The effects of clipping and burning on the allocation of total nonstructural carbohydrates and selected mineral nutrients in *Imperata cylindrica* (L.) Raeuschel

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DECLARATION

"I declare that THE EFFECTS OF CLIPPING AND BURNING ON THE ALLOCATION OF TOTAL NONSTRUCTURAL CARBOHYDRATES AND SELECTED MINERAL NUTRIENTS IN *IMPERATA CYLINDRICA* (L.) RAEUSCHEL **is my own work and that all the sources I have used or quoted have been indicated and acknowledged by means of complete references."**

signed ______________________

F MITCHELL

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ABSTRACT

The rhizomatous grass, *Imperata cylindrica*, occurs in the Cape Flats Nature Reserve (CFNR), South Africa. It is recognised globally as a weed of crop plants. The response of this weed to defoliation, in the forms of clipping and burning, was studied in terms of its total nonstructural carbohydrates and mineral nutrition. This study will serve as a starting point for later studies aiming to control this weed. It was confirmed that the underground stems or rhizomes serve as the major storage tissue for total nonstructural carbohydrates and mineral nutrients. These rhizomes also make up the largest part of its biomass and hence defoliation was found not to significantly decrease stem total nonstructural carbohydrates or mineral nutrients. The burn treatment induced faster replacement of above ground material than the other defoliation treatments. The burn and basal clipping treatments induced higher leaf nitrogen and phosphorus levels following defoliation. These two treatments also led to significantly higher number of tillers after defoliation and were also the only treatments which induced flowering. The one-off defoliation which was applied at the start of this study, was found to be ineffective in taxing *I. cylindrica*'s resources to the point where it would be vulnerable to eradication. It is hence recommended that future studies on the grass should entail multiple defoliations in order to develop a defoliation regime which will exterminate the grass.

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1 Chapter 1 GENERAL INTRODUCTION

1.1. The grass plant - its morphology and physiology

The graminoid life form is selected for by conditions of frequent destruction of above ground parts as by fire or grazing (Bryant, Chapin & Clan 1983). Hence, it is easy to understand why grasses hold such a pre-eminent position as forage plants (Langer 1979). How do grasses manage to tolerate frequent defoliation? The answer can be found by studying the effects of defoliation on grass morphology and grass physiology.

1.1.1. The effect of clipping on biomass

The morphology of the grass plant provides the basis for its physiological response to disturbances such as defoliation. The vegetative grass plant consists of a number of above ground shoots, known as tillers, which are arranged into anatomically attached groups forming the whole plant or metapopulation (Fig. 1.1) (Langer 1979; Briske 1986). These metapopulations are produced by the continuous iteration of relatively short-lived tillers from the axillary buds associated with phytomers near the soil surface (Briske 1986). Each tiller consists of a number of foliar organs or phytomers (Langer 1979; Briske 1986). Each phytomer consists of a blade, a leaf sheath, and an axillary bud, a node, and an internode.

The axillary buds are found on the grass stem which is very short because the internodes separating the nodes are highly contracted. The stem cannot normally be seen from the outside, and what normally appears to be a stem, is actually laminae which are tightly folded together, giving the appearance of a stem. The stem can be exposed by removal of the outside laminae and leaf sheaths of the tiller. The older leaves of the grass plant are on the outside and new leaves originate from the inside of this composite structure. When all the leaves have been removed, one finds in the centre an apical dome, an intensely meristematic region, capable of producing leaf primordia along two opposite flanks in alternating order (Langer 1979) (Fig. 1.2). In the axil of each leaf, situated at each node, there is an axillary bud which under suitable conditions, may grow out to become a new tiller (Langer 1979). The very short stem provides the meristematic regions (axillary buds) with a measure of protection from defoliation, and provided conditions are favourable, the buds will produce new tillers following defoliation (Langer 1979) .

The arrangement of the tillers to form the grass plant or metapopulation, also affords it with resistance to defoliation. This structural organization also facilitates the allocation of resources within the metapopulation. Photoassimilate is imported by young leaves from older leaves after defoliation (Briske 1986). After the young leaves have reached half leaf expansion, they are able to produce their own photoassimilate. Later they also start to export photoassimilate to other sinks in the plant. Marshall & Sagar (1968) found that *Lolium multiflorum* has anatomically connected tillers that aid the resource allocation within the metapopulation. They found that juvenile tillers import resources from established parent tillers for a period of time, until their leaf areas have increased sufficiently. These tillers, although self-sufficient in terms of photoassimilates, may still be dependent on the parent tillers for water and minerals (Anderson-Taylor & Marshall 1983). After defoliation, independent tillers may once again import photoassimilate following a reduction in the carbon gain capacity of the tillers. The degree of import diminishes within several days as photosynthetic tissues are rapidly replaced (Briske 1986).

1.1.2. The effect of defoliation by fire on biomass

Just as grasses are able to resist grazing, so too are they able to withstand and survive fire. d'Antonio & Vitousek (1992) stated that there are four factors which make grasses relatively flammable and able to recover rapidly following fire. Firstly, the grass life form supports standing dead material that burns readily. Secondly, grass tissues have large surface/volume ratios and can dry out quickly, meaning they will ignite and burn under a wider range of conditions than woody tissues. Even though the grass life form has dead material as fuel and ignites fairly easily, the amount of fuel compared to a woodland fire is much less, and less heat is produced (Daubenmire 1968), so heat damage is not so extreme as it might otherwise be. Thirdly, grasses recover rapidly following fire because there is little above-ground structural tissue, and almost all new tissue fixes carbon and contributes to growth. Fourthly, grass canopies support a microclimate in which surface temperatures are higher, vapour pressure deficits are larger, and the drying of tissues more rapid than in woodlands or forests. From the above, one can conclude that conditions favouring fire are more frequent in grasslands and that fire is an integral part of grasslands (Mutch 1970; McNaughton 1986; d'Antonio & Vitousek 1992).

As such, it is not surprising that fire has been used by man since early times to maintain grasslands by retarding reversion to bush (Joubert 1977; Hayes & Seastedt 1989). Fire was used mainly to increase forage cover, but also for protection against wild animals and for hunting (Joubert 1977). However, burning of vegetation is not always good as pointed out by Marloth (1924). He distinguished between the northern and eastern parts, and the southwestern parts of South Africa, in terms of fire. His discussion centred around the damaging effects of fire on the flora of the south-western part of the Cape Floristic Region (CFR). Marloth (1924) stated that fire impoverishes mountain flora by bringing about the extinction of species. Where 'maquis' of evergreen shrubs once covered the hills and the lower mountains of the south-west, they became occupied by fields of monocotyledonous plants with underground dormant organs. Fire also resulted in greatly increased water run-off in winter, and reduced the capacity of the mountain to capture and retain moisture (Marloth 1924).

Cowling, Holmes & Rebelo (1992) compared the western and eastern parts of the Cape Floristic Region (CFR) in terms of species richness. The rationale for the comparison was the increasing frequency of lightning strikes from west to east, the increasing summer rainfall and soil fertility from west to east. The east also has higher cover of fast-growing C_4-grasses due to the higher summer rainfall and increased soil fertility which encourages farmers to burn fynbos on a short rotation (3-4 years) (Cowling *et al.* 1992). This led to the assumption that in terms of alpha diversity the eastern part would be poorer. However, Cowling *et al.* (1992) could find no significant difference in total richness or shrub richness. This was ascribed to the ability of shrubs from the eastern part to resprout following fire. Marloth's fears about fire in the western CFR seem justified because Taylor (1972) stated that fynbos of the Cape Flats contains many species that prefer to regenerate from seed as opposed to resprouting. Fire in the drier, less fertile western parts could be deleterious. Because of the significantly lower number of lightning strikes per unit area in the west, one can assume that species growing there, will not respond as well as species in the east, which have been subjected to more fires over time. It would thus be expected that the species from the east should be adapted to deal with the more sporadic occurrence of fire.

Phenology also plays an important role in the response of species to a fire-prone system. Daubenmire (1968) found that fire going through a mixed planting of grass species, damaged those which had started growth early, whereas others escaped injury. This relationship between damage and phenology probably accounts for the widely observed phenomenon of fire damaging *Poa pratensis* in the midcontinental grasslands of North America, whereas associated species are stimulated. *Poa* is a genus of northern derivation that starts growth early, whereas the native dominants such as *Andropogon*, *Sophastrum*, and *Panicum*, are of southern extraction and remain dormant until the warm season is more advanced. In the Transvaal and Natal too, the later the date of burning after the start of the rainy season, which causes resumption of growth, the greater the damage to grasses (Daubenmire 1968).

1.1.3. The effect of clipping on total nonstructural carbohydrates (TNCs)

Resistance to grazing, or the ability for regrowth, is also dependent on the amount of intercalary and apical meristems remaining, following defoliation. Should sufficient meristems be available, carbohydrate reserves will be mobilized if the plant is not under moisture stress or any other stress (Busso, Richards & Chatterton 1990). Growth will be inhibited irrespective whether sufficient meristems or reserves are available, or not. Any stress limiting growth will override the presence of the meristems or reserves. However, Rusdy *et al.* (1995a) found that nitrogen fertilization did not significantly affect TNC content. Thus, some other factor must be limiting the use of reserves for regrowth.

Both photosynthates and total nonstructural carbohydrates are needed for regrowth following defoliation (Naidoo & Steinke 1979), when the remaining tissues cannot provide enough energy for respiration (growth demands) and the recovery of lost foliage (White 1973; Caldwell *et al.* 1981; Busso *et al.* 1990). When do the photosynthates take over from the stored carbohydrates in the recovery process? Previously, it was believed that total nonstructural carbohydrates played a greater role than photosynthates in the recovery from defoliation (Daer & Willard 1981). However, it has been found that the role stored carbohydrates play in regrowth, especially of grasses, decreases greatly once the plant has replaced some of its lost photosynthetic area (Richards & Caldwell 1985; Chapin, Shaver & Kedrowski 1986a).

1.1.4. The effect of fire on total nonstructural carbohydrates (TNCs)

There is no major difference between defoliation by clipping and defoliation by fire, as in both cases the aboveground material is removed. Examples include sites in South Africa (Natal and Transvaal), Venezuela, and New Zealand (Daubenmire 1968). Regrowth is initially dependent on TNCs which are quickly taken over by photosynthates, once new photosynthetic material is present. However, questions are raised on the quality of plant removal. With grazing not all plant material is removed, whereas in most instances with clipping and fire, all aboveground material is destroyed.

1.1.5. The effect of clipping and fire on nutrients

Upon defoliation, plants require active meristems and reserve carbohydrates in order to regrow. When moisture or nutrients are limiting, regrowth is inhibited, resulting in the below ground accumulation of carbohydrates in grasses. It is only when the moisture or nutrient stress have been removed that the accumulated reserves will be available for regrowth (White 1973; Bryant *et al.* 1983; Chapin, Vitousek & Van Cleve 1986b). The role of mineral nutrients in regrowth, following defoliation, can only be understood by looking at (i) how each mineral nutrient is cycled through a given biological system, (ii) what function the particular mineral nutrient performs, and (iii) how that function is affected by defoliation.

The nutrient cycle involves three components, namely, (i) an inorganic store in the soil, (ii) a biomass store which includes living organisms above and below the soil, and (iii) an organic store, on and in the soil, provided by residues and excreta of living organisms (White 1987) (Fig. 1.3). As stated above it is necessary to look at each mineral nutrient separately, because not only does each mineral nutrient perform a particular function, but it is also found in different concentrations within the components of the nutrient cycle, be it nitrogen or potassium.

plant, it is found that they vary with time. The concentrations are generally higher when the plant is young and then decline with time (Jarrell & Beverly 1981). This makes it very difficult to define the minimum concentration that is required to support maximum growth without reference to the stage of growth at which the observations are made; young plants will apparently require higher concentrations for maximum growth than older plants (Leigh & Storey 1991).

It is known that mineral nutrients are not allocated synchronously (Abrahamson & Caswell 1982; Benner & Bazzaz 1988). The concentrations also vary greatly between plant tissues and at different growth stages (Abrahams & Caswell 1982). Immobile nutrients (for example, calcium, magnesium, sodium) increase until the end of the growing season, unless there are large leaching losses. For mobile nutrients (for example, nitrogen, phosphorus and potassium) that are translocated to storage organs or reproductive parts, the timing of a maximum nutrient pool depends predictably upon the type of plant. For elements of intermediate mobility (for example, magnesium) the seasonal pattern of nutrient pool size is less predictable (Epstein 1972; Loneragan, Snowball & Rodson 1976; Abrahamson & Caswell 1982; Chapin & Van Cleve 1989). For mobile nutrients in deciduous plants the nutrient pool generally plateaus during the middle of the growing season. In perennial deciduous plants, the aboveground pool of mobile nutrients actually declines in autumn, as these nutrients are translocated belowground to storage organs. In evergreen plants, mobile nutrients often continue to increase until shortly before the end of the growing season (Chapin & Van Cleve 1989).

There are 17 elements which have been deemed essential for plant growth and development. These elements have been divided into macronutrients and micronutrients, depending on the quantity of a particular element that is required by a plant. The macronutrients are needed in concentrations exceeding 1 000 ppm and include nitrogen (N), calcium (Ca), magnesium (Mg), potassium (K), phosphorus (P) and sulphur (S). The micronutrients are needed in concentrations less than 100 ppm and include copper (Cu), iron (Fe), manganese (Mn), zinc (Zn), boron (B), molybdenum (Mo) and chlorine (Cl) (Marschner 1987; White 1987).

In general, nutrient cycling is enhanced by grazing, because nutrients are returned to the soil in a form which is immediately and directly available to plants. This has added benefits to plants, as shown by plants subjected to the grazing and defecation by geese. These plants had a longer growing season than control plants. The net effect is greater annual production in grazed or fertilized plants relative to controls (Cargill 1984). This effect is negated by the clipping of plants, as the clipped material would have to decompose before nutrients are returned to the soil. In this study, clipped material was removed following clipping, and hence mineral nutrients were lost from the cycle.

Several questions about the effects of fire remain, for example: (i) the reduction of humus both in and overlying the soil - along with associated changes in the C:N ratio; (ii) the tendency towards lowering the soil pH, which appears to be particularly marked in South African fynbos and forest soils; (iii) the viscitudes of water runoff or moisture infiltration, which depend on the density of plant cover or degree of exposure due to frequent burning, and ultimately, their influence on stream flow; and (iv) the effect of burning on soil temperature and its influence on plant physiology - for example, the fact that certain species cast seeds that germinate all the more readily once a fire has passed over them (Joubert 1977). Fire increases the rate at which nutrients are cycled through a biological system by volatilization of certain mineral nutrients and by making certain mineral nutrients more available to the plant and to runoff and leaching.

Plants growing in nutrient-poor soils, for example, those found in lowland fynbos sites (Low 1983), are said to be unable to procure sufficient resources to support rapid growth. The evolutionary response to resource limitation is an inherently slow growth rate (Bryant *et al.* 1983; Chapin *et al.* 1986b). Such plants grow slowly even when fertilizers are applied because they have low capacities to photosynthesize and absorb nutrients. The above plants are usually evergreens, which, although slow-growing in comparison to deciduous plants, have an advantage over the latter in nutrient-limited environments (Bryant *et al.* 1983). Although, the terms evergreen and deciduous are strictly applied to shrubs and trees, it seems that *Imperata cylindrica* could be responding as an evergreen plant, when growing in suboptimal conditions. When growing in tropical environments, *I. cylindrica* has a high growth rate (8-20 t/ha/yr) and it is also a strong competitor for water, light and nutrients (Kuusipalo *et al.* 1995). It should also be remembered that *I. cylindrica* is a highly plastic in terms of form (Holm *et al.* 1977a), and many ecotypes (due to high genetic variability) can be found, allowing the plant to grow in a wide range of conditions (Holm *et al.* 1977a; Patterson 1980; Brook 1989). The data of Chapin, Johnson & McKendrick (1980) seem to support the former scenario of slow growth rate; when looking at the seasonal course of nitrogen concentration in the current leaves of the graminoid, *Eriophorum vaginatum*, and the first year leaves of the evergreen shrub, *Ledum palustre*. The nitrogen concentration varied very little over the course of a year for each of the two species. This is in contrast to the deciduous species which had a seasonal pattern for nitrogen concentration (Chapin *et al.* 1980). However, in contrast to shrubs and trees, a grass, *E. vaginatum*, could respond with an increased productivity when fertilized with nitrogen (Wedin 1995) or when a fire releases mineral nutrients to the soil. On soils with low N availability, species which produce more dry matter per unit N incorporated (high N use efficiency), may outcompete those less efficient at using N (Chapin *et al.* 1980; Vitousek 1982). The Cape Flats Nature Reserve (CFNR) is not subjected to (large scale) herbivory by any ungulate or large herbivore. Thus, the aboveground material is a perennial feature changing only when old leaves are replaced by new leaves, or when sporadic fires occur.

I. cylindrica is known to have low forage value (Van Oudtshoorn 1992; Rusdy *et al.* 1995b). This seems to indicate that the protein content of the blades is low, indicating a high nitrogen use efficiency, a property it shares with evergreen plants (Wedin 1995). Returning to the high genetic variability of *I. cylindrica*, Patterson, Flint & Dickens (1980) tested whether temperature and photoperiod would cause new ecotypes to be produced from plants from four habitats in the United States. They found that individuals grown at 29/23°C were taller and produced more dry weight than those grown at 23/13°C, regardless of the plants' origin. The two photoperiods used, 16 hours and gear the primary and secondary products of their metabolism to growth of shoot and root systems (Pate 1983).

Grasslands have, on average, very low concentrations of available soil N and show large increases in productivity in response to N additions (Wedin 1995). Dominant grasses in these systems tend to have low tissue N concentrations (i.e., high C/N ratios) in both live and senesced tissues compared to grasses of shorter arid grasslands or managed grasslands. The low tissue N concentrations reflect the species' high N-use efficiency, the ratio of net productivity to N uptake. These dominant tall grasses also maintain large root systems, with over half of the annual net primary production allocated below ground, and tend to have a bunch or tussock growth form (Tilman & Wedin 1990).

Wedin & Tilman (1990) found that differences in photosynthetic pathway (C_3 vs C_4) explained much of the divergence in N cycling under the grass species they studied. In most native humid grasslands, the dominant species are C_4 grasses. Because C_4 species have reduced requirements for N-containing photosynthetic enzymes, they generally have lower leaf N concentrations than C_3 species (Field & Mooney 1986). Thus, the high N-use efficiency of these C_4 grasses is partly explained by their high photosynthetic N-use efficiency (rate of CO_2 uptake per unit leaf N). These grasses would have long-term ecological (and ultimately, evolutionary) advantage in nitrogen-poor sites (Barbour *et al.* 1987).

Clipping can entail two possibilities: (i) cutting of plants without removal of cut material, or (ii) cutting and removal of plant material. The former accelerates nutrient cycling through a biological system, whilst the latter results in a removal of nutrients from a particular biological system, only replenished through slow atmospheric precipitation. Stock & Lewis (1986a) found that atmospheric input of organic and inorganic nitrogen to the Pella Fynbos Biome Intensive Study site to be low (1.99 kg ha^{-1} y^{-1}) compared to higher rainfall heathland and upland peat ecosystems of the northern temperate latitudes (8.7-19.0 kg ha^{-1} y^{-1}). They calculated that atmospheric input alone would take 10-80 years to replace if initially all nitrogen was lost from the ecosystem through fire. Despite this, the atmospheric input of nitrogen is important to the nitrogen economy of the Pella site (Stock & Lewis 1986a). DeBano & Conrad (1978) found that about 11% of the nitrogen in plants, litter, and upper 10 cm of soil from chaparral, was lost through burning. This loss is significant because a means of replenishment must be available otherwise the ecosystem would have been depleted considering the great loss of nitrogen through volatilization.

Wallace & Macko (1993), in a comparison of two grasses, found that clipping enhanced nutrient uptake by *Phleum pratense*, apparently due to compensatory uptake to replace what was lost in the removal of above ground tissue. The clipped individuals increased their nutrient uptake above that of unclipped individuals. In contrast, *Andropogon gerardi*, was not stimulated by clipping in the same manner (Wallace & Macko 1993).

What effect does fire have for the cycling of nitrogen? Some researchers reported significant loss of N from grass fires, others reported no iincreases or reduction in soil nitrogen, while yet others found that the soil nitrogen was increased (Daubenmire 1968; DeBano *et al.* 1979; Raison 1979; Cass, Savage & Wallis 1984; Stock & Lewis 1986b). Why these divergent findings? When plant tissue burns, most of the nitrogen and sulphur are volatilized. Even if some nitrogen remains in the ash following a fire, it can easily be removed by wind or water from the soil surface. This results in an immediate loss of nitrogen from the system, which is only replaced by rain over a prolong period of time (Daubenmire 1968; Raison 1979; Groves 1983; Cass *et al.* 1984). Studies where nutrient deficiencies have been caused by fire are reported by Daubenmire (1968). Examples where the nitrogen input by rainfall more or less equals the loss from a typical fire cycle are also quoted by Daubenmire (1968), namely, *Molinia* grassland in Britain, and in the Northern Territory of Australia.

It should be remembered that ecosystems do not respond similarly to the volatilization of nitrogen by fire. Replacement of nitrogen in the above systems is mainly ascribed to precipitation and microbial input (Daubenmire 1968; Stock & Lewis 1986a). Other factors influence precipitation and microbial activity which vary from area to area. The quality of the precipitation is often dependent on location, specifically whether the ecosystem is close to industrial areas, or not (Stock & Lewis 1986a). Microbial activity is often dependent on the quality of the soil, increasing with increasing soil organic matter. Thus, in the above systems, nitrogen is lost and relatively quickly replaced, whilst in other systems replacement is a slow process. It is this latter factor which gets the credit for the beneficial effect fire has on soil nitrogen. The heating of the soil improves bacterial decomposition which enhances the nitrification process (Daubenmire

1968; Neuenschwander & Wright 1984). The establishment or persistence of legumes following a fire can also lead to an improvement in soil nitrogen (Daubenmire 1968). Studies where fire increased the amount of nitrogen available have been cited by Daubenmire (1968) and DeBano *et al.* (1979). Although nitrogen is easily lost through volatilization, sufficient amounts could be left after the fire, to result in either a minimal response or the absence of a response of post-fire vegetation to nitrogen fertilizers.

Soil type also affects the availability of nutrients to plants. Wallace & Macko (1993) found that *Andropogon gerardii* had a 50 cm competitive radius (the size of the area from which each plant procured nutrients) for nitrogen, whilst *Phleum pratense* had a depletion radius of 20 cm. Both these species grew in well drained, clayey soils. In contrast, Tilman (1989) found that *Schizachyrium scoparium* growing in sandy soil had a competitive radius of 70 cm. The larger radius for the latter species is an indication of the lower nutrient availability of nitrogen in sandy soils compared to the smaller radii found for the other two species growing in clayey soils.

How does the plant maintain its productivity with the loss of nitrogen following fire? Seastedt (1985) showed that burning caused more inorganic nitrogen in bulk precipitation to reach the soil on burned sites than on unburned sites. The premise being that water is the medium through which mineral nutrients reach plant tissues; it being limited so would mineral nutrients (Schulze 1991). This was attributed to microbial immobilization on standing dead material and litter on unburned sites. Hayes & Seastedt (1989) stated that while fire may increase volatilization of nitrogen, other effects could enhance conservation mechanisms or increase the efficiency with which vegetation cycles nitrogen. They found that differences between burnt and unburnt prairie soils were insignificant in terms of soil water nitrate. Thus, although burning volatilizes above ground plant material, the soil water nitrogen is unaffected.

Mes (1958) found for *Hyparrhenia hirta*, *H. schimperi*, *Themeda triandra*, and *Eragrostis atherstonei* that when plants were cut or burnt, the new leaves had a higher water, nitrogen and generally a higher ash content than new leaves on undisturbed plants. Mes (1958) also found that the water content and the nitrogen content of the leaves of the burnt plants of *H. hirta*, *T. triandra* and *E. atherstonei* were much higher than in leaves of unburnt plants. Ash analyses, in general, showed a higher ash content in the leaves of the burnt plants. Reasons cited for these results were that the new growth in undisturbed plants is shaded by old dead leaves and is protected against wind and sun. One could expect the transpiration of the leaves to be lower and their water content to be higher than that of the exposed leaves in burnt plants. That shaded leaves may have a higher water content was found with cut plants protected by a loose covering of detached dead leaves. Even the ash content was increased in these shaded plants. The difference between artificially shaded and undisturbed plants is that in the latter the old dead leaves and stems are still attached to the plant. Moreover, the old stems, as has been mentioned, are not necessarily dead. It is possible that they still absorb water and nutrients and in so doing compete with new leaf growth (Mes 1958).

