1}{2}}$). They showed that the decay of *P. pectinatus* was very rapid ($T_{\frac{1}{2}}$ = 35 days) when compared with emergent species where it varied between 90 days for *Juncus effusus* L. and 361 - 426 days for *P. australis*. *C. dactylon*, despite being equated with the emergent macrophytes in its diphasic pattern of decomposition, had a very rapid initial decay rate, losing 50% of its mass in 18 days (dried) and 28 days (fresh). Since decay is a biologically mediated process, it is expected to proceed more rapidly under warm aerobic conditions (Flanagan and Bunnell, 1976; Godshalk and Wetzel, 1978a, c and d; Howard-Williams and Davies, 1978; Saunders, 1976). On the Pongolo floodplain submersion occurs in summer when the water is aerobic, owing to the shallow nature of the lakes (Breen *et al.*, 1978), and temperatures are high (Table 9.2).

The pattern of decay has important implications in the interpretations of $T_{\frac{1}{2}}$. In species such as *P. pectinatus* in which the above-sediment standing crop decomposes each year (Howard-Williams and Davies, 1979) and in *P. crispus* which is an annual, losing the total standing crop each year (Rogers and Breen, 1980), $T_{\frac{1}{2}}$ refers to the loss of 50% of the total material which is synonymous with the decomposable material. In *C. dactylon* and probably in some emergent macrophytes, however, only a portion of the above-ground standing crop decomposes each year. The remainder sprouts during exposure. In this situation the decomposable fraction does not equal the total standing crop and thus if $T_{\frac{1}{2}}$ were defined in terms of the potentially decomposable fraction only, the rate would be higher. We were not able to express our data in this form due to the termination of the decomposition experiment after 30 days. However, from the difference between above-ground standing crop before and after inundation it may be estimated that only 76% decomposes under natural conditions. If $T_{\frac{1}{2}}$ is calculated on this basis, i.e. assuming that 76% of the material in the bags was decomposable, then it is reduced to 20 days and 14 days for fresh and dried material respectively.

Three explanations have been advanced to account for the increases in the concentration of nutrients such as nitrogen and phosphorus observed during the later stages of decay : an increase in the proportion of micro-organisms colonising the decomposing material (Odum and de la Cruz, 1967; de la Cruz, 1975), the complexing of proteins with finely divided detritus

(Saunders, 1976; Suberkropp *et al.*, 1976; Howard-Williams and Davies, 1979) and differential decomposition rates (Minderman, 1968; Godshalk and Wetzel, 1978c). We were not able to continue our decomposition experiment for a sufficiently long period to note whether an increase in nitrogen or phosphorus might occur. However, from the data showing changes in the composition of the *C. dactylon* remaining in the lake after submersion, it is evident that nitrogen, phosphorus, potassium and magnesium increased after the initial decline to concentrations above those at submersion. Since under these conditions the finely divided litter was being lost continually and the ash-free component remained fairly constant, an increasing development of the epiphyton offers the most plausible explanation.

## 9.3 Implications for the Floodplain

The importance of aquatic macrophytes in nutrient cycling and detritus formation in aquatic systems is well established (Melchiorri-Santolini and Hopton, 1972; Wetzel, 1975). The significance of the *C. dactylon* meadows to the floodplain lakes of the Pongolo river may be gauged from the relationship between the standing crop which is inundated and the rate of decomposition. As the water levels recede, the area *C. dactylon* increases and with it the standing crop (Table 9.3). On submersion, therefore, the potential input to the aquatic system depends on the period and extent of exposure, and on the duration of the following period of submersion. During 1976 the exposure period was 161 days and the total area around Namanini lake which became exposed was 89.5 ha. Only 22.3 ha was covered with *C. dactylon* and the total above-ground standing crop was 14 363 kg. Half of the total mass (7182 kg) containing 73 kg of nitrogen and 12 kg of phosphorus would be lost during the first 30 days of submersion (Table 9.4). Assuming the water content of the lake to be 1.2 x $10^6$ $m^3$ at high flood level (Breen *et al.*, 1978) the amount released would be sufficient to raise the concentration of nitrogen and phosphorus in the water by 61 and 10 $\mu g\ l^{-1}$ respectively. These levels are significant when compared with the range of concentrations recorded in the lake (Table 9.2). During the total period of submergence, however, the input is considerably larger since the standing crop of the grazeable fraction decreases from 14 363 to 4316 kg (Chapter 6).

