

ECOLOGICAL IMPACTS OF HIGHVELD GERBILS (*TATERA BRANTSII*) ON A REHABILITATED ASH DISPOSAL SITE

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ABSTRACT

Ecological Impacts of Highveld Gerbils (*Tatera brantsii*) on a Rehabilitated Ash Disposal Site

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Tatera brantsii was numerically dominant in the small mammal community on the plateaux of the rehabilitated ash disposal sites of ESKOM's Hendrina Power Station in 1998 and 1999 (Vermaak 2000). The species seemed well adapted to exploit this environment and, through biopedturbation, had altered the topsoil structure and chemistry. The consequences of this and other activities also affected the rehabilitated plant community of the PFA-dam habitat. Burrowing appeared limited to just under the topsoil layer, and seemed more extensive than burrows of this species in natural ecosystems. The burrow system architecture was mapped and quantified, and localised increases in nitrates, phosphorous and organic carbon in immediately associated substrate were noted. However, this substrate enrichment was transient, and disappeared following the abandonment, and subsequent collapse of burrow systems, when gerbil colonies migrated away from the area. The mixing of soil horizons also resulted in a more homogeneous substrate, which was more friable, and thus drier. The high pH and salinity of the topsoil layer in areas undisturbed by gerbil burrowing, and concentrations of particular elements associated with either the topsoil covering or the ash, were reduced as a consequence of substrate mixing in disturbed areas. Gerbil impacts on the substrate of this habitat seemed to promote pedogenesis, eliminating the sharp distinction between the topsoil covering and the ash below, but the re-exposed ash of the burrow mounds would become subject to erosion, and reduce the effectiveness of the rehabilitation effort. Gerbil activities increased the number of plant species, especially ruderal forbs, comprising the plant community of the PFA-dam habitat, but plant community diversity was not significantly increased. However, numerical dominance by few tussock grass species was diminished, possibly reflecting burial under mounds of excavated substrate. The biomass and cover of some grass species were reduced in areas of gerbil impacts, and plant life-cycles appeared to be completed sooner in areas affected by gerbil activities. These effects may be as a result of the drier substrate produced following the collapse of the extensive network of abandoned burrows. The succession of this plant community towards an underutilised grassland state, the expected outcome of the rehabilitation effort, was minimally affected by gerbil activities. The effects of *T. brantsii* activities in this PFA-dam habitat were not as distinct as the effects noted by other authors studying fossorial rodent impacts in less disturbed habitats. This could be because further disturbances in this habitat would merely add to the currently disturbed state, whereas disturbance in more natural habitats, would show more of a change from the initial state.

Keywords: biopedturbation; burrows; disturbance; fossorial rodents; industrial habitats; PFA-dams; plant succession; rehabilitation; small mammals; soil properties; South Africa

UITTREKSEL

Ekologiese Impakte van die Hoorveld se Nagmuis (*Tatera brantsii*) op 'n Gerehabiliteerde As-stortingsterrein

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Tatera brantsii was numeries dominant in die klein soogdiergemeenskap op die plato's van die gerehabiliteerde as-stortingsterrein van Eskom se Hendrina kragstasie in 1998 en 1999 (Vermaak 2000). Die spesie blyk goed aangepas te wees om hierdie omgewing te gebruik, en het die bogrond se struktuur en chemie gewysig deur "biopedturbation". Hierdie en ander aktiwiteite het ook die gerehabiliteerde plantgemeenskap van die PFA-dam beïnvloed. Tonnelgraving blyk beperk te wees tot die area net onder die bogrondlaag, en blyk ook meer ekstensief te wees as hierdie spesie se tonnelwerk in natuurlike ekosisteme. Die tonnelsisteem se argitektuur was gekarteer en gekwantifiseer, en gelokaliseerde vermeerdering van nitrate, fosfor en organiese koolstof in direk geassosieerde substraat was genoteer. Hierdie substraatverryking was egter tydelik en het verdwyn sodra die tonnells verlaat is en gevolglik verval het sodra die nagmuis-kolonies migreer het. Die vermenging van grondhorisone het 'n meer homogene substraat tot gevolg gehad wat meer krummelrig en dus droër was. Die hoë pH en soutinhoud van die bogrondlaag in areas onverstoord deur nagmuis-grawery en konsentrasies van spesifieke elemente wat óf met die grondlaag bedekking óf met die as geassosieër is, was verminder as gevolg van substraatvermenging in versteurde areas. Dit wou voorkom of die impak van die nagmuis op die substraat van hierdie habitat "pedogenese" bevorder het en die sterk onderskeid tussen grondbedekking en die aslaag daaronder geëlimineer het, maar die blootgestelde as in die tonnelhopies was aan erosie onderhewig, en het die effektiwiteit van die rehabiliteringsaksie verminder. Nagmuis-aktiwiteite het die hoeveelheid plantspesies vermeerder, veral "ruderales" kruie, wat die plantgemeenskap van die PFA-dam habitat behels het, maar die plantgemeenskap se diversiteit was nie merkbaar vermeerder nie. Die numeriese dominansie van 'n paar polgrasspesies is egter verminder, moontlik as gevolg van begrawing onder hope omgedolwe substraat. Die biomassa en dekking van sommige grasspesies was verminder in die gebiede waar nagmuis-impak gehad het, en plante se lewenssiklusse blyk vinniger voltooi te word in gebiede wat deur nagmuis-aktiwiteite geraak was. Hierdie gevolge is moontlik as gevolg van die droër substraat wat gevorm is nadat die ekstensiewe netwerk van verlate tonnells ingeval het. Die "suksessie" van hierdie plantgemeenskap na 'n "lae-verbruik" grasveld-staat (toestand) – die verwagte resultaat van die rehabiliteringsprogram – was minimal beïnvloed deur nagmuis-aktiwiteite. Die effek van *T. brantsii* in hierdie PFA-dam habitat was nie so duidelik soos die effek wat ander outeurs tydens die studie van "fossoriële" knaagdier-impak in minder versteurde habitats gevind het nie. Dit kon wees omdat die verdere versteuring van hierdie habitat slegs bygedra het tot die reeds versteurde habitat, waar versteuring in 'n meer natuurlike habitat 'n groter onderskeid sou toon met die oorspronklike stand van sake.

Sleutelwoorde: "biopedturbation"; "fossoriële" knaagdier; grond einskappe; industriële habitat; klein soogdiere; PFA-damme; plante-"suksessie"; rehabilitasie; Suid Afrika tonnelwerk; versteuring

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CHAPTER 1

INTRODUCTION

The taxonomically diverse small mammal group is an important intermediate component of most terrestrial ecosystems (Golley, Ryszkowski & Sokur 1975; Hayward & Phillipson 1982). Small mammals have been shown to play a significant role in regulating the transfer of energy and nutrients between the producers, consumers and decomposers in these ecosystems (Golley *et al.* 1975; Hayward & Phillipson 1982). As such, the direct and indirect impacts on the structure and dynamics of plant communities by terrestrial small mammals (e.g. through the destruction of plants by feeding, or in altering the composition of the substrate by digging) can be considerable (Dean & Milton 1991a, b; Hulme 1996; Olff & Ritchie 1998; Whitford & Kay 1999). Populations of small mammals are able to respond quickly to changes in environmental resources and conditions as a result of their short generation times and high reproductive rates. This makes them ideal subjects to study as part of the monitoring process for recovering ecosystems (Bourlière 1975).

A small mammal that potentially has a significant impact on the grass and forb plant communities, in southern African grasslands and savanna is the Highveld gerbil, *Tatera brantsii* (A. Smith, 1836). These gerbils are found in colonies composed of a number of complex burrow system refuges, with only the limited area around each refuge exploited by the resident gerbil (de Moor 1969; Skinner & Smithers 1990). Korn & Korn (1989) showed that as gerbil colonies moved across an area of grassy savanna over time, this possibly being motivated by the depletion of food resources in the immediate vicinity of burrows, the characteristics of local plant communities were altered by the activities of the gerbils. Dominant grass biomass was reduced, forb biomass was increased, and the plant community as a whole became more diverse as a result of feeding and extensive digging activity which may have altered substrate characteristics (Korn & Korn 1989).

Tatera brantsii is a common species on the rehabilitated grasslands of ash disposal sites at Hendrina Power Station in Mpumalanga, South Africa (Vermaak 2000). Given their demonstrated and considerable impact on plant communities in natural ecosystems, it was hypothesised that this species has a significant impact on the establishment and succession of plant communities on these ash disposal sites. In particular, this study assesses the nature and extent of gerbil activities on rehabilitation success in a revegetated plant community.

1.1 Why Small Mammals are Used as Indicators of Rehabilitation Success

Owing to their small size, terrestrial small mammals (here defined as mammal species with an adult body weight of less than two kilograms; Entwistle & Stephenson, 2000) are able to survive in marginal environments where larger mammals struggle to access adequate resources. They are highly adaptable and many of them are regarded as pioneer species, where they commonly herald the invasion or re-colonisation of mammal fauna in new or recently restored habitats.

The terrestrial small mammal group is taxonomically dominated by rodent species, which are among the most versatile and adaptable of small mammals (Hayward & Phillipson 1982). Rodents have a cosmopolitan distribution, are able to exploit a wide variety of food resources and are opportunistic, adjusting to seasonal changes in resources (Bourlière 1975; Golley *et al.* 1975). They exploit the different micro-habitats of an environment, which may facilitate the co-existence of several species (Kerley, Knight & Erasmus 1990). However, the same species does not necessarily occupy the same micro-habitat in similar environments which are spatially separated, competitive interactions within the small mammal community are more deterministic in this regard (Gliwicz 1987).

The versatility of generalist rodents pre-adapts them to colonise environments in the early stages of succession (Willan 1992). Further, these characteristics allow them to fulfil the role of suitable indicator species, and their ability to respond rapidly to changes in environmental resources makes them ideal study subjects when investigating succession and habitat health.

Small body size confers several advantages on terrestrial mammals (Bourlière 1975). These include: ● access to food resources poorly exploited by larger vertebrates (e.g., insectivores exploiting invertebrates), where the cost required to locate and acquire such specialised, high-energy resources would exceed the energetic value of the resource to a larger mammal.

- utilisation of specific micro-habitats that are often small in area, and non-food resources that are limiting, or inaccessible to larger species.

- energetic costs of the construction of refuges, which offer protection from harsh environmental conditions and predators, are not prohibitively expensive, as they would be for a larger mammal.

- concealment from sight-hunting predators, assisted by having crepuscular or nocturnal activity periods, or enhanced by a camouflaging coat for diurnal activity. This also allows small mammals to live undetected in close proximity to humans (Willan 1992).

- many terrestrial small mammals have comparatively higher reproductive power. Namely, shorter gestation and maturation periods, earlier age at first reproduction, high conception rates, large litters, and the potential of producing several litters in a single season (i.e., polyestrous). Small mammals are thus able to respond quickly to short-term favourable conditions, whereas larger mammal species are unable to because of their longer gestation and maturation periods.

These advantages aid small mammals in the successful exploitation of restrictive environmental conditions and limited resources. Their populations also recover rapidly following an ecological disaster (e.g.: drought, flood, fire, disease), and where necessary, fragment into several smaller populations, diversifying into different niches, to cope with changing environmental conditions (Bourlière 1975). The ability to adapt to habitats at the extremes of the species range, and their short generation times, promotes peripheral populations of terrestrial small mammals to undergo parapatric speciation. New races develop from this adapted pool of individuals as these populations have little interaction with the parent population because of the low vagility of terrestrial small mammals. In addition, local selection pressure of the marginal habitat assists in stabilising novel adaptations (Bush 1975).

Small body size, however, also has disadvantages for terrestrial mammals (Bourlière 1975). These include: ● being homeothermic, small mammals have comparatively higher energy requirements because of their higher mass-specific metabolic rates, associated with their high surface area to volume ratios. This requires them to expend more energy on thermoregulation than larger mammals, or small poikilothermic organisms (Schmidt-Nielsen 1990).

- higher costs of locomotion (i.e. more energy is used to move a unit of body mass over a distance interval; Schmidt-Nielsen 1990).

- a proportionately higher daily food intake *per biomass* of small mammal in order to maintain these comparatively higher daily energy expenditures, and a reliance on energy-rich foods.

- a shortened life span, which precludes learning from the experience of adults and forces greater reliance on rigid, genetically-based behaviour and skills.

These disadvantages, particularly the enhanced energy demands of terrestrial small mammals on natural resources, which tend to be localised as a result of their low vagility, increase the effect of their impact in local environments. On a gram-for-gram basis, small mammals have a greater impact on food resources and are more efficient in mineralising organic material than large mammals or invertebrates (Hayward & Phillipson 1982). However, their total impact on available primary production in ecosystems rarely exceeds 3 % (Golley *et al.* 1975). The overall impact of small mammals may be modest but, because of the concentration of such impact, should not be disregarded, particularly in terms of the mineralisation of organic material (Bourlière 1975; Hayward & Phillipson 1982).

1.1.1 Habitat requirements of small mammals

Increased habitat complexity, resulting in more niches because of greater plant density, diversity and cover, allows greater abundance, diversity and species richness in the terrestrial small mammal community (Green & Taylor 1975; Rowe-Rowe & Meester 1982; Happold & Happold 1989; Ogue 1995; Rosenstock 1996; Monadjem 1997). In ecosystems where resources are limited, competitive

interactions among small mammals result in the fine differentiation of niches. A resident community (persistent throughout the year) of small mammals has defined niches, delimited by the strict partitioning of resources according to their availability during the unfavourable season. The maximum use of niches is achieved where niche dimensions have minimal overlap, allowing the survival of the resident species through the unfavourable season (Gliwicz 1987).

Habitat structure is one of the main determinants of small mammal community compositions, particularly in grasslands (Grant, Birney, French & Swift 1982). Cover, in particular, is vital in determining micro-habitat selection. As a niche dimension, cover is one of the most important habitat resources for small mammals as it provides shade, protection from predators and food. The majority of small mammal species forage under cover as much as possible to avoid avian predators, particularly in more open environments, like deserts (Abramsky 1988; Kerley *et al.* 1990) and grasslands (Green & Taylor 1975; Kern 1981). Small mammals rarely abandon areas of protective cover, but may do so if excesses of food resources are available in an open area, where the benefits of the risk warrant exposure (Monadjem & Perrin 1998). However, even if food resources are abundant (e.g., in cereal crop landscapes), they are not as important as the availability of cover as a refuge for small mammals (Díaz 1994). Dependence on, or independence of, cover may be one of the primary aspects which separate two species that would otherwise utilise the same resources (Abramsky 1988). Further, as an environment changes during the process of succession (e.g., during the progression of coastal dune forest rehabilitation; Ferreira & van Aarde 1996), the influence of habitat characteristics may supercede the effects of competitive interactions in altering small mammal community structure.

Both the height and density of cover are important for different guilds of small mammals. Insectivores appear to be associated with low ground cover in fynbos (Els & Kerley 1996) and in regenerating forests (Parker 1989), possibly indicating the association of insect prey with this stratum. During the early phases of forest regeneration, this micro-habitat supports higher insect densities, whereas small mammal herbivores are associated with the taller plants of later succession. Maximum small mammal diversity occurs at an intermediate height where these two strata of cover overlap (Parker 1989). In grasslands, the quantity of cover a habitat provides may be important in determining small mammal community characteristics. While most small mammal species prefer areas with good cover (70-90 %), others require higher levels of cover, and some species are able to tolerate less cover due to anti-predator adaptations (Kern 1981). One such adaption is the saltatorial locomotion utilised by many gerbil species (Skinner & Smithers 1990). Anti-predator adaptations by small mammals are also common in desert habitats where the cover provided by the habitat is limited (Abramsky 1988; Kerley *et al.* 1990).

Where cover is reduced in habitats, such as by the grazing of large herbivores in grasslands (Grant *et al.* 1982) or by clear-cutting in forests (Parker 1989), small mammal community biomass and energetic components, as well as abundance, diversity and evenness, are often reduced compared to similar undisturbed habitats. Increases in cover, brought about by a reduction in grazing pressure by large mammals, for example (Rosenstock 1996), results in elevated small mammal abundance and diversity in a number of natural environments, ranging from deserts (Abramsky 1988; Kerley *et al.* 1990) and grasslands (Green & Taylor 1975; Kern 1981; Grant *et al.* 1982; Happold & Happold 1989; Ouge 1995) to forest (Parker 1989) and fynbos (Els & Kerley 1996). A similar trend has been noted in transformed ecosystems, such as agricultural ecosystems (Díaz 1994) and reclaimed grasslands (e.g., an opencast coal mine; Hingtgen & Clark 1984).

1.1.2 Why *Tatera brantsii* was selected for study

Tatera brantsii was numerically dominant on the plateaux of the study environment (Vermaak 2000). The traits which facilitate the ability of this species to exploit the PFA-dam environment are characteristic of the gerbil group and are reviewed below with emphasis on *T. brantsii*.

All gerbils found in southern Africa are nocturnal, adapted to arid or semi-arid habitats, and are omnivores, able to utilise transient food resources that are seasonally, or only locally available (Skinner & Smithers 1990). Certain gerbil species tend to be more herbivorous, such as *Gerbillurus paeba* and *Desmodillus auricularis*, but this might be the result of food availability (Kerley 1989; Kerley 1992a). Some gerbil species are also known to hoard seeds (e.g., *D. auricularis*), while others (e.g., *T. brantsii* & *Tatera leucogaster*) do not rely on this strategy and consume seeds only when they are seasonally

available (Pettifer & Nel 1977). However, some *Tatera* species do cover seeds with sand, which may be a primitive form of scatter-hoarding (Pettifer & Nel 1977).

Gerbils tend towards bipedalism and use saltatorial (hopping) locomotion (Skinner & Smithers 1990), which has a lower energetic cost associated with locomotion than running (Schmidt-Nielsen 1990). This adaptation allows a foraging gerbil to move rapidly and with considerable manoeuvrability, thereby avoiding predators, and making them more independent of cover (Christian 1977; Kern 1981; Abramsky 1988; Kerley *et al.* 1990; Kerley 1992b; Ouge 1995). As further protection against predators, and also as a refuge from harsh environmental conditions, gerbil species also excavate labyrinthine burrow systems. Those from the genus *Tatera* are particularly extensive and complex, with numerous entrances and blind tunnels (e.g., *T. brantsii*; Bronner 1992, and *T. indica*; Bhadauria & Mathur 1994).

The arid environments favoured by most gerbil species would be expected to promote breeding following the unpredictable rains. However, this is not the case as many species can breed throughout the year in their protected burrow systems (in particular, those better physiologically adapted to aridity, i.e. *D. auricularis*, *G. paeba* and *T. brantsii*), implying that the aridity of the environment does not restrict their breeding success (Perrin & Swanepoel 1987; Korn 1989; Skinner & Smithers 1990).

The gerbil species investigated in this study, *T. brantsii*, weighs approximately 80 g and has an average total length of 270 mm (Skinner & Smithers 1990). *Tatera brantsii* has been studied quite extensively as the species is known as a reservoir for bubonic plague (de Moor 1969). It is an omnivorous generalist feeder, and exploits seasonally available insects and plants (Skinner & Smithers 1990). This species is able to adapt its feeding strategy to different environments, thus having an impact on all stages of plant life cycles. Reproduction is aseasonal, occurring throughout the year, but peaking in the wet season and tapering off in the dry season (Korn 1989; Skinner & Smithers 1990), resulting in a year-round impact on local plant communities. Litter sizes are smaller than other gerbil species in Southern Africa, perhaps as a consequence of a lower protein diet (Perrin & Swanepoel 1987; Skinner & Smithers 1990).

Their burrow systems are typically extensive and intricate, showing considerable variability in length, branching tunnels and the number of access holes (Skinner & Smithers 1990; Bronner 1992). They are territorial and restrict their range of activities (e.g., foraging, searching for mates, defending territory, or digging new burrows) from their burrows to 0.489 ha (males), or 0.186 ha (females; de Moor 1969). These ranges are determined from two standard diameters, which encompass more than 95 % of an individual gerbil's points of capture (de Moor 1969; Skinner & Smithers 1990). Standard diameters were calculated by de Moor (1969) by first determining the centre of activity of each individual rodent (the geometric centre of all the points where it had been captured). Then, by calculating the standard deviation between each point of capture and the centre, and assuming these distances to be radii, the standard diameter could be determined. This limited range of activity could also imply that this gerbil species may utilise the feeding strategies of a central place forager (Jackson 2001).

The area of a colony of *T. brantsii* can be as expansive as 65-70 ha (Skinner & Smithers 1990). The principal activity in this area would presumably be feeding, most likely on available herbage (Perrin & Swanepoel 1987; Korn & Korn 1989). As food resources are depleted, and individuals move to exploit new resources, the colony cluster also seems to retain its cohesion (Korn & Korn 1989).

1.2 Roles of Terrestrial Small Mammals in Ecosystems

Small mammals perform four main functional roles in ecosystems, namely, the destruction of components, the movement of components, the alteration of habitats, and as intermediates in energy and nutrient cycles (Golley *et al.* 1975).

1.2.1 Destruction of components

This is usually taken to mean consumption of food items, but also includes incidental damage caused by moving through the habitat, the removal of vegetation for nesting material and localized effects on vegetation and soil associated with digging activities. Such impacts are not necessarily negative and may sometimes be required to maintain the dynamics of certain habitats, where destruction of dominant species serves to open up the environment and enhance diversity by encouraging the recruitment of other plant species (Batzli & Pitelka 1970; Golley *et al.* 1975; Hayward & Phillipson 1982). Small mammal

consumption assists in regulating the abundance of some plant species at certain equilibrium levels (Batzli & Pitelka 1970; Fleming 1975), thus maintaining the characteristic composition of a plant community (Brown & Heske 1990; Skarpe 1991; Weltzin, Archer & Heitschmidt 1997).