Even though these results seem to suggest that fire benefits plants, it is not always the case. Slash-and-burn agriculture initially enhances the nutrient regime but afterwards this is reduced drastically. Reasons for this reduction in fertility are (i) the destruction of soil ectomycorrhizae, (ii) the release of nutrients in a single large pulse, with their availability exceeding the exchange capacity of the soil, and (iii) the increased leaching of nutrients from the root zone because of (i) and (ii) (Barbour *et al.* 1987). Slash-and-burn agriculture is used extensively in Third World countries by subsistence farmers. Cash crops are planted in cleared forests, and although yields are good after the first harvest, they diminish thereafter, prompting the farmer to delve deeper into the forest for more land. The effect of fire in these forests, as compared to grasslands, differs in that the magnitude by which the pulse release of nutrients exceeds the exchange capacity of the soil, is not as large in grasslands (Daubenmire 1968; Raison 1979). The amount of nutrients stored in the soil of a tropical forest, more or less equals the amount of nutrients found in the plant biomass, whereas for grassland the amount of nutrients in the plant biomass is considerably less than what is found in the soil (Daubenmire 1968; Cass *et al.* 1984; White 1987). Fires in forests are also much hotter than fire in grasslands, which also leads to increased volatilization of nitrogen (Daubenmire 1968; DeBano *et al.* 1979).

All other nutrients are changed to simple salts that are water soluble and hence immediately available to the plant (Daubenmire 1968; Raison 1979). Burning increases the soil pH because an excess of basic cations (potassium, calcium and magnesium) is released in the ash. These elements occur in the ash as oxides which may be converted to carbonates which are acid soluble only (Cass *et al.* 1984).

Where does the nitrogen come from when the plant is recovering from defoliation? Chapin *et al.* (1980) stated that the spring decrease in nitrogen concentration of below-ground stems and roots of deciduous shrubs, also suggested that much of the nitrogen in the leaves was moved from below ground. When nitrogen is unavailable due to frozen soil or due to low soil availability, then the nitrogen contributing towards new growth can be ascribed to below-ground plant reserves.

1.1.5.2. Phosphorus (P)

Phosphorus is a constituent of nucleic acids and lipids, and it also plays a role in co-enzyme regulation (Lawlor 1991) which affects the growth and metabolism of plants (cell division and expansion, respiration, and photosynthesis) (Marschner 1987). It also aids the uptake of potassium and counteracts the effects of excess nitrogen (Day & Ludeke 1993). Phosphorus is the most likely nutrient, after nitrogen, to limit plant growth (Stock & Allsopp 1992; Day & Ludeke 1993). Plants growing optimally, usually have 0.3 to 0.5 % of their dry weight as phosphorus. Lower phosphorus levels result in growth retardation and a reddish colouration because of enhanced anthocyanin formation. Phosphorus deficiency leads to retarded leaf and cell expansion rather than diminished chlorophyll formation, resulting in higher chlorophyll per unit leaf area, but lower photosynthetic efficiency per unit area of chlorophyll (Marschner 1987). It also causes stunting of the root system which decreases the uptake of mineral nutrients (Day & Ludeke 1993). Soils with more than 1% organic matter, usually have a low availability of phosphorus, because of the desorption and adsorption of phosphorus. The dissolution and precipitation of inorganic phosphates does not affect these soils. Soils with lower organic matter are however dependent on the dissolution and precipitation of inorganic phosphates (Marschner 1987).

The sandy soils of the coastal fynbos of the south-western Cape are low in phosphorus, ranging between 16.2 and 37.5 kg ha^{-1} (Low 1983; Brown & Mitchell 1986; Mitchell, Brown & Jongens-Roberts 1984), which compares well with Australian heathlands, rather than Chile-California shrublands (Mitchell *et al.* 1984). Low (1983) warns against using absolute concentrations or pool sizes and also states, in addition, that he had found similar trends in coastal fynbos topsoil.

Brown & Mitchell (1986) found that fire at a sand plain lowland fynbos site caused an initial increase in resin-extractable phosphorus. This increase lasted for four months, after which it returned to levels comparable to those before the fire. Brown & Mitchell (1986) attributed this increase to three factors, namely, (i) fire combusts both plant and above ground litter, (ii) high soil temperatures caused by the fire leads to physical mineralization of phosphorus, and (iii) although still to be empirically proved, it seems as if during winter, conditions following fire are more favourable for microbes which release bound phosphorus.

Andriesse & Koopmans (1984) and Andriesse & Schelhaas (1987) studied the effects of burning on forest soils. They found significant increases in available soil phosphorus in Sarawak and total phosphorus in Sri Lanka, which they attributed to mineralization of phosphorus. It should be noted that these studies were conducted in forests which generally resulted in much higher outputs of mineral nutrients following fire. In contrast, decreases in total phosphorus were found in Thailand (Daubenmire 1968).

Atmospheric deposition of phosphorus at the Pella site, South Africa (0.189 kg P ha^{-1}) compared well with inputs from British heathland ecosystems (0.2-1.0 kg P ha^{-1}), contributing an estimated 4.5% to the annual soluble soil phosphorus pool (Brown, Mitchell & Stock 1984). This is much lower than the total nitrogen input from rainfall found by Stock & Lewis (1986a). However, it could be more significant than the deposition of nitrogen because phosphorus is unlikely to be affected to the same extent as nitrogen by volatilization (Stock & Lewis 1986a) or leaching (Day & Ludeke 1993) from the ecosystem.

Chapin & McNaughton (1989) showed that phosphorus was very important for the regrowth of a defoliated plant. They started with the premise that compensatory growth (enhanced growth in response to grazing) can only take place when environmental conditions (water, light and nutrients) are abundant and can be readily exploited, to replace tissues lost to herbivores. Their study was done in the Serengeti, an area with high soil fertility, which also contained grasses which exhibited compensatory growth following defoliation. When three of these grasses were grown under conditions of phosphorus deficiency, all showed a reduction in biomass yield compared to those grown under optimal nutrient conditions (Chapin & McNaughton 1989).

1.1.5.3. Potassium (K)

Potassium is essential for ionic regulation, pH stabilization and osmotic regulation in the cell (Leigh & Storey 1991). Potassium is also required for enzyme activation, membrane transport processes, protein synthesis and photosynthesis (Marschner 1987). Its uptake is highly selective and closely coupled to metabolic activity (Marschner 1987).

Plants growing optimally should have ~2-5% of their dry mass as potassium. Low potassium levels lead to the mobilization of the element from mature tissues and relocation to younger tissues. Severe deficiency results in organs becoming chlorotic and then necrotic (Marschner 1987).

1.1.5.4. Iron (Fe)

Iron is important because it is a constituent of hemoproteins (for example, the cytochromes), which are essential for the redox systems in chloroplasts and mitochondria. In the leaves, iron deficiency leads to lower chloroplast volume (lower chlorophyll content per unit leaf area) and lower protein synthesis, resulting in lower protein per chloroplast. The lower protein is a result of the relationship between the concentration of iron and the number of ribosomes (Marschner 1987).

Iron deficiency in the roots (except those of grasses), leads to inhibition of elongation, an increase in the diameter of the apical root zones, an abundant root hair formation, and the formation of rhizodermal cells with a distinct wall labyrinth typical of transfer cells.

Grasses respond differently to iron deficiency than other plants. Their roots release nonproteinogenic amino acids which form highly stable complexes with Fe (III) and which are very effective in dissolving FeOOH at high pH (Marschner 1987).

For optimal growth, plants normally require 50-150 mg/kg dry weight iron in their leaves. Physiological inactivation of iron leads to lime-induced chlorosis of the leaves, even though iron levels may be similar or higher to those found in green leaves (Marschner 1987). Plants exhibiting lime-induced chlorosis grow in alkaline soils, and are said to be iron inefficient. Andriesse & Koopmans (1984) found that exchangeable iron is increased by almost 500% when soil is heated to 150°C.

1.1.5.5. Magnesium (Mg)

Magnesium is a constituent of chlorophyll and plays a role in the ionic regulation of enzyme activity (Lawlor 1991). In photosynthesis it is responsible for the activation of RuBP carboxylase. It also plays an important role in protein synthesis; acting as a bridging element for the aggregation of ribosome subunits (Marschner 1987).

Plants growing optimally have ~0.5% of their dry weight as magnesium. Lower levels lead to the chlorosis of fully expanded leaves. They also lead to lower protein nitrogen and increased nonprotein nitrogen (Marschner 1987).

1.1.5.6. Sodium (Na)

Sodium is a beneficial element, meaning that it is either only essential for certain plant

Intrinsic mechanisms are physiological responses to herbivory (McNaughton, 1979).

The extrinsic effects of herbivory are indirect, and include (1) increased light, (2) an improved water supply, (3) increased nutrient supply to the remaining (uneaten) tissues. The fourth effect of herbivory is a direct change to plant metabolism, growth, and development. Herbivory can lead to an increase in light intensity by the removal of shading leaves. This leads to an increase in photosynthetic rate per unit area of remaining leaves, which can then lead to a higher assimilation rate per unit area in the new leaves that are produced following defoliation (McNaughton, 1979).

Herbivory improves the water supply of the plant. After defoliation, the roots have a smaller sink to supply. Thus, water may no longer limit carbon dioxide uptake by the leaves, and this results in an increase in the photosynthetic rate of the plant. Herbivory may also improve the nutrient supply available to the remaining tissues, which lead to compensatory growth. This may be similar to the improved water status, where the demand on the nutrient or water pool is reduced. It can also be a long-term effect where herbivory facilitates the recycling of plant material. This recycling of nutrients is speculated to be more beneficial to the plants than the initial detrimental effects of herbivory (Mattson & Addy, 1975).

The intrinsic mechanism of compensatory growth refers to the physiological changes within the plant that leads to compensatory growth following defoliation. These physiological changes may include meristem activation, increasing cell division and cell elongation rates, decrease in tissue senescence, rejuvenation of the remaining tissues, and a change in the allocation of stored and newly produced assimilates (McNaughton, 1979). It is widely accepted that there is a balance between assimilated carbohydrates and nutrient uptake in a defoliated plant. Following defoliation, stored carbohydrates are mobilized in order to replace lost material. The new tissues produced, act as sinks for the assimilates, but may later also contribute to the total photosynthetic area. This leads to compensatory growth following defoliation (McNaughton, 1979).

1.2. *Imperata cylindrica* as a weed

Imperata cylindrica is a rhizomatous, perennial C_4 grass, native to tropical and subtropical areas of the eastern hemisphere (Dickens & Moore 1974; Holm *et al.* 1977a). The grass has a global distribution and is regarded in many regions, especially the tropics, as a weed. Holm *et al.* (1977b) ranked *I. cylindrica* as the world's seventh worst weed. It is placed in a category of plants regarded as a group apart, since they are cited more than any other of the world's weeds, and cause the most problems in the largest number of crops (Drake *et al.* 1989; Bromilow 1995). The grass is present in South Africa and behaves as a weed, but its rank of importance is unknown (Holm *et al.* 1977a). In South Africa it has been recognized to be a problem plant in industrial areas and along roadsides, and it also has the potential to become a problem in tropical crops such as coffee (Bromilow 1995). Gibbs Russell *et al.* (1991) recognized it as a weed, mainly because of the difficulty in eradicating the underground rhizomes, which occur in South Africa's fynbos, savanna and grassland biomes. The grass may have been introduced to South Africa by accident, but was probably introduced intentionally because it is said to be an effective soil binder (Meredith 1955; Bromilow 1995).

I. cylindrica is not generally considered a serious weed in the Western Cape because it is not an aggressive invader of new areas, although it is widespread in the south-western Cape and southern Cape (Bond & Goldblatt 1984). It seems as if *I. cylindrica* is an opportunist which colonizes disturbed wet areas. This pattern has also been found in parts of the world where slash-and-burn cultivation is in use (Dove 1986). After the land has been used for cropping it lies fallow. It is during this fallow period that secondary succession occurs, with *I. cylindrica* more often than not, being in the guild of invaders in cleared tropical forest areas (Ramakrishnan & Vitousek 1989). However, even if it colonizes open areas, it must have an advantage in order to persist (Thompson 1991). One of the most probable reasons for it not being too successful in the Western Cape could be because it is a C_4 species. Brook (1989) states that *I. cylindrica* is a poor competitor on fertile soils, easily outcompeted by other species. It is more successful on infertile soils as it has a low nutrient demand per unit dry matter production, and a high efficiency of nutrient uptake, which may be facilitated by mycorrhizas (Brook 1989).

Vogel, Fuls & Ellis (1978) showed that grasses show a characteristic distribution across South Africa, with C_4 species occurring in areas with a mean daily temperature above 25°C, and C_3 species more abundant in the colder areas of South Africa, namely the winter rainfall area of the Western Cape and the cold summits of the Drakensberg range. Precipitation could not account for the distribution of C_3 and C_4 species because of too much overlap (Vogel *et al.* 1978). Thompson (1991) suggests that *Spartina anglica*, a

C_4 grass, grows in cooler areas (5-10°C) but still maintains photosynthetic rates equal to C_3 species. Whether this is also true for *I. cylindrica* is uncertain and needs to be investigated.

It seems as if *I. cylindrica* propagates primarily vegetatively by means of its underground rhizome system (Ayeni & Duke 1985; Anoko, Akobundu & Okonkwo 1991; Brook 1989; Bryson & Carter 1993; Otsamo *et al.* 1995). *I. cylindrica* usually flowers only after disturbance or stress, such as burning, cutting or drought. Seeds remain viable for one year only and germination rates of 80-90% have been found under favourable conditions (Brook 1989). The viability of *I. cylindrica* seed, following defoliation, must still be investigated for individuals growing in the Cape Flats Nature Reserve (CFNR). Even if the seeds are found to be viable, it should be remembered that the CFNR is an island surrounded by developed land, and hence areas for colonization are limited. Thus, establishment is going to be a greater problem for the plant. Chapin *et al.* (1986b) stated that the graminoid *Eriophorum vaginatum* grows in an environment (tussock tundra), where establishment of new individuals from seed is infrequent. This is probably because vegetative reproduction is cheaper than investing large amounts of stored reserves into sexual reproduction. (Brook 1989).

I. cylindrica is suspected of having an allelopathic effect on particularly crop species (Brook 1989; Kuusipalo *et al.* 1995). Crushed *I. cylindrica* leaves have been found to decrease growth in rice, maize and soybean (Brook 1989). Extracts from leaves have been found to suppress growth in tomato. Hussain & Abidi (1991) found that extracts obtained from *I. cylindrica* tissues retarded seed germination of co-occurring species. They also did a mulching experiment that showed that *I. cylindrica* litter made soil unsuitable for growth of various species. The toxins in the extracts were identified as caffeic, *p*-coumaric, *p*-hydroxybenzoic, syringic, chlorogenic and vanillic acids (Hussain & Abidi 1991). All of the above compounds are water-soluble and inhibited germination, radicle growth and plumule growth of tested species (Hussain, Abidi & Malik 1994). The results found by Hussain & Abidi (1991) agreed in most instances with that of Hussain *et al.* (1994). Dakshini & Dakshini (1991) analysed a number of leachates, for example, leaf leachate, root/rhizome leachate, and soil for phenolic compounds. They found that the quality and quantity of phenolic fractions changed with the presence or absence of *I. cylindrica*. The phenolic compounds caused an allelopathic effect on other species. All phenolics tested were water-soluble as leachates were prepared in an aqueous medium (Dakshini & Dakshini 1991). The water-solubility of the compounds allow it to be easily leached from the plant into the soil and thus preventing any other plant from establishing itself, either vegetatively or through seed (Dakshini & Dakshini 1991).

I. cylindrica can be controlled mechanically, chemically, biologically and/or culturally (Brook 1989). Mechanical control usually entails grazing, slash-and-burn, or tillage. It is usually the first control method used by farmers, as only labour and simple tools are required. However, burning requires much less labour (15 man days/ha) when compared to cutting of the grass (75 man days/ha) (Brook 1989). Often stands of *I. cylindrica* will be burned and thereafter the soil would be ploughed to expose the buried rhizomes to the sun. Cultivation makes it easier to introduce crops or shade trees into the area (Conroy, Bagnall-Oakley & Gunawan 1995). Chemicals associated with chemical control include dalapon, paraquat, imazapyr and glyphosate (Willard *et al.* 1996). Chemical control is expensive because of labour and the multiple applications which are needed to effectively control the weed. Combining chemical and mechanical control gives the best economic and management result, and is used when chemicals can be afforded.

Willard *et al.* (1991) found that mowing *I. cylindrica*, with or without the use of herbicides, significantly reduced shoot and rhizome biomass. They also suggested that mowing could perhaps deplete belowground carbohydrate reserves. This is especially true if the weed is given a long enough rest period between mowings. Willard *et al.* (1991) confirmed that mowing and chemical control together, reduced *I. cylindrica* shoot and rhizome biomass more than chemical control alone. They also found that clipping the chemically treated plants a year after the initial clipping, reduced shoot and rhizome biomass even further. One treatment only actually increased the biomass. The use of sulfometuron without any prior clipping, resulted in increased shoot and rhizome biomass. Possible reasons for this was the release of *I. cylindrica* from interspecific competition from broadleaf species, which are more vulnerable to chemical spraying. The chemical could also have broken apical dominance in *I. cylindrica* and released dormancy in axillary buds in the rhizomes (Willard *et al.* 1991). In order to eliminate the weed, it is necessary to eliminate the rhizomes where most of the energy for regrowth is stored. A reduction in shoot and rhizome biomass of 80% and more (compared to the controls) is acceptable. They only achieved this when glyphosate, imazapyr or dalapon was followed with discing. Thus, follow-up programs of control are necessary to reduce shoot and rhizome biomass to acceptable levels. This is also standard practice in infested areas, where land is cleared by slashing or burning and then applying glyphosate at 1.8 kg/ha, followed up with a lesser concentration if any regrowth appears (Conroy *et al.* 1995).

I. cylindrica is particularly a problem in former forested areas of moist tropical regions, for example, in southeast Asia (Otsamo *et al.* 1995). Cultural control of *I. cylindrica* in these forests has been attempted by planting fast-growing trees within stands of the weed.This is however often difficult because of compact and nutrient-deficient soil, hydrologic instability, large variation in surface temperatures of the soil, grass competition, allelopathy, and the high fire susceptibility of the grass (Kuusipalo *et al.* 1995).

I. cylindrica is known to be intolerant of shade as would be expected of a C_4 plant (Brook 1989). Patterson (1980) found that shading significantly reduced total plant dry weight, leaf area, the dry weights of roots, stems, leaves, and rhizomes, and number of rhizomes and leaves. Prior to planting any shade trees, it is necessary to use complete plowing of large infested areas, as opposed to strip plowing of areas (Wilcut *et al.* 1988a; Otsamo *et al.* 1995). Plowed strips are often easily reinfested with *I. cylindrica*, mainly because of its high capacity to spread horizontally using its rhizomes. Young tree seedlings are often inhibited by the reinfestation. Once an area has been completely plowed, trees should be planted and fertilized with nitrogen, phosphorus and potassium. Fertilization has been found to significantly increase the basal cover of the tree species used in the experiment; tripling the basal cover of *Paraserianthes falcataria*, and doubling the basal cover of *Acacia mangium* and *Gmelina arborea*. Cultural control in the Cape Flats Nature Reserve (CFNR) has not been given any consideration because *I. cylindrica* is not regarded as a threat to the CFNR's vegetation. If this changes, a fynbos species from the CFNR, which is comparable to the trees used to reclaim *Imperata*-infested land, will have to be used. It will have to be similar in terms of growth rate and also basal cover.

Anoko *et al.* (1991) successfully established leguminous hedgerow trees (*Gliricidia sepium* and *Leucaena leucocephala*) by simply cutting 4 metre strips through an *Imperata* field. No plowing of soil was done. Although successful, it is still recommended that complete plowing be done just in case of underground reinfestation by *I. cylindrica*. Anoko *et al.* (1991) found little or no tillering, and no flowering of *I. cylindrica* in *Gliricidia* and *Leucaena* hedgerows. Significant differences were found in rhizome biomass for shaded plants and controls, shading affecting the branching of rhizomes. Shoot biomass also decreased but to a lesser extent than rhizome biomass. All these mentioned results were consistent with previous work done by Patterson (1980).

Moosavi-Nia & Dore (1979) found that *I. cylindrica* becomes more sensitive to glyphosate spraying with decreasing light conditions. The direct effect of shading was reducing the total rhizome production, thus increasing the shoot to root ratio. Shading also caused a depletion of the total nonstructural carbohydrate content of the underground tissues, which indicated that the relative increase in photosynthetic tissue did not compensate for the reduced light (Moosavi-Nia & Dore 1979). Standard practice in rubber and oil palm plantations is to eradicate *I. cylindrica* from the land using herbicides, and then introducing a legume crop which excludes reinfestation through shade (Conroy *et al.* 1995).

The gall midge, *Orsiollella javanica*, has been found to be host specific to *I. cylindrica* resulting in 25% infestation when the grass is cut before introduction (Brook 1989; Soenarjo 1986). Unfortunately, the gall midge is preyed upon by the an egg-larval parasitic ant (*Platygaster* sp.) and it also fails to attack the rhizome, instead attacking primarily the shoots (Brook 1989). The ragged stunt virus was found to infect *I. cylindrica*, besides its natural host, *Echinochloa crus-galli* var. *oryzicola*, causing leaf yellowing and swelling of small veins (Brook 1989).

1.3. *Imperata cylindrica* in the Cape Flats Nature Reserve (CFNR)

The Cape Flats Nature Reserve (CFNR) is located on the University of the Western Cape campus, Bellville South (Fig.1.4). It was proclaimed in 1977 under Section 12(4) of the Nature Conservation Ordinance of 1974 and has since increased in size, from about 20 ha (Low 1982a; Feely 1988) to around 30 ha with the addition of an adjacent area in 1989. This study was done in an area consisting mainly of dunes and dune 'streets' or dune slacks , and in a sandy flatland close to a vlei (Figs 1.5 and 1.6). *I. cylindrica* occurs mainly in the dune slacks and on the sandy flatland close to the vlei. It for temperate floras in the world (Goldblatt 1978; Cowling *et al.* 1992). Thus classifying fynbos floristically is a long term objective. According to Campbell (1986) the whole fynbos biome would only be classified floristically in about 20 years at the rate of work at that stage. Despite this, the problem of identifying the specimens found in the field remains. The structural approach has been used by all past researchers (for example, Marloth, Adamson, Taylor, and Kruger), to classify fynbos (Campbell 1986; Cowling & Holmes 1992). However, it is only since Campbell (1985), that a complete typology for the whole of the fynbos biome was produced (Cowling & Holmes 1992). The structural approach classifies on the basis of the relative proportions of their growth forms, in particular restioids, ericoids and proteoids (Cowling & Richardson 1995).

In order to put the Reserve in a broader context, the typology of Campbell (1985) was used because it included the whole of the fynbos biome. The scheme also not only looks at fynbos and strandveld, but also how these vegetation types fit into the fynbos biome. This scheme was also used by Cowling & Holmes (1992) to classify fynbos, as they criticized previous structural classification attempts by Taylor (1978) and Kruger (1979) as being too loosely and broadly defined. Campbell (1985) divided fynbos plant communities into fynbos and non-fynbos elements (Fig. 1.7). These were then subdivided into groups and further down into series. This scheme was based on data collected from 507 plots on 22 transects located throughout the mountains of the fynbos biome (Cowling & Holmes 1992).

In Campbell's (1985) scheme, the vegetation of the CFNR is composed of:

Non-fynbos

(i) Forest and thicket, consisting mainly of *Olea exasperata* and *Rhus* spp.

Fynbos

(ii) Cape fynbos shrubland, consisting of *Metalasia muricata*, *Ehrharta villosa*

The comparison of the three habitats by Low (1982a), Fredericks (1992) and Campbell (1985) are shown in Table 1.1. From Table 1.2 there is no series from Campbell (1985) which corresponds to the vegetation of the sandy flats (occurring between dunes). Possible reasons for this is that:

1. the physiognomy of the *Imperata* stands resembles grassland vegetation more than fynbos vegetation,
2. Campbell's transects were confined to mountainous areas in the fynbos biome,
3. *Imperata cylindrica* is a weed which has become naturalized in the CFNR and presumably replaced indigenous vegetation.

It is clear that even though Campbell (1985) presents a typology applicable to the whole of the fynbos biome, it is still too broad. The scheme provides a good framework, as did Acocks (1975) from which to work from. However, it falls short when working on autecological or ecophysiological projects which are often confined to a very small area. However, Campbell's (1985) scheme will continue to provide the framework from which detailed floristic studies are made. The results of these floristic studies will in all likelihood lead to modification and additions to the scheme developed by Campbell

(1985).

Fredericks (1992) found three communities in the CFNR (Fig. 1.8, Table 1.1), namely, (1) Imperato-Metalasietum muricatae rhoetosum (I-Mmr), (2) Passerino-Rhoetum laevigatae willdenowietosum (P-Rlw), and (3) Eucleo-Oleetum exasperatae kedrostietosum (E-Oek). These three communities occur in three distinct habitats as indicated by Low (1982a). It would seem that the most likely vegetation replaced by the I-Mmr community, would be the P-Rlw community. This community has its dominant species as *Rhus laevigata*, *Willdenowia teres*, *Ischyrolepis eleocharis*, *Ehrharta villosa*, and *Aspalathus hispida*. This community is not easily placed in Campbell's (1985) scheme.