Input into the aquatic system also derives from the ungrazeable fraction. Although it was not possible to estimate its rate of disappearance during inundation, total input may be approximated by the difference between standing crop before (*c*. 160 000 kg) and after inundation (71 000 kg). These data indicate that losses from the ungrazeable were approximately ten times those from the grazeable fraction. However, until more is known of the pattern of loss and the utilisation of the ungrazeable fraction during submergence, its significance as a source of energy and nutrients for the aquatic system cannot be precisely established.

## 9.4 Conclusions and Future Research Priorities

Large amounts of material and nutrients are released when *C. dactylon* meadows are inundated. Indications are that extended periods of flooding will result in nutrients and organic matter being flushed from the system. Thus the extended periods of high floods, such as occurred during the construction of the Pongolapoort Dam, could have an adverse effect on the functioning of the system. From the data in Table 9.4 it is evident that, with the exception of a short lag during the first 25 days of exposure, the amounts of N, P and total biomass that can be released into the water increases with increasing period of exposure. Thus the interval between consecutive periods of inundation should exceed 25 days. The optimum interval may be determined only after a consideration of the contribution of *C. dactylon* to the terrestrial grazers during the period of exposure (Chapter 7) and contribution to the aquatic phase by other inundated communities.

Thus the effects of different flood regimes on the flushing from, or retention within the floodplain system of organic material and nutrients especially from the ungrazeable fraction, as well as the effects of extended periods of inundation on the vigour of *C. dactylon* needs to be investigated in more detail so that management options can be formulated. In addition, the contribution of organic material and nutrients to the aquatic phase by communities other than *C. dactylon* also requires investigation.

# CHAPTER 10

## GENERAL DISCUSSION AND CONCLUSIONS

### 10.1 Introduction

The objective of the multidisciplinary research programme on the Pongolo river floodplain was to formulate guidelines for floodplain management. This can be achieved only if the interrelationships between the biotic and abiotic components are understood. As this study reports on the vegetation of the seasonally inundated areas in general and the *C. dactylon* Community in particular, their role in the functioning of the Pongolo floodplain system is emphasised in this discussion. An attempt is also made to illustrate the extent to which the dynamics of the producers influence the consumers.

### 10.2 Conceptual Model (Fig. 10.1)

The feature which dominated the functioning of the system under natural conditions (i.e. conditions prevailing prior to the construction of the Pongolapoort Dam) was the seasonal fluctuation in water level, involving a number of floods during summer, and water draining and evaporating from the system during the dry winter period. The fluctuating water level had both direct and indirect effects on the primary producers of the system, as well as organisms of higher trophic levels and they can be depicted in a conceptual model (Fig. 10.1). From the model it is evident that they differ greatly between summer and winter, and it is appropriate to discuss the conceptual model in two sections, winter conditions and summer conditions.

#### 10.2.1 Winter conditions

The occurrence of floods and local rainfall decreased rapidly after February (Fig. 10.1). Water drained from the floodplain back into the river and water level decreased from HFL to MRL. The remains of *C. dactylon* become exposed as floodwater subsided. Under the wet conditions prevailing immediately after exposure, growth of *C. dactylon* was rapid and crop growth rate high, providing a palatable source of grazing for domestic stock. As the dry season progressed and the exposure period increased, conditions on the exposed area became drier, the crop growth rate of *C. dactylon* on the areas exposed for the longest period decreased, and the grass became less palatable. Despite this, the amount of grazing increased progressively as new wet areas became exposed by the receding water. Thus grazers followed the highly productive, palatable grass zone, tending to utilize the higher-lying areas less frequently.

During the total exposure period *C. dactylon* contributed *c.* 914 kg $ha^{-1}$ dry mass, *c.* 17 kg $ha^{-1}$ nitrogen and *c.* 2 kg $ha^{-1}$ phosphorus to the terrestrial grazers from the area surrounding Namanini lake. Most of this must be regarded as an export from the system (Fig. 10.1), as the grazers spend most of their time off the floodplain, although some would return as faecal detritus. This has considerable significance because it represents a net loss of nutrients from the floodplain which has to be replenished if productivity is to be maintained. The annual floods have largely balanced this loss in the past by depositing a fresh layer of silt, but the impounding of the river will deprive the floodplain of this source of nutrients.