The destructive impacts by small mammals on plants can take several forms, of which foliage consumption is perhaps the most conspicuous. Other than the complete consumption of plants, grazing affects plants in several indirect ways that may have beneficial as well as detrimental effects. Light grazing (or the removal of above-ground grass foliage only once per growth season in an arid environment; Chaieb, Henchi & Boukhris 1996) produces an increase in plant productivity, especially if the grazed patch is large enough to eliminate the competitive effects of surrounding plants (Semmartin & Oosterheld 1996). Plants adapted to grazing (i.e. predictable damage to the primary shoot) may also be stimulated to overcompensate by producing more seeds, with the activation of secondary shoots (Järemo, Nilsson & Tuomi 1996). Also, plants of initially greater biomass tend to produce shoots of higher mass, and if neighbouring plants are more severely damaged, further increases in shoot mass may result (Bonser & Reader 1995). Plants in dry grassland environments may produce deeper roots after light grazing (Chaieb *et al.* 1996). However, when resources are limited, biomass recovery from light grazing may be poor (Hulme 1996) and secondary damage can result from fungal infections (Palmisano & Fox 1997). Also the fluids involved in plant repair attract opportunistic insects that may further damage the plant (Louda 1995).

By contrast, heavy grazing (reduction of up to 50 % biomass, or continuous grazing) can elevate plant mortality as they struggle to recover from the damage, especially if environmental resources are limited (Hulme 1996). A heavily-grazed plant community on a prairie dog colony evidenced higher evapotranspiration rates, and thus a higher water demand by community plants (Day & Detling 1994). In arid grasslands, heavy grazing reduces cover and litter that keep the topsoil cool and suppress evaporative water loss. Also, cover and litter assist water infiltration into the soil and reduce runoff losses, which is important in arid environments. Intense grazing further acts to reduce the larger-base perennial grasses and replace them with smaller annual grasses, so that even more soil surfaces are exposed. This is because perennial grasses that are over-grazed are prevented from storing carbohydrates to survive the dry season as they continually utilise storage products to replace lost foliage which reduces their vigour. As a result, they are unable to compete effectively with annuals which then become dominant in the community (Kelly & Walker 1976).

Grazing by small mammalian herbivores can have a considerable impact in semi-arid areas. For instance, exclusion of rabbits resulted in a sixfold increase in grassland productivity in New Zealand (Norbury & Norbury 1996). In South African savanna, Korn (1987) estimated that the biomass of grazing rodents per hectare approximated that of larger mammalian herbivores. Because of their higher mass-specific metabolic rate, and thus increased energy demands, an equivalent biomass of rodents may exert a greater trophic impact than larger herbivores. Using allometric scaling, Korn (1987) calculated that one kilogram of herbivorous rodents consumed as much energy as eight kilograms of impala and 12.7 kilograms of cattle. However, allometric scaling is not a preferred method to estimate of trophic impact because the assumptions are unlikely to be satisfied under natural conditions.

Rodent grazing can also change the population dynamics of certain plant species, inhibiting growth rates and delaying maturity. This can be severely detrimental to the populations of a plant species with a 2-3 year life span (Palmisano & Fox 1997). Plant damage from rodent impact (e.g., seasonal gnawing of tree bark) can cause abnormal growth (stripping older trees of bark higher up the trunk) or death (stripping young trees of bark at the base of the trunk; Taylor & Perrin 1996).

Grazing impacts tend to be higher close to small mammal burrow entrances, decreasing along a proximity gradient with increasing distance in grasslands. Plant cover is increased along the gradient, and plant species richness increases up to an intermediate point, then decreases thereafter (English & Bowers 1994). Similar impacts, attributable to grazing and other plant damaging effects like scent marking, were shown to occur in different environments (e.g., woodlands), with increased plant mortality and reduced plant vigour found closer to burrow entrances (Swihart & Picone 1991).

Seeds are food resources favoured by small mammals as they are highly nutritious, and granivory, where seeds comprise more than half of the diet, is a common ecological strategy, particularly in north American and Israeli deserts (Kerley 1991; Kerley & Whitford 1994). Rodents preferentially select larger seeds to maximise their foraging efficiency (Hoffmann, Redente & McEwen 1995), and the

extent of this impact may significantly reduce the density of large-seeded annual species, particularly winter annuals (Guo, Thompson, Valone & Brown 1995). Also, seed predation of more competitive large-seeded winter annuals by keystone rodent species can assist in the maintenance of specific habitat types (Brown & Heske 1990). As seed predation occurs in most environments, plants generally produce seeds in excess of that which can be utilised by consumers. Miller (1994), for instance, reported that the preferential consumption of seeds by rodents of one *Acacia* species in South African savanna depleted up to 25 % of the annual seed crop, which still left sufficient seeds for recruitment during the following year. In agricultural ecosystems, the abundance of seed is generally underutilised by rodents as other environmental resources (e.g., cover) limit the number of individuals that can utilise the available seed bank (Díaz 1994).

Granivory by rodents may have a significant effect on the outcome of ecological rehabilitation, not only through direct seed predation, but also by altering the seed mixtures used during initial revegetation through selective seed predation. Owing to concerns about environmentally damaging techniques of rodent control, Everett & Monsen (1990) recommended that seeding mixtures should mimic natural seed dispersion strategies, and provide seed in excess of that required to satiate the resident population of rodents.

Seedlings, especially their cotyledons, are nutritious food resources, and may be selected in preference to available seed (Clements & Young 1996). In most habitats, seedling predation by rodents may exceed that of other animal groups in this herbivorous guild (Hulme 1994), but where the habitat favours another animal group (e.g., slugs in moist coastal woodland), the proportion of rodent impact on seedling mortality is reduced (Paterson, Binggeli & Rushton 1996). Selective rodent grazing on the seedlings of certain species may impede their establishment (Clements & Young 1996), and this impact may be sufficient to maintain grassland habitats by preventing the dominance of particular woody forb species (Weltzin *et al.* 1997).

1.2.2 Movement of components

The most obvious components moved by terrestrial small mammals are seeds, which assists in plant dispersal. Small mammals can assist the spread of plants by burying caches of seeds, bulbs and corms either in their burrows (larder-hoarding) or in several sites within their territories (scatter-hoarding). The uneaten items often germinate, thereby facilitating their dispersal (Golley *et al.* 1975; Pettifer & Nel 1977; Huntly & Reichman 1994).

Organic material and substrate chemical components are also redistributed in habitats by small mammal activity (Golley *et al.* 1975; Pettifer & Nel 1977; Hayward & Phillipson 1982).

A more subtle form of small mammal-mediated movement of components involves the consequences of digging. Mixing of soils from different horizons of the soil profile increases the quantity of organic matter in the substrate, can redistribute chemical components from different strata in the soil profile, and assist decomposition processes. Any organic material deposited in burrows (faeces, plant material) is more quickly degraded by the increased amounts of nitrogen-fixing fungi associated with rodent waste, further enriching the substrate. The cycling of chemicals and nutrients through the substrate may thus be accelerated (Golley *et al.* 1975). Substrate mixing by burrowing small mammals may act to significantly reduce heavy metal contaminants in surface soil, and thus limit their erosional dispersion away from the contaminated area (Mace, Graham & Amrhein 1997).

Some terrestrial small mammals are also implicated in the pollination of plants, though this particular ecological role is known primarily from bats (Fleming 1975). Rodent and bat pollinators are likely to be generalists, pollinating flowers of different plant species as they become available throughout the season, or consuming alternative foods when nectar is unavailable. This discourages plants from evolving specialist pollination structures, as is the case with insect pollinators (Begon, Harper & Townsend 1990).

1.2.3 Alteration of habitats

The role small mammals play in altering habitats is performed mainly by fossorial forms (biopedturbation), where the construction of burrow systems and digging changes the micro-relief of the

habitat, the most obvious of which, are mima mounds. This alteration of micro-topography can affect drainage patterns and water flow through the habitat. Also, with the reduction of soil density, and increased friability, water infiltration is improved. Burrow construction can also aid substrate cycling and enrichment, which may then change the plant community structure of the habitat (Golley *et al.* 1975; Whitford & Kay 1999; Reichman & Seabloom 2002).

Burrowing in arid areas is one way that soluble nutrients are raised to the surface, and insoluble material becomes available for weathering. It is one of the principal methods of soil turnover (Whitford & Kay 1999). The direction of water movement (and associated mobile ions) in arid soils is upward as it is driven by the influence of evaporation. Arid soils usually have increased concentrations of soluble salts (products of weathering) which are generally of a more alkaline nature. As the process of leaching is minimal, or absent, soils tend to become saline (Tivy 1990). Burrow systems in general benefit arid areas by allowing increased water infiltration into the soil (Whitford & Kay 1999). This can be as high as 5.25 l ($\times 10^3$) litres (at a rate of 20.002 l/min. [data converted to modern units]) before any overflow (Eloff 1953).

Burrows of small mammals may reduce surface runoff and erosion, which is of benefit to landfill sites with minimal topsoil, but improved infiltration of water into the soil can also result in the migration of aqueously mobile metal ions (such as Caesium) from deeper in the landfill to the surface soil (Hakonson 1999). Burrows on hillsides alter the movement of soil down-slope, accelerating it at both low and high angles (midrange angles are invariant with the standard linear ratio of increasing soil erosion to slope; Reichman & Seabloom 2002).

Diggings, even on a small scale, provide micro-sites where detritus, seeds and water can accumulate. Plant germination is often facilitated by these protective hollows, particularly in more arid environments (Dean & Milton 1991b; Whitford & Kay 1999). On a larger scale, small mammal burrow systems (especially in colonies) can disrupt the root system continuity of a perennial grass sward, thereby allowing poorly competitive annuals and seedlings a better chance of survival as they are able to acquire more water (Milton & Dean 1991). Patches of disturbance caused by burrowing rodent colonies maintain higher plant community diversity by providing refugia for the annuals of the community, and seem to have a higher nutrient status than surrounding areas (Martinsen, Cushman & Whitman 1990; Dean & Milton 1991a; Whitford & Kay 1999; Reichman & Seabloom 2002).

The burial of plants under burrow system excavations is analogous to consumption with the more numerous (dominant) species being more affected. As annual species seem to recover more readily than perennials, dominance by perennial grasses is reduced and annual forbs are able to establish, thereby increasing the diversity of the plant community (Korn & Korn 1989; Dean & Milton 1991a). Decomposing, buried plants also provide nutrients to the plant community, and nearby plants benefit not only from the increased availability of nutrients, but also from the reduced competition (Reichman & Seabloom 2002).

1.2.4 Effects on energy and nutrient cycles

Mineralisation of organic material is necessary, especially in grassland ecosystems, to regulate the availability of nutrients. Small mammals are highly effective in this role, processing almost all the energy they assimilate from an ecosystem, and reserving only about two percent for production. This is primarily due to their high energy demands, but also because of the rapid turnover rate of small mammal populations (allowing prompt response to changes in producer demographics), their adaptability, and their ability to utilise a variety of food resources (Hayward & Phillipson 1982).

In addition, not all food harvested is assimilated, but is still degraded as small pieces of litter and faeces. The mobility of small mammals assists in the transport of nutrients throughout the ecosystem (e.g., soil enrichment, from the decay of organic matter associated with the burrows of certain species). This more direct linkage of the producer and decomposer components of an ecosystem benefits the entire system, making it energetically more efficient. In this regard, small mammals may act in an analogous way to fire in grassland systems (Golley *et al.* 1975; Hayward & Phillipson 1982).

The energetic processing efficiency of temperate rodents has been illustrated by Hayward & Phillipson (1982), who showed that efficiencies of digestion ranged from 67 % (grazing herbivore) to 90 % (granivore), the remainder voided as undigested fibre. Of the digested amount, 95 % to 98 % is assimilated, with between 2 % and 5 % being rejected as waste, particularly urine. On average, less than

3 % of the assimilated energy is used for production (ranging from 65 % in the early stages of life, to 0 % in the latter stages). The remainder of the assimilated energy (92-95 %) is used to sustain the metabolic status of the small mammals.

Despite accumulating only minimal amounts of the initial energy available in an ecosystem in secondary production (increased biomass and reproduction), the abundance of small mammals allows them to fulfil a crucial role as prey (Golley *et al.* 1975; Hayward & Phillipson 1982). Most predators are not prey-species specific and tend to take those small mammals that are most prevalent at any given time. Fluctuations in abundance of small mammals, often in stable medium- to long- term cycles, helps regulate the populations of predator species (Begon *et al.* 1990).

As predators, insectivorous small mammals may increase the abundance of plant species their invertebrate prey feed on by limiting their prey populations. Alternatively, if their invertebrate prey are parasites of plant-damaging invertebrates, small mammal feeding may indirectly impact negatively on plants by increasing the populations of their consumers (Hayward & Phillipson 1982). These two effects also apply to carnivorous small mammals, which by reducing the populations of herbivorous smaller mammals, increase plant abundance, and by being consumed by predators higher up the food chain, effect an increase in plant impact in the ecosystem (Norrdahl & Korpimäki 1995). If, however, both the primary and secondary predator guilds act on the herbivore, and additionally the secondary guild has an impact on the primary predator, the primary small mammal predator performs the role of the initial controller of the prey population, and the role of the secondary predator is to stabilise the system by containing excesses of abundance in both populations (Norrdahl & Korpimäki 1995).

1.3 Impacts of Small Mammals on Plant Communities

Minor disturbances in natural ecosystems induce recovery to one or more steady states of relative equilibrium (Inouye 1995), whereas a major disturbance could cause the system to undergo a transitional recovery to an alternative steady state (Milton & Hoffman 1994). The transition between two states can also be controlled by the focussed impact on competitive plant species of a keystone predator (Brown & Heske 1990).

From predominantly northern hemisphere studies, burrowing small mammals have been reported to increase plant diversity (Martinsen *et al.* 1990; Williams 1992; Stockrahm, Olson & Harper 1993; Huntly & Reichman 1994). This is especially by increasing species richness, as a result of disturbance of the environment, which facilitates plant establishment, combined with grazing, which reduces the effects of interspecific plant competition (Stockrahm *et al.* 1993). The individual activities of subterranean, herbivorous small mammals seem to have a synergistic overall effect, altering the composition of plant communities, reducing standing biomass and changing plant productivity (Huntly & Reichman 1994). These combined effects may maintain the particular character of a plant community (e.g., for short-grass prairie; Williams 1992). Specifically, the excavations of burrowing rodents bury, and thereby kill, existing vegetation and provide germination sites for competitively inferior species. Most buried plants seem to be dominant perennial grasses which are replaced by dicotyledonous forbs (Martinsen *et al.* 1990). A similar effect on plant communities seems to occur for the southern hemisphere. Korn & Korn (1989) showed that burrowing and grazing by *T. brantsii* reduced plant biomass in the vicinity of their colonies. By decreasing the density of dominant grasses, plant diversity and evenness was increased, largely because of increased establishment and growth of dicotyledonous plants.

Low levels of disturbance in grassland, aggregated intense disturbance patches, or high levels of disturbance in productive environments serve to increase plant diversity, as local extinctions provide opportunities for colonisation from regional species pools. However, non-selective, broad-scale or selective impacts on rarer species that are poor competitors can decrease diversity. Similarly, grazing in arid or poor soil environments also decreases diversity (Olf & Ritchie 1998). To a great extent, the outcome of grazing on plant community diversity seems to depend on environmental gradients of soil fertility and moisture content (Olf & Ritchie 1998). Also, when considering different time scales, an apparent increase in herbivory-induced diversity in the short-term may merely be the forerunner of successional change to a plant community of defended and/or grazing-tolerant species (Milton & Hoffman 1994).

Some ecosystems (e.g., savanna) require disturbances to maintain plant communities in a dynamic

state of equilibrium. In the natural environment, drought, migrations of large indigenous herbivores and grazing pressure fulfil this role and maintain a cohort of perennial palatable grass species and clumps of woodland (Skarpe 1991). This disturbance, whether natural or a management technique (e.g., burning; Kern 1981), needs to be sufficient in scope and frequency to prevent the development of a homogeneous grass-dominated sward with a low species diversity, but not so severe as to promote the development of a herbaceous-plant dominated ecosystem with a poor ability to support grazers (Skarpe 1991). Some savanna management techniques in protected areas thus utilise controlled burning to maintain the characteristic diversity of this ecosystem, where burn disturbances are made to mimic aggregated patches of intense disruption and occur at different times (Parr & Brockett 1999).

Herbivore impacts on plant community succession may have different effects depending on the plant community characteristics. Those plant communities where herbivory impacts primarily on intermediate seres which consist of grass, shrubs and pioneer trees, and result in a forest-type of steady state, or climax plant community of woody forms, tend to have accelerated succession. The primary defence of intermediate seral species is compensatory growth, compared to later seral species which utilise physical (e.g., thorns) and chemical (e.g., toxic or indigestible compounds) defences. Any impact tends to focus on the intermediate species, reducing their competitive ability (Davidson 1993). If, however, herbivory impacts on earlier successional seres, or those seres which result in a grassland-type of steady state, the process of succession is retarded. In the first case, the essential fulcrum point of the intermediate sere is never reached, and in the second, the high impact on the intermediate seral species favours plant communities of ruderal or other annual species typical of secondary succession (Davidson 1993). Granivorous impact seems to be focussed on larger-seeded, later successional species, and also acts to retard succession (Davidson 1993).

Grazing by rodents may maintain a sub-climax state of forbs and annual grasses by selectively consuming seed or seedlings of later seral species, but may also encourage secondary succession through their disturbance activities (digging or forming runways). Rodents may also benefit grassland communities by grazing later seral shrubs and woody plants, allowing the re-establishment of perennial grasses (Hayward & Phillipson 1982).

1.4 Environmental Rehabilitation

The area chosen for this study was the ash disposal site of Hendrina Power Station, operated by the Electricity Supply Commission (ESKOM) of South Africa. This coal-fired power generating station is located within the grassland biome of the South African highveld, in Mpumalanga Province (Rutherford & Westfall 1994; Eskom 1996) and the ash disposal site associated with it consists of several pulverised fuel ash (PFA) lagoons, or ash dams, as they are known in South Africa.

ESKOM has used the low-grade portion of locally-abundant coal deposits to fuel Hendrina Power Station, and the product of burned low-grade coal, pulverised fuel ash, is highly inert, alkaline, saline, and sterile. Low-grade coal also produces more ash (because of the greater soil proportion), and thus substantial amounts need to be recycled or disposed of. Ash recycling in South Africa in 2000 was between 4 and 5 % (M.D. Michael 2000, pers. comm.*), which required that the majority of fuel ash produced needed to be disposed of in an ecologically acceptable way.

Existing environmental legislation (Anonymous 1998) requires that PFA-dams be rehabilitated by topsoiling and seeding with indigenous grasses at the end of their useful lifespan.

1.4.1 Reasons for environmental rehabilitation

It is recommended that damaged ecosystems are rehabilitated in order to preserve essential biodiversity and ecosystem services, as the management of protected areas alone are insufficient to achieve this successfully. This is becoming more important now, as human environmental impacts on all environments is increasing rapidly. But to restore an ecosystem to the exact parameters it possessed before it was damaged is virtually impossible because the sequence of events that preceded the final state cannot be repeated exactly. Thus, the best that can be hoped for is to "return an ecosystem to a close

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approximation of its condition prior to disturbance" (Cairns 1995).

According to Higgs (1997), the minimum requirements for effective restoration are meeting the technical aspects which give an ecosystem fidelity, but this does not imply that such restoration is *good*. Ecosystem fidelity requires that the restored ecosystem has a structure and species composition comparable to similar surrounding natural ecosystems, that the system has functioning biogeochemical cycles and that it is sustainable with enough resilience to endure stochastic events with its characteristic identity remaining intact. The process of restoration also needs to be efficient, introducing the concepts of economic value of restoration and the achievement of restoration in the most effective time. And lastly, the restoration should include awareness of, and planning for, the factors which affect it in the long-term in order to be considered good restoration (Higgs 1997).

The rehabilitation of any environment disturbed by industry in South Africa is required by law (Act No. 107, 1998) since accepting the strictures of the Convention of Biological Diversity in 1995. However the environmental legislation (Anonymous 1998) is vague on what ecological rehabilitation entails, stating only that where any disturbances "...cannot be altogether avoided, are minimised and remedied..." (section 2, subsection 4: i-viii; Anonymous 1998). This presumably means that the guidelines set by Barnard (1995), that the economic value of the new [rehabilitated] resource has to be at least equal to the value of the [natural] resources that will be destroyed during development, still apply and that the rehabilitation has to be sustainable.

1.4.2 Small mammals and environmental rehabilitation

From the onset of rehabilitation, the habitat is subject to invasions (immigration) by opportunistic small mammals, which seek to exploit the new area. Initial colonisers, which form the pioneer small mammal community, seem to be less dependant on cover (Grant *et al.* 1982; Hingtgen & Clark 1984) and reproduce rapidly, allowing them to out-compete other small mammal species (Ferreira & van Aarde 1996). Consequently, recently rehabilitated areas are also characterised by low diversity of small mammals. Diversity increases as the rehabilitated ecosystem ages and the habitat resource of cover increases (Hingtgen & Clark 1984; Ferreira & van Aarde 1996).

Impacts by small mammals on ecosystem recovery may initially include the consumption of seed planted to start revegetation (Everett & Monsen 1990) and the destruction of planted trees and shrubs (Hingtgen & Clark 1984). The rapid mineralisation of nutrients by rodents may, however, catalyse the re-establishment of grassland ecosystem cycles (Hingtgen & Clark 1984). Considering their higher mass-specific metabolic rates, and relatively greater abundance in recovering ecosystems, the impacts of small mammals on revegetated ecosystems may equal or exceed that of larger mammals.

The PFA-dams at Hendrina power station fall well within the natural distribution zone of *T. brantsii* (Skinner & Smithers 1990). Within the phytosociological plant communities on the plateaux of the rehabilitated PFA-dams (Morgenthal 2003), *T. brantsii* occurs in significantly greater numbers than on the slopes or in the adjacent control areas of natural veld (Vermaak 2000). It is also the second most dominant species in the PFA-dam habitat in terms of density, and the most dominant species in terms of biomass (Vermaak 2000).