The Cape Flats Nature Reserve (CFNR) falls within the western part of the Cape Floristic Region (CFR) (Fig. 1.4). This area has a mediterranean-type climate, with dry summers and wet winters. The vegetation of this region was divided by Acocks (1975) into 'Coastal Macchia' (Veld Type 47), 'Macchia' (Veld Type 69), and 'False Macchia' (Veld Type 69). Taylor (1978) recognised that besides these three veld types, Capensis or the Cape Floristic Region also contained 'Strandveld' (Veld Type 34) and Coastal Rhenosterbosveld (Veld Type 46). Strandveld has more in common with the vegetation of the CFNR, in that both contain *Euclea racemosa* and *Rhus* species. Taylor (1978) also recognized that Acock's (1975) definition of 'Strandveld' was too narrow, occurring according to Acocks (1975) mainly on the west coast. Kruger (1979) placed the vegetation of the Cape Flats within a Coastal Fynbos category (subcategory: 'Fynbos of Coastal Sands'). Boucher & Moll (1981) divided mediterranean shrublands into three categories, (i) 'Strandveld', (ii) 'Coastal Renosterveld', and (iii) 'Inland Renosterveld'. As with Acocks (1975), the CFNR's vegetations falls within Boucher & Moll's (1981) 'Strandveld' category.

What is Strandveld? Liengme's (1987) definition of Strandveld is as follows: "Strandveld comprises three successionally related communities: Pioneer Littoral Vegetation, Successional Littoral Dune Vegetation and Dune Scrub. Strandveld contains elements of Capensis and Karoo-Namib floras, as well as Tongaland-Pondoland and Afromontane elements." Taylor (1983) stated that Strandveld has been used in the past as a landscape type which often included more than one vegetation type. Boucher's (1983) Strandveld includes broad-sclerophyll woody scrub of dunes near the coast, and also includes ericoid, fynbos-like scrub.

What is fynbos? Acocks (1975) recognized three veld types for the fynbos biome, namely 'Macchia' or Veld Type 69 (now referred to as Fynbos), 'Coastal Macchia' or Veld Type 47 (now referred to as Coastal Fynbos), and 'False Macchia' or Veld Type 70 (now referred to as False Fynbos). Cowling & Holmes (1992) states that Acocks (1975) causes confusion because his concept of a veld type is an agroecological unit of vegetation 'whose range of variation is small enough to permit it to have the same farming potentialities'. Acocks (1975) concede this, stating that the vegetation is too complex to easily and simply divide into different types. He cites the lack of a few dominant species, as found in forest and other vegetation, to be the cause of his cursory treatment of fynbos. Acocks (1975) listed the families and genera occurring as dominants in the fynbos biome:

Macchia (Fynbos):

Proteaceae, Ericaceae, Fabaceae, Restionaceae, Cyperaceae, Poaceae, Rhamnaceae, Penaeaceae, Rosaceae, Bruniaceae, Geraniaceae, Haemodoraceae, Liliaceae, Orchidaceae, Asteraceae, Rutaceae, Thymeleaeaceae, Aizoaceae, Boraginaceae, Verbenaceae, Campanulaceae, Polygalaceae, Grubbiaceae, Amaryllidaceae, Iridaceae.

Coastal Fynbos:

Shrub and trees: *Euclea racemosa*, *Rhus laevigata*, *Rhus lucida*, *Olea exasperata*, *Rhus glauca*, *Nylandtia spinosa*.

False Fynbos:

Dominant grass, *Aristida junciformis*, and other tropical grassveld species.

Dominant Asteraceae include *Othonna*, *Euryops*, *Ursinnia*.

Acocks (1975) limited his definition of 'Strandveld' (Veld Type 34) to the west coast, forming a band with Redelinghuys in the south and the Olifantsriver in the north. When looking at the species that he listed for Strandveld, there is overlap with 'Coastal Fynbos' (Veld Type 47). The species common to both are: *Rhus glauca*, *Euclea racemosa*, and *Rhus laevigata*.

Taylor (1978) improved on Acocks (1975) broad classification of fynbos. He defined fynbos as vegetation having the characteristic restioid element (wiry aphyllous hemicryptophytes), an ericoid element (dwarf and low evergreen ericoid shrubs), and a frequent but not constant proteoid element (tall broad-sclerophyllous shrubs). Taylor (1978) distinguished between three vegetation types which make up fynbos, namely, 'Mountain Fynbos', 'Arid Fynbos', and 'Coastal Fynbos'. He also recognized two other vegetation types as belonging to the Cape Floristic Kingdom, but not to fynbos, namely, 'Strandveld',and 'Coastal Renosterveld'. Kruger (1979) supported the classification of Taylor (1978), stating that the only constant and differential floristic element is the Restionaceae which may dominate communities or at least the herb stratum in certain habitats.

Moll & Jarman (1984) defined Cape fynbos as "Evergreen sclerophyllous shrublands, on oligotrophic soils, comprising essentially Cape Floristic Kingdom elements, consisting predominantly of either functionally isobilateral picophyllous and/or microphyllous to mesophyllous-leaved shrubs (ericoids and Proteaceae) and usually associated with evergreen aphyllous and/or narrow-leaved sclerophyllous hemicryptophytes (Restionaceae)". Vegetation dominated by elements from the Cape Floristic Kingdom, and the presence of one, two or all three of the restioid, ericoid and proteoid elements, will designate it as being fynbos (Moll & Jarman 1984).

Campbell (1985) in his definition stressed the importance of restioids in fynbos, but also that of Ericaceae and proteoids. Features differentiating types of fynbos include leafy sedges, non-ericaceous ericoids, ericoid Asteraceae, stoeboids, aphyllous grasses, leaf spinescence, Penaceae, and Brunniaceae. (Campbell 1985).

The above definitions cause confusion about fynbos, which makes the classification of the habitats in the Cape Flats Nature Reserve (CFNR) difficult. Acocks (1975) included the Cape Flats in his 'Coastal Fynbos' (Veld Type 47), which has both the ericoid and restioid elements (the flats habitat) and the tropical scrub elements (the dune habitat). Acocks (1975) did not include the Cape Flats as an area which had Strandveld vegetation (only a minor exception at Scarborough).

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1.5. Figures

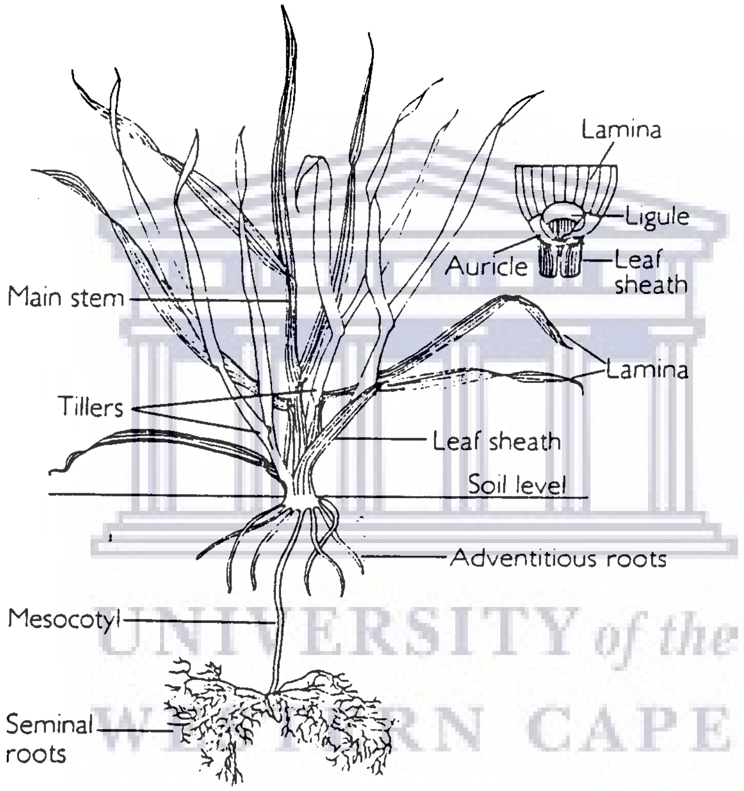


Figure 1.1. The grass plant with its aboveground tillers, arranged into anatomically attached groups forming the whole plant or metapopulation (Langer 1979).

Figure 1.2. The dome-shaped, vegetative stem apex showing alternating leaf primordia at varying stages of development (Langer 1979).

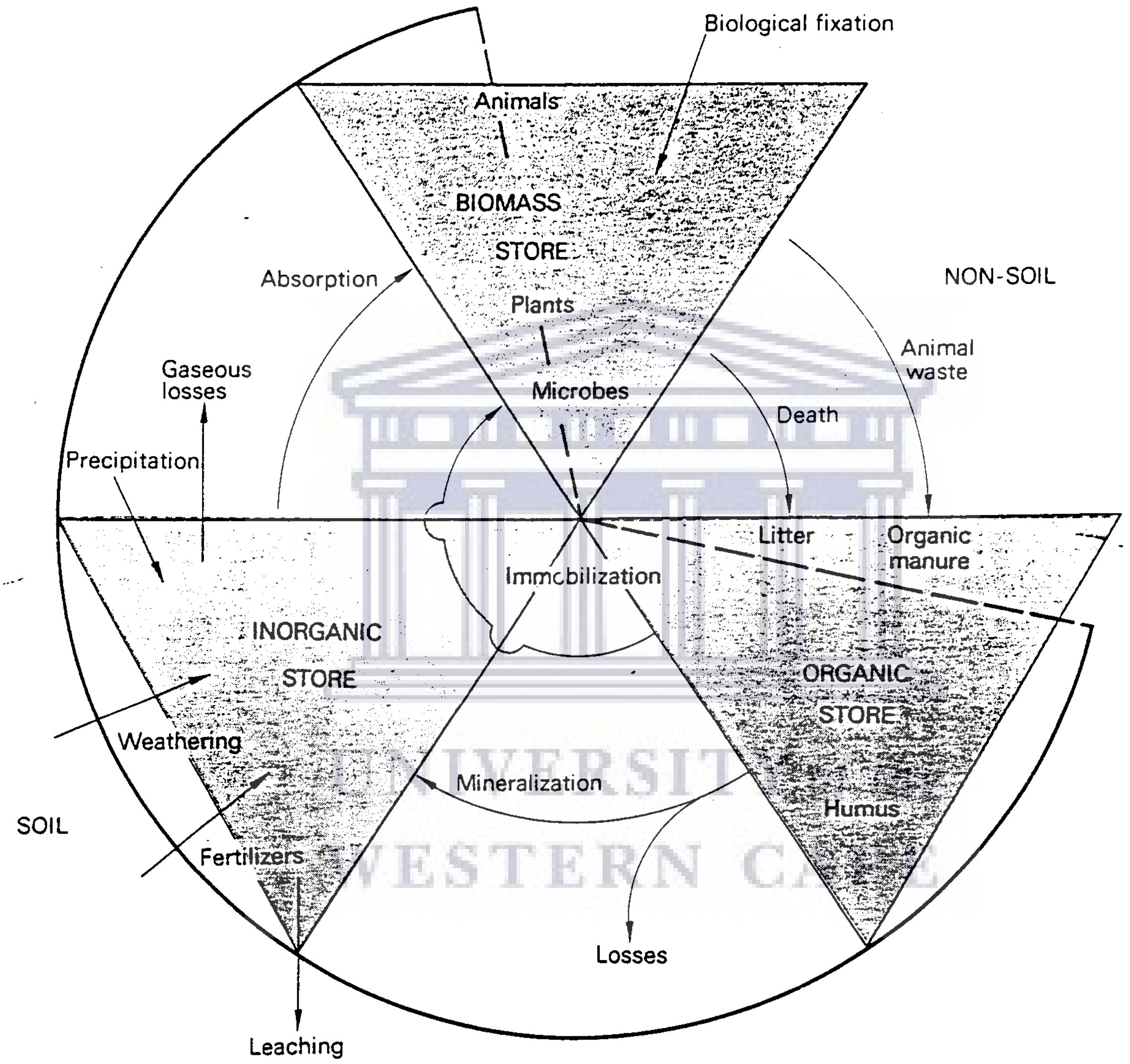


Figure 1.3. Fundamentals of a nutrient cycle (White 1987).

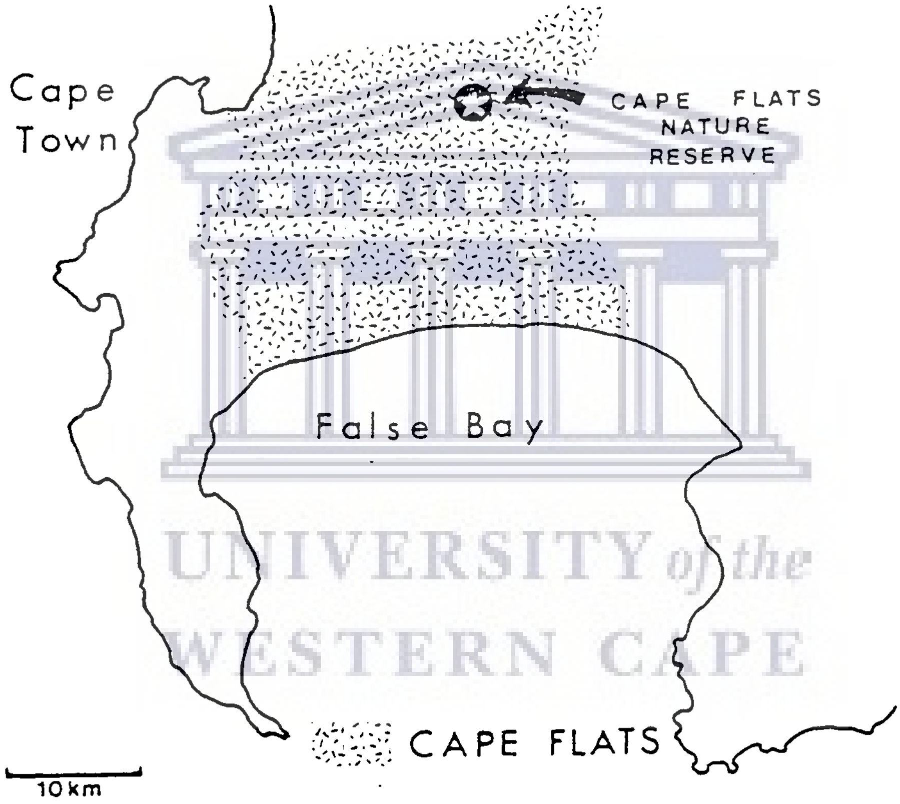
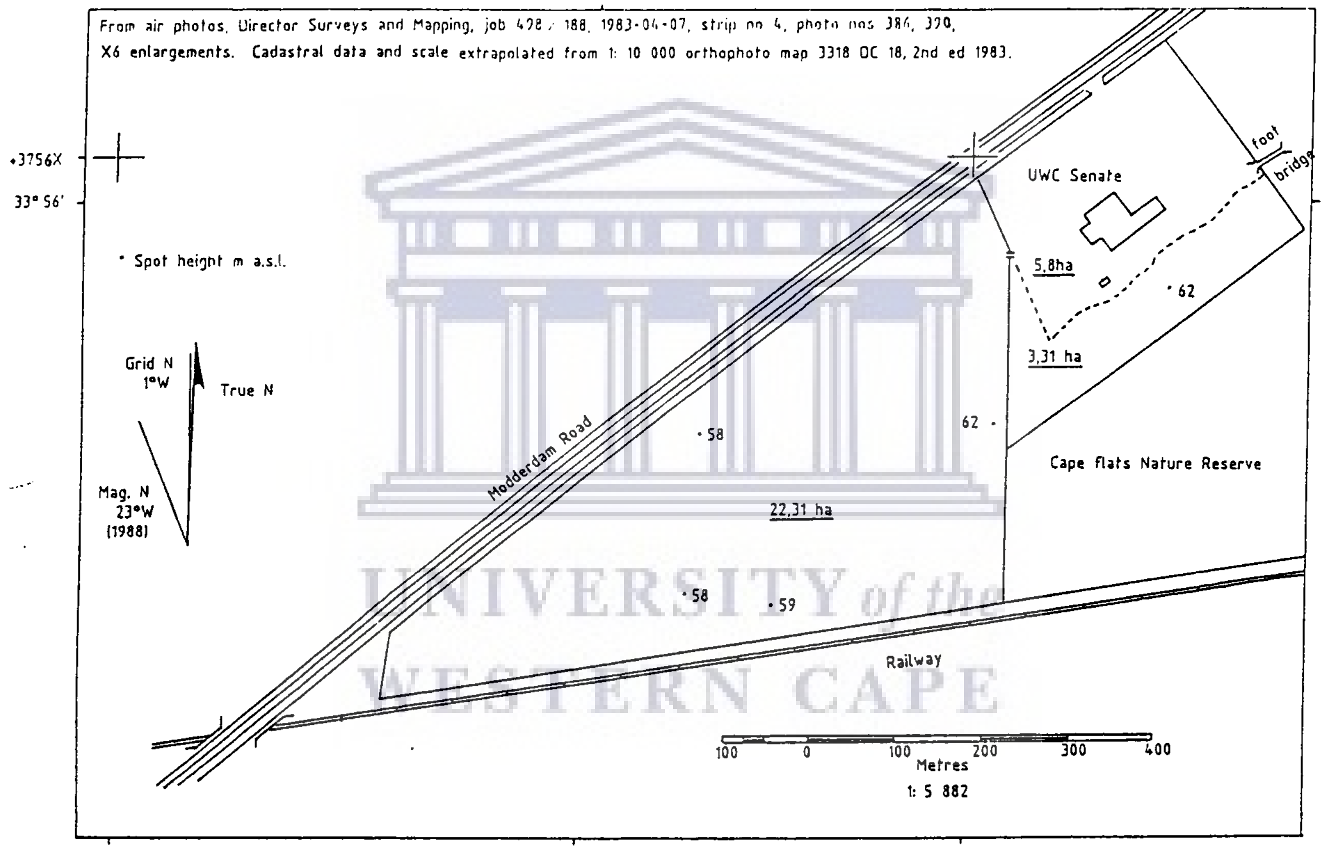


Figure 1.4. The location of the Cape Flats Nature Reserve (CFNR) on the Cape Flats (Low 1982b).



From air photos, Director Surveys and Mapping, job 428 / 188, 1983-04-07, strip no 4, photo nos 386, 390, X6 enlargements. Cadastral data and scale extrapolated from 1: 10 000 orthophoto map 3318 OC 18, 2nd ed 1983.

Figure 1.5. Triangle and western Cape Flats Nature Reserve (CFNR) (Feely 1988).

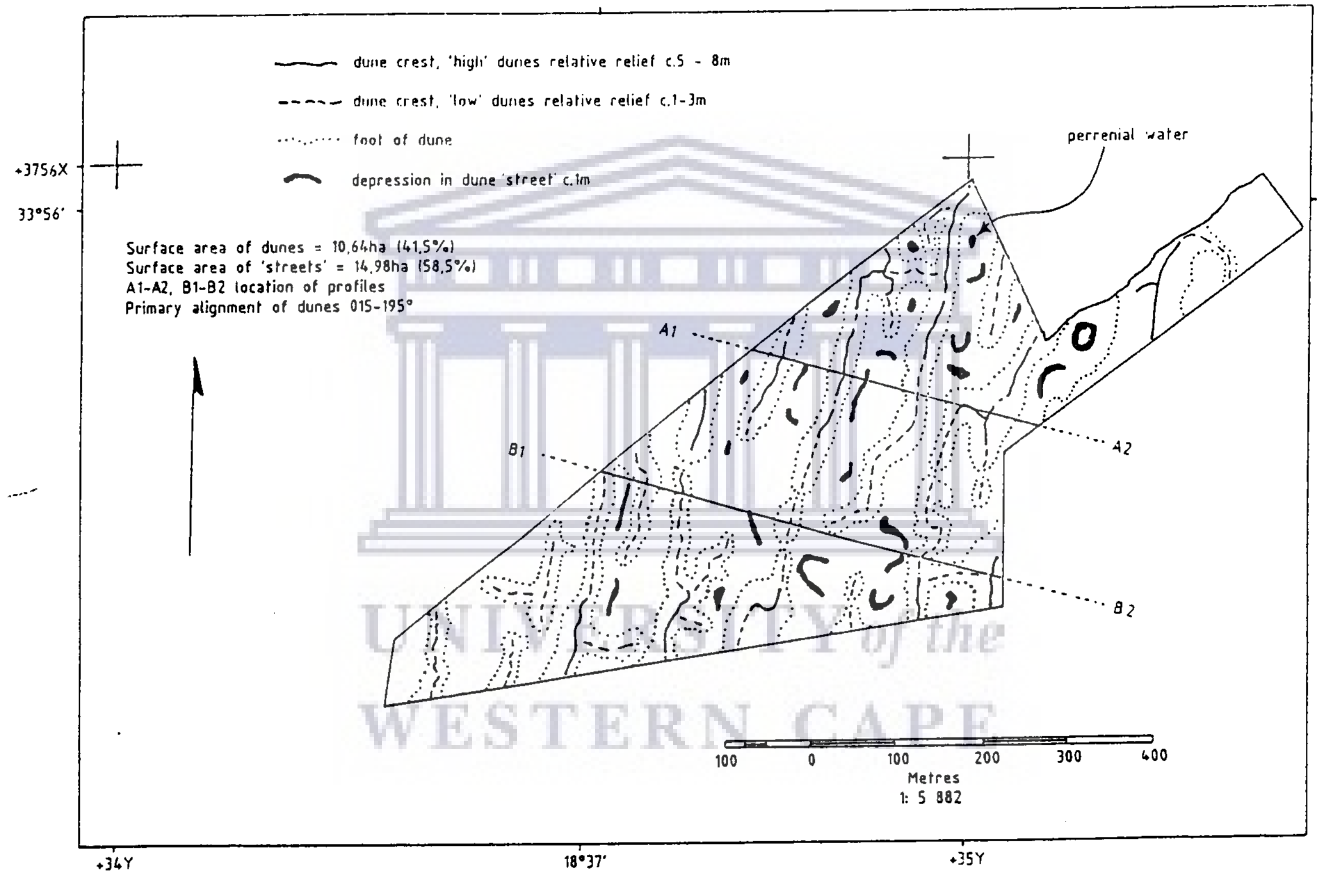


Figure 1.6. The Triangle - Longitudinal dunes and dune streets, and vlei area (perennial water) (Feely 1988).

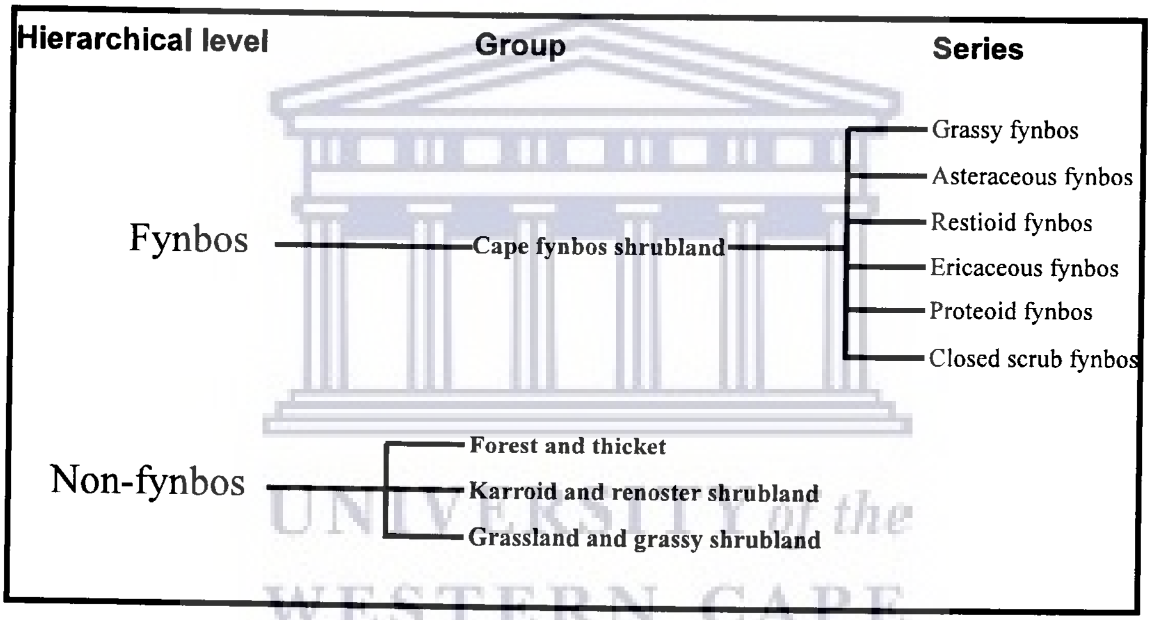


Figure 1.7. Hierarchical classification of fynbos plant communities, based on Campbell (1985) (modified from Cowling & Holmes 1992)

Table 1.2: Differences in soil environmental variables measured in each community of the Cape Flats Nature Reserve (CFNR) (Fredericks 1992).