Approximately half (47%; 825 kg $ha^{-1}$) of the *C. dactylon* produced during the exposure period was not grazed, but because it was out of the water it contributed little, if anything, to the aquatic phase at this time. The floodplain lakes, having little or no inflow during winter, must therefore be almost entirely dependent on autochthonous production for ecosystem functioning (Fig. 10.1) during this period. The decrease in windrun favours clearing of the water column by sediment deposition, and the cooling associated with the advent of winter promotes the germination of *P. crispus* turions (Rogers and Breen, 1980). Thus as winter progresses dense growths of *P. crispus* appear which, together with their epiphyton, provide a major energy source for the primary consumers (Fig. 10.1). The consumers include fish and invertebrates, and at the time of peak standing crop, large numbers of white-faced duck. Feeding by consumers increases the rate of nutrient cycling and contributes to the detritus pool (Heeg and Breen, in press). The detritus input is extremely important in floodplain functioning because it serves as a food source for fish (Kok, 1978) and invertebrate fauna (Walley, 1980; Heeg and Breen, in press), both of which are utilized by higher trophic levels. After *P. crispus* has attained its peak standing crop it enters a senescent phase, during which it continues to serve as a major energy source to primary consumers, particularly bacteria and snails (Rogers and Breen, 1980). As senescence proceeds, decomposition and grazing take place, releasing nutrients into the water and increasing the detritus pool (Fig. 10.1). The input of *P. crispus* to the water (using values obtained at the time of peak standing crop, Rogers and Breen, 1980) during the period September to December has been estimated as *c.* 420 kg $ha^{-1}$ dry mass, 10 kg $ha^{-1}$ nitrogen and 2 kg $ha^{-1}$ phosphorus. In addition, the epiphyton may add nitrogen by fixation (e.g. in the case of Tete lake up to *c.* 1 tonne $yr^{-1}$ was added by fixation, Rogers, F.E.J., 1981).

A part of the *P. crispus* production is exported from the system after transfer to waterfowl. Rogers, K.H. (1980) has estimated that *c.* 31 kg $ha^{-1}$ of *P. crispus* was consumed by waterfowl at Tete lake, but since some of this, particularly nutrients, returns in the faeces, losses from the system in this way are considered small. Phytoplankton production has been shown to be very low throughout the year and consequently the submerged hydrophytes are regarded as being the major sources of energy and nutrients during winter (Fig. 10.1). Rogers and Breen (1980) have demonstrated that the standing stock of nutrients in *P. crispus* greatly exceeds that in the lake water during the time of isolation from the river. Sediments must therefore be the major source of nutrients for their growth, and Everson (1980) has shown that the major site of phosphorus uptake is the roots. Since a part of *P. crispus* is exported each year by waterfowl, and some is flushed out as detritus during floods, it is clear that this loss must be made up if productivity is to be maintained. As with the *C. dactylon* it was probably replenished each year with a new deposit of silt. As the silt will in future be trapped in the dam, this source will no longer be available to the lakes. A decreased nutrient input will bring about a reduction in production of rooted plants, which in turn will result in a decrease in production of the floodplain system as a whole. This detrimental effect could be reduced if the *C. dactylon* meadows were artificially fertilized and irrigated. A discussion of this proposal is included under section 10.3.