Highveld gerbils are ideally suited to pioneer the invasion of a rehabilitated PFA-dam as they are opportunistic, omnivorous and physiologically well adapted to the arid conditions of this environment. Also, because they are less reliant on cover and construct burrow system refuges (Skinner & Smithers 1990), they are more independent of the exposed and extreme conditions of the PFA-dam habitat.

Their influence on grassland ecosystems may be considerable, of a similar magnitude to pocket gopher disturbance in rangelands of northern America (Korn & Korn 1989). Old gerbil colonies in a savanna ecosystem showed more than a 47 % reduction of aboveground plant biomass, and about 34 % reduction of root biomass, compared to areas undisturbed by gerbils. Plant height was also reduced. Plant diversity and evenness were, however, increased and a higher ratio of dicotyledonous legumes was found on gerbil colonies. Selective grazing and burrow system excavation by these gerbils may therefore contribute towards the maintenance of the characteristic patch diversity of savanna (Korn & Korn 1989). However, the observations recorded by Korn & Korn (1989) may not necessarily have occurred only as a result of gerbil activities. Medium and large mammalian herbivores were not excluded from the study

area, and thus any grazing or trampling impact from them may have contributed to the observed impacts.

Whether or not similar impacts by *T. brantsii* are manifest in rehabilitated habitats, such as the plateaux of PFA-dams at Hendrina Power Station, has never been established.

1.5. Aims of this Study

Knowledge of ecological impacts of small mammals in South African in general, and rehabilitated environments in particular, is lacking, and this indicates a clear need for the close examination of small mammal impacts in restored environments, and specifically, the gerbil-mediated factors in this environment. The results of a similar study in a natural habitat (Korn & Korn 1989) may not necessarily apply to this rehabilitated grassland habitat, as natural environments are far more robust, having developed over a longer period of time, adapting to changes rather than being subject to certain defined criteria within a set of artificial parameters (Inouye 1995).

The rehabilitated plant communities of the PFA-dams were dominated by perennial grasses, with some annual grasses and forbs in areas without gerbil colonies, and consisted of several steady states at sub-climax stages (Morgenthal 2003). In areas colonised by *T. brantsii*, many more forb species were noted, but it was unclear whether gerbil impact advanced the process of succession or retarded it. The high *T. brantsii* densities observed (37.098 / ha; Vermaak 2000) potentially affected the overall success of the rehabilitation effort, but the extent of this effect was unknown.

This study investigated the effects of *T. brantsii* colonies on substrate structure and chemistry, and on plant community characteristics on the plateau of a PFA-dam at Hendrina power station.

Given their demonstrated and considerable impact in natural ecosystems, the study attempted to establish whether digging by *T. brantsii* had a significant impact on the structure, moisture content and chemistry of the PFA-dam substrate, and further, whether the composition of the resident plant community would be altered by the consequences of digging and/or feeding, possibly impacting the process of succession in the PFA-dam environment. However, as the results of small mammal impacts in natural environments may not necessarily apply to a rehabilitated environment (Inouye 1995), it may be found that gerbil impacts have no effect in this habitat.

CHAPTER 2

METHODS

2.1 Study Area

2.1.1 Location and Climate

The study area is located on one of the five pulverised fuel ash lagoons at Hendrina Power Station, a coal-fired electricity generating plant operated by the Electricity Supply Commission (ESKOM) of South Africa. The power station is located on the farm Boschmanskop (26°03'S, 29°35'E) in Mpumalanga Province.

The region has a temperate climate with warm, wet summers (December-February), and cool, dry winters (June-August). The average annual precipitation for the region from 1990 to 1999 was 692 mm, with the highest average monthly precipitation (90-138 mm) recorded between December and February, and the lowest average monthly precipitation (3-6 mm) occurring between June and August. Mean daily temperatures, namely the difference between the lowest and highest daily temperature, vary from 19.4° C in summer and from 10.8° C in winter. During this study (1998 & 1999), the climate followed the long-term monthly precipitation and temperature trends (Figs. 2.1-2.4). However, the annual precipitation was slightly lower than the 10-year mean in 1998 (679 mm), and markedly lower in 1999 (436 mm, South African Weather Bureau; Anonymous 2002). The lower precipitation in 1999 may have reduced the productivity of the plant communities assessed in that year.

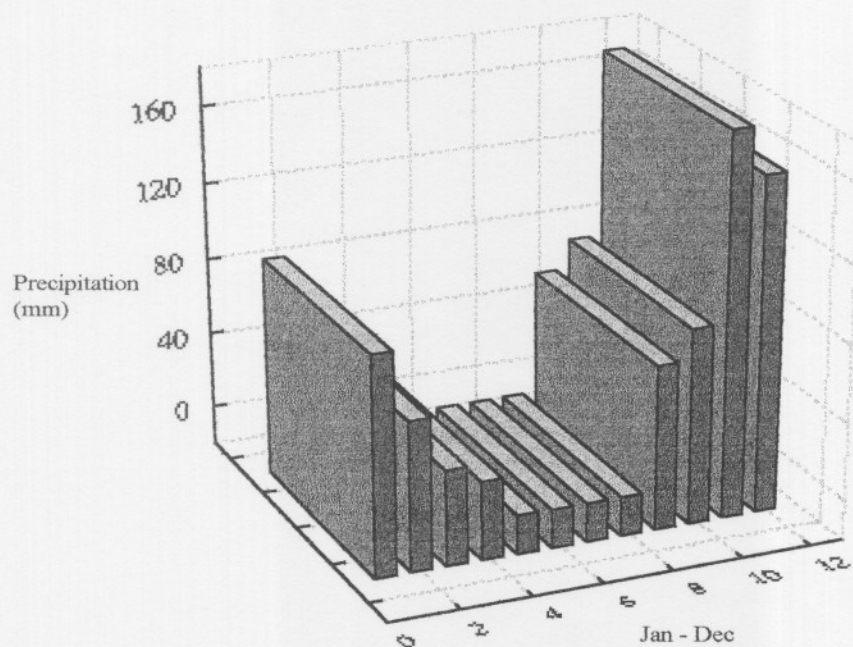


Figure 2.1: Monthly precipitation at Hendrina Power Station in 1998.

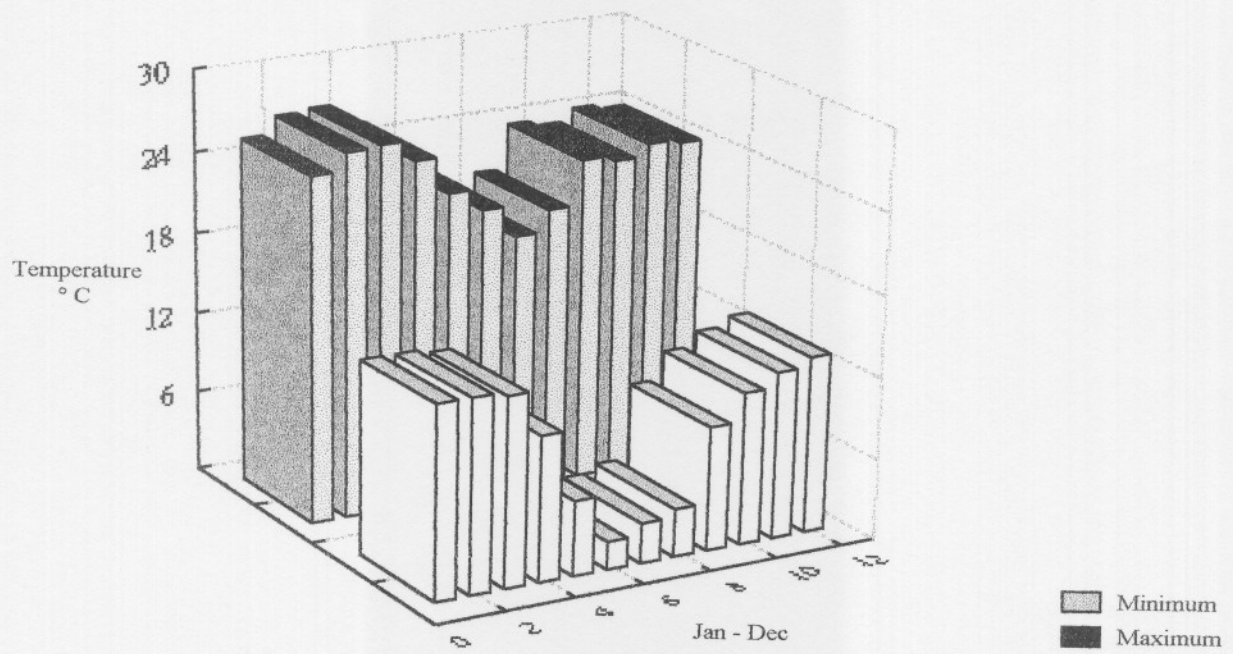


Figure 2.2: Daily minimum and maximum temperature per month at Hendrina Power Station in 1998.

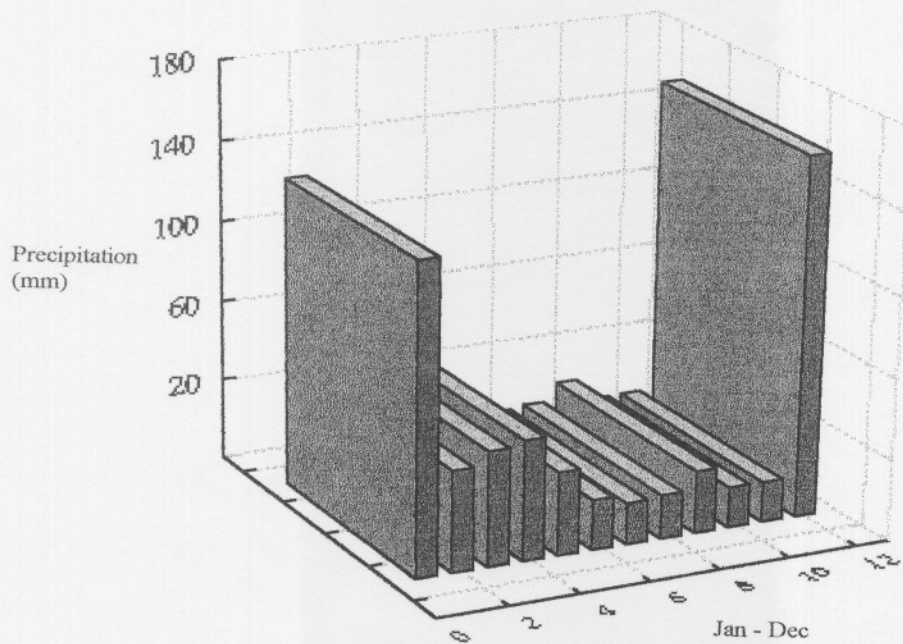


Figure 2.3: Monthly precipitation at Hendrina Power Station in 1999.

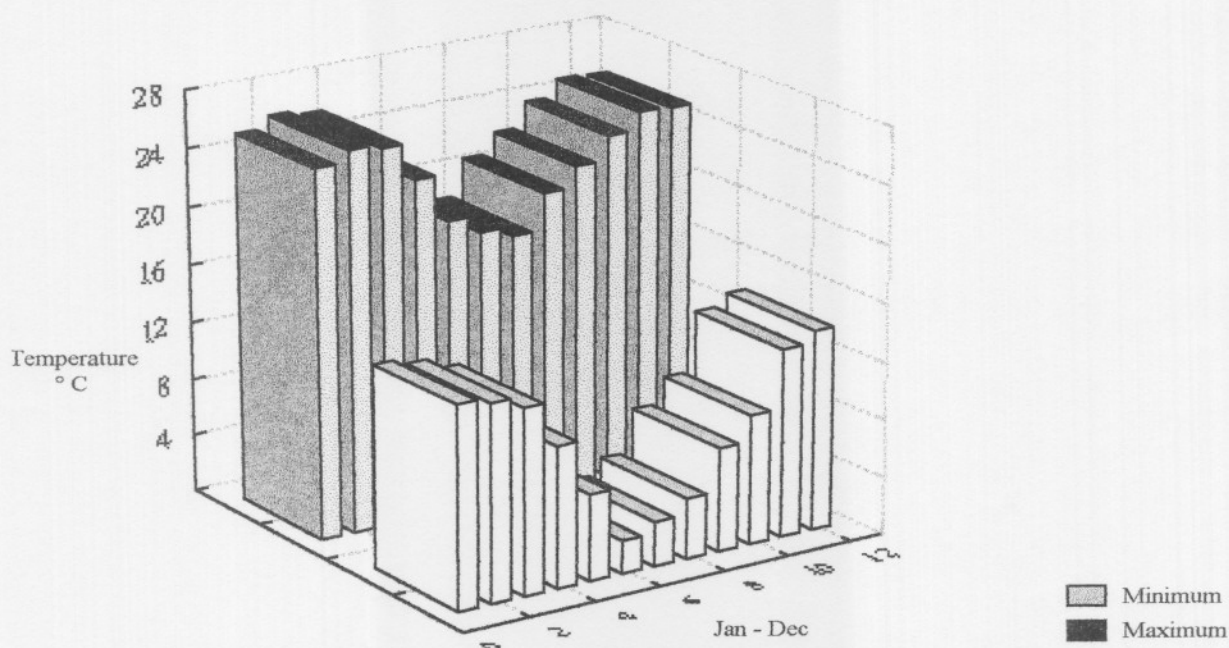


Figure 2.4: Daily minimum and maximum temperature per month at Hendrina Power Station in 1999.

2.1.2 Flora

The study area falls within the grassland biome of South Africa, and more specifically, the Moist Grassland portion of this biome (annual precipitation > 625 mm). The plant community is dominated by sour, unpalatable grasses, which provide good plant canopy cover, and show highest productivity levels in the wet summer months. Soils usually have low nutrient concentrations as a result of leaching and fire frequency is higher (Rutherford & Westfall 1994).

Acoks (1988) classified the natural vegetation of the area as Sour Grassveld (under False Grassveld types) and as the eastern variation of the Bankenveld (veld type: 61c). The most commonly occurring grass species of this veld type are: *Tristachya leucothrix*; *Eragrostis racemosa*; *Heteropogon contortus*; *Trachypogon spicatus*; *Digitaria tricholaenoides*; *Themeda triandra* and *Brachiaria serrata* with *Digitaria monodactyla* occurring less commonly. Where the veld is loosely sandy, local plant communities may be dominated by *Eragrostis curvula* or *E. racemosa* among others (Acoks 1988).

2.1.3 Ash disposal

Ash recycling is substantial in some developed countries, such as the USA, where up to 30 % (~ 18 million tonnes) of the total 1992 production of 60 million tonnes was recycled (Manz 1997), or in the UK, where 60 % (4.8 million tonnes) of the 1992 production (~8 million tonnes) was recycled (Shaw 1992). In South Africa, recycling is more limited and amounted to only about 19% (5.6 million tonnes) of a total ash production (30 million tonnes) in 1992 (Manz 1997). The recycling of ash usually involves the production of ash bricks and in cement extension (Graham 1997). Currently (2000) the production of ash by ESKOM power stations is 20-25 million tonnes, of which approximately only about four to five percent (~1 million tonnes) is recycled annually (M.D. Michael 2000, pers. comm.*).

Large quantities of ash, therefore, need to be disposed off in a safe and ecologically-sensitive way. The usual method used by ESKOM is to dump the ash in PFA-dams which are similar to slurry dams. Ash from power plants is composed of the minute particles of burned and pulverised low-grade coal, precipitated from blast furnaces by electrostatic or hydrostatic precipitators. These particles are dumped in a lagoon as a highly saline, slurry solution to reduce clogging of the transportation pipes. The typical consistency of this ash is 10-20 % bottom ash (that which remains after burning) and 80-90 % PFA from precipitation of the fly-ash (addendum to Eskom report: TRR/S/91/103/rw, Michael 1991).

The PFA-dam is built by pouring the slurry onto a concrete base and damming it with compacted ash along its edges. The purpose of the concrete base is to allow drainage of the water component of the slurry, which has an extremely high pH, to be recycled via a closed-water system to the power station, so as not to contaminate local ground water. This mound builds up until it reaches its designed height, which may vary according to the ability of the underlying ground to support the weight of the ash dump above it. Thereafter it is ecologically rehabilitated with a skin of topsoil, which is then seeded, usually with selected grass species, to prevent erosion and wind-borne dust pollution (M.D. Michael 2000, pers. comm.*).

2.1.4 The PFA-dam environment

PFA-dams in the Mpumalanga highveld are constructed to conform to the general shape of mine dumps, and as such, share a number of common problems. They consist of artificial hills and are often the highest points in the area, usually because they are located on relatively flat terrain. They are therefore subject to intense wind erosion where wind-blown detritus (especially dust) can become a hazard (Thurlow 1937). Their flanks are quite steep, which makes them susceptible to water erosion (Jaaback & Muzzell 1971) and they are arid, with their surfaces exposed to extremes of temperature (Jusaitis & Pillman 1997; Piha, Vallack, Michael & Reeler 1995).

The typical character of the substrate is one of extreme conditions, both structurally and chemically, and is summarised from Grunwald, Iverson & Szafoni (1995) as follows:

Water availability is essential for seed germination and subsequent plant survival, and the maintenance of soil water is a function of the ability of the soil texture to retain water. Irrigation of mine dumps is often prohibitively costly (with the associated dangers of salinisation and alkalinisation in arid soils; Tivy 1990), and alternative means of water retention need to be applied. These include mulches (which reduce evaporation and facilitate infiltration) and judicious grading of slopes to enhance water collection and retention. This also has the further advantage of controlling erosion.

Fortunately, PFA-dam substrate has the ability to retain high levels of plant-available water (Aitken, Campbell & Bell 1984). The textures of artificial soils are often quite different from natural soils, and in the process of PFA-dam construction, they can be severely compacted. This may change the soil atmosphere so that it becomes waterlogged and reduces the availability of oxygen. Compact dense soils also resist root penetration.

Extremes of pH are common problems on mine dumps, with direct damage to plants occurring at both ends of the pH scale. Acidity decreases the availability of essential plant nutrients (e.g., Ca, K, Mg & P), impairs nitrogen-fixation and increases the availability of toxic heavy metals (e.g., Al & Mn; Rees & Sidrak 1955; Rees & Sidrak 1956). Alkalinity increases the availability of calcium, potassium, magnesium and sulphur ions, impairs the release of potential toxic ions (e.g., B, Cu, Fe, Mn, P & Zn) and increases the infectiveness of some soil pathogens. Amelioration of these pH extremes has involved the mixing in of quantities of substrate of the opposite pH and encouraging leaching.

PFA-dam substrates are often low in essential nutrients like phosphorous and especially nitrogen, and leaching can further diminish what nutrients are available as there is little organic matter to either slow water flow through the soil or, in degrading, replace lost nutrients. Addition of chemical fertilisers and the incorporation of organic waste (sewage) can benefit soil rehabilitation immensely. In addition, PFA-dam substrates can also contain toxically high levels of boron (Jones & Lewis 1960; Aitken *et al.* 1984).

Salinity or sodicity (excessive Na concentration) are common in arid alkaline soils where evaporation rates are high, and both interfere with the osmotic uptake of water by plants. Leaching seems to be the only means of reducing salinity or sodicity. Ash substrates however, do weather relatively quickly, with an almost exponential drop in toxicity levels over the first few years. This yields the result that biologically available nitrogen becomes the primary limiting factor for plant growth (Jones & Lewis 1960).

High soil temperature is a factor of air temperature, exposure to radiant energy (strongly influenced by soil colour), precipitation and evaporation, soil thermal conductivity and surface cover. Surface cover is the most influential factor in controlling soil temperature, and is most easily controlled by

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plants growing in the soil. Proper selection of plants for drought tolerance and light exposure is essential for mine dump rehabilitation (Grunwald *et al.* 1995).

A long-term solution to mine dump amelioration involves topsoiling followed by revegetation to stabilise the soil and slopes, and to reduce associated pollution (Phillips 1937; Thurlow 1937; Jaaback & Muzzell 1971; Kimmerer 1984).

2.1.5 The process of revegetation

Natural revegetation of mine dumps occurs slowly (Kimmerer 1984; Shaw 1992). Initially, plants aggregate on more favourable micro-sites, these being colonised by hardy individuals of pioneer species from adjacent species pools surrounding the mine dump site. This is followed by rapid adaption (within several generations) of more tolerant races (ecotypes) to the hostile environment. This initial colony of changed vegetation then begins to alter its immediate environment and thereby alleviate extreme environmental inhospitability. Further, it functions as a locus from which colonisation of the rest of the mine dump can proceed (Kimmerer 1984).

On metal mine dumps, this process takes a minimum of 10 years for any vegetation to become established, 16 years before a patchy distribution of a basic plant community occurs and 30 years before any significant amount of cover develops (Kimmerer 1984). A suitable pioneer community can take 10-20 years to develop on china clay waste (Roberts, Marrs, Skeffington & Bradshaw 1981), and on fly-ash disposal sites, a forb-grass pioneer community may take 7 years to develop (Shaw 1992). In all cases the accumulation of nitrogen in the substrate and soil developmental processes based on the production and integration of organic material were crucial for successful revegetation.

Rehabilitative revegetation attempts to accelerate this process of succession to minimise the long-term negative impacts of industrial disturbance or destruction on the environment. Accordingly, the plants used for revegetation (usually grasses) need to be given the best possible chance of establishment and survival. Methods used included supplying adequate nutrients in the form of fertilisers and ensuring that seed (e.g., through the process of hydroseeding; Jaaback & Muzzell 1971) and seedlings have enough water, which requires initial irrigation.

Revegetation of pulverised fuel ash usually involves covering the disposal site ash with topsoil and seeding it with plant species adapted to the harsh environment (Aitken *et al.* 1984; Mulhern, Robel, Furness & Hensley 1989; Piha *et al.* 1995; Shaw 1996; Jusaitis & Pillman 1997; Pillman & Jusaitis 1997; van Rensburg, de Sousa Correia, Booysen & Ginster 1998). These plants must also be able to survive the prevailing climatic conditions, so plants that are indigenous to the area are usually selected for the seeding mixtures. The efficacy of this method is improved if topsoil from an already rehabilitated PFA-dam is used, as it already contains a seed bank of adapted species, which would stand an improved chance of survival (Shaw 1996).