E-Oek - Eucleo-Oleetum exasperatae kedrostietosum (community 8)

I-Mmr - Imperato-Metalasietum muricatae passerinetosum (community 14)

P-Rlw - Passerino-Rhoetum laevigatae wildenowietosum (community 11)

Community	**pH**	**P (mg/kg)**	**mmol/kg Ca**	**mmol/kg Mg**	**mmol/kg Na**
E-Oek (#8)	8.15	23.43	72.47	5.76	5.49
P-Rlw (#11)	8.24	17.04	74.81	5.44	5.66
I-Mmr (#14)	8.25	29.35	71.25	4.83	3.92
Community	**mmol/kg K**	**%clay**	**%silt**	**%coarse sand**	**%medium sand**
E-Oek (#8)	1.36	1.55	1.27	14.95	36.61
P-Rlw (#11)	1.38	1.50	1.50	9.53	43.99
I-Mmr (#14)	1.52	3.00	0.01	9.12	43.45
Community	**% fine sand**	**bulk dens. (g/ml)**	**%N**	**% org. matter**	
E-Oek (#8)	45.64	1.48	0.05	1.00	
P-Rlw (#11)	44.73	1.48	0.05	0.83	
I-Mmr (#14)	49.43	1.60	0.06	1.10	

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Materials and methods. This section should provide sufficient details of the techniques to enable the work to be repeated. Do not describe or refer to commonplace statistical tests in Methods but allude to them briefly in Results.

Results. This should state the results, drawing attention in the text to important details shown in tables and figures.

Discussion. This should point out the significance of the results in relation to the reasons for doing the work, and place them in the context of other work.

Acknowledgements.

References (see Specifications).

Tables (see Specifications). These should be referred to in the text as Table 1, etc. Do not present the same data in both figure and table form.

Figure legends (see Specifications). Figures should be referred to in the text as Fig. 1, etc. (note Figs 1 and 2 with no period). Illustrations (see Specifications) should be referred to as Figures.

Technical reports

These are reports of new methods, techniques or apparatus. They will be accepted only if they are of sufficiently general interest. They should normally be structured like a standard paper but be shorter in length.

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The editors welcome short review articles on topical subjects which are of general interest to the readership. Intending authors are advised to consult with the editors before preparing essays for submission.

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Journal of Applied Ecology, Dr N. Webb (zoological material), Institute of Terrestrial Ecology, Furzebrook Research Station, Wareham, Dorset BH20 5AS, UK; Dr H.A.P. Ingram (botanical material), Department of Biological Sciences, The University, Dundee DD1 4HN, UK.

Journal of Ecology, Dr P. Moore, Biosphere Science Division, King's College, Campden Hill Road, Kensington, London W8 7AH, UK.

Specifications

Figures

Figures in the form of line diagrams should be produced according to the style seen in recent issues, and should either be drawn by hand or produced on a good-quality printer. Where possible, they should be no bigger than A4 and designed appropriately if they are to be reduced in size for publication. Insert all lettering in soft pencil on a transparent overlay or indicate it on a photocopy, and label each figure with authors' names and figure number. Photographs should be glossy prints of good contrast. Where several photographs are used together to make one figure, they should be well matched for tonal range. Lettering or arrows should be placed on by authors using suitable transfer film. Colour photographs may be allowed if colour is an essential feature of the result but the author may be asked to contribute to the cost. Four photocopies/copies should be provided for circulation to referees.

Figure legends

Legends should be grouped on a separate sheet, and furnish enough detail so that the figure can be understood without reference to the text.

Tables

Each table should be on a separate page, numbered and accompanied by a title at the top.

References

References to work by up to three authors in the text should be in full on first mention, e.g. (Able, Baker & Charles 1986), then subsequently abbreviated (Able *et al.* 1986). When different groups of authors with the same first author and date occur, they should be cited thus: (Able, Baker & Charles 1986a; Able, David & Edwards 1986b), then subsequently abbreviated to (Able *et al.* 1986a; Able *et al.* 1986b). If the number of authors exceeds three, they should always be abbreviated thus: (Frank *et al.* 1986). The references in the list should be in alphabetical order with the journal name unabbreviated. The format for papers, entire books and chapters in books is as follows:

Boutin, C. & Harper, J.L. (1991) A comparative study of the population dynamics of five species of *Veronica* in natural habitats. *Journal of Ecology* **79**, 199–221.

Cockburn, A. (1991) *An Introduction to Evolutionary Ecology*. Blackwell Scientific Publications, Oxford.

Sibly, R.M. (1981) Strategies of digestion and defecation. *Physiological Ecology* (eds C. R. Townsend & P. Calow), pp. 109–139. Blackwell Scientific Publications, Oxford.

Platenkamp, G.A.J. (1989) *Phenotypic plasticity and genetic differentiation in the demography of the grass* Anthoxanthum odoratum *L.* Ph D thesis, University of California, Davis.

References should be cited as 'in press' only if the paper has been accepted for publication. Other references should be cited as 'unpublished' and not included in the list. Three copies of any paper cited as 'in press' must be included with the typescript so that they can be sent to referees. Work not yet submitted for publication may be cited in the text and attributed to its author as: 'full author name, unpublished data'.

Units and symbols

Authors are requested to use the International System of Units (SI, Système International d'Unités) where possible for all measurements (see *Quantities, Units and Symbols*, 2nd edn (1975) The Royal Society, London). Note that mathematical expressions should contain symbols, not abbreviations. If the paper contains many symbols, it is recommended that they should be defined as early in the text as possible, or within a subsection of the Materials and methods section.

Scientific names

Give the Latin names of each species in full, together with the authority for its name, at first mention in the main text. If there are many species, cite a *Flora* or check-list which may be consulted for authorities instead of listing them in the text. Do not give authorities for species cited from published references. Use scientific names in the text (with colloquial names in parentheses, if desired).

Makers' names

When a special piece of equipment has been used it should be described so that the reader can trace its specifications by writing to the manufacturer; thus: Data were collected using a solid-state data logger (CR21X, Campbell Scientific, UT, USA).

Mathematical material

Mathematical expressions should be carefully represented, denoting Greek symbols and small fonts by a note in the margin; superscripts and subscripts by the marks V and , respectively, and bold font by zig-zag underline. Suffixes and operators such as d, log, ln and exp will be set in Roman type; matrices and vectors will be set in bold type; other algebraic symbols will be set in italic. Make sure that there is no confusion between similar characters like l ('ell') and 1 ('one'). Also make sure that expressions are spaced as you would like them to appear, and if there are several equations they should be identified by a number in parentheses.

Numbers in tables

Do not use an excessive number of digits when writing a decimal number to represent the mean of a set of measurements (the number of digits should reflect the precision of the measurement).

Numbers in text

Numbers from one to nine should be spelled out except when used with units; e.g. two eyes but 10 stomata and 5°C.

Journal: Functional Ecology

1. The effects of clipping and burning on the allocation of total nonstructural carbohydrates in *Imperata cylindrica*

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4. Allocation, defoliation, total nonstructural carbohydrates

Summary

1. *Imperata cylindrica*, a rhizomatous grass species, occurring in the Cape Flats Nature Reserve, South Africa was studied. This grass is known globally as a weed in a number of crops.

2. Different defoliation treatments did not induce the expected decrease in total nonstructural carbohydrates. This substantiates the claim that total nonstructural carbohydrates are of less importance in the regrowth of grasses, following defoliation, as opposed to shrubs.

3. Plants that received the burn treatment replaced above ground material faster than the other defoliation treatments. This could be due to the mineral enrichment of the soil following the fire.

4. Only the burn and basal clipping treatments induced flowering.

Key-words:

Imperata cylindrica, total nonstructural carbohydrates, allocation, defoliation, clipping, burning.

2.1. Introduction

It is logical to assume that once a plant is defoliated it must replace lost material in order to survive and remain competitive in its environment. Hence, plant growth is generally proportional to the balance of carbon gains and carbon losses. The components of the carbon balance provide us with a theoretical understanding of how carbon is gained or lost, and how this affects growth and productivity (Amthor & McCree 1990). Photosynthesis is the main physiological process through which the plant acquires carbon. Stress that limits the uptake of atmospheric carbon dioxide and its subsequent diffusion further into the leaf, will limit the carbon gain of the plant (Amthor & McCree 1990). Respiration refers to the oxidation of organic compounds by a series of enzyme-catalyzed reactions in living cells, releasing energy used in growth, maintenance and repair, intercellular transport, and mineral nutrient assimilation (Penning de Vries 1975). Carbon is also lost from the plant through abscission, leaching, herbivory, volatilization and exudation (Mooney 1972).

The carbon in a plant can be divided into two categories, namely, structural carbon and nonstructural carbon. Structural carbon increases through a process called growth, which is dependent on photosynthesis and respiration. As the name implies, structural carbon is found in the structures of the plant, be it tissues or organs (Amthor & McCree 1990).

Nonstructural carbon refers to the carbon that can be accumulated and then readily be mobilized for metabolism or for translocation to other plant parts. There is still much debate over which compounds present the principal source of carbon for regrowth.

White (1973) suggested that nonstructural carbohydrates are the main carbon reserves used for regrowth in grasses. White (1973) stated that in 1927, Graber and co-workers considered not only nonstructural carbohydrates to be an important reserve energy source, but also nitrogenous compounds. White (1973) conceded that nitrogenous compounds might be used for respiration, and although evidence of this phenomenon was presented (Davidson & Milthorpe 1966), nitrogenous compounds are not alternately stored and utilized as is the case with nonstructural carbohydrates.

Another factor which affects the correlation between regrowth following defoliation and nonstructural carbohydrates, is photosynthesis during the 'recovery' period (Richards 1986). Upon removal of photosynthetic tissue, regrowth and maintenance of remaining tissues is dependent on stored nonstructural carbohydrates (Caldwell *et al.* 1981). Thereafter, as photosynthetic surface area is replaced, the role of regrowth and maintenance of the recovering plant is gradually taken over by recently assimilated photosynthetic carbon (Caldwell *et al.* 1981; Richards 1986).

Observations and conclusions made by Caldwell *et al.* (1981) and Richards (1986) were based on the responses of *Agropyron* bunchgrasses. Thus, the responses mentioned earlier, are specific to these grasses. Defoliated grass plants decrease stored carbohydrates immediately and continue using them for only a few days (Davidson & Milthorpe 1966; White 1973). It is probably this quick response of grasses, following disturbance, which prompts McNaughton (1986) to suggest that grasses compensate for defoliation. Whether it is beneficial or not, is perhaps not the right question to ask. As McNaughton (1986) pointed out: "... grasses (as species ecotypes, or genotypes) that dominate grazed grasslands but disappear in the absence of the grazers, are obligate grazophiles and would not exist in the absence of the grazers." It is known that grazing maintains grasslands. The absence of defoliation results in a significant increase in tree density (Medina & Silva 1990). At the ecosystem level, defoliation by grazing or fire seems to be beneficial in that it maintains the grassland and prevents a shift to savanna or bushveld. At the individual plant level, the grass has to endure the removal of its photosynthetic area. Whether this causes it to break out of its moribund state and to grow faster without the constraints of old or dying material, is not debated here. What is important is that defoliation, of whatever kind, usually translates into a loss for the plant. Whether the plant compensates or overcompensates, it has to find those resources required for growth from the environment, be it light, nutrients or water.

The aim of this study was to determine the allocation and concentration patterns of biomass and total nonstructural carbohydrates of *I. cylindrica* to its tissues, and how this was affected by fire and clipping. The allocation and concentration were studied over a period of fifteen weeks. Allocation refers to the differential movement of materials to and from organs (Fitter & Setters 1988). It is also known that mineral nutrients are not allocated synchronously (Abrahamson & Caswell 1982, Benner & Bazzaz 1988) and that the concentrations also vary greatly between plant tissues and at different growth stages (Abrahams & Caswell 1982). It would thus not be surprising if the same was to be found in this study for carbon. Because of scant research on resource allocation patterns, this study aims to ascertain where carbon is stored and/or translocated in *I. cylindrica*, and also to see whether there is any relation between resource allocation and biomass allocation.

2.2. Materials and Methods

This study was conducted in the Cape Flats Nature Reserve (CFNR), which is located on the University of the Western Cape campus in Bellville (33°56' and 18°37') (Fig. 2.1).

2.2.1. Experimental Design and Ecological Measurements

A randomized block experiment with four treatments, harvested on 15 consecutive weeks and replicated twice, was used. The four treatments included a control, a burn treatment, clipping at ground level (basal clipping), and clipping at 20 cm above the ground (partial clipping). Two plots were prepared in the Cape Flats Nature Reserve, one near the vlei and the other in a dune slack. Each of the sites were divided into $1m^2$ blocks whereafter the treatments were applied. At least one metre was left between the treatments to ensure that the effect of fire on the unburnt blocks was minimized.

Each plot had 15 blocks per treatment. Every week, a block was randomly selected for harvesting of plant material. From within the $1m^2$ block, above ground material was removed from a 50x50 cm area, while a 20x20x20 cm volume of belowground material and soil was removed from within the same block. Prior to harvesting, measurements such as live tiller number, live tiller height (taken from the tallest live tiller in the plot), inflorescence number, and inflorescence height (taken from the tallest inflorescence) were taken (Fig. 2.2). After harvesting, the plant material was sifted to remove any remaining soil from the roots, and then taken to the lab. Plant material was then oven dried to constant dry weight at 65°C and then sifted again to remove soil and other debris. The plant material was sorted into different tissue categories, namely leaves (tillers), stems (rhizomes), roots, and inflorescences. Plant material was then weighed and put through a Wiley intermediate mill using a 40 mesh screen. The milled material was placed in glass vials, redried (65°C) before sealing, and stored in dessicators until samples were analysed.

2.2.2. Chemical Analyses

Total nonstructural carbohydrates were extracted from 1500 mg tissue samples, using the modified Weinmann method (Smith 1981). The samples were boiled for 5 min in 15 cm^3 distilled water. After cooling, 183 units of amyloglucosidase enzyme (from *Asperilligus niger*, Sigma Chemical Company), buffered to a pH of 4.5, were added and the tubes incubated at 55°C for 24 h (Van der Heyden 1992).

Samples were then filtered through Whatman No. 1 filter paper. Precipitation of proteins, pigments and other contaminants was achieved by adding lead acetate. Samples were then centrifuged at 8000 g for 20 minutes to remove the precipitate. The aliquots were acid hydrolysed (1 cm^3 1N H_2SO_4, 100°C water bath, 15 min), and neutralized with 1 cm^3 1N NaOH. This was followed by quantification of reducing power by titration (Smith 1981).

2.3. Results

2.3.1. Ecological Parameters

The effects of the treatments on form (tiller number, tiller height, inflorescence number, and inflorescence height) over the 15 week study period are shown in figures 2.2 a - d.

Tiller density

The largest significant difference between the treatments in terms of number of tillers per m^2, appears to have occurred during week 9 for the partial clip and control treatments. The burn treatment was significantly higher than the control treatment during weeks 6, 7, 9, and 14. The basal clip was significantly higher than the control treatment during weeks 13, 14 and 15. There was no significant difference between the basal clip and burn treatments over the 15 week study period (Fig. 2.2). In general the control treatment had fewer tillers per unit area..

Tiller height

Tiller height was taken as the height of the highest tiller in the measured plot. Thus, it was not surprising to find that the highest tillers were found in the control plots. This is in contrast with the control treatment having the lowest tiller number. This can be explained when looking at an uncut *I. cylindrica* stand (control). The grass looks very thick, tall and dense. However, most of the standing mass consists of dead tillers and only live tillers were counted. In general the control had significantly taller tillers than the other treatments. No significant differences were found when comparing only the basal clip, partial clip, and burn treatments.

Inflorescence number and height

Besides having significantly higher tiller numbers when compared to the control treatment, the basal clip and burn treatments were also the only treatments to induce flowering. The fire resulted in higher inflorescence density (week 8) but no significant difference in inflorescence height (Fig. 2.2).

2.3.2. Total nonstructural carbohydrates

Total nonstructural carbohydrate allocation (g/m^2)

The stem had significantly higher levels of TNC allocated ($p \leq 0.05$) to it than other tissues, indicating that it is the main storage organ of TNCs. This result was also found by Rusdy *et al.* (1995). The allocation patterns appear similar for the treatments, except for the inflorescences produced with the burn and basal clip treatments (Fig. 2.3). The partial clip treatment also shows the possible overestimation of tillers caused by lack of differentiation between remaining and new tillers.

Total nonstructural carbohydrate concentration (g/kg dry weight)

The stem is the primary storage organ for total nonstructural carbohydrates (TNCs), in terms of the concentration of TNCs (g/kg dry weight, $p \leq 0.01$).No significant differences could be found between tissues other than the stem, irrespective of the treatment (Fig. 2.4).

There was no significant difference in root, leaf, or inflorescence TNC concentration between the different treatments.

2.3.3. Allocation of biomass (g/m^2)

Biomass allocation appears very similar to the TNC allocation. This is mainly caused by the higher allocation of biomass to the stem and the resulting allocation of TNCs to this tissue. No significant differences were found between treatments or within a particular treatment. Again, the partial clip treatment shows higher leaf biomass (although not significantly different) compared to other treatments, caused by lack of differentiation between remaining and new tillers (Fig. 2.5).

2.4. Discussion

Burning and clipping caused a significantly higher number of tillers to be produced relatively early in the 6-10 week period for the burn treatment, and later during weeks 13 and 15, for the basal clip treatment, when compared to the control (Fig. 2.2). However, in terms of tiller height, the control had significantly taller tillers than the burn, basal clip, or partial clip treatments (Fig. 2.2). One would expect that the energy for the increased tiller numbers of the burn and basal clip treatments, would have come from the stored reserves held belowground. However, no decrease in stored total nonstructural carbohydrates (TNCs) occuredr (Figs. 2.3 and 2.4). There are a number of possible reasons for this. Firstly, the importance of stored carbohydrates following defoliation have been questioned by Ryle & Powell (1975), Richards & Caldwell (1985) and Danckwerts & Gordon (1987).

Richards & Caldwell (1985) found that for *Agropyron spicatum*, 4 to 11% of regrowth was due to stored carbohydrates, and the remainder was due to photosynthates. Yet, one would still expect a decrease in stem carbohydrates because burning and basal clipping removed 100% of the photosynthetic material. Richards & Caldwell (1985) removed only 85% of the aboveground material in their experiment. It would thus be expected that the dependency of *I. cylindrica* on the stored carbohydrates would be greater and that a decrease in stored reserves would be seen.

Initially, stored carbohydrates would be important to replace the lost photosynthetic material, and once this has occurred, the new leaves would produce photosynthates which would take over from the stored carbohydrates as an energy source (White 1973;

Naidoo & Steinke 1979; Caldwell *et al.* 1981; Chapin, Shaver & Kedrowski 1986a; Busso, Richards & Chatterton 1990).

A possible explanation why there was no reduction in the stem TNCs could be the difference in growth form between *I. cylindrica* and the *Agropyron* species used by Richards & Caldwell (1985). The *Agropyron* species are bunchgrasses (grasses without stolons or rhizomes; growth habit of forming a bunch or tussock) (Mullahey & Tanner 1997) while *I. cylindrica* is a rhizomatous grass. Although bunchgrasses have extensive root systems, they cannot be compared to the shoot systems of rhizomatous grass species in terms of size. *I. cylindrica* has an extensive underground system of interconnected rhizomes which seem to buffer the grass against any superficial defoliation, such as removing only the aboveground tillers. The results obtained Rusdy *et al.* (1995) seem to support the last statement. They used potted *I. cylindrica* which did show a decrease in stem TNCs following defoliation. This seem to indicate that these plants did not have the large underground store of reserves available to them under natural conditions.

It is probably this feature of *I. cylindrica* which makes it so difficult to eradicate. A stand of *I. cylindrica* in the field does not react as separate organisms, but rather as one individual. Removal of only the aboveground material, seems to stimulate the grass as it releases it from the stagnation of maintaining old, moribund tissue. In order to control *I. cylindrica*, clipping has to be applied at frequent intervals (Willard *et al.* 1996) and used in conjunction with other control methods (Patterson 1980, Anoko, Akobundu & Okonkwo 1991, Willard *et al.* 1996)

Another possibility could be the high proportion that the stem contributes to the total biomass of *I. cylindrica*, and also the high proportion of TNCs that is stored there. The decrease in TNCs during the first few weeks, can easily go undetected, mainly because of the high proportion of TNCs allocated to the stem. Stored carbohydrates are only used in the first few days in the recovery of lost photosynthetic tissues, and because weekly sampling was done in this study, a transient drop in TNCs could easily be missed.

The results show that burnt plots replace aboveground material quicker than basal clip plots. This is an expected result because burning, unlike clipping, returns mineral nutrients to the soil in the form of ash, which is readily usable by the grass. In terms of TNCs there is no distinction between any of the treatments and thus mineral enrichment by the fire seems to be the reason for this result.

The burn and basal clip treatments were also the only treatments which produced inflorescences. There was no significant difference between the number of inflorescences and the height of the inflorescences produced. The viability of the seeds remains questionable, because *I. cylindrica* tend to propagate itself mainly through vegetative means (Ayeni & Duke 1985, Anoko *et al.* 1991; Bryson & Carter 1993; Otsamo *et al.* 1995).

I. cylindrica is an opportunistic colonizer of disturbed, often wet, nutrient-poor areas. This is mainly prevalent where slash-and-burn cultivation is practised. Once established, it is often difficult to eradicate, although on nutrient-rich sites it is replaced by more competitive species (Brook 1989). *I. cylindrica* is a better competitor on nutrient poor soils because it has a low nutrient demand per unit dry matter production (it is relatively sclerophyllous), and possesses a high efficiency of nutrient uptake (Brook 1989).

I. cylindrica's strategy, once it establishes itself in an area, seems to be a wait-and-see approach. It builds up a large store of carbon below ground which it only uses when a disturbance induces it to flower. It seems as if *I. cylindrica* flowers irrespective of whether the end result will produce viable seed, or not. The reason for stating this is that some weeks prior to the start of this study, a natural fire went through a stand of *I. cylindrica*, and it produced taller inflorescences than the experimental plots of this study. The difference between that flowering and what I have found can be gauged by the amount of seed that was produced in the former's case, with seed covering the ground where the grass stood. So it seems as if *I. cylindrica* is obliged to make use of its reserves irrespective of the quality of the disturbance. Thus, its stored reserves are much more prone to any sporadic disturbance which might occur. Although this study could not duplicate the large flowering and seed dispersal observed elsewhere, weeks before this study was conducted, it must have had an impact on the stored reserves below ground.

Another effect that disturbances, such as fire and clipping have on *I. cylindrica*, is to ameliorate the nutrient status of the plant. Stands of *I. cylindrica* contain large amounts of dead and moribund tissue. When a fire moves through such a stand of *I. cylindrica*, it removes the dead and stagnating material, releasing *I. cylindrica* from maintaining this material. The loss of this material to grasses, like *I. cylindrica*, are minimal as the aboveground material contains little structural tissue (d'Antonio & Vitousek 1992). The loss of old material leads to an improvement in nutrient status of the plant, which activates new meristems to produce new growth. It is only when the moisture or nutrient stress has been removed that the accumulated reserves will be used for regrowth (White 1973, Bryant, Chapin & Clan 1983, Chapin, Vitousek & Van Cleve 1986b).

2.5. Acknowledgements

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2.7. Figures

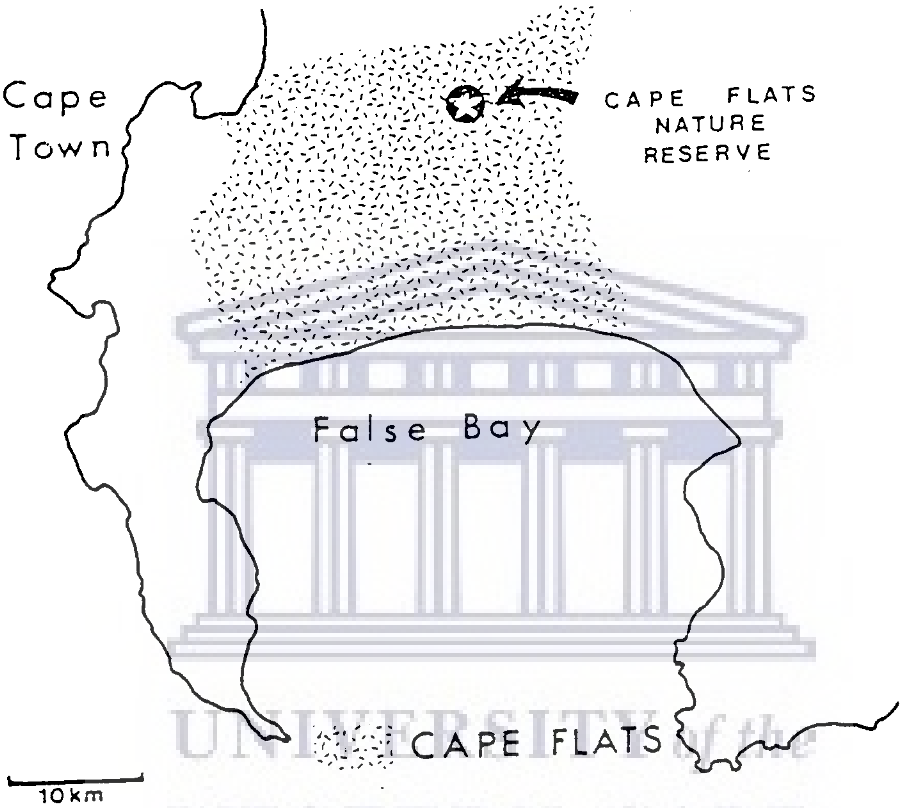

Figure 2.1. Location of the study area on the Cape Flats (Low 1982b).