### 10.2.2 Summer conditions

The first summer floods reached the floodplain during November (Chapter 4). Nutrients being released by the decomposition of remaining *P. crispus* and detritus are flushed from the system. The vegetation between MRL and HFL becomes inundated, making it available to aquatic grazers and decomposer organisms, thereby bringing about transfer of energy and nutrients to the aquatic phase of the floodplain system (Fig. 10.1). Of the six communities growing on the seasonally inundated area (Chapter 5), the two occupying the higher-lying areas of the floodplain (i.e. *Ficus sycomorus* - *Rauvolfia caffra* and *Acacia xanthophloea* - *Dyschoriste depressa* Communities) probably contribute little to the aquatic phase. This is because they are flooded for relatively short periods and comprise plants that do not readily decompose. The main input from these communities is therefore from litter (fruits, leaves, twigs, etc.). The *Phragmites* Communities, although occupying low-lying areas on the floodplain and therefore inundated for relatively long periods, do not rapidly decompose. They thus also contribute little to the aquatic phase during floods. Some plants in the *Cyperus fastigiatus* - *Echinochloa pyramidalis* Community do decompose readily, while others (e.g. *Echinochloa pyramidalis*) assume a 'wet season' form and continue growing under flooded conditions. The input from this community due to release following decomposition might be significant but it was not assessed in the present study. The *Cynodon dactylon* Community is fairly extensive and undergoes a marked reduction in standing crop during summer inundation (Fig. 10.1). It is thus one of the major sources of energy and nutrients during the flooding phase. In the present study *c*. 4310 kg $ha^{-1}$ of *C. dactylon* material (grazeable and ungrazeable fraction ) containing *c*. 46 kg $ha^{-1}$ nitrogen and *c*. 6 kg $ha^{-1}$ phosphorus was transferred to the aquatic phase, by both decomposition and grazing by aquatic organisms.

Decomposition of *C. dactylon* material is rapid, half being lost during the first 20 days of inundation. Under natural conditions the 'average' flood had a duration of 5.8 days (Pitman and Weiss, 1979). During a 6 day inundation period approximately 25% of the material and 20% of the nitrogen and phosphorus would be transferred to the aquatic phase. An inundation period of < 6 days would therefore be too short to allow the transfer of all the decomposable *C. dactylon* material. Initially (October - December) the interval between floods was long (Fig. 4.7), allowing water to drain from the floodplain before the onset of the next flood. These intervals between floods, together with favourable soil moisture conditions, high summer temperatures and recent silt deposition, favour regrowth of *C. dactylon*, such that when the next flood occurred there would be an increased amount of *C. dactylon* available for incorporation into the aquatic phase. Thus under natural conditions *C. dactylon* goes through a series of cycles as summer flood pulses occur, of decomposition/grazing during inundation and regrowth/grazing during exposure. This situation did not persist for the entire summer because from about mid-December the frequency and intensity of floods increased (Fig. 4.7; Fig. 10.1). Consequently the *C. dactylon* areas were inundated for *c*. 120 days (Fig. 4.7; Table 4.3), due mainly to the decreased intervals between floods, which did not allow the floodplain to drain and therefore maintained high water levels (Fig. 10.1). The significance of the initial summer cycles of inundation and exposure in determining the total input of *C. dactylon*, has not been assessed because the impounding of the Pongolo river created unnatural conditions, such that during this study only one flood occurred in a year. It seems probable, however, that the natural flooding regime would have resulted in greater input from *C. dactylon* than that estimated in this study. Thus the assessment of significance of the *C. dactylon* given here is conservative. However, despite this conservative estimate, *C. dactylon* is shown to be extremely important in the floodplain system, as it contributed ten times more dry mass and between three and five times more phosphorus and nitrogen to the aquatic phase than did *P. crispus*. In addition, approximately thirty times more *C. dactylon* than *P. crispus* was removed by grazers which used the system intermittently.

*C. dactylon*, and to a lesser extent *P. crispus*, play important roles in the functioning of the Pongolo floodplain system, the growth and production of both these plants being determined by the annual hydrological cycle (Fig. 10.1). The construction of an impoundment on the Pongolo river above the floodplain has affected the hydrological regime of the floodplain (Fig. 4.7). The effect of the dam has been to prolong the period of inundation due to attenuation of floods, so that although there may be some fluctuation in flow, summer conditions on the floodplain have been characterised by extended periods of high water levels (Fig. 4.7). Once irrigation gets under way frequency and duration of floods is expected to decrease. The presence of the dam will also alter the rate of flood development and subsidence. Under natural conditions the time from the onset of flooding to peak flood is approximately $^4/_{10}$ of the time required for water level to decrease from peak floodlevel, to pre-flood level (Pitman and Weiss, 1979). The rate of change in river flow is far more rapid than under natural conditions and it can be expected that the rate of exposure of the floodplain will be more rapid than occurred under natural conditions. This will reduce *C. dactylon* production, which is at a maximum immediately following floods, because water stress will develop earlier than occurred under natural conditions. The amount available to grazers and the input to the aquatic phase will thus also be reduced.