Recent attention has focussed on alternative methods of amelioration as the supply of topsoil is limited and therefore expensive. In the USA, Mulhern *et al.* (1989) reported successful rehabilitation of fly-ash where cattle manure and fertiliser were added directly to the ash to facilitate establishment by herbaceous plants (forbs), or where woodchips and fertiliser were added directly to the ash (for trees). However, on bottom ash, they failed to establish any vegetative growth directly on the substrate, following any combination of fertiliser, hay, woodchips or manure (Mulhern *et al.* 1989).

A study in Australia has shown that if seeds of suitable plant species are protected from desiccating wind and high temperatures (by either being seeded in shallow topsoil, 5-10 cm, or in compost stabilised with coarse organic mulch, hydromulch or erosion control fabric) they germinate in protected seed beds and establish well (Jusaitis & Pillman 1997). Also, if suitable plant species are grown in containers to develop sufficient root volume, and are then transplanted directly into ash as islands of vegetation, they become established with judicious application of nitrate fertilisers (Pillman & Jusaitis 1997).

In Zimbabwe, limited success establishing plants on raw ash was achieved for a nitrogen-fixing tree species (*Acacia gerrardii*), but the high salinity and toxic surface boron levels limited grass survival and prohibited the survival of other plants like herbaceous legumes. Concern that the tree species would destabilise the PFA-dam wall was also raised (Piha *et al.* 1995).

In South Africa, most efforts to rehabilitate PFA-dams still involve topsoiling and seeding with indigenous grass species. Experimentation with various methods to alleviate dependence on the use of topsoil has shown that amelioration with composting, manure and fertilisation proved effective in establishing a grass community dominated by *Cynodon dactylon* and *Eragrostis curvula*. These two perennial grasses have growth forms complementary towards the control of erosion (van Rensburg *et al.* 1998).

2.1.6 Description of ash disposal sites

The disposal site at Hendrina Power Station consisted of four PFA-dams in 1998, located contiguously from the northeast (PFA-dam A) to the southwest (PFA-dam D; Fig. 2.5, compiled from addendums to Eskom report: TRR/S/91/103/rw, Michael 1991). The northernmost three PFA-dams (A-C) were joined consecutively to each other with a gap between the lower (Southwest) base of PFA-dam C and the upper (Northeast) base of PFA-dam D. Construction of a fifth PFA-dam (E), began in 1998. PFA-dam D was still in active service at the start of this study in 1998, but was decommissioned in 1999, when PFA-dam E became operational. PFA-dams A-C, as well as the lower two-thirds of PFA-dam D (slopes) had been completely revegetated at the start of this study.

Land adjoining the PFA-dams has also been transformed by the activities of the power station. The northern boundary of the area borders on the power station, while the northwest boundary adjoins a railway line and a coal-loading area. To the northeast, there are abandoned opencast coal mines, that during their operation, severely disturbed the natural habitats in the area. This area has been only partially rehabilitated following the cessation of mining. The southwestern, southern, and parts of the eastern side of the area are bordered by highly transformed vegetation, mostly a monoculture of maize fields.

PFA-dam A was first rehabilitated in the early 1980's with pampas grass (*Cortaderia* sp.) and *Pennisetum clandestinum* sods, with the unsuccessful addition of an experimental grass seed mix on the plateau in 1986 (of which very few species survived). In 1995 the pampas grass was removed as it posed a health hazard. The plateau was coated with 50 mm of topsoil, which was presumably fertilised and subsequently revegetated with an indigenous grass seed mixture (possibly similar to the mix used on the slopes of PFA-dams A and C during 1992-1994; Table 2.1).

These revegetation practices on the ash disposal sites at Hendrina Power Station resulted in the establishment of an *Eragrostis curvula*-*Cynodon dactylon* phytosociological plant community (Morgenthal 2003). Diagnosis is facilitated by two common forb species (*Cyperus esculentus* & *Chamaecrista biensis*). The sub-community on PFA-dam A, is characterised and dominated by the grasses *Hyparrhenia hirta* and *Eragrostis curvula*, with the plant community variant on the plateau described as *Lepidium bonariensis*-*Eragrostis trichophora*. This variant shows a prevalence of the grass *Pennisetum clandestinum* and reduced abundance of *Hyparrhenia hirta*. Dominant forbs in the community are *Conyza bonariensis* and *Tagetes minuta*, with *Lepidium bonariensis*, *Acanthospermum glabratum*, *Hypochaeris radicata* and *Verbena bonariensis* serving as characteristic diagnostic species (Morgenthal 2003).

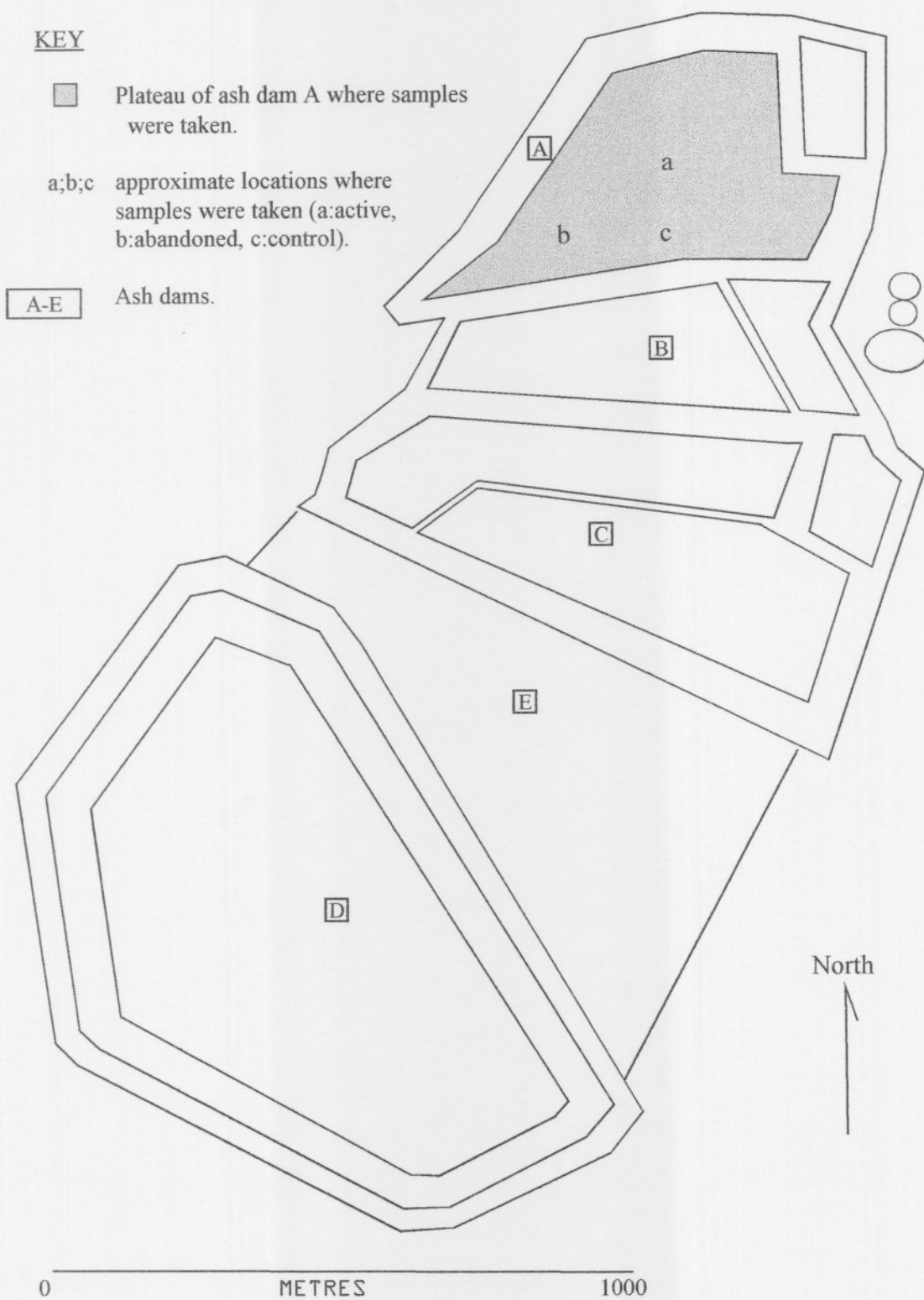


Figure 2.5: Outline sketch map of the PFA-dams at Hendrina Power Station.

Table: 2.1 Species and mechanisms used in the ecological rehabilitation of PFA-dam A. This information is courtesy of Eskom report N° TRR/S/91/103/rw and addenda (Michael 1991).

	PFA-dam A	Possible seed mix, plateau of A, 1995	Kg/ha.
Species	1980's : <i>Cortaderia</i> sp.	<i>Eragrostis curvula</i>	3.0
	<i>Pennisetum clandestinum</i>	<i>Eragrostis teff</i>	3.0
	1986 : <i>Agrostis</i> sp.	<i>Chloris gayana</i>	2.0
	<i>Atriplex</i> sp.	<i>Cynodon dactylon</i>	2.0
	<i>Cenchrus ciliaris</i>	<i>Digitaria eriantha</i>	2.0
	<i>Chloris gayana</i>	<i>Enneapogon cenchoides</i>	2.0
	<i>Cynodon dactylon</i>	<i>Chloris virgata</i>	1.0
	<i>Digitaria eriantha</i>	<i>Eragrostis chloromelas</i>	1.0
	<i>Eragrostis curvula</i>	<i>Eragrostis echinocloidea</i>	1.0
	<i>Eragrostis teff</i>	<i>Eragrostis lehmanniana</i>	1.0
	<i>Festuca arundinaceae</i>	<i>Hyparrhenia hirta</i>	1.0
	<i>Lolium multiflorum</i>	<i>Themeda triandra</i>	1.0
	<i>Lotus corniculatus</i>		
	<i>Medicago sativa</i>		
	<i>Pennisetum americanum</i>		
	<i>Secale cereale</i>		
	<i>Sorghum</i> sp.		
	<i>Trifolium</i> sp.		
	<i>Viscia dasycarpa</i>		
	1995 : 50mm	10cm	
Topsoil			
Fertilisation	0	Superphosphate	250
		4:3:4 (30) + Zn	200

2.2 Experimental Design

Three aspects of *Tatera brantsii* activity were investigated: the topography of burrow systems; the impact of gerbil diggings on substrate characteristics; and the impacts of gerbil activities on the local plant community. The study was initiated in May 1998, when data on the impacts of gerbils on plant communities and substrate characteristics were collected. More burrow data were collected in July 1998, and again in September 1998. Further plant data were collected in March 1999 and additional burrow data were collected in June 1999.

To assess the impacts of gerbil activity on substrate characteristics and plant community structure, three areas (hereafter termed "impact zones"), characterised by varying levels of gerbil activity within the vegetation variant on the plateau, were identified and studied. These impact zones were:

- 1) Control zones (undisturbed by gerbil burrow construction).
- 2) Active zones (areas where gerbils were excavating burrows and living in them).
- 3) Abandoned zones (areas which gerbils had vacated and where burrow systems had collapsed).

Within the *Lepidium bonariensis*-*Eragrostis trichophora* variant, the active zones were colonised before May 1998, probably between January and May 1998. This impact zone was characterised by intermediate and ongoing levels of disturbance in 1998. The abandoned zones were probably colonised by gerbils in 1997, or even earlier (maybe late 1996), but were vacated by gerbils before the first survey in 1998. No active burrow entrances were found in this area. This impact zone had presumably experienced the greatest levels of gerbil disturbance. The control impact zone was located in an area not yet disturbed by gerbil activity in 1998. During the March 1999 survey, fewer burrows were being constructed in the active impact zone as gerbils seemed to be moving elsewhere and activity was tapering off but had not yet ceased. Abandoned zones had not been re-invaded. Control zones remained undisturbed by gerbil burrow

impacts.

Within the plant community variant, three 100 m² grids (10 m by 10 m) were selected at random from each of the three impact zones (Global Positioning System coordinates, taken from the centre of each grid, are given in Table: 2.2). Each grid was then divided into 100 1m² quadrats, from which three quadrats were randomly selected. The quadrats were earmarked for extensive botanical sampling and for three consecutive 10 cm soil cores (for a total depth of 30 cm) to be taken from the centre of each quadrat.

Although nine quadrats were sampled in each of the active and abandoned zones in 1998, only six quadrats were sampled in control zones due to time constraints. In 1999 however, nine quadrats were sampled from each of the impact zones.

Table: 2.2 Global Positioning points for the grids used in this study.

Ash dam A
Active 1: 26°02'44.8"S 29°36'16.5"E
Active 2: 26°02'49.2"S 29°36'16.1"E
Active 3: 26°02'47.0"S 29°36'14.7"E
Abandoned 1: 26°02'49.5"S 29°36'14.8"E
Abandoned 2: 26°02'49.0"S 29°36'10.1"E
Abandoned 3: 26°02'51.0"S 29°36'10.7"E
Control 1: 26°02'47.1"S 29°36'21.8"E
Control 2: 26°02'48.1"S 29°36'17.7"E
Control 3: 26°02'50.4"S 29°36'19.8"E

2.2.1 Burrow system architecture

Nine randomly-selected active burrow systems (chosen on the basis of fresh footprints and evidence of excavated substrate from nocturnal activities) were mapped and the extent of their topography was quantified (illustrated in Appendix 1). For each burrow system, total length (in cm) was measured, and the number of access holes and nests were counted. Five of these burrow systems were intensively studied, additionally noting the number of chambers and cul-de-sac tunnels, and accurately mapped in order to determine the architecture of the burrow system and burrow volume. Map points were spaced about 30 cm apart, and/or wherever a tunnel branched or changed direction. At each map point, tunnel or chamber height, tunnel width, and the depth of the tunnel or chamber floor from the surface were measured (all in cm). The diameter of each tunnel was calculated from the height and width parameters at each map point and the mean tunnel diameter from all the map points of a system was used to calculate burrow volume, by considering the system a cylinder, and using the formula: $\pi r^2 l$ (r = radius, l = length, both in cm). No width values were taken at map points in chambers, instead map points were placed as close to the edges of the chamber as possible to give an idea of its area (illustrated in Figs. B1-B5, Appendix 1). For purposes of volume calculations, chambers were considered as if they were tunnels of the same length, resulting in slight underestimates.

The mass of the substrate excavated by gerbils was collected from each hole of the five systems that were mapped to give an indication of the substrate turnover per burrow. The mass of the substrate excavated per night was determined from a further 20 randomly selected active holes by clearing away any prior mounds in order to collect, on a plastic sheet, only freshly excavated substrates. It was assumed that the substrate collected at each hole was excavated by only one gerbil.

During burrow system excavation, substrate cores were taken next to the tunnels for the purposes

of assessing root biomass in the immediate vicinity of them. These were compared with roots extracted from additional soil cores taken in the control quadrats.

2.2.2 Substrate structure and chemistry

Substrate properties of the three impact zones were compared by taking substrate core samples (with a manual soil corer) from the centres of the randomly determined quadrats within each grid at three depths (0-10 cm, 10-20 cm & 20-30 cm). These samples were sealed in airtight plastic bags, and stored for later analysis. The cores were analysed at the Research Institute for Reclamation Ecology (North-West University) to determine the particle size distribution and chemical composition of the substrate.

Substrate particles were grouped into four categories: Gravel (particles >2 mm); Sand (very coarse, coarse & medium-sand); Silt (fine- & very fine-sand and silt); and Clay. Soil moisture content was determined by drying sub-samples of substrate to a constant weight in a laboratory oven at ~50° C.

Substrate chemical composition was assessed for: pH; salinity (determined from substrate electro-conductivity, in mS/cm); % Carbon; biologically important macro-elements (NO₃, NH₄, P, HCO₃, K, Na, Ca, Mg, SO₄ & Cl in mmol/l); biologically important micro-elements (B, Fe, Mn, Cu & Zn in µmol/l) and biologically toxic heavy metals (Al & Se in mg/l).

Additional substrate cores (10 cm deep) were taken from the floors of excavated tunnels, to assess the substrate chemical composition in the immediate vicinity of tunnels. These were analysed for: pH; salinity; % C; and macro-elements (NO₃, NH₄, P & HCO₃).

2.2.3 Plant community characteristics

The vegetation in each impact zone was assessed using two complementary sampling methods, namely dropped-point transects (similar to the wheel-point method) and rigid 1 m² quadrats, each method was chosen for its suitability in assessing certain aspects of the plant community (Barbour, Burk & Pitts 1987).

A dropped-point transect was undertaken by dropping a pointer at ~1 metre intervals along ten, 10 m transects (1 m apart) within each grid, yielding 100 sample points. At each drop-point, the following characteristics were noted for the nearest rooted plant species within 30 cm:

- occurrence (to calculate frequency, as percentage);
- cover, expressed as *basal* (where the dropped point hit the stem); *crown* (where the point traversed the foliage near the stem) or *zero* (the point outside the crown but still within 30 cm of the stem);
- reproductive state or phenology (seedling, non-flowering mature plant, mature plant in flower, mature plant with seed, mature plant with chaff & dead).

If no rooted plant was within a 30 cm radius of the point, bare ground was recorded.

Three 1 m² quadrats (of the hundred available) were randomly chosen from each grid, and each plant species within the quadrat was assessed according to:

- density (number of individuals per 1 m²);
- phenology (using the same categories as for the transect assessment technique above);
- dry-weight biomass (all plants harvested were dried for 72 hours at ~50° C in a laboratory oven).

For each quadrat and transect, species richness, as well as Shannon-Wiener diversity and evenness indices were calculated, additionally, these indices were also calculated for grasses and forbs.

2.3 Plant Ecological Status

The plant species sampled in this study, as well as certain general characteristics, are summarised in Table: 2.3. Species identification, annual/perennial and grass/forb status follow Morgenthal (2003). Unidentified species, and incompletely identified species (described as species 1-5, or as X species 1, etc), were at least classified as grasses or forbs (Table 2.3).

Ecological Status designations for grass species follow definitions defined by van Oudtshoorn (1991) as follows:

- Decreaser: Palatable climax grasses abundant in veld in good condition. These species decrease when the veld is over-grazed or underutilised.
- Increaser I: Unpalatable robust climax grasses abundant in underutilised veld. These species increase when veld remains under-grazed.
- Increaser II: Pioneer and sub-climax grass species which are abundant in over-grazed veld. These species produce large quantities of seed and increase following a disturbance to the veld.
- Increaser III: Unpalatable dense climax grass species common in over-grazed veld receiving higher precipitation. These species are strong competitors and increase as a result of over-grazing weakening the more palatable grasses.

Other indicators added to the ecological status column following the advice of T. Morgenthal (T.L. Morgenthal 2000, pers. comm.*).

- Exotic: Grass species not native to the southern African region, no ecological indication is given.
- Cultivated Land: Forb species typically found in areas which are cultivated.
- Grassland: Forb species typically associated with the plant community comprising grasslands.
- Weed: Forb species, often ruderal or pioneer, not indigenous to the area (an invader). These species indicate areas of disturbance.

2.4 Statistical Analysis

The data were analysed with the Statistica 5.1 software package (StatSoft, Inc. 1984-1996). Each data suite analysed was first tested for normality (using the Kolmogorov-Smirnov D-statistic), and if satisfied, for homogeneity of variance using Levene's test. If these criteria were fulfilled, parametric analytical methods were used as they are considered more able to statistically describe data than non-parametric tests (Zar 1984). Data were sometimes transformed to a log_e-scale to avoid using a non-parametric method if this transformation resulted in a normal distribution.

Data for the three impact zones were compared using one-way analysis of variance (ANOVA) utilising means for parametric tests, and with the Kruskal-Wallis ANOVA using medians for non-parametric tests. Where significant differences were indicated, specific relationships were established between variables utilising parametric post-hoc comparisons of means (Tukey's honest significant difference test) or parametric t-tests. The non-parametric equivalent test used, was the Mann-Whitney U-test (the Z-value thereof). However, if the sample size was small, approximations of the Z-value were used (a Z(adjusted)-value), in which the data were corrected for continuity (Statsoft, Inc. 1984-1996).

Principal Component Analyses, which rank statistically significant components in order of importance along three factor axes, were used to examine multivariate differences among impact zones. Specifically, this was to determine which variables affected by gerbil activity differed most markedly among impact zones.

Data from the control zones of the two consecutive years of sampling on PFA-dam A (1998 & 1999) were compared to assess differences in the plant community that could be attributed to sampling at different points of the growth season.

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Table: 2.3 Plant Species and reference characteristics from the plant community sampled on PFA-dam A of Hendrina Power Station.