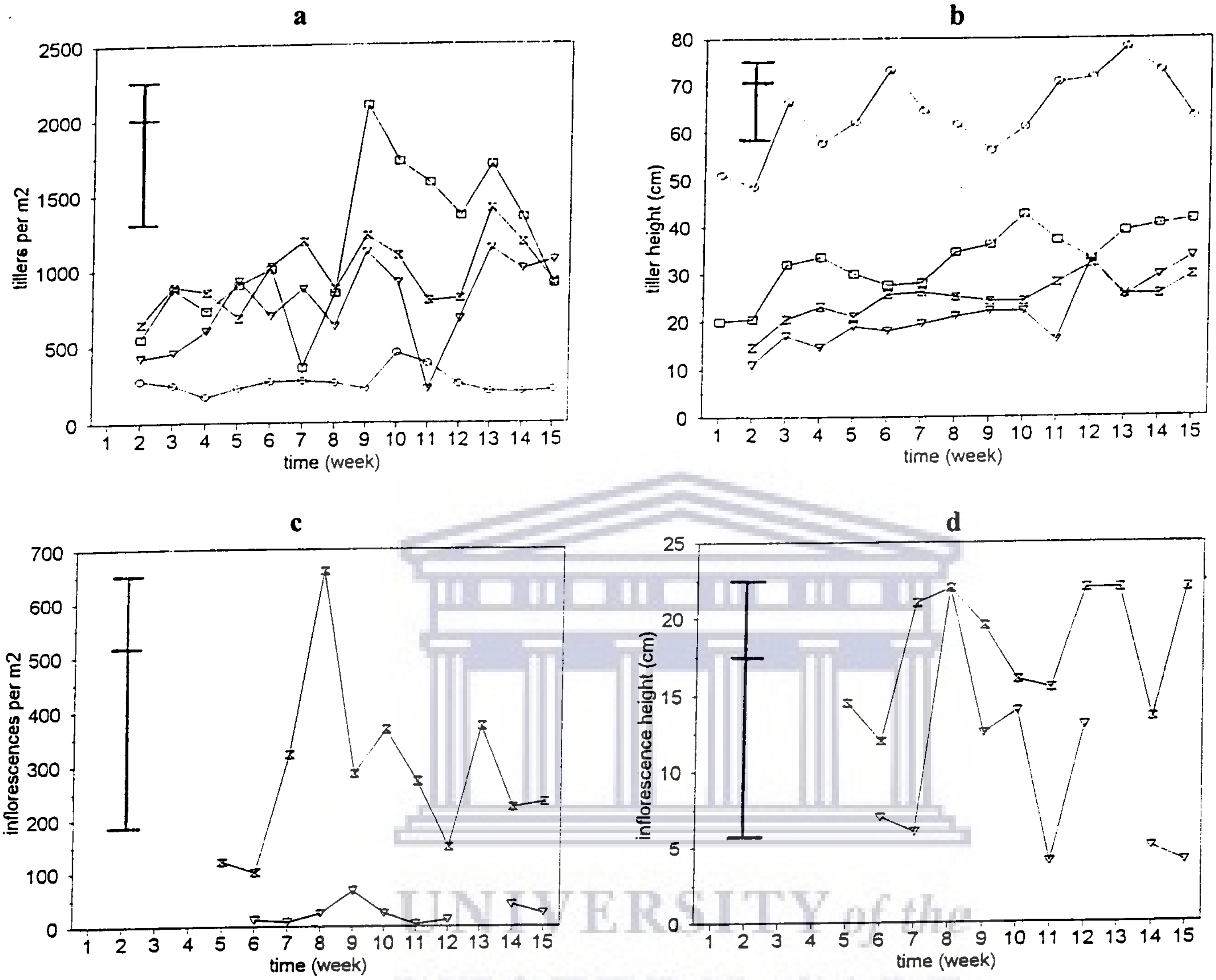

Figure 2.2. Change in (a) tiller density, (b) tiller height, (c) inflorescence density, (d) inflorescence height of *Imperata cylindrica* over fifteen weeks. ○=control, ⧖=burn, ▽=basal clip, □=partial clip. Vertical bar represent least significance differences of 0.01 and 0.05 respectively.

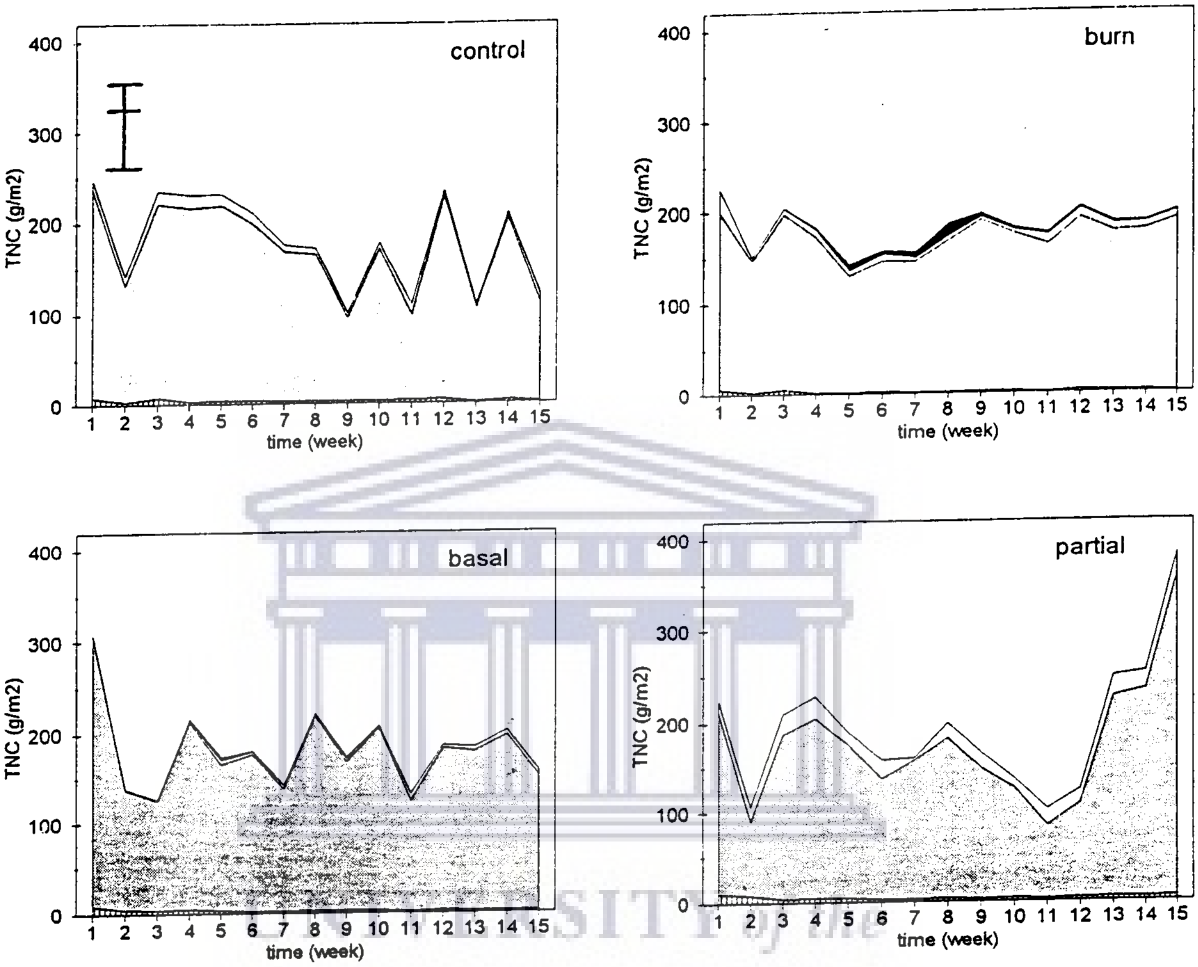

Figure 2.3. Total nonstructural carbohydrate allocation of *Imperata cylindrica* over fifteen weeks: Shading: Vertical lines, roots; stipling, stems; open, leaves; closed, inflorescences. Vertical bar represent least significance differences of 0.01 and 0.05 respectively.

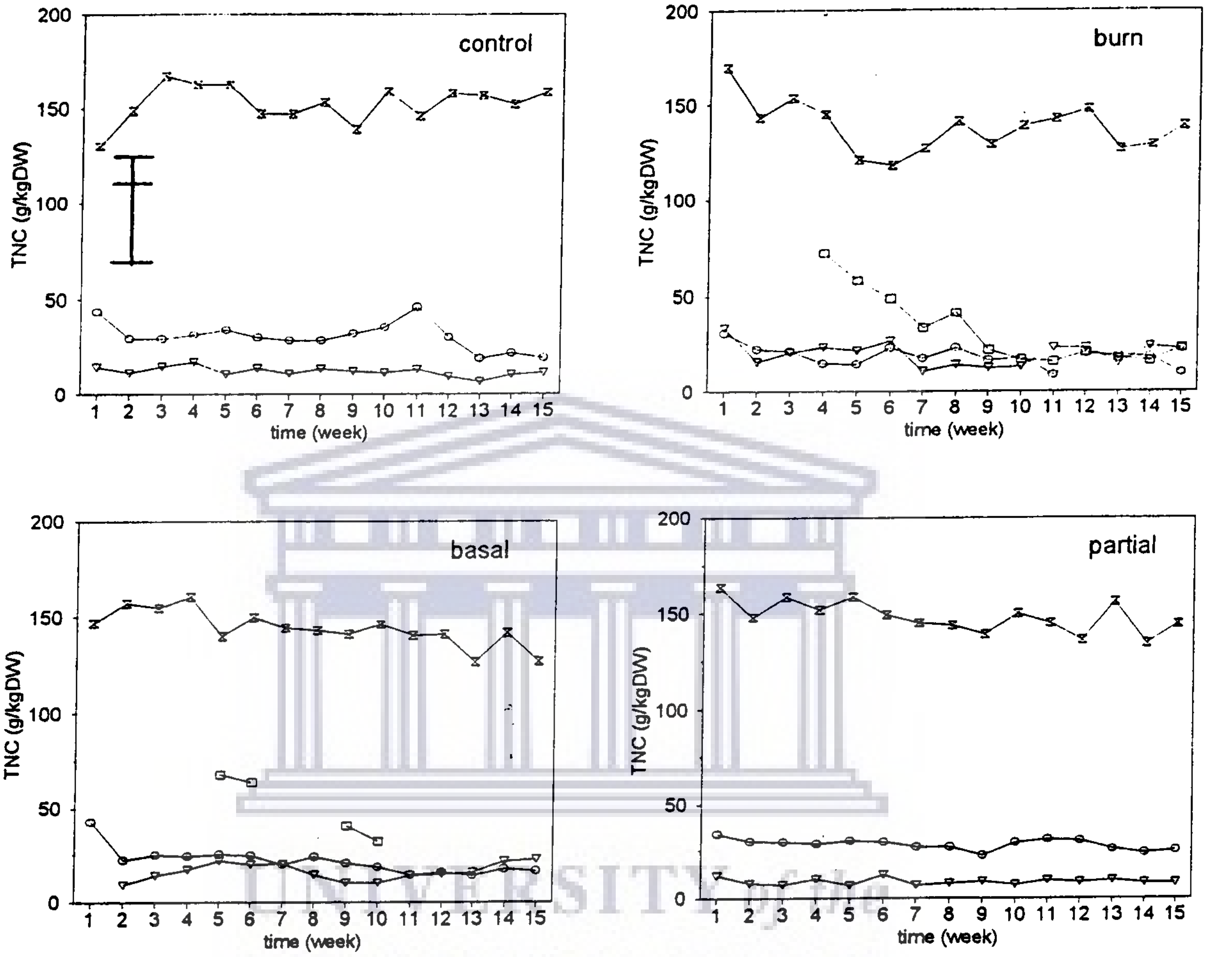

Figure 2.4. Total nonstructural carbohydrate concentration of *Imperata cylindrica* over fifteen weeks. o=roots, ⧖=stems, ∇=leaves, □=inflorescences. Vertical bar represent least significance differences of 0.01 and 0.05 respectively.

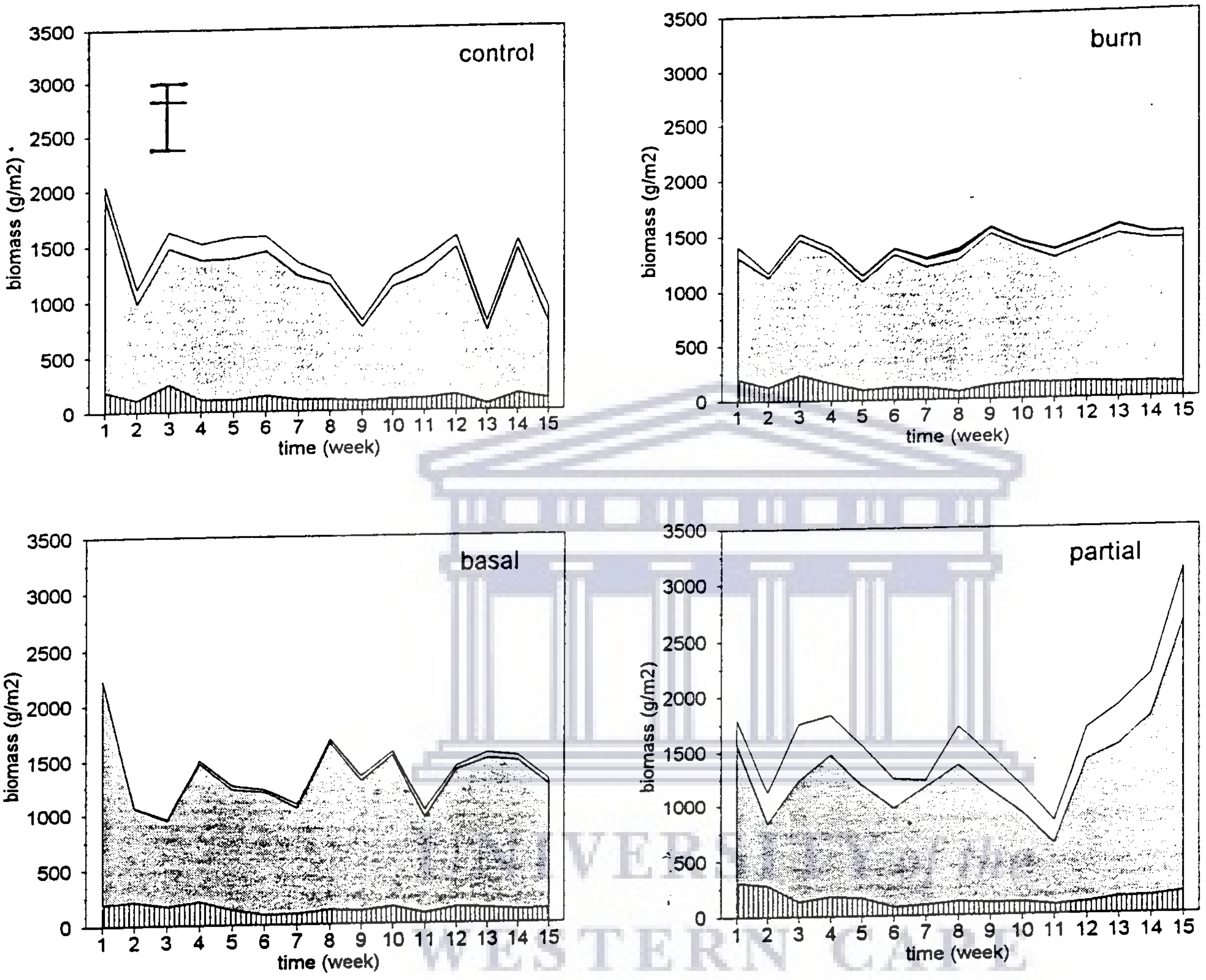

Figure 2.5. Biomass allocation of *Imperata cylindrica* over fifteen weeks. Shading: Vertical lines, roots; stipling, stems; open, leaves; closed, inflorescences. Vertical bar represent least significance differences of 0.01 and 0.05 respectively.

Chapter 3 MINERAL NUTRITION AND DEFOLIATION

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Acknowledgements.

References (see Specifications).

Tables (see Specifications). These should be referred to in the text as Table 1, etc. Do not present the same data in both figure and table form.

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Cockburn, A. (1991) *An Introduction to Evolutionary Ecology*. Blackwell Scientific Publications, Oxford.

Sibly, R.M. (1981) Strategies of digestion and defecation. *Physiological Ecology* (eds C. R. Townsend & P. Calow), pp. 109–139. Blackwell Scientific Publications, Oxford.

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Do not use an excessive number of digits when writing a decimal number to represent the mean of a set of measurements (the number of digits should reflect the precision of the measurement).

Numbers in text

Numbers from one to nine should be spelled out except when used with units; e.g. two eyes but 10 stomata and 5°C.

Journal: Functional Ecology

1. The effects of clipping and burning on the allocation of selected mineral elements in *Imperata cylindrica*

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4. Allocation, defoliation, mineral nutrients

Summary

1. The effect of different defoliation treatments on *Imperata cylindrica*, a rhizomatous grass species, occurring in the Cape Flats Nature Reserve, South Africa was studied. This grass is globally known to be a weed of crop plants.

2. The underground stem is the major storage organ for mineral nutrients.

3. The burn and basal clipping treatments induced raised leaf nitrogen and phosphorus levels, following defoliation.

4. Only the burn and basal clipping treatments induced flowering.

Key-words:

Imperata cylindrica, mineral nutrition, allocation, defoliation, clipping, burning.

3.1. Introduction

Defoliation increases the cycling of nutrients through a given system. Defoliation by fire and herbivory benefits plants, because nutrients are returned to the soil, where they can be utilized immediately. Cuttings of the aboveground plant material takes longer to recycle as the severed plant material has to decompose before becoming available to plants. Should clipped material be removed, then this benefit would be lost.

The Cape Flats Nature Reserve occurs on soils which are known to be nutrient-poor (Low 1983). It is thus conceivable that the *Imperata cylindrica* stands, which grow on these nutrient-poor soils, operate with a strategy which optimises the use of nutrients by mobilizing and recycling the limited nutrients, in order to survive (Bowen 1984). These stands of *I. cylindrica* are also fire-prone and need to safeguard these nutrients against any sporadic fire. This they do by having a large underground biomass, which stores the limited nutrients out of reach of fire (Westman & Rogers 1977). As already stated in the previous chapter, this underground store of reserves buffers the plant against any sporadic disturbance, such as fire.

The concept of allocation has been used by researchers in at least two ways. Firstly, biomass allocation can be extrapolated to give one a general idea of how other resources, be it carbohydrates or a mineral nutrient, are allocated within a given plant. The second approach does away with this extrapolation, and suggests rather that biomass together with other resources, need to be measured, to ascertain whether this pattern, as suggested by the first premise, is indeed true (Abrahamson & Caswell 1982).

The aim of this study was to determine the allocation and concentration patterns of selected mineral nutrients (nitrogen, phosphorus, potassium, magnesium, iron and the non-essential element, sodium) of *I. cylindrica* to its tissues, and how this is affected by fire and clipping. Like the carbon allocation study, the study period covered fifteen weeks. The allocation or movement of mineral nutrients (or any other resource) differs from one organ to another (Fitter & Setters 1988). Mineral nutrients are also not allocated synchronously (Abrahamson & Caswell 1982, Benner & Bazzaz 1988) and the concentrations also vary greatly between plant tissues and at different growth stages (Abrahams & Caswell 1982). It is for this reason, and also the scant research on resource allocation patterns, that this study aims to ascertain where resources are stored or translocated for *I. cylindrica*, and also to see whether there is any relation between resource allocation and biomass allocation.

3.2. Materials and methods

This study was conducted in the Cape Flats Nature Reserve (CFNR), which is located on the University of the Western Cape campus in Bellville (33°58' and 18°32') (Fig. 3.1).

3.2.1. Experimental procedures

The experimental design is the same as discussed in Chapter 2.

3.2.2. Chemical analyses

3.2.2.1. Digestion and analysis of plant material

Plant samples were digested using the hydrogen peroxide - sulphuric acid digestion method (Allen 1989). About 800 mg oven-dried plant material was placed in a digestion tube with 8.8 cm^3 digestion mixture. The digestion tubes were then randomly placed in a heating block. The starting temperature was 150°C, which allowed for the evaporation of water. Hereafter, the temperature was raised consecutively to 220°C, 250°C, 280°C, 300°C at one hour intervals, and finally to 350°C for 1½ hours. A faint yellow colour indicated that all plant material was digested. Samples that had not yet reached this point, were heated further until complete digestion of plant material was achieved. The tubes were then removed and allowed to cool. In order to prevent the digest from solidifying, and to ensure that the iron dissolved, water was added just before the tubes cooled down completely.

The solution was then quantitatively transferred to a 50 cm^3 volumetric flask and made to volume with distilled water and used in the following manner:
25 cm^3 for nitrogen analyses,
20 cm^3 for the phosphorus analyses,
and the remaining 5 cm^3 for the mineral nutrient determinations.

A standard curve was obtained by digesting aliquots with 0.1 to 18.0 mg N (depending on the tissue analysed), and also a blank.

3.2.2.2 Nitrogen

The Kjeldahl method was used to determine total nitrogen concentration. Excess NaOH was added to the acid digest, which was then distilled with a Buchi nitrogen distillation unit (Allen 1989). The distillate was captured in an Erlenmeyer flask containing 5cm^3

2% boric acid and titrated against 0.01 M standardized HCl solution.

3.2.2.3 Phosphorus

The Murphy & Riley (1962) method was used to determine the total phosphorus concentration. Eight cm^3 of the Murphy and Riley solution was added to 20 cm^3 of the digest in a 50 cm^3 volumetric flask and filled to volume with distilled water. An hour was allowed for colour development, after which the absorbance was read at 882 nm using a Pharmacia Novaspec II UV spectrophotometer.

3.2.2.4. Mineral nutrients

For the determination of the other mineral nutrients, potassium, magnesium, iron, and sodium, one cm^3 of the initial 5 cm^3 was made up to 50 cm^3. The concentrations of these elements was then determined by means of atomic absorption spectrophotometry.

3.3. Results

3.3.1. Nitrogen

Significantly higher levels of nitrogen were allocated to the stem than to other tissues ($p \leq 0.05$), regardless of treatment (Fig. 3.2). This was caused by the higher biomass of the stems when compared to other tissues (Fig. 3.3). There were no significant differences between the stem allocation pattern for the different treatments, except for the significantly higher stem nitrogen ($p \leq 0.01$) found for weeks 6 and 15, belonging to the control and partial clip treatments, respectively. Comparing the allocation of the other tissues for the different treatments showed no significant difference ($p \leq 0.05$).

The stem nitrogen concentration was significantly lower than the leaf and inflorescence nitrogen concentration for the burn and basal clipping treatments ($p \leq 0,05$; Fig. 3.4) This indicated that the significantly higher stem nitrogen allocation was due to the stem having higher biomass than the other tissues.

A comparison of stem nitrogen concentrations showed no significant differences between treatments. No significant difference was found when comparing root nitrogen concentrations. The leaf nitrogen concentrations were significantly different ($p \leq 0.05$). The burn and basal clip treatments, in general, were significantly higher ($p \leq 0.05$) than the control and partial clip treatments from week 2 up to the end of the study period. The inflorescence nitrogen concentrations of the burn and basal clip treatments were not significantly different. There were significant differences in the nitrogen concentration of the burn treatments' inflorescences over the 15 week study period. No significant difference were found during weeks 4 to 6, but the nitrogen concentrations were significantly higher (($p \leq 0.05$) than for weeks 7 to 15.

3.3.2. Phosphorus

As with nitrogen, higher levels of phosphorus were allocated to the stems than to other tissues ($p \leq 0.05$) (Fig. 3.5). Similarly, there were no significant differences between the allocation patterns for the different treatments, except for a few peaks caused by high stem phosphorus values such as at week 15 of the partial clip treatment. These peaks were probably artifacts caused by an uneven spread of biomass between the sample plots. This is shown by the way they parallel biomass allocation pattern (Fig. 3.3) rather than concentration (Fig. 3.6).