Maintenance of floodplain productivity is therefore contingent upon sound management, and proposals are set out below.

## 10.3 Management Proposals

### 10.3.1 Water release programme for the Pongolapoort Dam (Fig. 10.2)

In order to maintain the floodplain as a functional unit, plant communities of the seasonally flooded areas will have to be periodically inundated. To achieve this, the water level on the floodplain will have to be raised to HFL, if only for brief periods. An increase in water level to MRL will not be satisfactory, as an important community such as *C. dactylon* which occupies an intermediate position would not be inundated. This would deprive the aquatic system of an energy and nutrient input during summer (following inundation) and subject this community to continual grazing pressure and increased moisture stress.

The water release programme set out below was formulated taking four main considerations into account; the response of the vegetation, particularly the *C. dactylon* Community, to the annual exposure-inundation cycle; the hydrological regime prevailing on the floodplain during the present study; the flooding regime under natural conditions; and the fact that most of the water stored in the Pongolapoort Dam will be required for irrigation purposes. The proposed flooding programme would require summer flooding with low water levels during winter (Fig. 10.2). The first summer flood should occur during the first half of November. A flow of 56 $m^3$ $s^{-1}$ for a period of six days would ensure that seven of the major floodplain lakes received floodwater (Table 4.4), and most of the *C. dactylon* areas would be inundated. Water level should then be decreased to the pre-flood level for a period of 21-28 days. This would allow for some regrowth of *C. dactylon* thereby increasing the energy and nutrient input to the aquatic system during the following flood. This second flood should be larger than the first (i.e. up to 85 $m^3$ $s^{-1}$) and take place over a five day period during mid-December. A flood of this magnitude would result in sixteen floodplain lakes receiving floodwater (Table 4.4) and all major *C. dactylon* areas being inundated. A 21-28 day period of low flow (*c*. 7 $m^3$ $s^{-1}$ or less) following this flood would again allow regrowth of *C. dactylon* thereby further increasing potential input to the aquatic system. After this low flow period, an extended flood of *c*. 42 days with flow levels fluctuating between 28 $m^3$ $s^{-1}$ and 56 $m^3$ $s^{-1}$ (average 42 $m^3$ $s^{-1}$) is proposed before flow is reduced to 28 $m^3$ $s^{-1}$ during the first 14 days of March, prior to a reduction to 7 $m^3$ $s^{-1}$ or less for the duration of the winter period. The gradual decrease from *c*. 56 $m^3$ $s^{-1}$ to < 7 $m^3$ $s^{-1}$

is designed to allow gradual drainage and exposure of *C. dactylon* areas, thus ensuring a continual supply of lush grazing for cattle. This flood programme would require 242 x $10^6$ $m^3$ of water which is 23% of the mean annual runoff of the Pongolapoort Dam catchment area (or 10% of the full supply capacity of the dam). Winter river flow could be maintained at $< 7$ $m^3$ $s^{-1}$ or discontinued if runoff from agricultural lands maintains a flow in the river. This flood programme is designed to maintain the functioning of the floodplain system by maximising the *C. dactylon* input to the aquatic phase during summer, while allowing it to be utilized by terrestrial grazers during winter.

The proposed exposure period of *c*. 230 days during winter is longer than the exposure period during the present study (161 days). However, during the present study, although growth of *C. dactylon* decreased slightly between 98 and 161 days after exposure, standing crop was still increasing after 161 days. Thus the 161 day period did not have a serious detrimental effect on *C. dactylon* input to the aquatic system. Although the proposed flood programme extends the exposure period by 70 days, this will occur during September and October when rainfall is much higher than during the May to August period (Table 4.1; Musil *et al*., 1973). This additional rainfall should be sufficient to maintain *C. dactylon* areas. Should a decrease in standing crop occur during this period, input to the aquatic system is unlikely to be markedly reduced, as the flood pulses proposed during the first half of summer are designed to increase energy and nutrient input ot the aquatic system. These floods will therefore serve a dual purpose as they will also stimulate fish breeding and migration.