Species Name	Species Number	Annual / Perennial	Grass / Forb	Ecological Status
<i>Eragrostis plana</i>	1	Perennial	Grass	increaser II
<i>Pennisetum clandestinum</i>	2	Perennial	Grass	exotic
<i>Cynodon dactylon</i>	3	Perennial	Grass	increaser II
<i>Chamaecrista biensis</i>	4	Annual	Forb	grassland
<i>Conyza canadensis</i>	5	Annual	Forb	weed
<i>Tagetes minuta</i>	6	Annual	Forb	weed
<i>Eragrostis curvula</i>	7	Perennial	Grass	increaser II
<i>Schkuhria pinnata</i>	8	Annual	Forb	weed
<i>Hyparrhenia hirta</i>	9	Perennial	Grass	increaser I
<i>Cyperus esculentus</i>	10	Ann./ Per.	Forb	weed
Unidentified dead forb	11	Annual	Forb	
<i>Lepidium bonariensis</i>	12	Annual	Forb	weed
<i>Pseudofolium undulatum</i>	13	Annual	Forb	weed
<i>Conyza bonariensis</i>	14	Annual	Forb	weed
<i>Oxalis</i> species 1	15	Perennial	Forb	grassland
<i>Acanthospermum glabratum</i>	16	Annual	Forb	weed
<i>Setaria pallide-fusca</i>	17	Perennial	Grass	increaser II
<i>Bulbostylis humilis</i>	18	Annual	Forb	
<i>Cyperus usitatus</i>	19	Ann./ Per.	Forb	
<i>Verbena bonariensis</i>	20	Ann./ Per.	Forb	weed
<i>Eragrostis echinocloidea</i>	21	Perennial	Grass	increaser II
<i>Pelargonium luridum</i>	22	Perennial	Forb	grassland
Species 1	23		Forb	
<i>Sorrel</i> species 1	24		Forb	
<i>Bidens formosa</i>	25	Annual	Forb	weed
<i>Hibiscus trionium</i>	26		Forb	weed
<i>Cleome monophylla</i>	27	Annual	Forb	
<i>Flauria bidentis</i>	28	Annual	Forb	weed
<i>Panicum coloratum</i>	29	Perennial	Grass	decreaser
<i>Sporobolus africanus</i>	30	Perennial	Grass	increaser III
Species 3	31		Forb	
Species 2	32		Forb	
<i>Walafrida densiflora</i>	33	Perennial	Forb	
<i>Aristida congesta</i>	34	Ann./ Per.	Grass	increaser II
Species 4	35		Forb	
Species 5	36		Forb	
<i>Pogonarthria squarrosa</i>	37	Perennial	Grass	increaser II
<i>Cyperus</i> species 1	38	Ann./ Per.	Forb	weed
<i>Bidens bipinnata</i>	39	Annual	Forb	weed
<i>Amaranthus</i> species 1	40	Annual	Forb	weed
<i>Vigna vexillata</i>	41	Perennial	Forb	grassland
<i>Themeda triandra</i>	42	Perennial	Grass	decreaser
<i>Digitaria eriantha</i>	43	Perennial	Grass	decreaser
Bare Ground	44			

CHAPTER 3

RESULTS: BURROW SYSTEM DESCRIPTION AND QUANTIFICATION OF DIRECTLY ASSOCIATED IMPACTS

There are few studies detailing the architecture and quantifying the volume of individual gerbil burrow systems (Bronner 1992; Bhadauria & Mathur 1994), especially in rehabilitated landscapes. Most studies have focussed on the effects of gerbil burrowing activities on substrate and plant communities in natural ecosystems (Korn & Korn 1989; Dean & Milton 1991a; Whitford & Kay 1999). The present study is an attempt to address this lack of information by mapping the burrow systems of *Tatera brantsii* in detail and accurately measuring burrow topographies. The study also includes an estimation of substrates excavated by individual gerbils as an indication of substrate turnover, which can then be used in conjunction with gerbil density studies to quantify the extent of species impact in this and similar ecosystems.

Although not pursued in this study, it was found that organic material in tunnels was uncommon, and while none of the systems sampled contained more than a single nest, some chambers identified as nests (entrances plugged with loose soil), did contain vegetative organic material, possibly bedding. Detailed analysis of this material was not undertaken, however a number of arthropod species were extracted from the nesting material and several individuals of a flea species (*Chiaestopsylla rossi*), associated with *T. brantsii*, were identified using the Siphonaptera of Southern Africa (Segerman 1995) identification key. Nest material may provide niches for other organisms, and despite that burrows are not occupied for extended periods of time because gerbils move away as food resources become depleted (Korn & Korn 1989), this is another form, albeit short-lived, of ecological impact.

3.1 Burrow system architecture

The five intensively mapped burrow systems are shown in Appendix 1 (Figs. B1 - B5). The results of all investigated burrow systems, and associated activities are summarised in Table 3.1.

Table: 3.1 Tunnel and burrow system characteristics of *Tatera brantsii* burrows on the plateaux of the rehabilitated PFA-dams at Hendrina Power Station. n = number of measurements from 5 systems.

Aspect	No. systems	n	Range	Mean±SD
Average Tunnel:				
height (cm)	5	280	3 - 16	5.0±1.2
width (cm)	5	287	3 - 17	6.6±2.4
depth (cm)	5	285	5 - 37	16.0±6.3
Average Chamber:				
height (cm)	5	93	2 - 12	5.3±1.7
depth (cm)	5	90	6 - 38	15.7±7.4
Overall System:				
length (cm)	9	9	767 - 2387	1289.8±464.8
no. chambers	5	5	3 - 12	6.0±3.7
no. nests	9	9	0 - 1	0.3±0.5
no. cul de sacs	5	5	8 - 12	9.8±1.6
no. access holes	9	9	4 - 10	6.7±2.1
Average System:				
volume (cm ³)	5	5	29104 - 78478	41650.0±20772.7
Substrate excavated:				
per night (g)	n/a	20	22 - 442	128.9±107.9
per hole (g)	5	35	0 - 23171	4950.8±4459.5
per system (g)	5	5	27282 - 55113	34643.2±10458.7
Active holes/transect	n/a	6	0 - 8	4.0±2.6

3.2 Localised effects of burrows on substrate chemistry

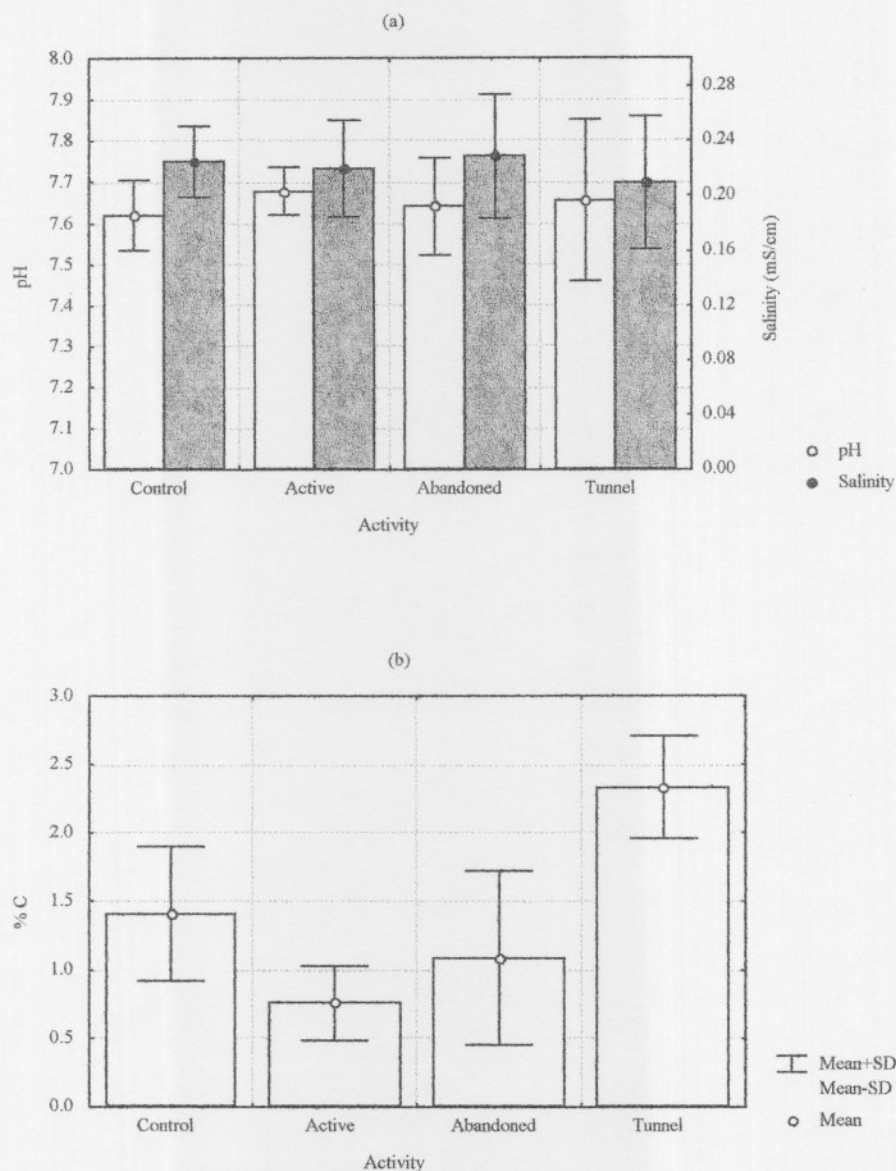


Figure 3.1: The pH, salinity & % Carbon of impact zone substrates at a depth of 10-20 cm compared to that of tunnels of burrows of *T. brantsii*. Bars denote mean values, vertical lines represent 1SD.

There were no significant differences in pH and salinity (data $\log_e$ transformed) of substrate samples taken from the floors of tunnels (Fig. 3.1a) relative to the general background values (i.e. those measured in substrate samples taken from the impact zones). However, the % Carbon in tunnel samples was significantly greater than in samples from any of the three impact zones ($H_{3,46}:31.366$, $P < 0.001$, Fig. 3.1b). The same trend was evidenced for Phosphorous levels, which were higher in tunnel substrate than any of the background (impact zone) values ($H_{3,46}:38.380$, $P < 0.001$, Fig. 3.2b). Nitrate concentrations $[\text{NO}_3]$ (data $\log_e$ transformed) in tunnel substrates were significantly greater than in control and active zones ($F_{3,42}:8.817$, $P < 0.001$, Fig. 3.2a), and ammonia concentrations $[\text{NH}_4]$ were significantly higher in

tunnels than background values in active or abandoned zones ($H_{3,46}:11.181$, $P < 0.05$, Fig. 3.2a). Conversely, bicarbonates [HCO_3] in tunnel substrates showed the opposite trend, and were significantly reduced when compared with those of the control zones ($F_{3,42}:3.382$, $P < 0.05$, Fig. 3.2b).

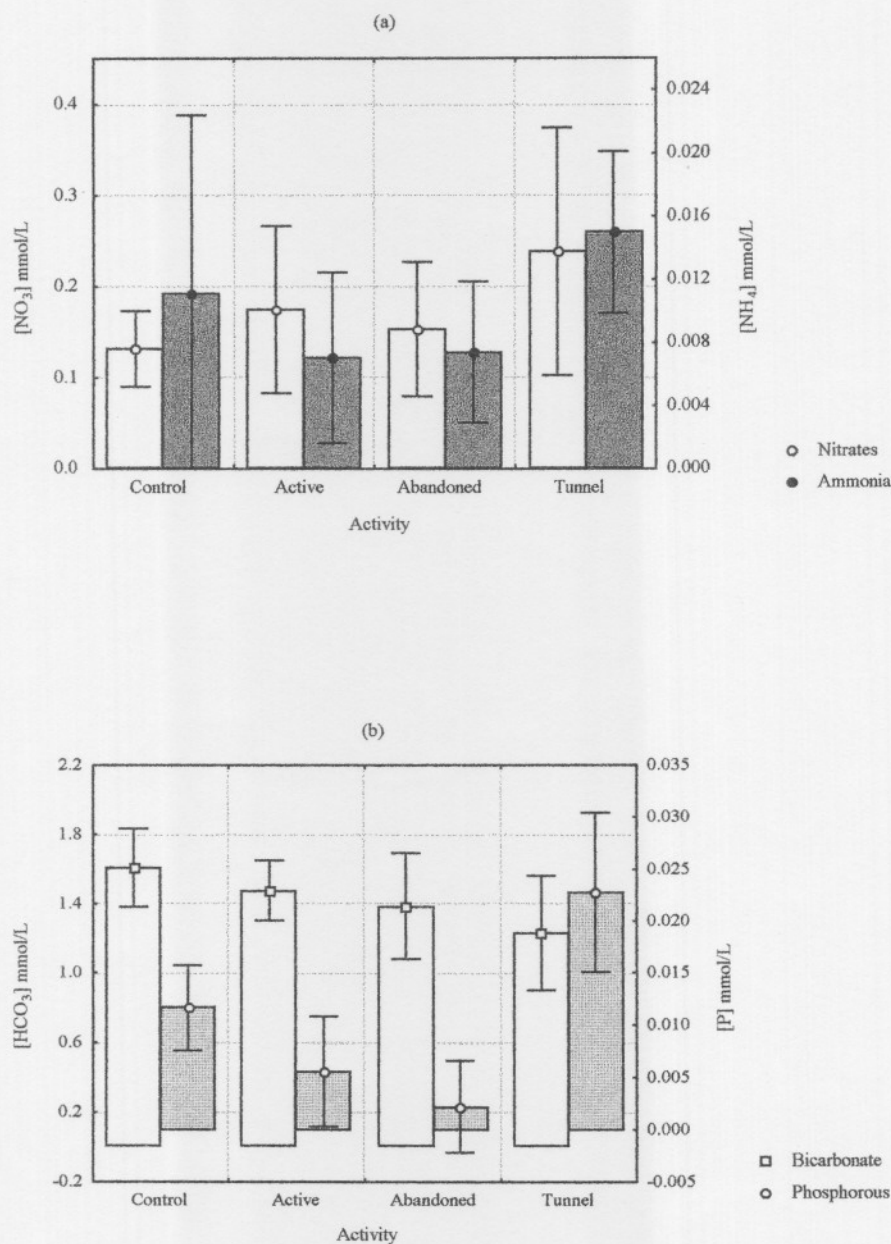


Figure 3.2: Concentrations of Nitrates [NO_3], Ammonia [NH_4], Bicarbonates [HCO_3] & Phosphorous [P] of impact zone substrates at a depth of 10-20 cm compared to that of tunnels of burrows of *T. brantsii*. Bars denote mean values, vertical lines represent 1SD.

3.3 Root biomass

Root biomass was reduced near tunnels, compared to samples from control zones at the same depths, significantly so in the 10-20 cm depth category ($F_{1,30}:6.485$, $P < 0.05$, Fig. 3.3).

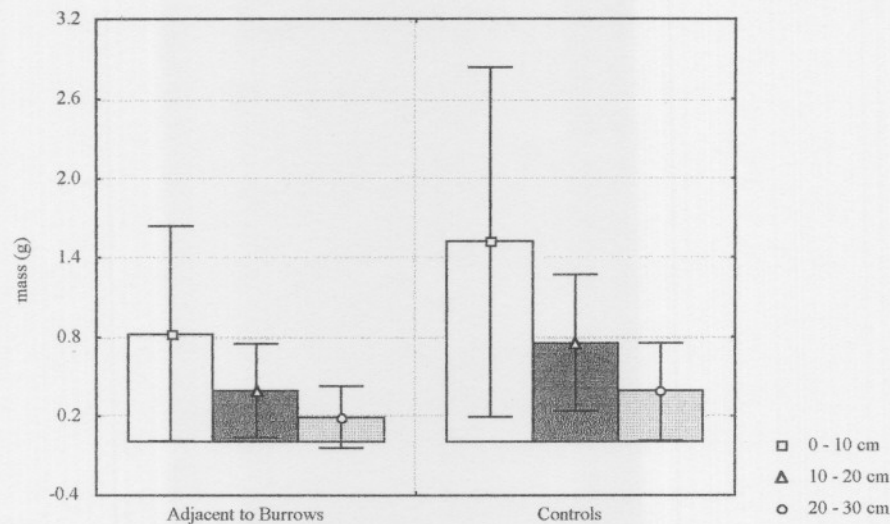


Figure 3.3: The root biomass adjacent to tunnels compared with that of control zones at three depths. Bars denote mean values, vertical lines represent 1SD.

3.4 Discussion

Burrowing was limited to the upper level of the substrate, under the topsoil layer, and was rarely deeper than 30 cm. Tunnel depths averaged approximately 16 cm, and generally exceeded this only when they enlarged into chambers. Tunnel diameters were fairly uniform and averaged between 5 and 6.5 cm. These parameters are similar to those found by Bronner (1992) in a natural grassland in Mpumulanga. Increased tunnel height was mostly associated with chambers, and it was observed that tunnels wider than average often showed evidence of side-wall collapse of the dry ash beneath the hardened topsoil crust.

The burrow systems comprised long, often convoluted tunnels interspersed with the occasional chamber (usually off a side tunnel). Most tunnels of a system terminated at an access hole but branching and blind tunnels were common. Length was highly variable, ranging from just under 8 m, to almost 24 m long, and are notably longer than burrow systems in a natural grassland (approximately 5 m - 7 m long; Bronner 1992).

If one calculates the number of systems per 10 x 10 m grid (dividing the mean number of active holes per transect by the mean number of access holes per system), and extrapolates to one hectare, the density of a *T. brantsii* colony on the plateau of the PFA-dam A is approximately 59.7 systems / ha. The volume of substrate excavated from a colony in this habitat (2.5 m³), exceeds by more than three times that of a *Tatera robusta* colony on the shortgrass plains of the Serengeti (0.7 m³; Whitford & Kay 1999).

The quantities of substrate excavated by gerbils were at least 27 kg (and could reach 55 kg) *per system*, most of it being removed through only a few access holes. However, as it would be unfeasible to expect to collect all the substrate excavated in a field sampling situation, the information recorded in Table 3.1 gives only a conservative estimate of the actual quantity.

Further, gerbil excavation, from an active burrow in this study, could reach almost half a kilogram from one hole in a single night. If one extrapolates from the average number of access holes per system, multiplied by the amount excavated per hole per night, a single gerbil could potentially excavate up to 0.9 kg of substrate a night during the construction phase of an active burrow. This is more than 11 times the average mass of an adult gerbil (Skinner & Smithers 1990). The potential impact on substrate cycling in the PFA-dam environment is quite vast, considering that *T. brantsii* was the second most abundant small mammal species on the PFA-dam plateaux at the time of this study, and comprised about 48 % of the small mammal community (Vermaak 2000). The densities of *T. brantsii* gerbils (Vermaak 2000) captured on the PFA-dams during the time period of this study (1998-1999), averaged 19.3 for males

(26.8 for females), potentially increasing the amount of substrate excavated *per night* by the gerbil community to 16.6 kg (males) and 23.1 kg (females) for a total of 39.7 kg.

This quantity however, represented only a trapping success of 14.8 % for *T. brantsii* (Vermaak 2000), so the possible amounts of excavated substrate may be greater still.

There were no food hoards and very few nests associated with *T. brantsii* burrow systems in this habitat. Thus, localised increases in carbon, nitrates, ammonia and phosphorous (Figs. 3.1 & 3.2) were probably as a result of deposited excreta and the decay processes associated with this organic matter (including the decay-organisms themselves). Small quantities of discarded food and other vegetative matter, as well as the decay of plant roots disrupted by burrowing, could increase the substrate organic content (% C) in the immediate vicinity of gerbil tunnels. Other biopedturbation studies, noting increased substrate nutrient status, concentrated on larger-scale disturbances than the substrate immediately surrounding tunnels, namely, the mounds of substrate excavated (Golley *et al* 1975; Huntly & Reichman 1994; Whitford & Kay 1999) or the area of the disturbance (Dean & Milton 1991a).

Bicarbonate levels are associated with higher pH and salinity in arid soils (Tivy 1990), partly as a result of the upward (evaporation-driven) movement of salts in the soil profile, but also, in the absence of leaching, as a product of weathering (see Section 4.4). The reduced HCO_3 concentrations in tunnel substrates, in the absence of any observed changes in pH and salinity, suggest that the substrate continuity, and the upward flow of salts, were not disrupted by the presence of gerbil tunnels. Instead, the decline in $[\text{HCO}_3]$ was probably associated with rainwater infiltration into the tunnels, and the subsequent leaching of soluble bicarbonates.

Direct damage, and the physical undermining of roots by tunnels, may have underlain the decrease in the biomass of roots above and immediately around tunnels (Fig. 3.3). Yet, tunnels also allow air to circulate freely, with the consequence that the substrate associated with the tunnels becomes drier as interstitial water evaporates, and this may have accounted for some of the observed decrease in the biomass of roots adjacent to tunnels. The average tunnel depth was 16.0 ± 6.3 cm, which could explain why the impact was greatest in the 10-20 cm depth category.

3.5 Conclusions

Tatera brantsii burrow systems in this habitat seemed quite extensive, but it must be kept in mind that the substrate consisted of fairly uniform ash below the topsoil, so gerbils had no need to dig through or around consolidated regions, concretions and/or rocks, as are found in natural substrates (Tivy 1990; Whitford & Kay 1999). The quantities of the substrate excavated by this species may therefore have been overestimations in comparison with natural ecosystems. However, the very uniformity of this substrate presented an opportunity to examine the intricacy of the burrow system architecture without the interference of impassable inclusions. Burrow systems of *T. brantsii* met the requirements of the concept of ecosystem engineering, in that the changes brought about in the environment by their digging were distinctive from abiotic processes, and were relatively larger than the physical processes operating in the system (Reichman & Seabloom 2002).

It was clear that gerbil digging activities had an impact on substrate chemistry (significantly altering the levels of biologically-important elements) and root biomass, and thereby a potential impact on plant productivity. Other studies (Korn & Korn 1989; Day & Detling 1994; Huntly & Reichman 1994), indicated that plant productivity was generally reduced above burrows and on colonies. However, in this study, impact was limited to the immediate vicinity of the burrows themselves, as evidenced by the absence of any significant changes in the prevailing general substrate conditions of pH and salinity compared to controls. The effects were also likely to be transient, as gerbils inhabit burrows for only a short period, and colonies tend to move over time as they deplete local resources (Korn & Korn 1989). Thus, at colony level, these substrate nutrient enrichment effects brought about directly by gerbil activities (the increased organic content and N-content in tunnels), probably had no more than a negligible impact, because they were too localised and short-lived to have any persistent or major ecological effect.

CHAPTER 4

RESULTS: IMPACTS OF GERBIL ACTIVITY ON SUBSTRATE STRUCTURE AND CHEMISTRY

Individual burrows may have a negligible impact on the structure and chemistry of the substrate (Section 3.2). However, the cumulative effect of a colony of burrows, with the addition of nutrients from the decay of buried organic matter, and the weathering of deeper substrates brought to the surface, may serve to increase the fertility of the substrate in this industrial habitat as it does in natural habitats (Whitford & Kay 1999). Biopedturbation increases the friability of substrates as excavated substrate is of a lower bulk density, and is an important aspect of pedogenesis (Golley *et al.* 1975; Whitford & Kay 1999). Higher water infiltration rates and enhanced erosion are also consequences of biopedturbation (Eloff 1953; Hakonson 1999; Whitford & Kay 1999; Reichman & Seabloom 2002).