As with nitrogen concentrations, no significant difference was found between plant tissues for the control and partial clip treatments. Phosphorus and nitrogen concentration were also similar when comparing the burn treatments. However, significance ($p \leq 0.05$) was only found for weeks 3, 4, 7, 9, 10, 14 and 15. The burn treatment's inflorescences had significantly higher phosphorus levels than leaves for weeks 4 to 6 ($p \leq 0.01$), after which it decreased during weeks 8 and 9 ($p \leq 0.05$), after which it again decreased to levels similar to those of the leaves (Fig. 3.6).

The stem phosphorus concentration did not differ significantly when compared across the treatments; neither did root phosphorus concentration. The leaf phosphorus concentration of the burn and basal clip treatments were, in general, higher ($p \leq 0.05$) than that of the control and partial clip treatments. Inflorescence phosphorus concentration did not differ significantly for the burn and basal clip treatments. The inflorescence phosphorus concentration of the burn treatment showed similar decreases to that found for nitrogen.

3.3.3. Potassium

Generally, stems had more potassium allocated to it than the other tissues ($p \leq 0.05$), again because of its higher biomass. No significant differences were found for the other tissues. (Fig. 3.7). The peaks that do appear significant are probably artifacts caused by an uneven spread of biomass found in the sampling plots. This is shown by the way they parallel the biomass allocation pattern (Fig. 3.3) rather than concentration (Fig. 3.6)..

The stem potassium concentration was not significantly different from the other tissues belonging to the control or partial clip treatments. Significant differences did appear between the leaf and root potassium concentrations of these two treatments, with the latter being significantly higher in some instances. Comparing the tissues of the control and partial clip treatments, a similar pattern of non-significance, as found with the nitrogen and phosphorus concentrations, was found. However, more significant differences were found for the potassium concentration than for the nitrogen and phosphorus concentrations, but not enough to detract from the general trend which seems to be present (Fig. 3.8).

The potassium concentration of the burn and basal clip treatments also share a pattern with the nitrogen and phosphorus concentrations of the same treatments. In the first few weeks (week 1 to 3) there was no significant difference ($p \leq 0.01$) between the leaf and stem potassium concentrations of the two treatments. From week 4 to week 9 (for the basal clip treatment) or week 10 (for the burn treatment), the leaf concentration was significantly higher than the stem concentration. During the following weeks, the difference between the two once again became insignificant. The inflorescence potassium concentration for both basal clip and burn treatments was not significantly different from the leaf concentration, except for week 5 in the case of the burn treatment, and week 10 for the basal clip treatment, where the former was significantly higher than the latter.

No significant differences were found when comparing stem or root potassium concentrations across treatments. The leaf potassium concentrations shared a similar pattern with the nitrogen and phosphorus concentrations, with the burn and basal clip treatments generally having a significantly higher potassium concentration than the control and partial clip treatments ($p \leq 0.01$). The inflorescence potassium concentrations were significantly different for week 10. However, the basal clip treatment only produced sufficient inflorescences for analysis in weeks 5, 9 and 10. Again, the inflorescence potassium concentration of the burn treatment decreased from week 3 to 14 ($p \leq 0.05$) (Fig. 3.8).

3.3.4. Iron

Very few significant differences ($p \leq 0.05$) were found in the iron allocation for tissues and treatments. The stem seemed to have higher levels of iron allocated to it, but this was significant only in a few instances (Fig. 3.9).

No significant differences were found for iron concentrations, irrespective whether comparing within or between treatments, probably due to the high levels of variation found (Fig. 3.10).

3.3.5. Magnesium

Generally, significantly more magnesium was allocated to stems than to other tissues ($p \leq 0.05$) (Fig. 3.11). An allocation pattern similar to the previously discussed mineral nutrients was found. The roots had high levels of magnesium allocated to them but these differences were not significant.

The root magnesium concentration of the control and partial clip treatments were generally significantly higher ($p \leq 0.05$) when compared to stems and leaves. Stem and root magnesium concentrations were not significantly affected by any of the treatments. The leaf magnesium concentration for the basal clip and burn treatments were significantly higher than for the control and partial clip treatments for weeks 5 to 8 ($p \leq 0.05$) (Fig 3.12).

3.3.6. Sodium

The stem had more sodium allocated to it than the other tissues ($p \leq 0.05$), except for weeks 9 to 11 of the control treatment, and week 2 of the partial clip treatment. No significant differences were found for the other tissues (Fig. 3.13).

The stem sodium concentration was not significantly different from the other tissues, irrespective of the treatment. Significant differences did appear between the leaf and root sodium concentrations, with the latter being significantly higher in some instances. The significance though did not occur across the whole of the 15 week study period, with a few weeks showing no significant difference (Fig. 3.14). No significant differences were found when comparing root, stem, leaf, or inflorescence sodium concentrations across treatments (Fig. 3.14).

3.4. Discussion

3.4.1. Nitrogen

3.4.1.1. Allocation patterns

The stem, as for total nonstructural carbohydrates, is the major storage organ for nitrogen and also the other mineral nutrients, mainly because of the high proportion it contributes to the total plant biomass (Figs 3.2 and 3.3). The biomass allocation and nitrogen allocation patterns appear similar. This is mainly due to the predominance of the stem. This similarity should thus not be surprising as the nitrogen allocation pattern, as well as other allocation patterns in this study, are largely a function of the large biomass of the underground stem

The biomass allocation pattern is mainly determined by the stem. The peaks and troughs which are seen, are mainly due to an uneven spread of biomass over the experimental plots (Fig. 3.3). Because of the relative stability of the stem, in terms of biomass, the pattern does not change from one treatment to the other. The only discernable change amongst the treatments is the presence of inflorescences in the burn and basal clip treatments, although in the latter's case it is difficult to see, because of the small contribution made by the inflorescences. Inflorescences start to appear from week 3 for the burn treatment and a week later for the basal clip treatment. Another difference is the partial clip treatments relatively higher, although not significant, biomass allocation to leaves. As already explained, this is probably an artifact of sampling. The partial clip treatment was expected to react similarly to the control treatment. However, at the end of the study, it seems to allocate more resources to its underground stems.

3.4.1.2. Concentration patterns

The nitrogen concentrations found during this study compare well those of other studies (Table 3.1). There were no significant differences between the nitrogen concentrations of the different tissues of the control treatment. The leaves did not have a higher nitrogen concentration than the other tissues, which would be surprising for most other plant (Fig. 3.4). *Imperata cylindrica*, however, is known to be of low nutritive value as forage (Rusdy *et al.* 1995). This seems to indicate the protein content of the blades is low, pointing to a high nitrogen use efficiency, a property it shares with evergreen plants (Wedin 1995). This result is very similar to that found by Chapin, Johnson & McKendrick (1980) for *Eriophorum vaginatum* (a graminoid) and *Ledum palustre* (an evergreen shrub). This is in contrast to the deciduous species which had a seasonal pattern for nitrogen concentration (Chapin *et al.* 1980). *Imperata cylindrica* could possibly respond as an evergreen plant because in the Cape Flats Nature Reserve (CFNR) it grows on oligotrophic soils. Thus, storing nitrogen and other mineral nutrients in leaves, would confer a selective advantage on the plant (Moore 1984).

Evergreen shrubs and trees do not respond to fertilization because of their inherent slow growth compared to deciduous species (Rundel 1991). However, grasses could respond with an increased productivity when fertilized with nitrogen (Wedin 1995) or when a fire releases mineral nutrients to the soil. On soils with low N availability, species which produce more dry matter per unit N incorporated (high N use efficiency), may outcompete those less efficient at using N (Chapin *et al.* 1980, Vitousek 1982).

It appears as if the nitrogen data of this study supports the view that *I. cylindrica* uses an opportunistic wait-and-see approach. It uses a strategy similar to an evergreen, that is, investing proportionately little mineral nutrient per unit dry weight and having a slow growth rate. However, when a fire occurs, *I. cylindrica* is able to take advantage of being released from maintaining moribund above ground material, and also from the improved mineral nutrient status. The response of the burn and basal clip treatments support this statement because the leaf nitrogen concentrations were significantly higher for these two treatments from week 2 until the end of the study period. The new growth produced had a significantly higher leaf nitrogen than the leaves it was replacing. The new growth would be able to have a higher photosynthetic capacity than the older leaves, which means it could quickly replace all of the lost aboveground photosynthetic material. As the new leaves age, so its photosynthetic capacity decreases (Waring 1991).

3.4.2. Phosphorus

3.4.2.1. Allocation patterns

The stem is also the major storage organ for phosphorus. The biomass allocation and phosphorus patterns appeared very similar, again due to the predominance of the stem (Figs 3.3 and 3.5).

As with nitrogen, this pattern should be expected as the stem contributes most of the total plant biomass.

3.4.2.2. Concentration patterns

The phosphorus levels found were very low when compared to levels found in other studies (Table 3.1). This is due to the nutrient-poor soils of the Cape Flats Nature Reserve, and is also an indication of the low nutritive value of *I. cylindrica*'s leaves.

The phosphorus levels showed a similar pattern to that of the nitrogen concentrations. There were no significant differences between the tissues of the control and partial clip treatments. The leaf phosphorus concentration of the burn and basal clip treatments were significantly higher than that of the control. The burn and basal clip treatments took two weeks before any regrowth of significance appears (Fig. 3.6). It was this new growth which exhibited the higher nitrogen and phosphorus levels. This is not surprising as new leaves have a higher photosynthetic capacity than older leaves (Waring 1991). However, in comparison to the phosphorus concentrations of other plants, the phosphorus concentrations found are extremely low. There is also a trend in evergreen plants, with low photosynthetic capacity and a relatively high weight per unit of surface area, to have very few nutrients in its foliage (Waring 1991). The stem is again the primary storage organ because of its biomass (Fig. 3.3). However, in terms of units per dry weight, it is not any different from the roots or the leaves.

3.4.3. Potassium, iron, magnesium and sodium

3.4.3.1. Allocation patterns

Potassium, iron, magenesium and sodium allocation patterns (Figs. 3.7, 3.9, 3.11, 3.13, respectively) look very similar to the biomass allocation pattern (Fig. 3.3).

3.4.3.2. Concentration patterns

3.4.3.2.1. Potassium

The potassium concentrations found in the tissues of *I. cylindrica* were extremely low compared to other plants (Fig. 3.8). Like nitrogen and phosphorus, this is caused by the oligotrophic soils of the CFNR.

There was a significant difference between the leaf and root potassium concentrations (Fig. 3.8). Generally, in the case of the control and partial clip treatments the roots had higher levels of potassium than the leaves. This pattern was reversed in the case of the burn and basal clip treatments, because of the new leaves produced.

3.4.3.2.2. Iron

The iron concentration found in this study compared well to levels found in other studies (Table 3.1). However, there were no significant differences for any of the tissues or treatments in terms of iron concentration (Fig. 3.10).

3.4.3.2.3. Magnesium

The root magnesium concentrations were generally significantly higher ($p \leq 0,05$) when compared to the stem and leaves. Stem and root magnesium concentrations were not significantly different, irrespective of the treatment. The leaf magnesium concentration for the basal clip and burn treatments were significantly higher than the control and partial clip treatments for the weeks 5 to 8 ($p \leq 0,05$) (Fig. 3.12). The higher magnesium concentration found in the leaves can be ascribed to the new leaves that were produced following basal clipping and burning.

3.4.3.2.4. Sodium

There was significant differences when comparing the leaf and root sodium concentrations, with the latter being significantly higher in some instances. This significant difference is however not evident across the entire 15 week study period, a few weeks showing no significant difference. No significant differences were found when comparing root, stem, leaf, or inflorescence sodium concentrations across treatments (Fig. 3.14).

It was expected that sodium could possibly partially replace potassium. However, no relation was found between sodium and potassium (Fig. 3.15).

3.5. Acknowledgements

This study was funded by the University of the Western Cape (UWC) and the Foundation for Research Development (FRD). The Agricultural Research Council - Range and Forage Institute (ARC-RFI) is thanked for the use of their laboratory. The Environmental Education Resource Unit (EERU) at UWC, also assisted this project.

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3.7. Figures

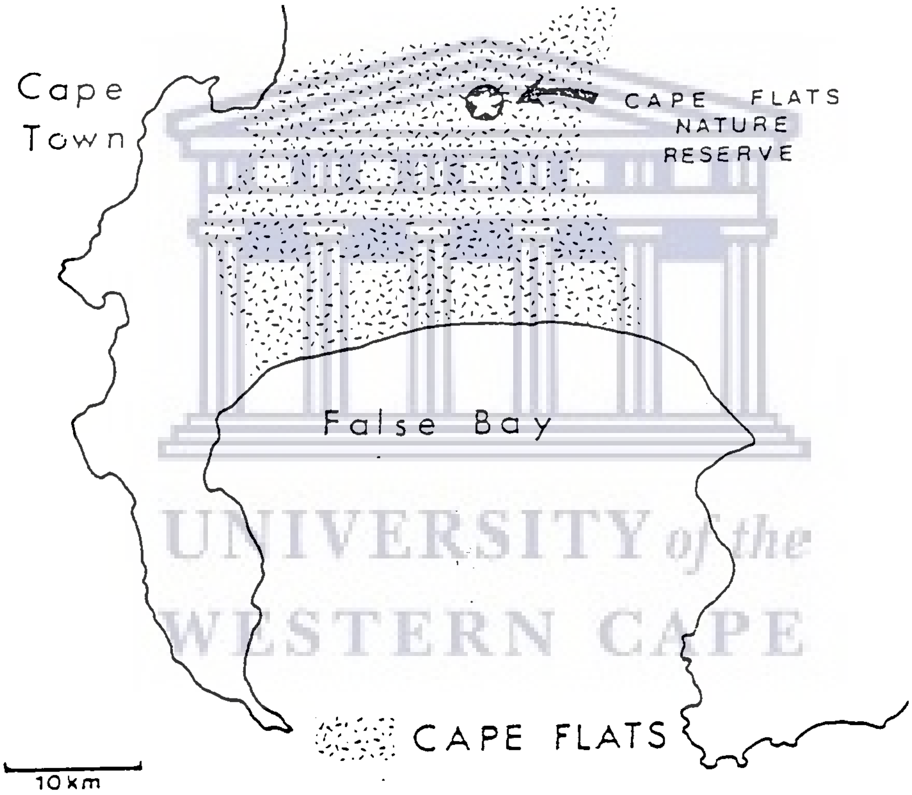

Figure 3.1. The location of the Cape Flats Nature Reserve (CFNR) on the Cape Flats (Low 1982b).

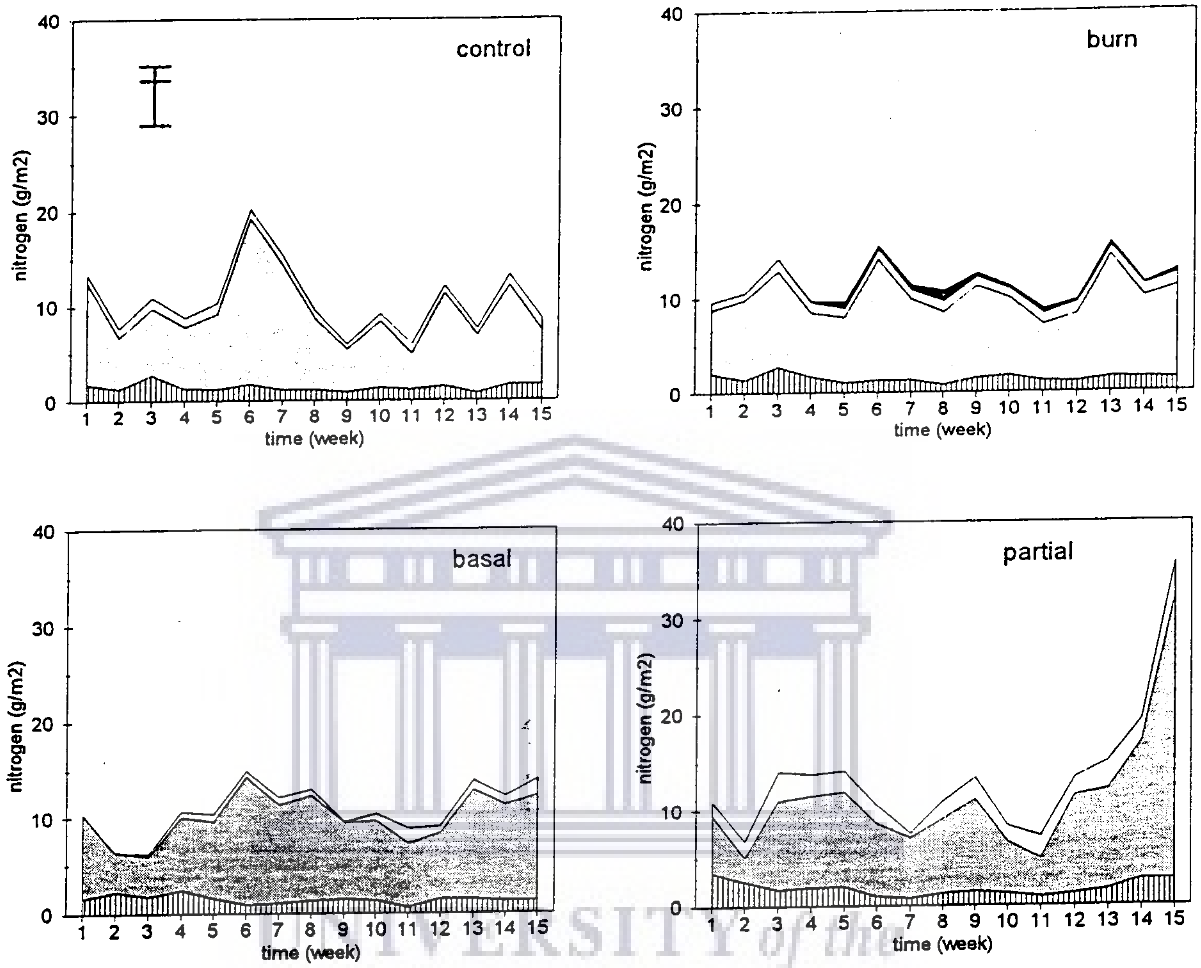

Figure 3.2. Nitrogen allocation (g/m^2) of *Imperata cylindrica* treatments (control, burn, basal clipping and partial clipping) over fifteen weeks. Shading: Vertical lines, roots; stipling, stems; open, leaves; closed, inflorescences. Vertical bar represent least significant differences of 0.01 and 0.05 respectively.

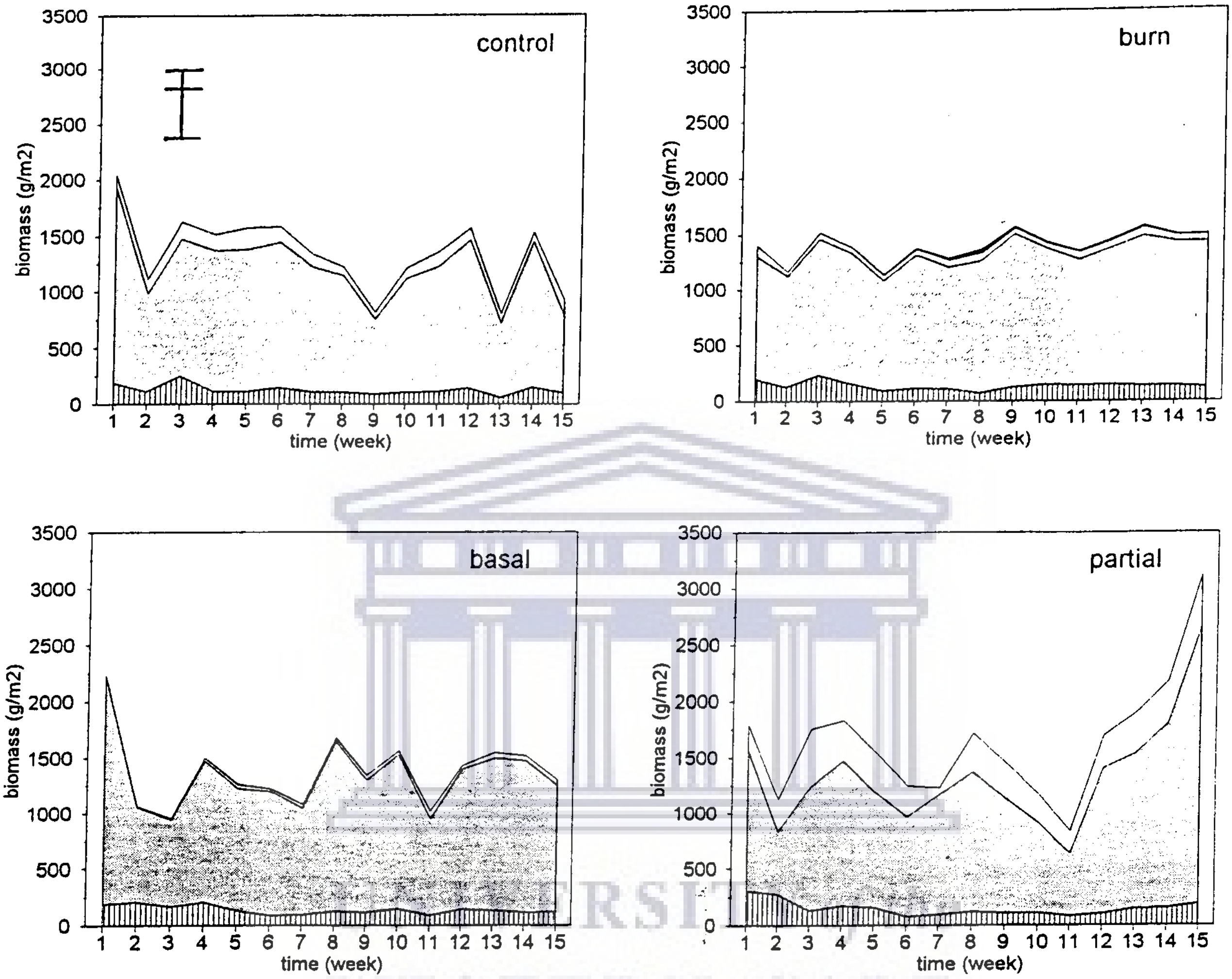

Figure 3.3. Biomass allocation (g/m^2) of *Imperata cylindrica* treatments (control, burn, basal clipping and partial clipping) over fifteen weeks. Shading: Vertical lines, roots; stipling, stems; open, leaves; closed, inflorescences. Vertical bar represent least significant differences of 0.01 and 0.05 respectively.

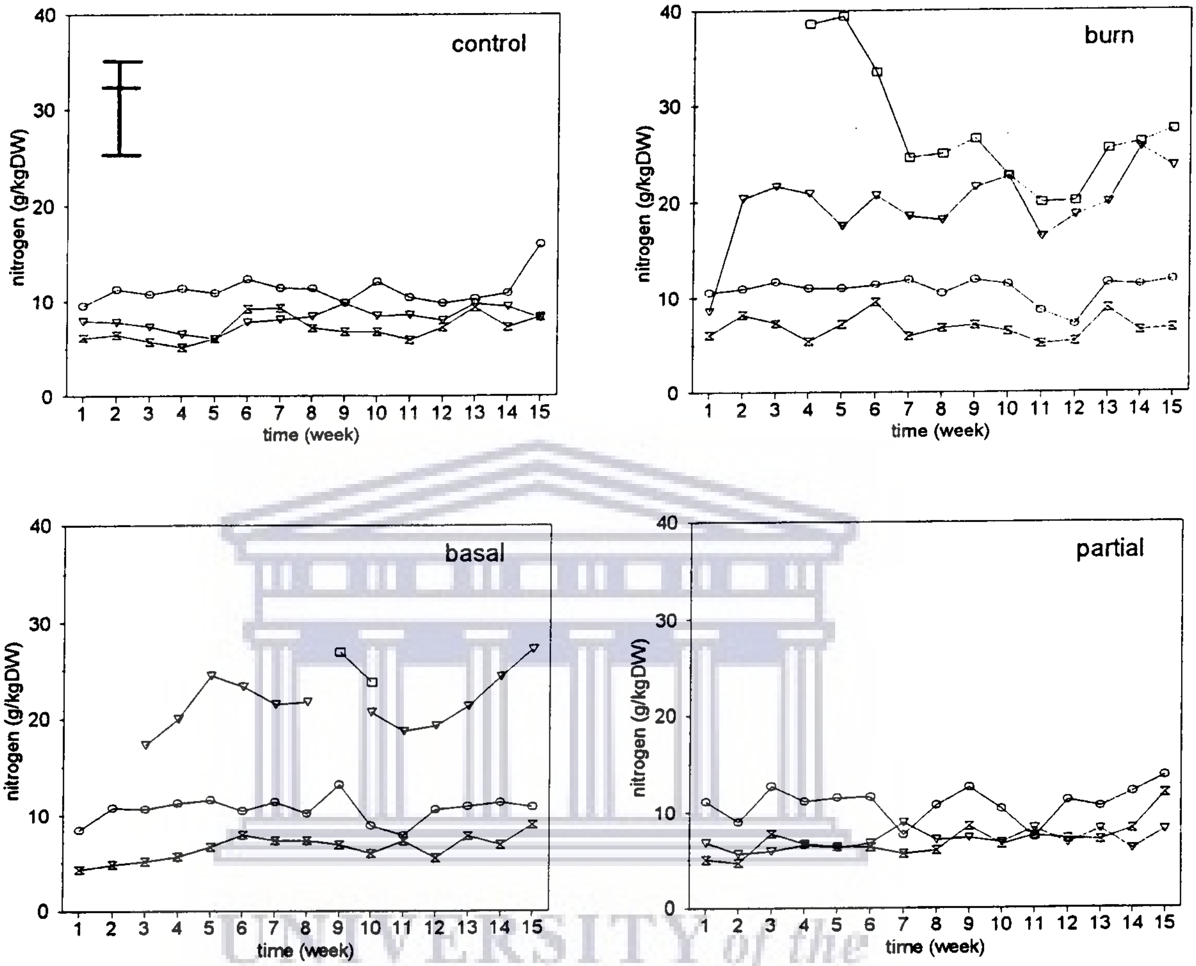

Figure 3.4. Nitrogen concentration (g/kg DW) of *Imperata cylindrica* treatments (control, burn, basal clipping and partial clipping) over fifteen weeks. ○=roots, ⧖=stems, ▽=leaves, □=inflorescences. Vertical bar represent least significant differences of 0.01 and 0.05 respectively.