As the water requirements for irrigation purposes are not known at this stage, it is not possible to establish if 10% of the full supply of the dam will be available for the floodplain. However, as irrigation from the Pongolapoort Dam will not commence for a number of years, the opportunity exists to determine if the above flood programme, particularly the 230 day low flow period during winter, has any detrimental effects on floodplain vegetation. In addition, since the long-term irrigation requirements are certain to result in a conflict in demand for the water, it is important to formulate alternative proposals which demand less of the water under the command of the Pongolapoort Dam. These proposals consist of a series of flood programmes which require decreasing amounts of water from the Pongolapoort Dam. By testing these programmes in a sequence of decreasing water requirements, the minimum water requirement which will maintain functioning of the floodplain can be established. This series of flood programmes should be preceeded by a flood season similar to what would be expected under natural conditions, so as to stabilise conditions on the floodplain. This preliminary flood season should extend from November to April (Fig. 4.6). Individual floods should be of short duration (*c*. 6 days), and during November, March and April flow rate during flooding should be between 56 $m^3$ $s^{-1}$ and 85 $m^3$ $s^{-1}$, increasing to between 100 $m^3$ $s^{-1}$ and 120 $m^3$ $s^{-1}$ during December and January. A peak flooding period, with flow rates up to 200 $m^3$ $s^{-1}$, should occur during February. During the dry season (May to October) flow rate should not exceed 21 $m^3$ $s^{-1}$.

Following this stabilisation period a series of flood programmes with decreasing water requirements should be implemented. The first (Proposal A; Fig. 10.2b) could consist of a single five day flood (i.e. 56 $m^3$ $s^{-1}$ for 3 days followed by 85 $m^3$ $s^{-1}$ for 2 days) during the November-December period, and a longer flood period during the second half of summer at a lower flow rate (*c*. 30 $m^3$ $s^{-1}$ for 60 days). This programme will require a total of *c*. 185 x $10^6$ $m^3$ of water, which is 18% of the mean annual runoff of the Pongolapoort Dam catchment area (or 7.5% of the full supply capacity of the dam). A second alternative proposal consists of five floods, each of five days duration (56 $m^3$ $s^{-1}$ for 3 days and 85 $m^3$ $s^{-1}$ for 2 days), at approximately monthly intervals between November and March. This programme (Proposal B; Fig. 10.2b) would require 146 x $10^6$ $m^3$ of water, which is 14% of the mean annual runoff of the Pongolapoort Dam catchment area (or 5.8% of the full supply capacity of the dam). This programme (Proposal B) could be modified, so as to further decrease the amount of water required, by reducing the floods during November, January and March to a maximum of 56 $m^3$ $s^{-1}$ for a 3 day period. This will require *c*. 100 x $10^6$ $m^3$ of water, i.e. 10% of the mean annual runoff of the Pongolapoort Dam catchment area or 4% of the full supply capacity of the dam.

It is possible that either the minimum water requirement of the floodplain will exceed the amount available, or that the amount of water required for irrigation purposes is so great, that even 4% - 5% of the full supply capacity of the dam will not be available for floodplain inundation. If this is the case alternative methods with which to maintain the floodplain will have to be considered. Heeg *et al.*, (1980) have suggested the use of inflatable weirs strategically placed in the main river channel. The placing of these weirs in the inlet and outlet channels of floodplain lakes may be more advantageous as this will enable water to be retained within the lake, until energy and nutrients from inundated floodplain vegetation have been incorporated into organisms of higher trophic levels. Before these proposals can be implemented, the rate of assimilation of the primary production of the floodplain into organisms of higher trophic levels will have to be determined. A hydraulic model will also have to be constructed to establish accurately the relationship between river flow and floodlevels. In addition to the use of weirs, irrigation and fertilization of *C. dactylon* meadows could also be considered. However, the effects of nutrient addition to the aquatic phase of the system (i.e. the overabundant development of algae and aquatic macrophytes eventually leading to the development of an anaerobic water column) will have to be examined before fertilization is implemented.

## 10.4 Conclusions

*Cynodon dactylon* and other primary producers are important in the functioning of the Pongolo river floodplain. Their importance is related to annual fluctuations in river flow. At this stage the minimum water requirement for maintaining floodplain functioning is not known. However, as water from the Pongolapoort Dam will not be required for irrigation purposes for a number of years, a period is available during which the minimum water requirements can be determined.

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