The present study attempted to establish what impacts *T. brantsii* had on substrate structure and chemistry in the PFA-dam industrial habitat.

4.1 Substrate structure and moisture

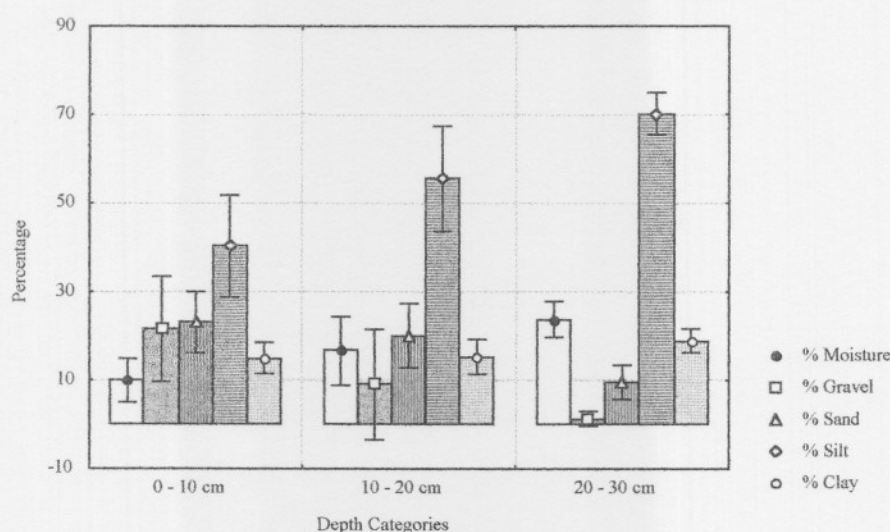


Figure 4.1: Percentages of substrate particle classes and % moisture at three depths in control zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

The distribution of substrate particles and percentage moisture in the top thirty centimetres of the soil profile, following ecological rehabilitation, and before gerbils started burrowing into the substrate, was assessed in the control zones (Fig. 4.1). From analysis of variance (ANOVA) it was found that the % gravel differed significantly with substrate depth ($H_{2,18}:8.933$, $P < 0.05$). Using U-tests, it appeared that at 0-10 cm the % gravel was greater than at 20-30 cm ($Z:2.882$, $P < 0.01$). The % sand at 0-10 cm and at 10-20 cm was significantly higher than at 20-30 cm ($F_{2,15}:7.802$, $P < 0.01$). The % silt increased significantly with increasing depth ($F_{2,15}:13.648$, $P < 0.001$), but the % of clay did not vary significantly with depth.

The % moisture differed significantly with depth ($H_{2,18}:9.836$, $P < 0.01$), and was lower at 0-10 cm than 20-30 cm ($Z:-2.882$, $P < 0.01$).

4.1.1 % Gravel content

The % gravel (Fig. 4.2) differed with depth in active ($H_{2,27}:10.136$, $P < 0.01$) and abandoned ($H_{2,27}:11.715$, $P < 0.01$) zones. In active zones, there was significantly more gravel at 0-10 cm than at 10-20 cm ($Z:2.517$, $P < 0.05$) and at 20-30 cm ($Z:2.870$, $P < 0.01$). Similarly, in abandoned zones, % gravel was higher at 0-10 cm than at 10-20 cm ($Z:2.075$, $P < 0.05$) or 20-30 cm ($Z:2.826$, $P < 0.01$), and % gravel was also significantly higher at 10-20 cm than at 20-30 cm ($Z:2.428$, $P < 0.05$).

Comparison of impact zones (all depth data pooled) showed that % gravel was significantly higher in the abandoned zones than in the control and active zones ($H_{2,72}:6.424$, $P < 0.05$). At 0-10 cm and 10-20 cm, samples from the impact zones contained similar percentages of gravel (no significant differences). However at 20-30 cm, impact zones differed with regard to % gravel ($H_{2,24}:8.830$, $P < 0.05$), being significantly lower in both control ($Z:-2.710$, $P < 0.01$) and active zones ($Z:-2.163$, $P < 0.05$) when compared to abandoned zones.

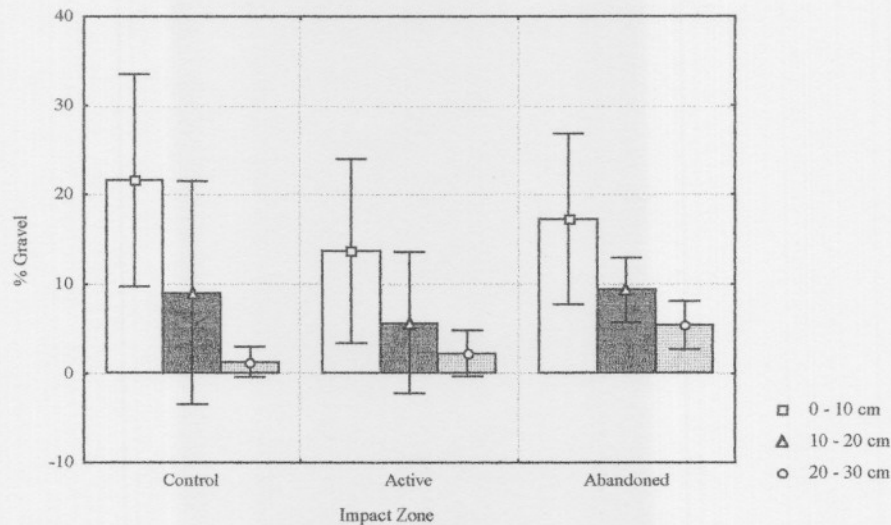


Figure 4.2: Comparison of substrate % gravel particle distributions at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

4.1.2 % Sand content

The percentage of sand did not differ significantly among depth categories in either the active or abandoned zones (Fig. 4.3). In the 0-10 cm and 10-20 cm depth categories, the abandoned zones had significantly greater % sand than the active or control zones (0-10 cm: $F_{2,21}:12.548$, $P < 0.001$ and 10-20 cm: $F_{2,21}:10.52$, $P < 0.001$). Also, in the 20-30 cm category the % sand was significantly higher in the abandoned zones than in the control zones ($F_{2,21}:8.430$, $P < 0.05$).

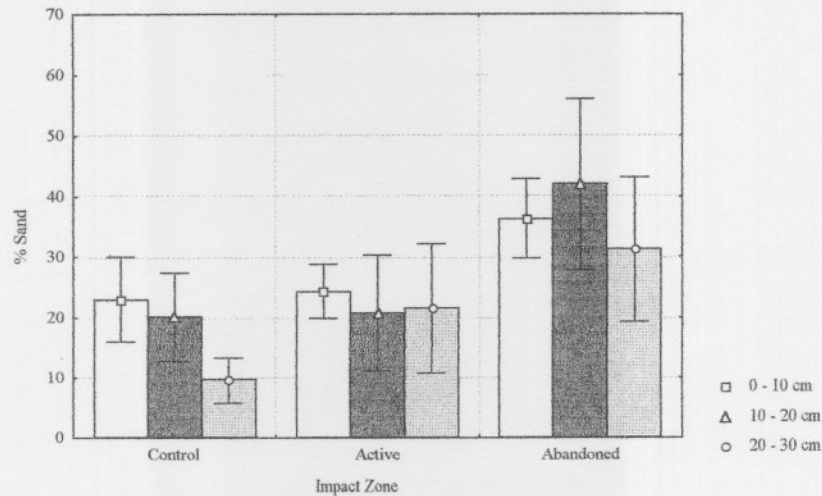


Figure 4.3: Comparison of substrate % sand particle distributions at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

4.1.3 % Silt content

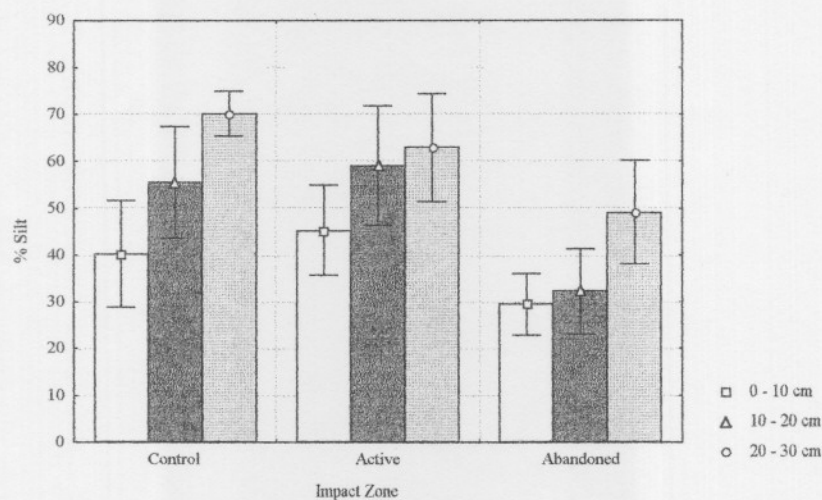


Figure 4.4: Comparison of substrate % silt particle distributions at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

In the active zones % silt was significantly lower at 0-10 cm than at both 10-20 cm and 20-30 cm ($F_{2,24}:6.037$, $P < 0.01$, Fig. 4.4), but the latter two depth categories did not differ significantly in silt percentage. In abandoned zones, % silt at 20-30 cm was significantly greater than at either 0-10 or at 10-20 cm ($F_{2,24}:9.505$, $P < 0.001$). In the topsoil layer (0-10 cm), the abandoned zones had significantly less % silt than active zones ($F_{2,21}:7.022$, $P < 0.01$), and at 10-20 cm, the % silt was significantly reduced compared to either the active or control zones ($F_{2,21}:14.595$, $P < 0.001$). No significant differences were found among impact zones at 20-30 cm.

4.1.4 % Clay content

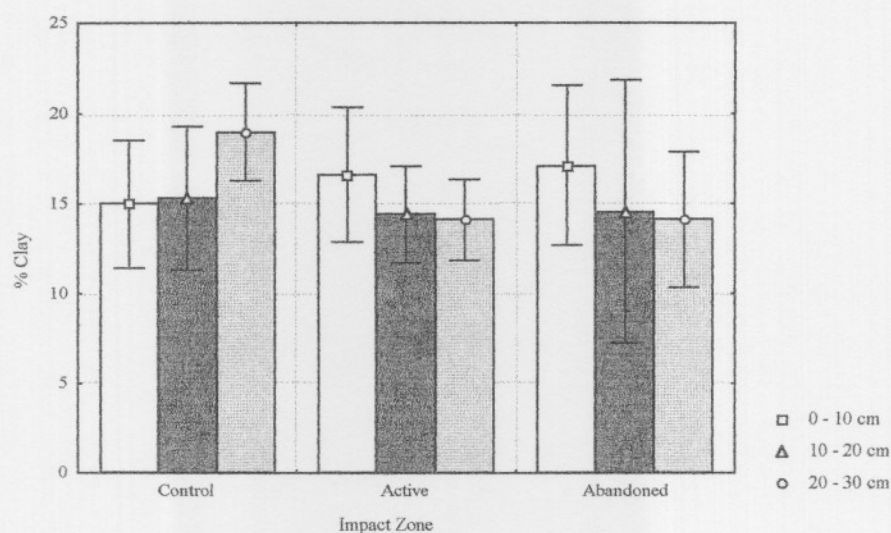


Figure 4.5: Comparison of substrate % clay particle distributions at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

The % clay of the substrate did not vary significantly with depth in any of the impact zones. However, at 20-30 cm the control zones had significantly elevated levels of % clay relative to either of the active or abandoned zones ($F_{2,21}:5.892$, $P < 0.01$, Fig. 4.5).

4.1.5 % Moisture content

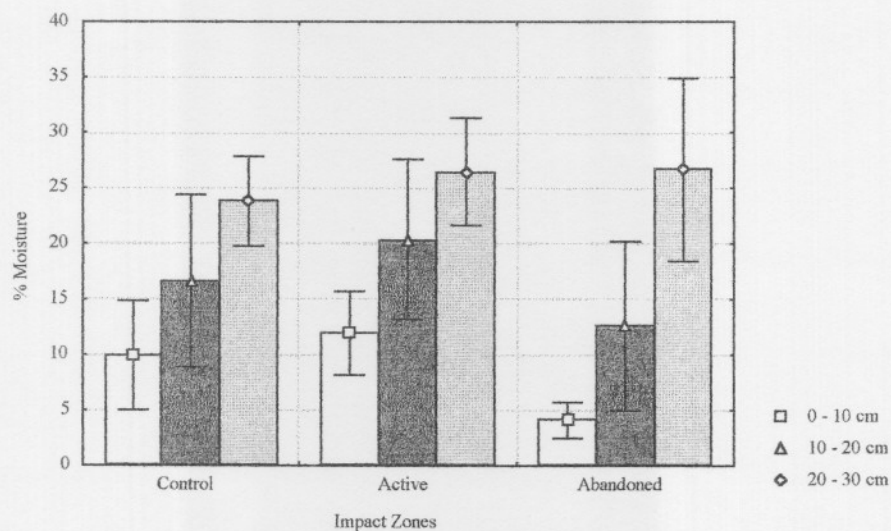


Figure 4.6: Comparison of substrate % moisture distribution at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

The % moisture data were $\log_e$ transformed to satisfy the ANOVA-related criterion of

homogeneity of variances. % Moisture differed significantly with depth in each impact zone (ie: active: $F_{2,24}:9.445$, $P < 0.001$; abandoned: $F_{2,24}:41.152$, $P < 0.001$, Fig. 4.6). From post hoc comparisons, the substrate appeared significantly drier at 0-10 cm than at 20-30 cm in active zones, and the % moisture increased with each depth category in abandoned zones. At a depth of 0-10 cm, the substrates in abandoned zones were significantly drier than in either of active or control zones ($F_{2,21}:19.730$, $P < 0.001$), but no differences were noted in % moisture among impact zones at 10-20 cm and 20-30 cm.

4.2 Substrate chemistry

4.2.1 pH, Salinity and % Carbon

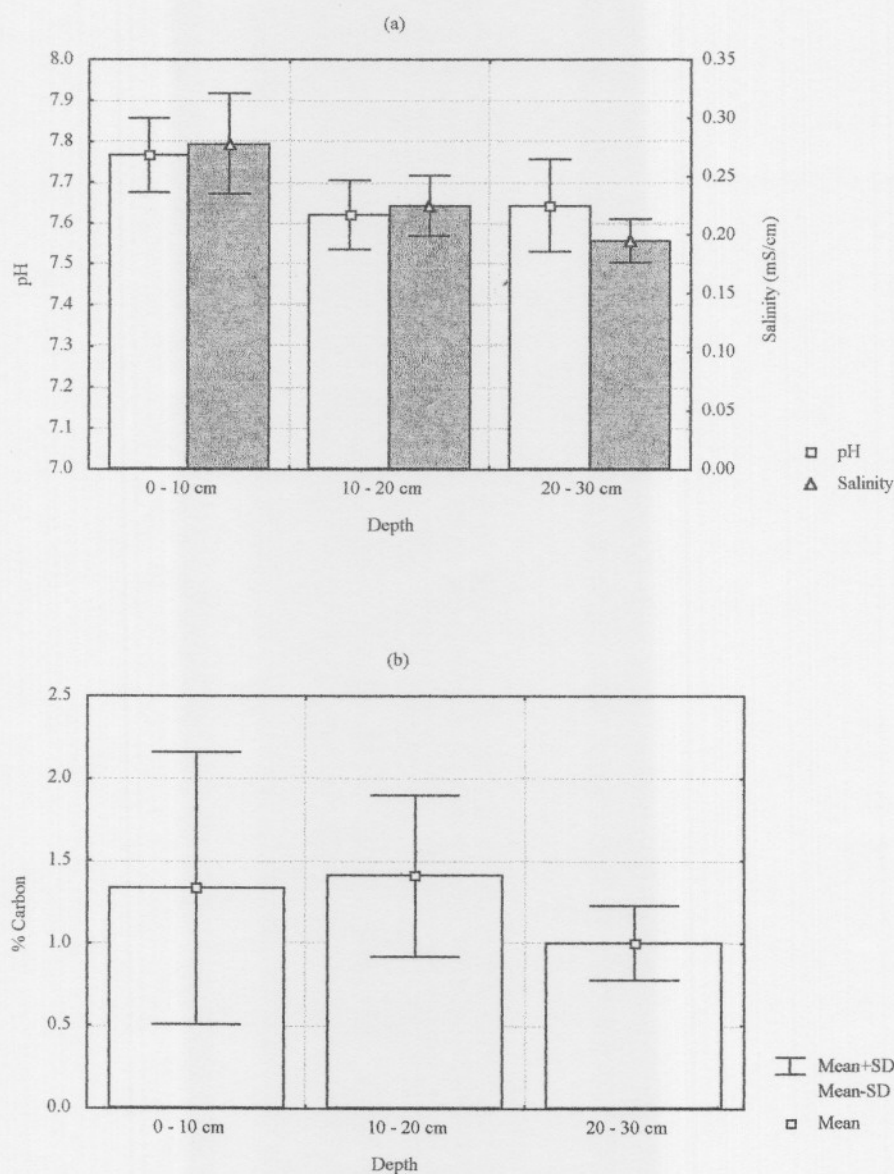


Figure 4.7: The pH, salinity & % Carbon of control zone substrates at three depths on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

The substrate characteristics of pH, salinity and % Carbon were assessed from control zones as an indication of substrate conditions before gerbils had an impact (Fig. 4.7). Substrate pH (log_e transformed) at 0-10 cm was significantly higher (7.767 ± 0.091) than at 10-20 cm (7.620 ± 0.085 ; $F_{2,15}:3.909$, $P < 0.05$), giving a more alkaline topsoil (Fig. 4.7a). The pH was lower at 20-30 cm (7.643 ± 0.114) but, because of variability in the sample data, any significant depth effects may have been masked. Substrate salinity (log_e transformed) was also significantly higher in the topsoil (0-10 cm) than deeper in the soil profile (10-20 & 20-30 cm; $F_{2,15}:12.074$, $P < 0.001$, Fig. 4.7a). The % Carbon did not vary significantly with depth in the control zone substrate (Fig. 4.7b).

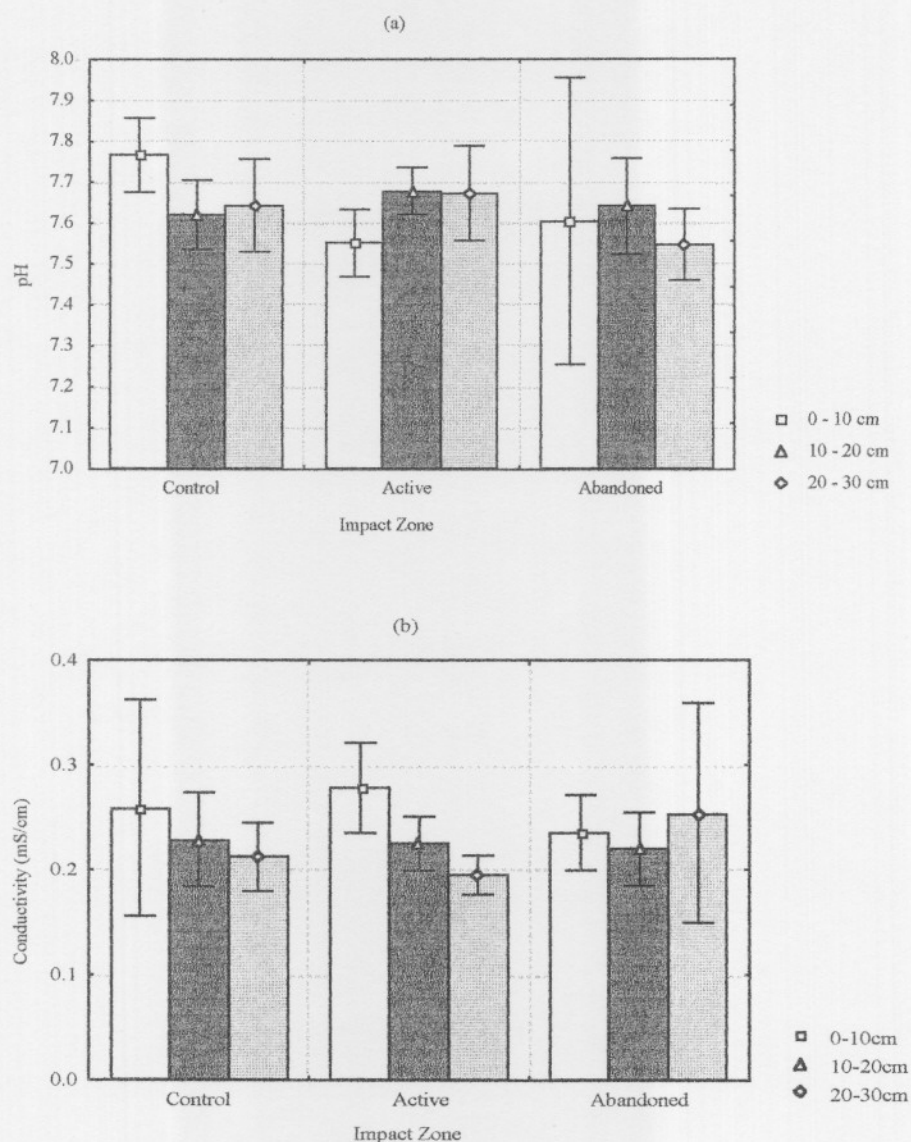


Figure 4.8: Comparisons of substrate pH and salinity at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

In contrast to the controls, the topsoil (0-10 cm) of the active zones was significantly more acidic (7.551 ± 0.082) than the substrate deeper in the soil profile (10-20: 7.679 ± 0.058 & 20-30: 7.673 ± 0.117 ; $F_{2,24}:5.946$, $P < 0.01$, Fig. 4.8). The pH of substrates from abandoned zones did not differ with depth. When comparing impact zones, gerbil activity had an effect on pH at 0-10 cm. Post hoc comparison of

means proved inconclusive, but t-tests revealed that control zones were significantly more alkaline (higher pH) than the active zones ($t_{df13}:4.773$, $P < 0.001$).