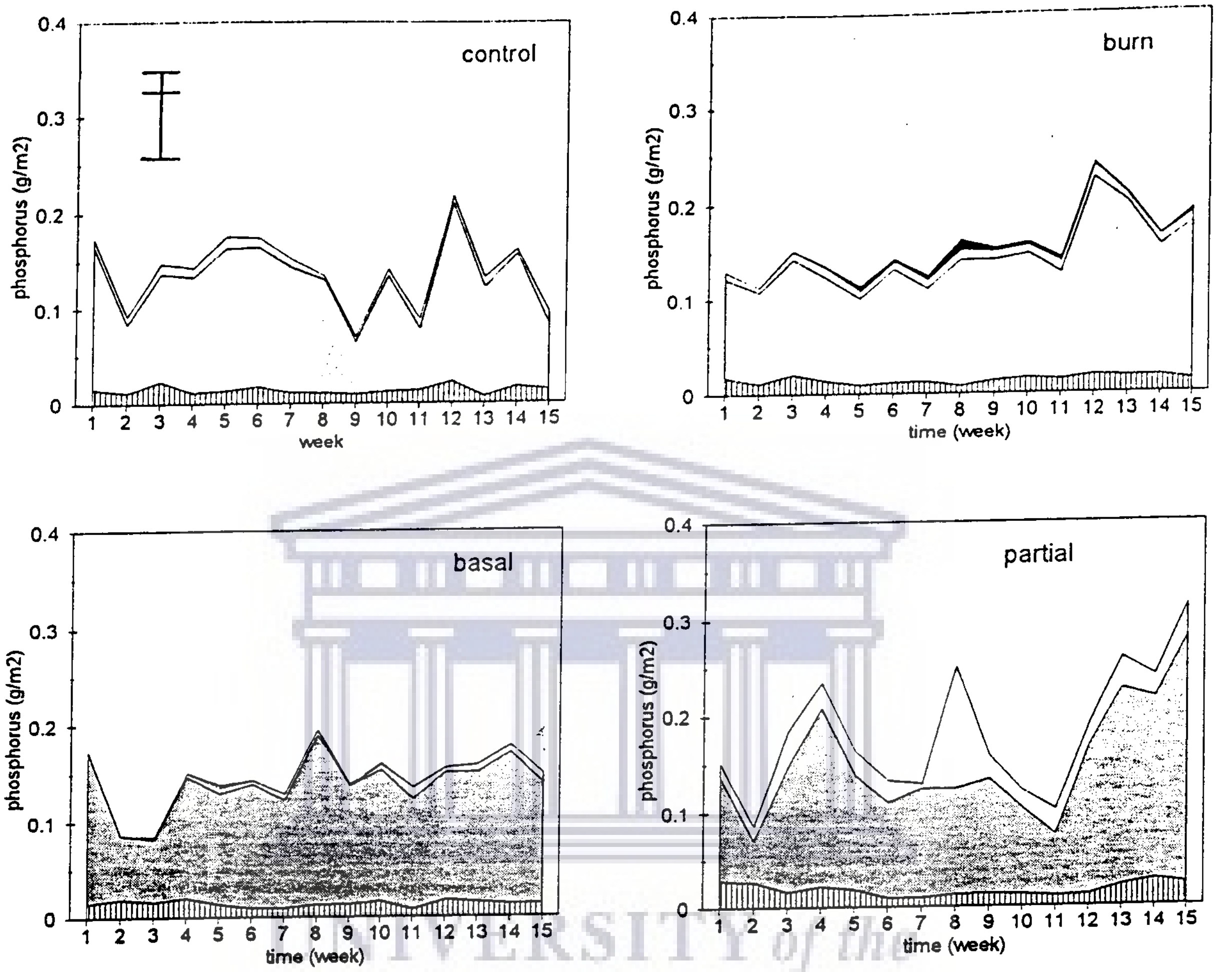

Figure 3.5. Phosphorus allocation (g/m^2) of *Imperata cylindrica* treatments (control, burn, basal clipping and partial clipping) over fifteen weeks. Shading: Vertical lines, roots; stipling, stems; open, leaves; closed, inflorescences. Vertical bar represent least significant differences of 0.01 and 0.05 respectively.

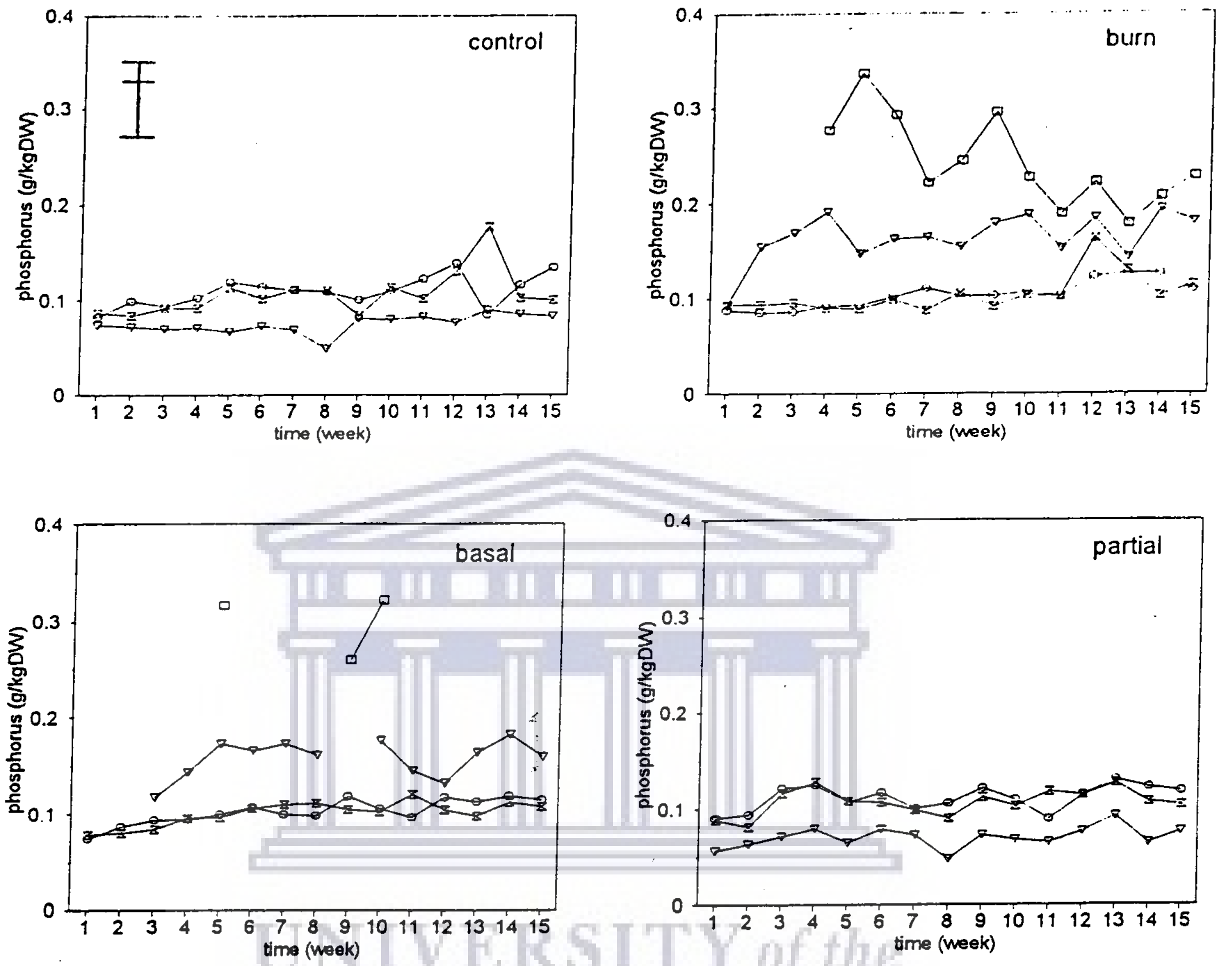

Figure 3.6. Phosphorus concentrations (g/kg DW) of *Imperata cylindrica* treatments (control, burn, basal clipping and partial clipping) over fifteen weeks. ○=roots, ⧖=stems, ▽=leaves, □=inflorescences. Vertical bar represent least significant differences of 0.01 and 0.05 respectively.

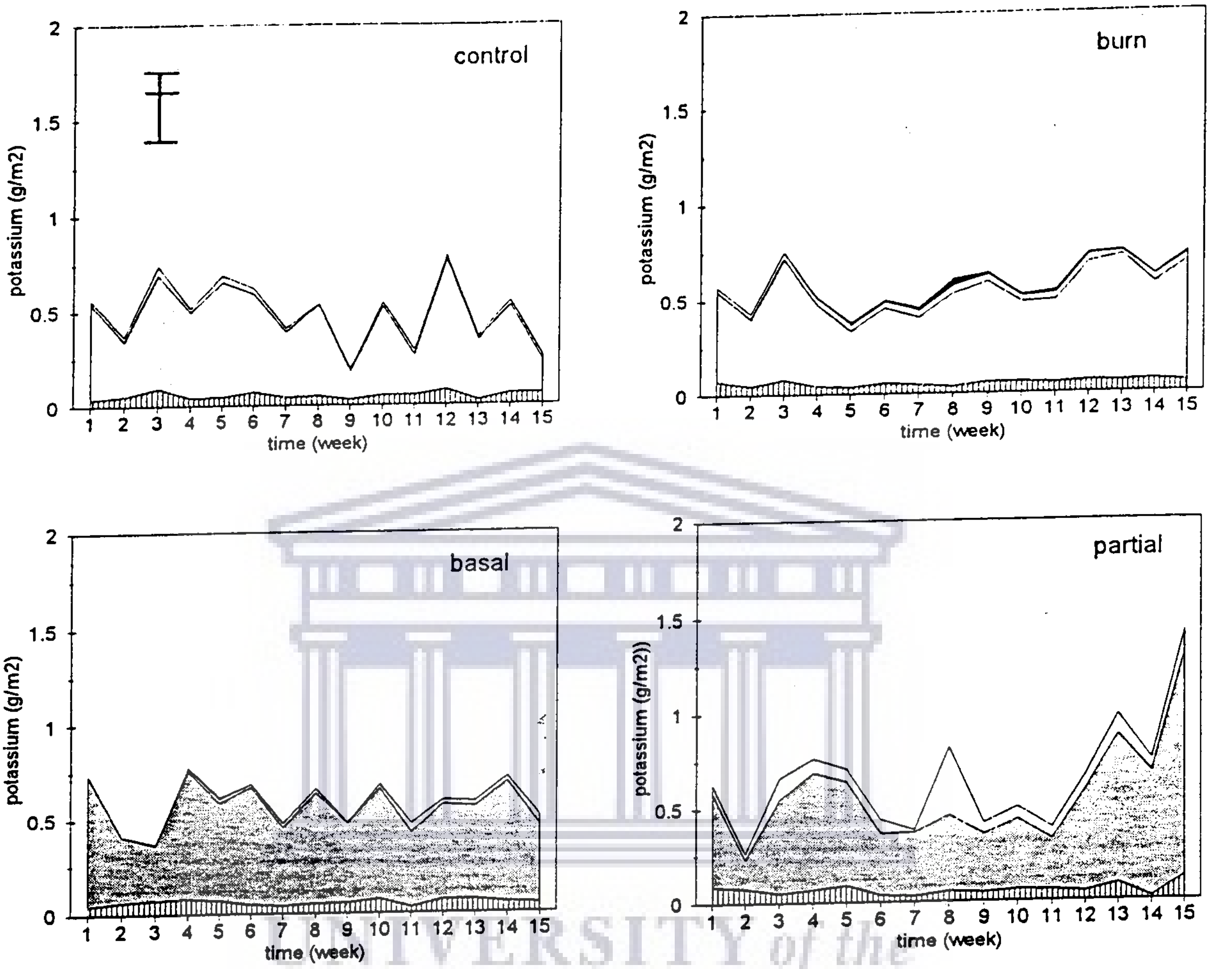

Figure 3.7. Potassium allocation (g/m^2) of *Imperata cylindrica* treatments (control, burn, basal clipping and partial clipping) over fifteen weeks. Shading: Vertical lines, roots; stipling, stems; open, leaves; closed, inflorescences. Vertical bar represent least significant differences of 0.01 and 0.05 respectively.

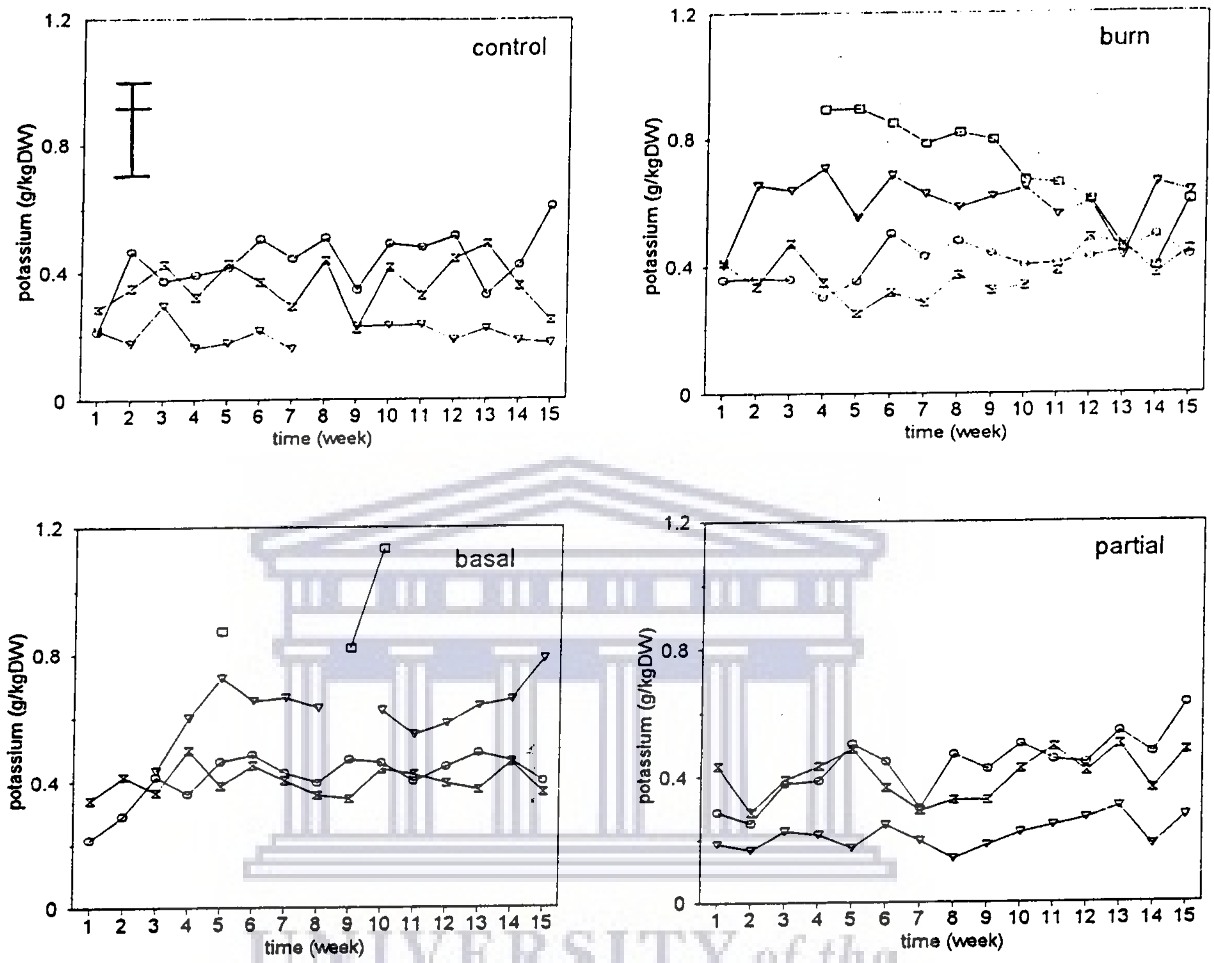

Figure 3.8. Potassium concentrations (g/kg DW) of *Imperata cylindrica* treatments (control, burn, basal clipping and partial clipping) over fifteen weeks. ○=roots, ⧖=stems, ▽=leaves, □=inflorescences. Vertical bar represent least significant differences of 0.01 and 0.05 respectively.

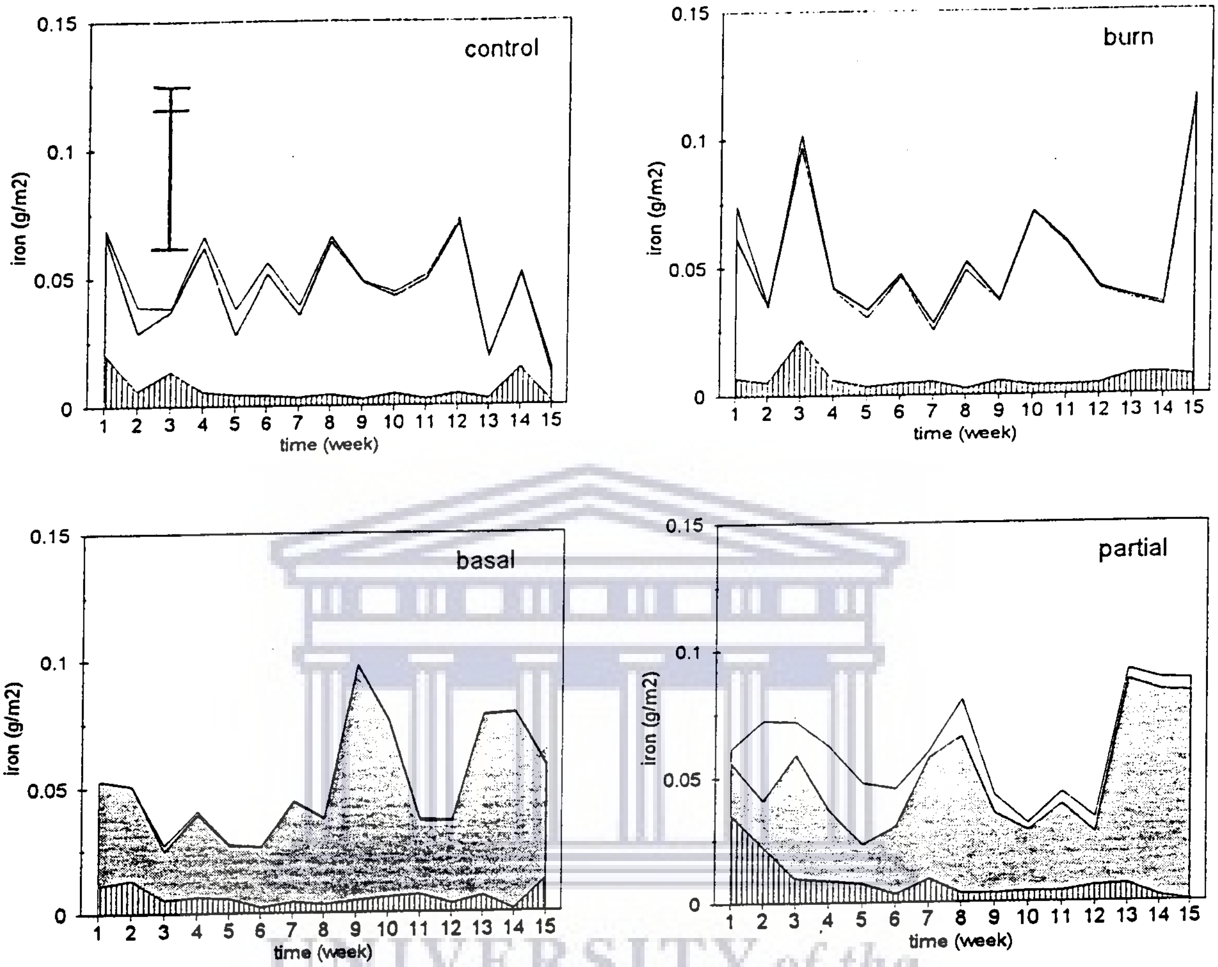

Figure 3.9. Iron allocation (g/m^2) of *Imperata cylindrica* treatments (control, burn, basal clipping and partial clipping) over fifteen weeks. Shading: Vertical lines, roots; stipling, stems; open, leaves; closed, inflorescences. Vertical bar represent least significant differences of 0.01 and 0.05 respectively.

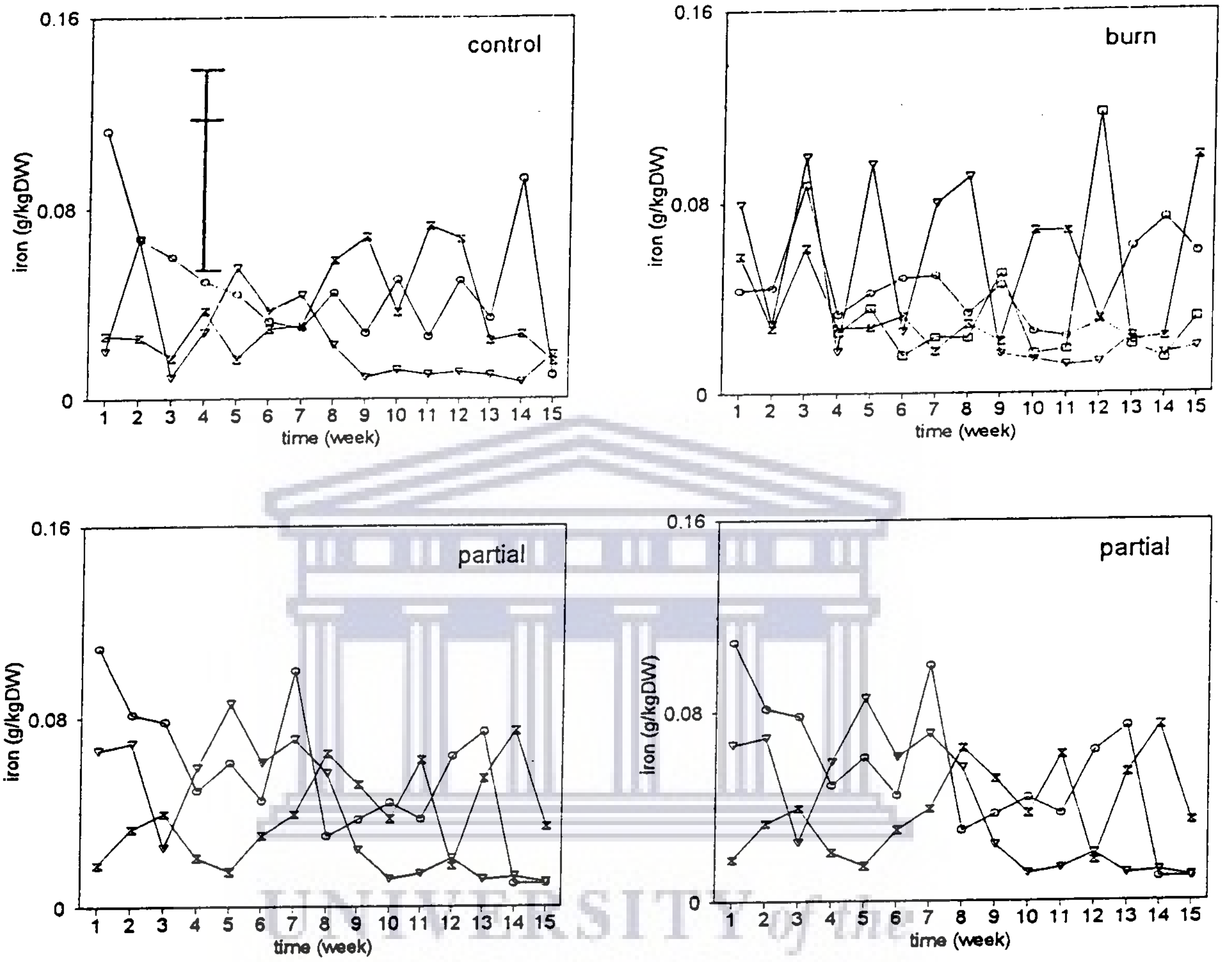

Figure 3.10. Iron concentrations (g/kg DW) of *Imperata cylindrica* treatments (control, burn, basal clipping and partial clipping) over fifteen weeks. ○=roots, ⧖=stems, ∇=leaves, □=inflorescences. Vertical bar represent least significant differences of 0.01 and 0.05 respectively.

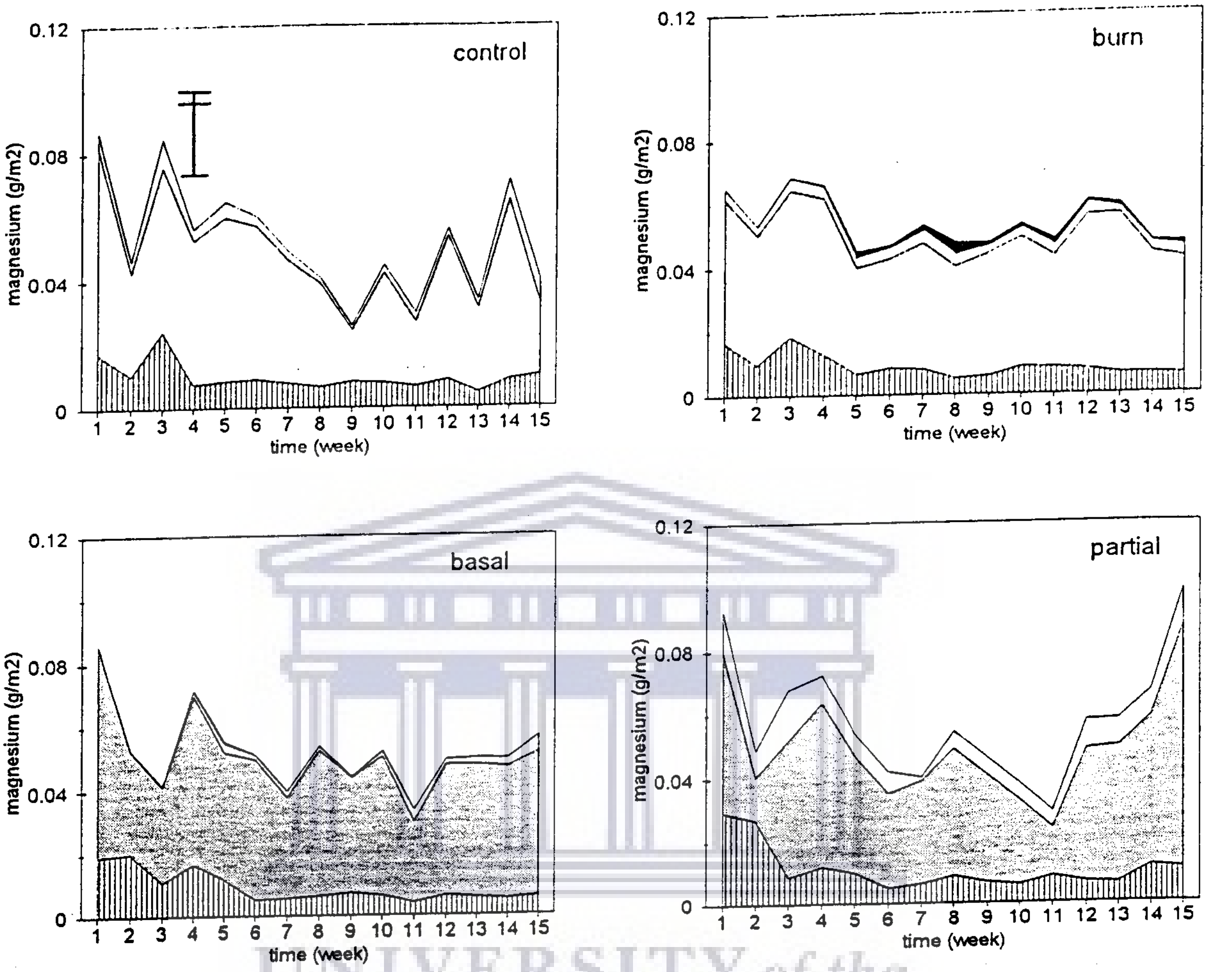

Figure 3.11. Magnesium allocation (g/m^2) of *Imperata cylindrica* treatments (control, burn, basal clipping and partial clipping) over fifteen weeks. Shading: Vertical lines, roots; stipling, stems; open, leaves; closed, inflorescences. Vertical bar represent least significant differences of 0.01 and 0.05 respectively.

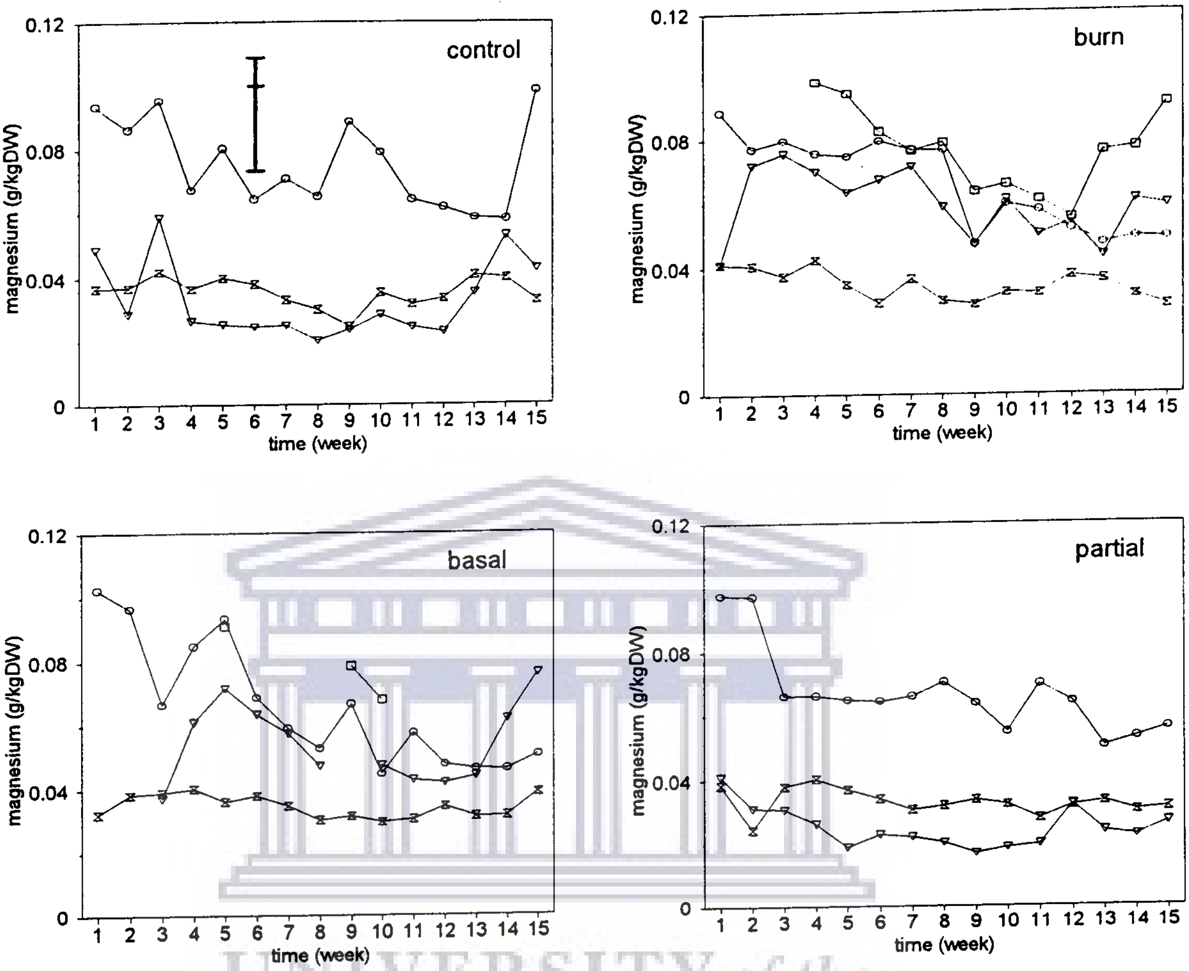

Figure 3.12. Magnesium concentrations (g/kg DW) of *Imperata cylindrica* treatments (control, burn, basal clipping and partial clipping) over fifteen weeks. ○=roots, ⧖=stems, ▽=leaves, □=inflorescences. Vertical bar represent least significant differences of 0.01 and 0.05 respectively.

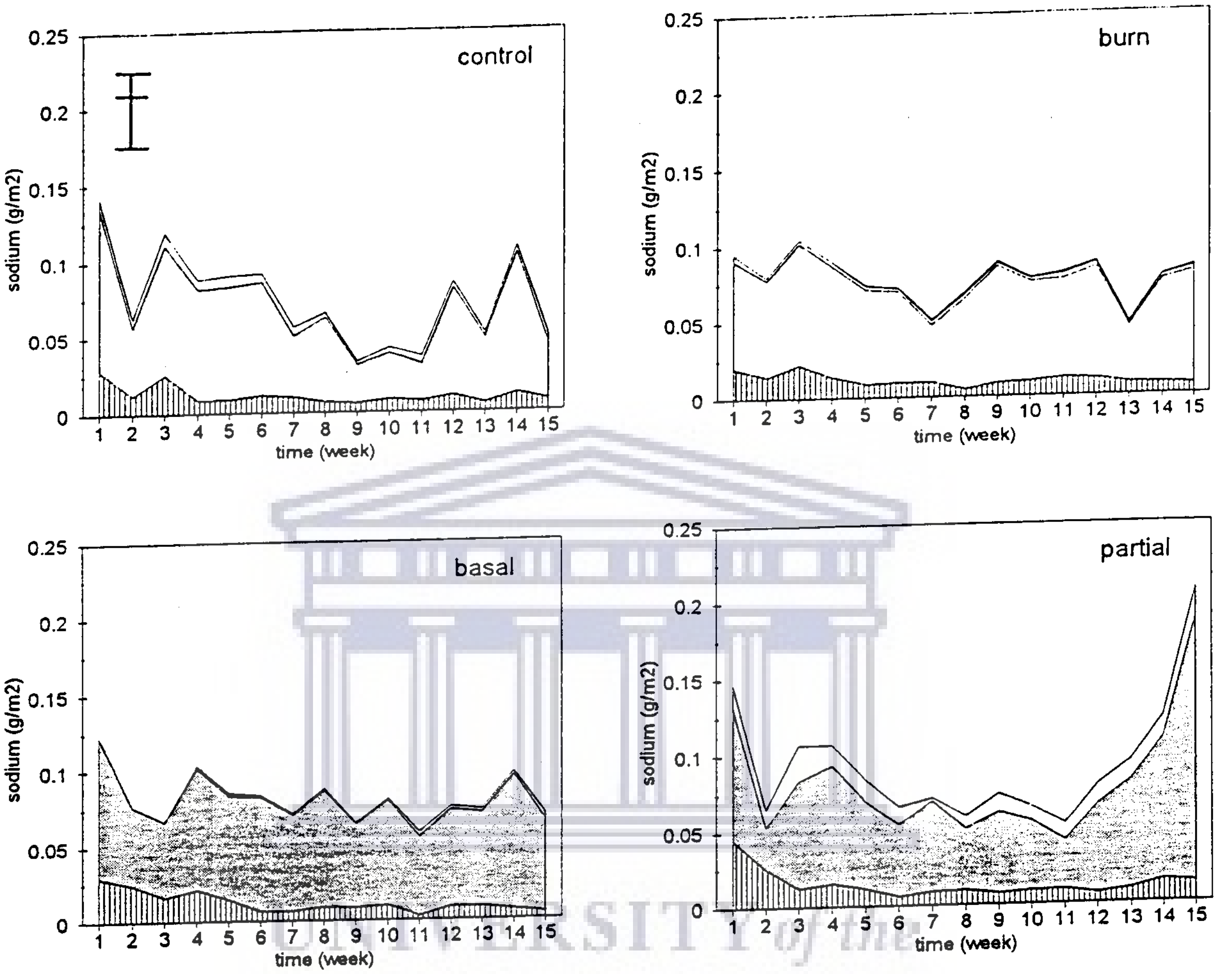

Figure 3.13. Sodium allocation (g/m^2) of *Imperata cylindrica* treatments (control, burn, basal clipping and partial clipping) over fifteen weeks. Shading: Vertical lines, roots; stipling, stems; open, leaves; closed, inflorescences. Vertical bar represent least significant differences of 0.01 and 0.05 respectively.

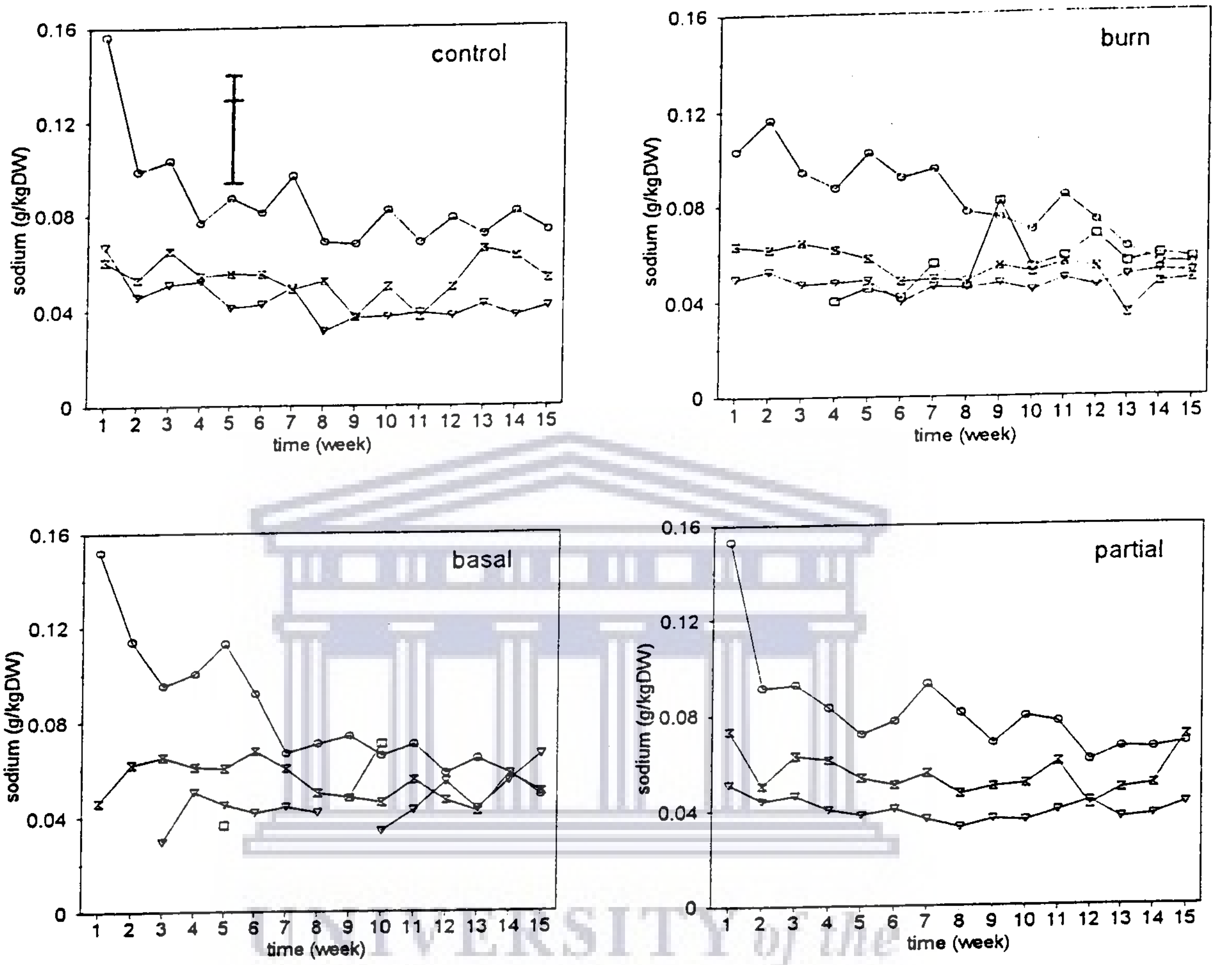

Figure 3.14. Sodium concentrations (g/kg DW) of *Imperata cylindrica* treatments (control, burn, basal clipping and partial clipping) over fifteen weeks. ○=roots, ⧖=stems, ∇=leaves, ☐=inflorescences. Vertical bar represent least significant differences of 0.01 and 0.05 respectively.

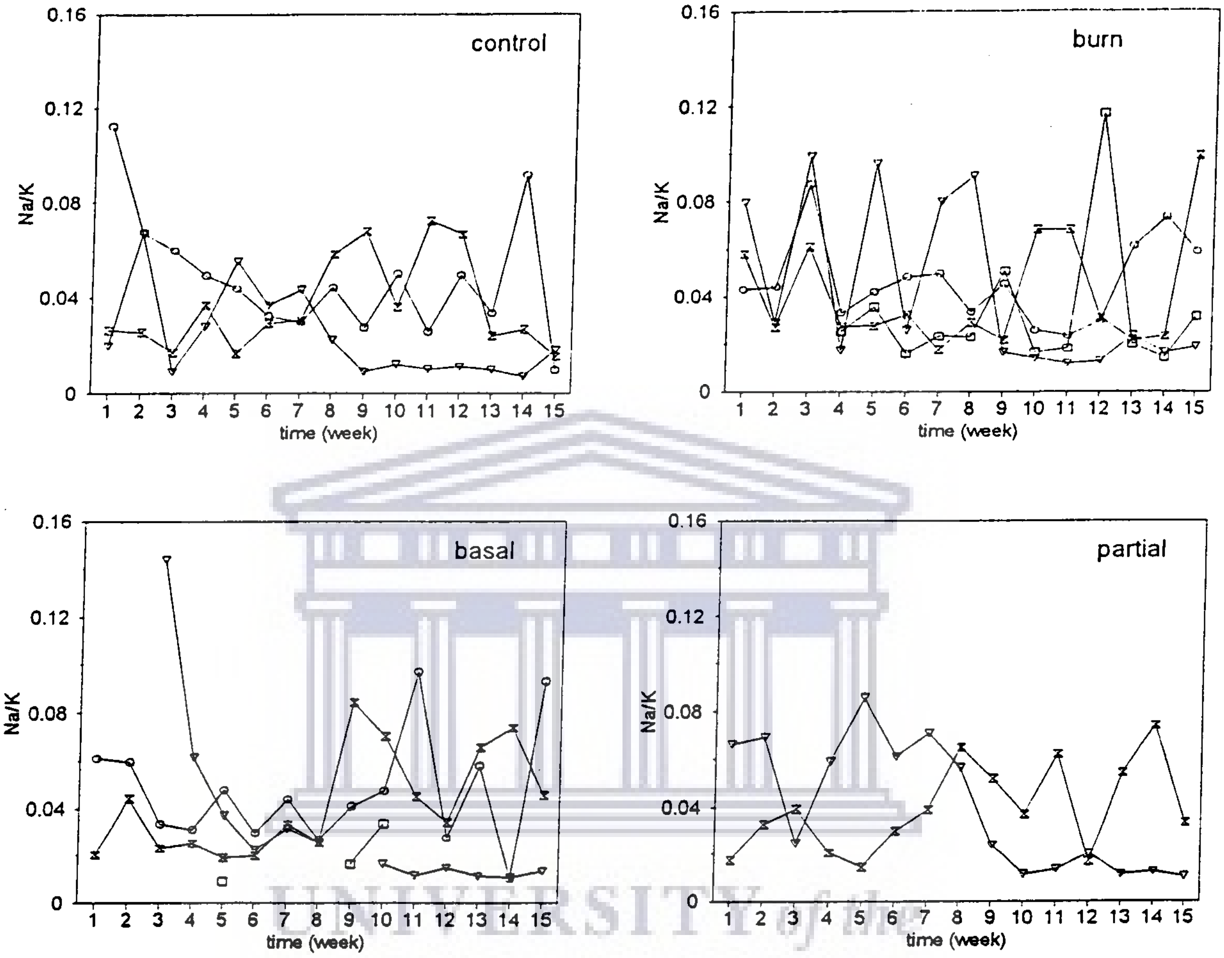

Figure 3.15. The ratio between sodium and potassium concentrations of *Imperata cylindrica* treatments (control, burn, basal clipping and partial clipping) over fifteen weeks. ○=roots, ⧗=stems, ∇=leaves, □=inflorescences. Vertical bar represent least significant differences of 0.01 and 0.05 respectively.

Element	Land plants (g.kg^{-1} dry matter)	Mean
N	10-50	20
P	1-8	2
S	0.5-8	1
K	5-50	10
Ca	5-50	10
Mg	1-10	2
Fe	0.05-1	0.1
Mn	0.02-0.3	0.05
Zn	0.01-0.1	0.02
Cu	0.002-0.02	0.006
Mo	0.0001-0.001	0.0002
B	0.005-0.1	0.02
Cl	0.2-10	0.1

Table 3.1 Average content of mineral bioelements in plants (Larcher 1980).

Chapter 4 SUMMARY AND RECOMMENDATIONS

The aim of this study was to determine the response of *I. cylindrica* to burning and clipping, in terms of its total nonstructural carbohydrates and mineral nutrients. This study had only one defoliation treatment which was found to be insufficient to eradicate *I. cylindrica.* It is therefore recommended that further studies should have multiple defoliations . This will lead the way to a defoliation regime which will cause the eradication of the grass.

Burning and basal clipping caused a significantly higher number of tillers to be produced compared to the control and the partial clip treatments. The production of new plant material did not affect the reserve storage of the burning or basal clipping treatments which suggests that more defoliation, be it burning or basal clipping, may be needed to induce a reduction in stored carbohydrates. Defoliation removes old and moribund material and also recycles mineral nutrients in the case of burning, however repeated defoliations should nullify these beneficial effects. The number of defoliations necessary to sufficiently tax the underground reserve storage of *I. cylindrica* will still need to be determined in later studies.

Burning and basal clipping also induced significantly higher leaf nitrogen concentrations mainly because of the growth produced following defoliation (Fig 3.3). Multiple defoliations should also lead to a reduction of the nitrogen pool of *I. cylindrica*. It is difficult to recommend a defoliation regime as this study had only one defoliation treatment. However, the period between defoliations should be less than 3 days because the dependency on stored carbohydrates for regrowth is at its greatest 2 to 3 days following defoliation (Richards & Caldwell 1985).

The depletion of *I. cylindrica*'s underground reserves, may yet prove to be its Achilles heel. However, successive burning or mowing cannot be guaranteed to be successful because of the rhizomatous nature of the grass. Eradication is also hampered by the plastic nature of *I. cylindrica* in terms of form; it being able to grow in a variety of habitats provided it succeeds in its colonisation of an area.

Four methods of control has already been mentioned, namely, mechanical, chemical, biological, and cultural. This study focussed solely on mechanical means of control because it is usually much cheaper and/or quicker than the other forms. In the Cape Flats Nature Reserve (CFNR) the most pragmatic form of controlling would be by burning stands *I. cylindrica*. Mowing or cutting would be too labour intensive and hence too expensive. Burning remains the cheapest option. Biological and chemical control will only be considered should *I. cylindrica* start to increase its area in the CFNR. This is highly unlikely to occur as *I. cylindrica* is not considered a threat to the CFNR's vegetation.

I. cylindrica's status in the CFNR is that as long as it does not spread, that is, become an invasive alien, it will be tolerated in the CFNR. Whether this is the correct perspective to have is not up for debate as the Environmental Education Research Unit (EERU), who manages the CFNR, already has to deal with a bigger menace in the form of aggressive Australian alien invasive plant species. The CFNR is also an island of conservation in a sea of developed land and thus the possibility of the grass spreading is remote.

What then is the value of this research? It is hoped that this study provides some insight into the response of rhizomatous grasses, not only *I. cylindrica*, to defoliation. This work can also be of value to regions where *I. cylindrica* is an aggressive invader, for example, in tropical crops such as rubber and rice. The eradication of the grass, however, is not solely based on whether it is aggressive or not. In South Africa and elsewhere it is often found on the sides of freeways, creating a potential visibility hazard in the event of it catching fire.

This study was a pilot study leaving many more questions unanswered than answered. Future studies are needed, as recommended above, to get an understanding of *I. cylindrica*'s response to disturbance. Once all pertinent questions the defoliation regime of *I. cylindrica* have been answered, then only can it be manage and controlled.