Salinity did not differ with depth in either of the active or abandoned impact zones, nor did salinity differ significantly among impact zones in each depth category.

There were significant differences in % Carbon (% C; data log_e transformed) among the depth samples in the active zones ($H_{2,27}:7.088$, $P < 0.05$, Fig. 4.9), with % C greater at 0-10 cm than at 10-20 cm ($Z:2.693$, $P < 0.01$). The % C did not vary significantly with depth in the abandoned zones. Also, in all depth categories, none of the three impact zones differed significantly from each other with regard to % C.

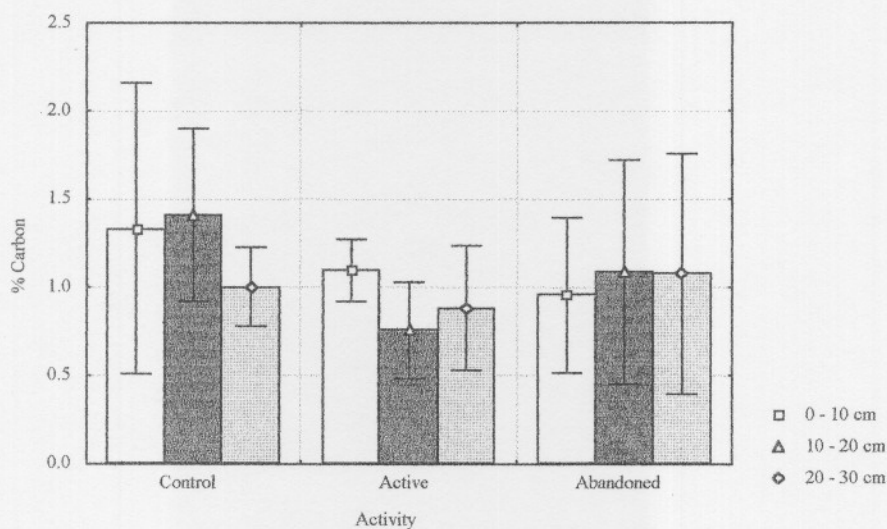


Figure 4.9: Comparison of substrate % Carbon at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

4.2.2 Macro-elements

In control zones, concentrations of nitrates [NO_3], ammonia [NH_4], Sodium [Na], sulphates [SO_4] and Chlorine [Cl] did not vary significantly with depth (Fig. 4.10). However, bicarbonate (HCO_3), and Calcium (Ca) concentrations decreased significantly with depth (HCO_3 : $H_{2,18}:10.993$, $P < 0.01$; Ca: $H_{2,18}:14.966$, $P < 0.001$, Fig.4.10). At both 0-10 cm ($Z:2.882$, $P < 0.01$) and 10-20 cm ($Z:2.242$, $P < 0.05$), [HCO_3] was greater than at 20-30 cm, and [Ca] at 0-10 cm was greater than at both 10-20 cm ($Z:2.882$, $P < 0.01$) and 20-30 cm ($Z:2.882$, $P < 0.01$). [Ca] at 10-20 cm was also greater than that at 20-30 cm ($Z:2.802$, $P < 0.01$). Potassium concentration [K] was significantly higher at 0-10 cm than at 10-20 cm ($t_{df10}:2.313$, $P < 0.05$). Phosphorous (P) and Magnesium (Mg) concentrations increased with increasing depth (P: $H_{2,18}:9.837$, $P < 0.01$; Mg: $F_{2,15}:6.249$, $P < 0.05$). [P] was lower at 0-10 cm than at either 10-20 cm ($Z:-2.482$, $P < 0.05$) or 20-30 cm ($Z_{(adj)}:-2.211$, $P < 0.05$), and [Mg] was significantly higher at 20-30 cm than at 0-10 cm (Fig.4.10).

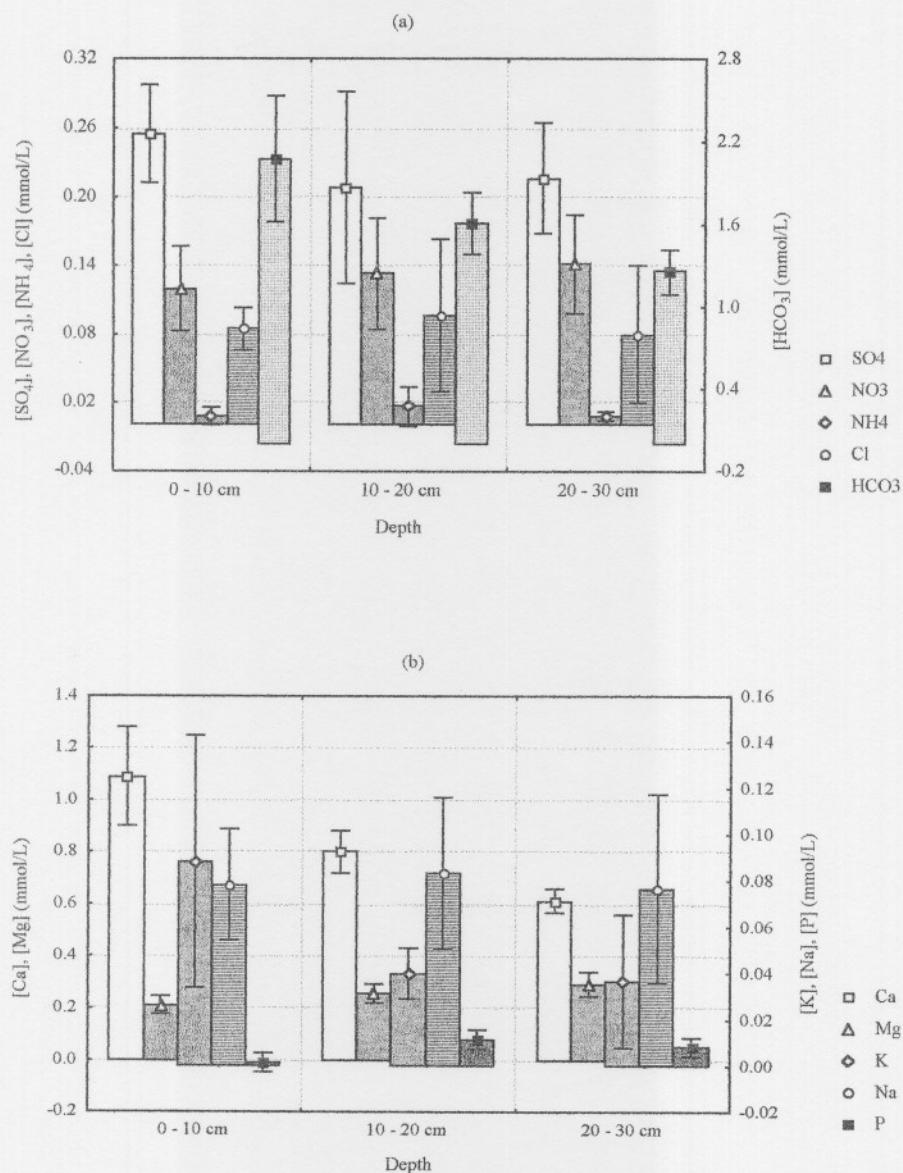


Figure 4.10: Concentrations of Nitrates $[NO_3]$, Ammonia $[NH_4]$, Calcium $[Ca]$, Bicarbonates $[HCO_3]$, Potassium $[P]$, Sodium $[Na]$, Phosphorous $[P]$, Magnesium $[Mg]$, Sulphates $[SO_4]$ & Chlorine $[Cl]$ at three depths from control zone substrates on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

Nitrates and Ammonia

Nitrate concentrations $[NO_3]$ in substrates (data log_e transformed) differed significantly among depth categories in active zones ($F_{2,24}; 7.301$, $P < 0.01$), being greater at 20-30 cm than at 10-20 cm (Fig. 4.11a). Variability in 0-10 cm sample data may, however, have obscured significant depth differences. No significant depth differences were found in abandoned zones, and $[NO_3]$ did not differ significantly among impact zones in any of the depth categories. Again, variability in 0-10 cm active zone samples may have masked significant differences.

Due to substantial variability in control zone samples, significant differences in ammonia

concentrations $[\text{NH}_4]$ (Fig. 4.11b) with depth were found only in the abandoned zones ($H_{2,27}:18.200$, $P < 0.001$), where $[\text{NH}_4]$ in the 0-10 cm depth category was lower than at 10-20 cm ($Z:-2.782$, $P < 0.01$) and 20-30 cm ($Z:-2.782$, $P < 0.01$). In the 10-20 cm depth category, impact zones did not differ significantly from each other. However, in the 20-30 cm depth category, the $[\text{NH}_4]$ did differ among impact zones ($H_{2,24}:7.383$, $P < 0.05$), being significantly lower in active zones compared to abandoned zones ($Z:-1.987$, $P < 0.05$).

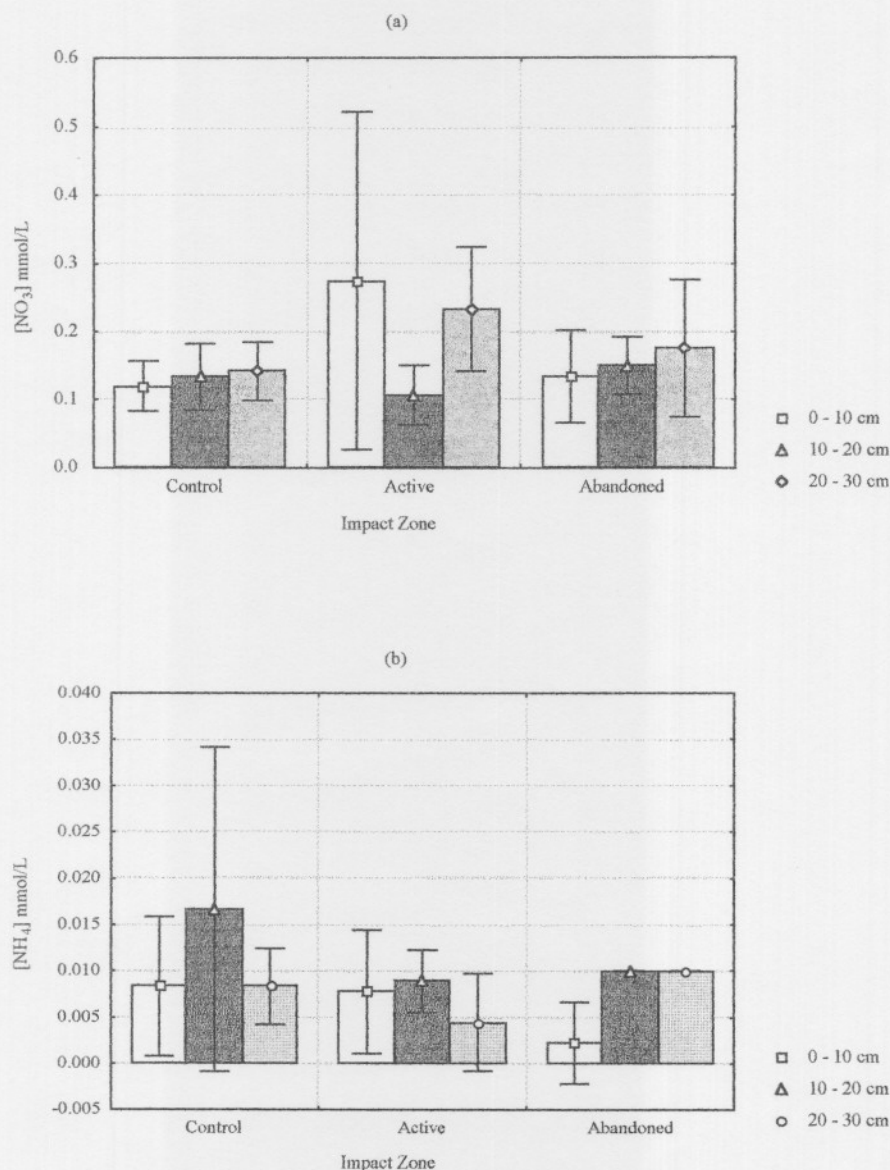


Figure 4.11: Comparisons of substrate $[\text{NO}_3]$ & $[\text{NH}_4]$ at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

Calcium and Bicarbonates (HCO_3)

Substrate Calcium concentrations (data $\log_e$ transformed) did not vary significantly with depth in the active or abandoned impact zones, and no significant difference in $[\text{Ca}]$ was noted for any depth category among the impact zones either (Fig 4.12a). Similarly, the $[\text{HCO}_3]$ in active and abandoned impact zones did not vary significantly with increasing depth (Fig. 4.12b). Among impact zones, in the 0-

10 cm depth category, $[\text{HCO}_3^-]$ was observed to be significantly lower in active and abandoned zones when compared to controls ($F_{2,21}:6.749$, $P < 0.01$).

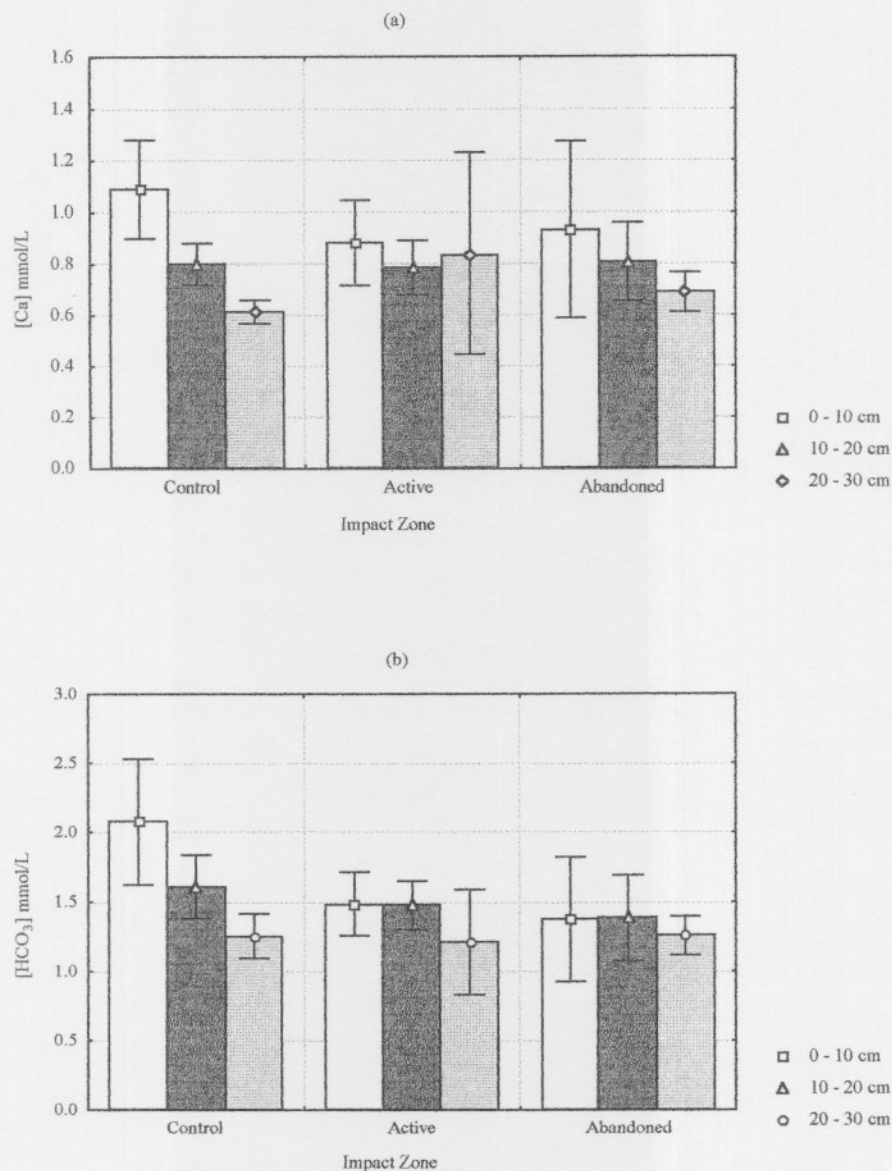


Figure 4.12: Comparisons of substrate $[\text{Ca}]$ & $[\text{HCO}_3^-]$ at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

Potassium and Sodium

Significant differences in $[\text{K}]$ with depth (data $\log_e$ transformed) were found in active zones ($F_{2,24}:3.762$, $P < 0.05$), where $[\text{K}]$ proved to be higher at 0-10 cm than at 10-20 cm ($t_{df16}:3.073$, $P < 0.01$). In the 0-10 cm depth category, the abandoned zones had significantly lower $[\text{K}]$ than the control zones ($F_{2,21}:4.312$, $P < 0.05$). The 10-20 cm and 20-30 cm depth categories did not show significant differences among impact zones (Fig. 4.13a), but variability in the abandoned zone samples at 10-20 cm, and the active zone samples at 20-30 cm, may have masked what differences there were.

The $[\text{Na}]$ (data $\log_e$ transformed) differed according to depth only on abandoned zones

($F_{2,24}:5.290$, $P < 0.05$), where it was significantly elevated at 20-30 cm compared to 10-20 cm. No significant differences in [Na] were found among impact zones in the different depth categories (Fig. 4.13b), however there was considerable variability among the samples from the active zones at 0-10 cm.

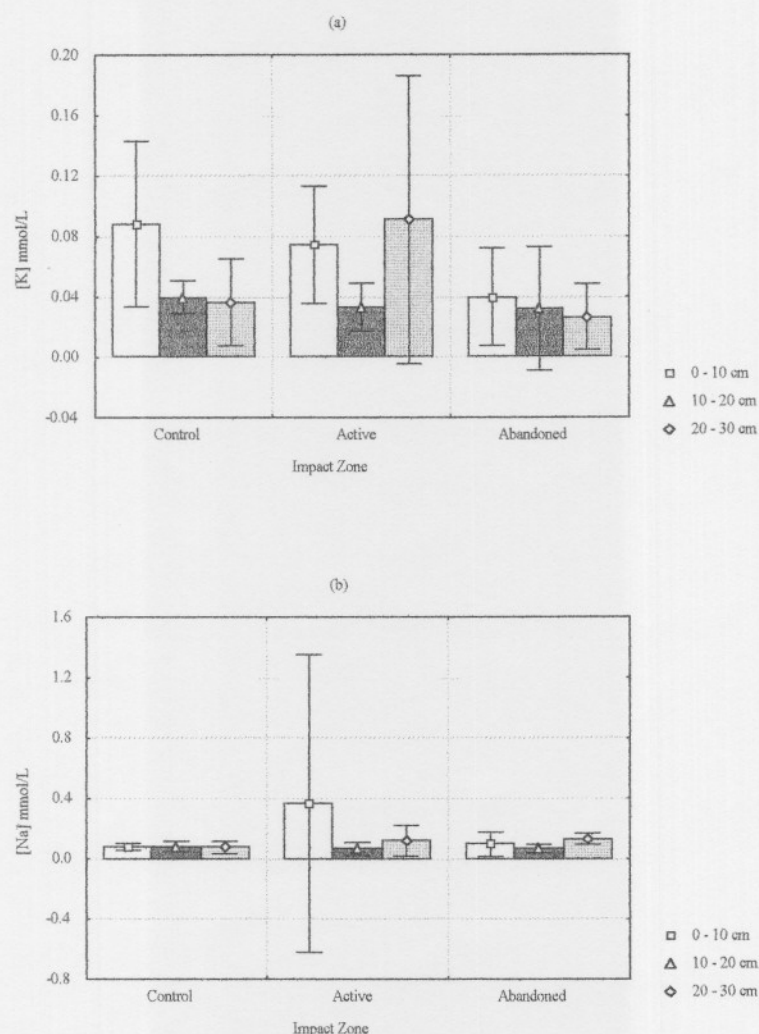


Figure 4.13: Comparisons of substrate [K] & [Na] at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

Phosphorous and Magnesium

Sampling yielded variable data, which may have obscured significant differences in the 0-10 cm and 20-30 cm depth categories, as well as within active and abandoned impact zones. Thus it was found that Phosphorous concentration [P] did not vary significantly with depth in active and abandoned zones. Within each depth category, significant differences in [P] were found only at 10-20 cm ($H_{2,24}:9.287$, $P < 0.01$), where [P] was lower in both active ($Z_{(adj)}:-2.061$, $P < 0.05$) and abandoned zones ($Z:-2.593$, $P < 0.01$) than controls (Fig. 4.14a).

Substrate Magnesium [Mg] (data $\log_e$ transformed) was significantly higher at 20-30 cm than at 0-10 cm and 10-20 cm in active zones ($F_{2,24}:11.667$, $P < 0.001$), but did not differ with depth in abandoned zones (Fig. 4.14b).

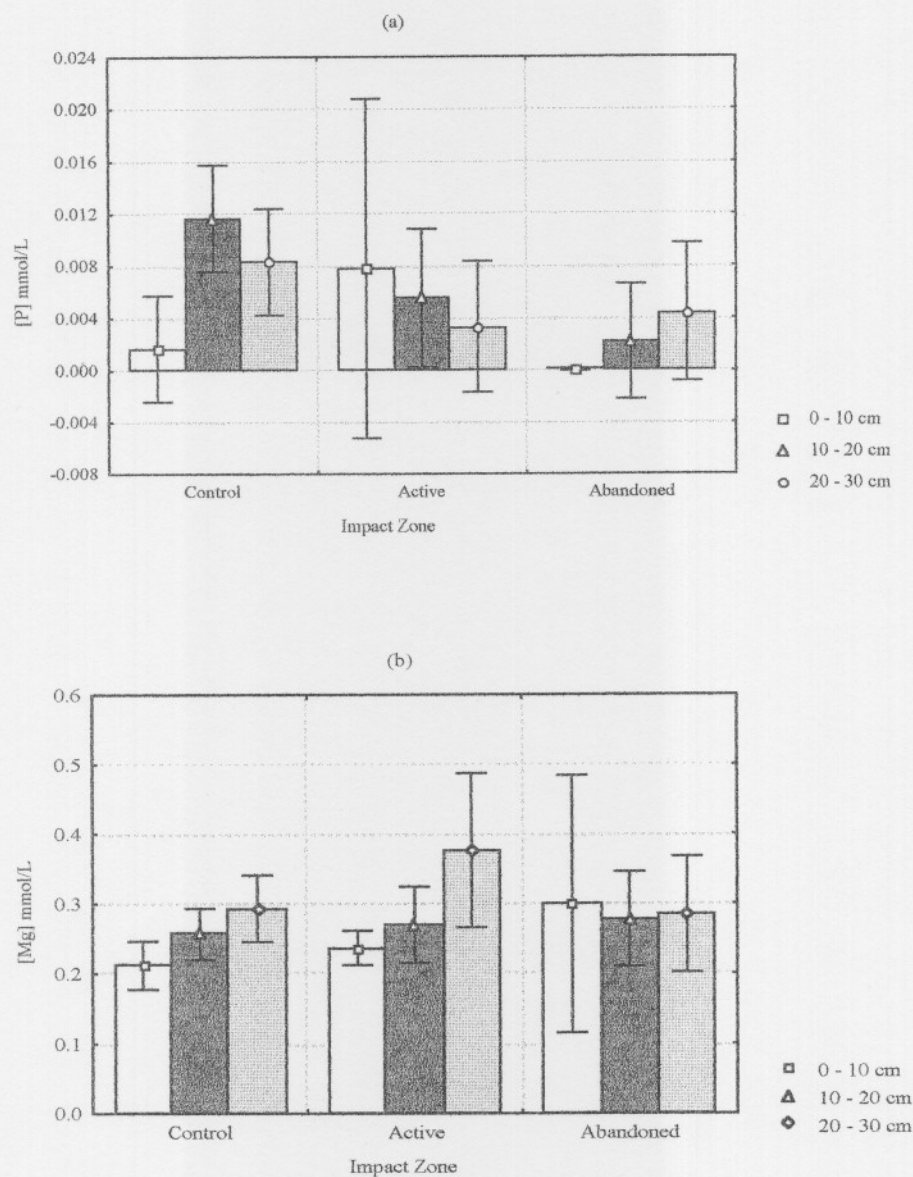


Figure 4.14: Comparisons of substrate [P] & [Mg] at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

Sulphates (SO_4) and Chlorine

The concentrations of sulphates [SO_4] (Fig. 4.15a) and Chlorine [Cl] (Fig. 4.15b) in the PFA-dam substrates did not differ significantly with depth or among impact zones, suggesting that these were not affected either by gerbil digging activity or the cessation of such activity.

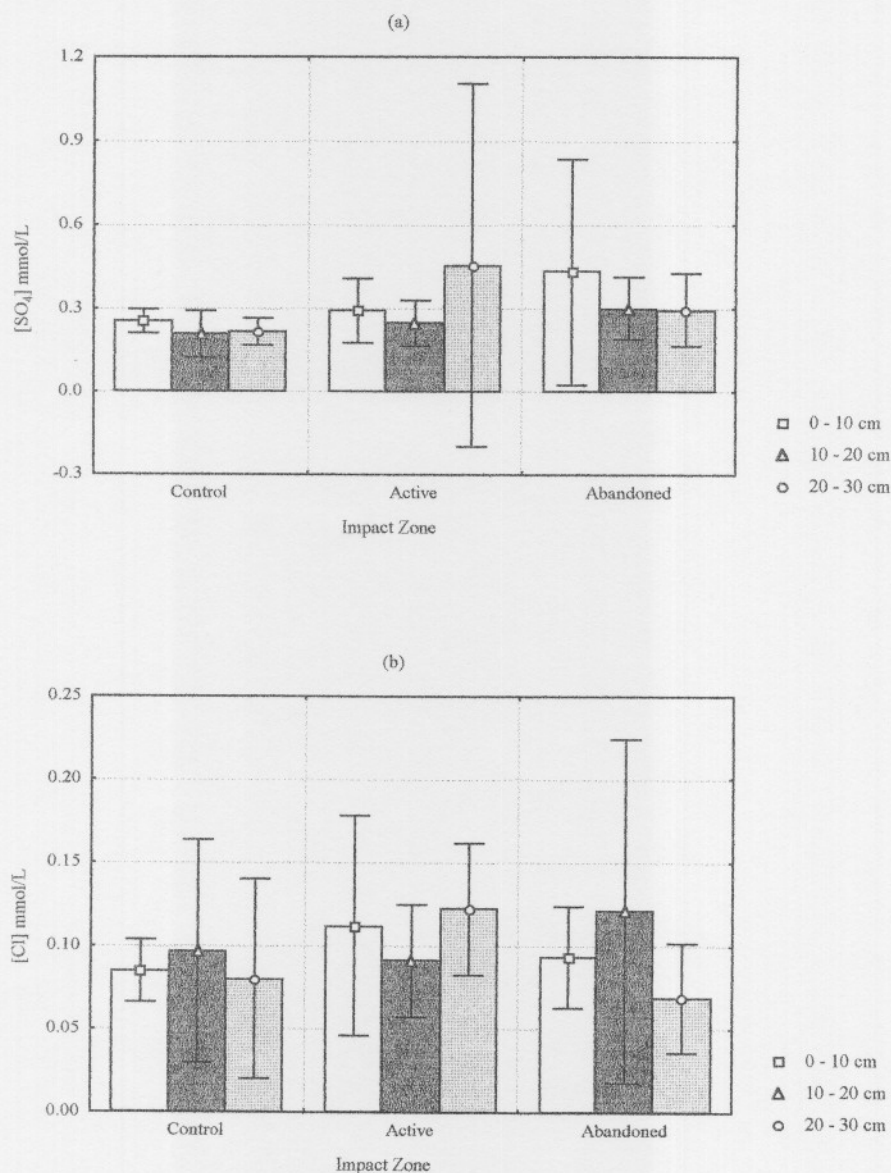


Figure 4.15: Comparisons of substrate $[SO_4]$ & $[Cl]$ at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

4.2.3 Micro-elements

All micro-element data were $\log_e$ transformed. In control zone substrates (Fig. 4.16), Boron concentrations increased significantly with depth ($F_{2,15}:22.653$, $P < 0.001$), and were significantly higher at 10-20 cm and 20-30 cm than at 0-10 cm. Iron ($F_{2,12}:5.049$, $P < 0.05$) and Manganese ($F_{2,10}:6.536$, $P < 0.05$) concentrations decreased with depth, where both the $[Fe]$ and the $[Mn]$ were greater at 0-10 cm and 10-20 cm than at 20-30 cm. The substrate had significantly greater Copper concentrations 10-20 cm than at 20-30 cm ($F_{2,13}:6.735$, $P < 0.01$). Substrate Zinc concentrations did not differ significantly with increasing depth in control zones.

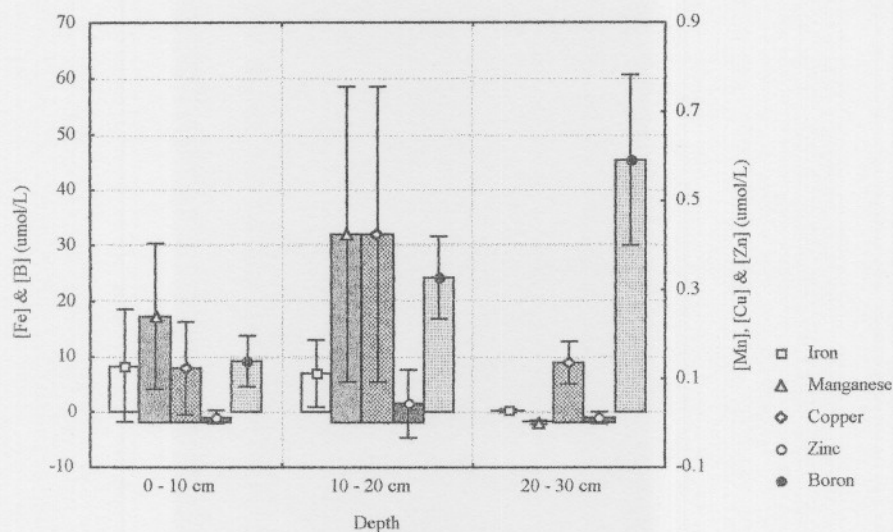


Figure 4.16: Concentrations of Boron [B], Iron [Fe], Manganese [Mn], Copper [Cu] & Zinc [Zn] at three depths from control zone substrates on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

Boron

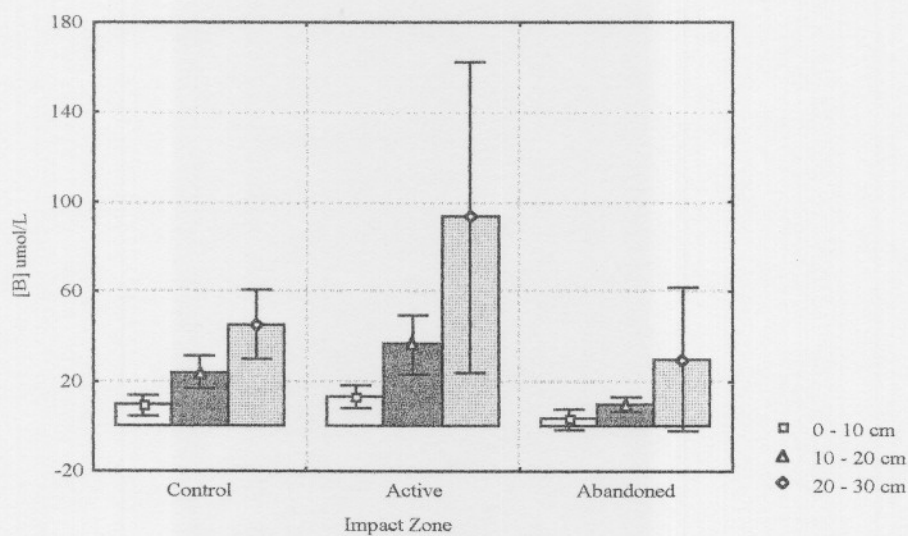


Figure 4.17: Comparison of substrate [B] at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

Substrate Boron concentration [B] (Fig. 4.17) differed significantly with depth in active zones ($F_{2,24}:35.289$, $P < 0.001$) and abandoned zones ($F_{2,19}:9.234$, $P < 0.01$). In active zones, the [B] declined significantly from 20-30 cm to 10-20 cm to 0-10 cm. In abandoned zones it was higher at 20-30 cm than at 0-10 cm and 10-20 cm. Among impact zones, at 20-30 cm, the active zones had a greater [B] than the

abandoned zones ($F_{2,21}:8.229$, $P < 0.01$), and at 10-20 cm both the active and control zones had greater [B] than abandoned zones ($F_{2,21}:28.593$, $P < 0.001$). No significant differences were found among impact zones at 0-10 cm.

Iron and Manganese

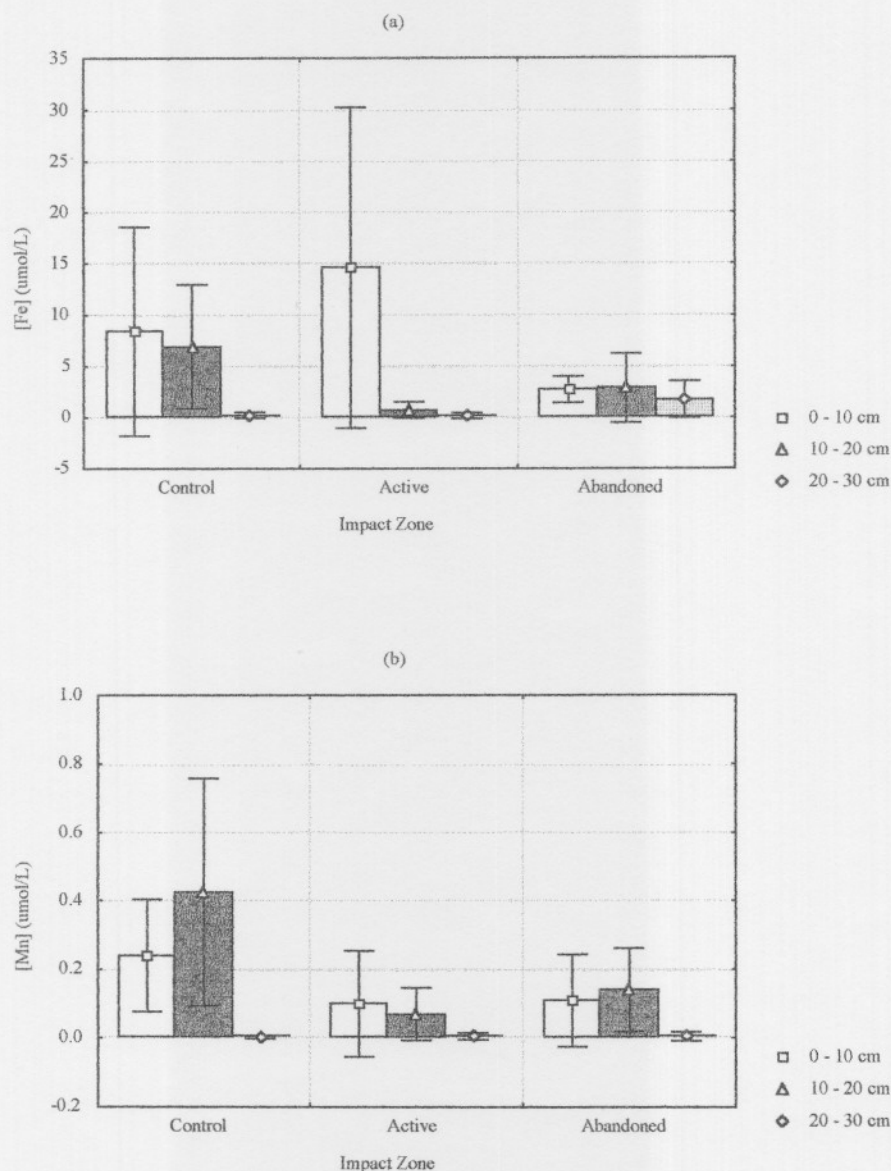


Figure 4.18: Comparisons of substrate [Fe] & [Mn] at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

Although there was considerable variability in the both the Iron and Manganese data, this was dampened by log_e transformation, and this allowed statistical trends to be detected. In the active zones ($F_{2,18}:30.616$, $P < 0.001$), the Iron concentration [Fe] decreased significantly with depth (Fig. 4.18a), with 0-10 cm higher than 10-20 cm which was higher than 20-30 cm. Iron concentration did not differ significantly with depth in the abandoned zones. The [Fe] differed among impact zones in the 0-10 cm

($F_{2,21}:4.980$, $P < 0.05$) and the 20-30 cm depth categories ($F_{2,15}:9.444$, $P < 0.01$). At 0-10 cm the active zones had greater [Fe] than abandoned zones and at 20-30 cm the abandoned zones had greater [Fe] than the active zones.

Manganese concentrations [Mn] (Fig. 4.18b) were significantly higher at 0-10 cm than at 10-20 cm or 20-30 cm in the active zones ($F_{2,9}:9.548$, $P < 0.01$). The [Mn] did not vary significantly with depth in abandoned zones. Among impact zones, only the 10-20 cm depth category showed any significant differences ($F_{2,18}:6.995$, $P < 0.01$), where the control zones had significantly reduced [Mn] compared to the active zones.

Copper and Zinc

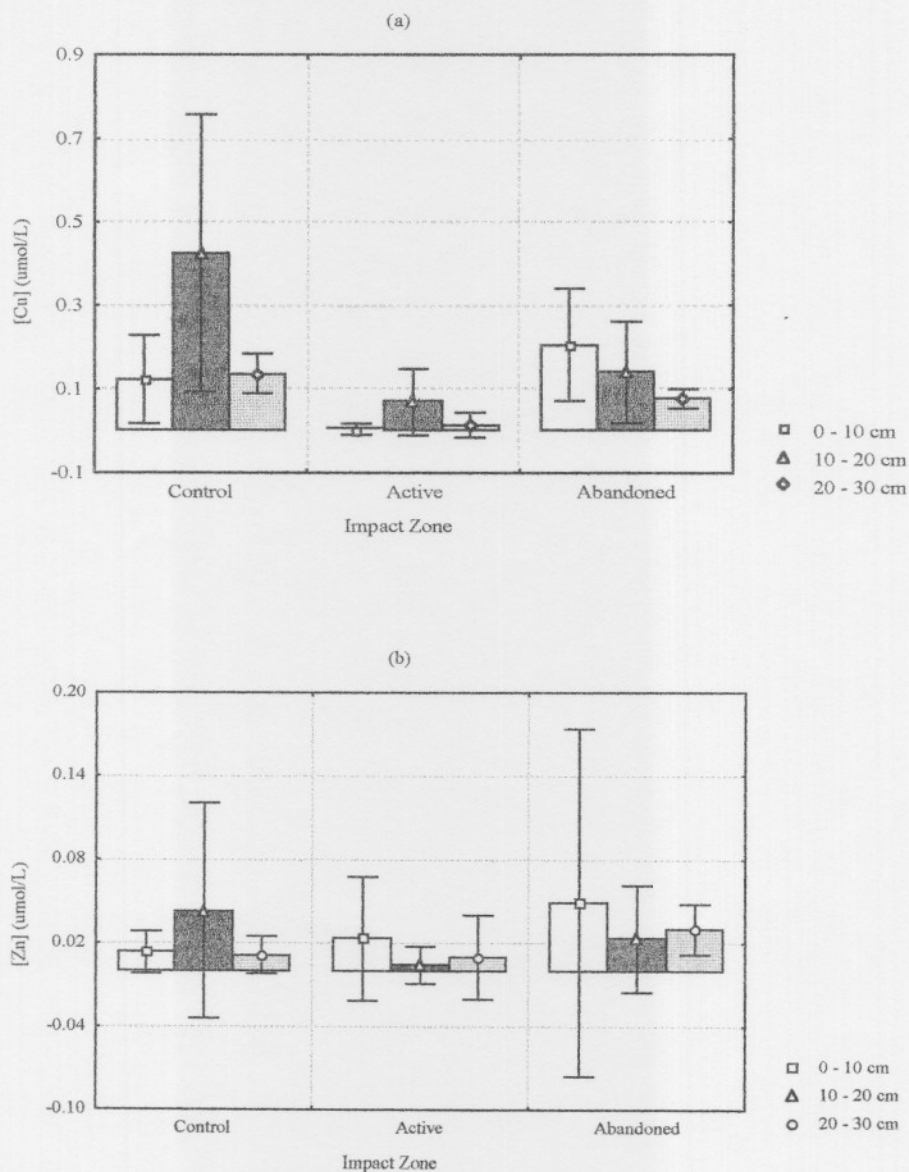


Figure 4.19: Comparisons of substrate [Cu] & [Zn] at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

No significant differences in substrate Copper concentrations with changing depth were apparent from analysis of the data from either of the active zones or abandoned zones (Fig. 4.19a). No differences among impact zones were found for the substrate [Cu] in the 0-10 cm depth category, but at 10-20 cm, both the active and abandoned zones had lower [Cu] than the control zones ($F_{2,17}:5.800$, $P < 0.05$), whereas in the 20-30 cm depth category the control and abandoned zones had significantly greater [Cu] than the active zones ($F_{2,15}:8.220$, $P < 0.01$).

Zinc concentrations did not differ significantly with depth in impact zones, or among impact zones for the different depth categories (Fig. 4.19b).

4.2.4 Heavy Metals

Aluminium and Selenium concentrations ($\log_e$ transformed) were not found to differ significantly with increasing depth (Fig. 4.20) in the control zone substrates. The data was still considerably variable, even after transformation, and thus no concentrations with regard to depth of these two elements could be established in the PFA-dam substrates following ecological rehabilitation.

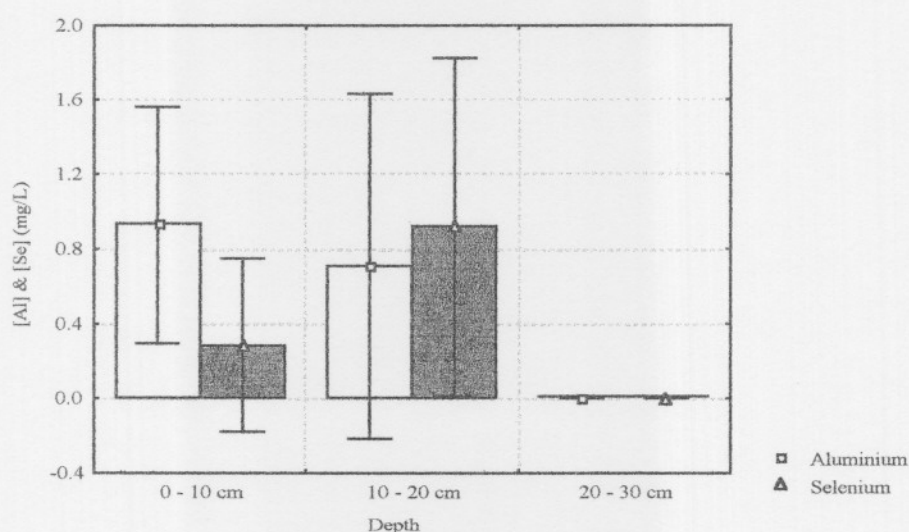


Figure 4.20: Concentrations of Aluminium [Al] & Selenium [Se] at three depths from control zone substrates on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

Aluminium and Selenium

Neither of the active nor abandoned impact zones showed any significant changes in substrate Aluminium and Selenium concentrations with depth, and no significant differences were found among impact zones in the three depth categories either (Figs. 4.21a & b).

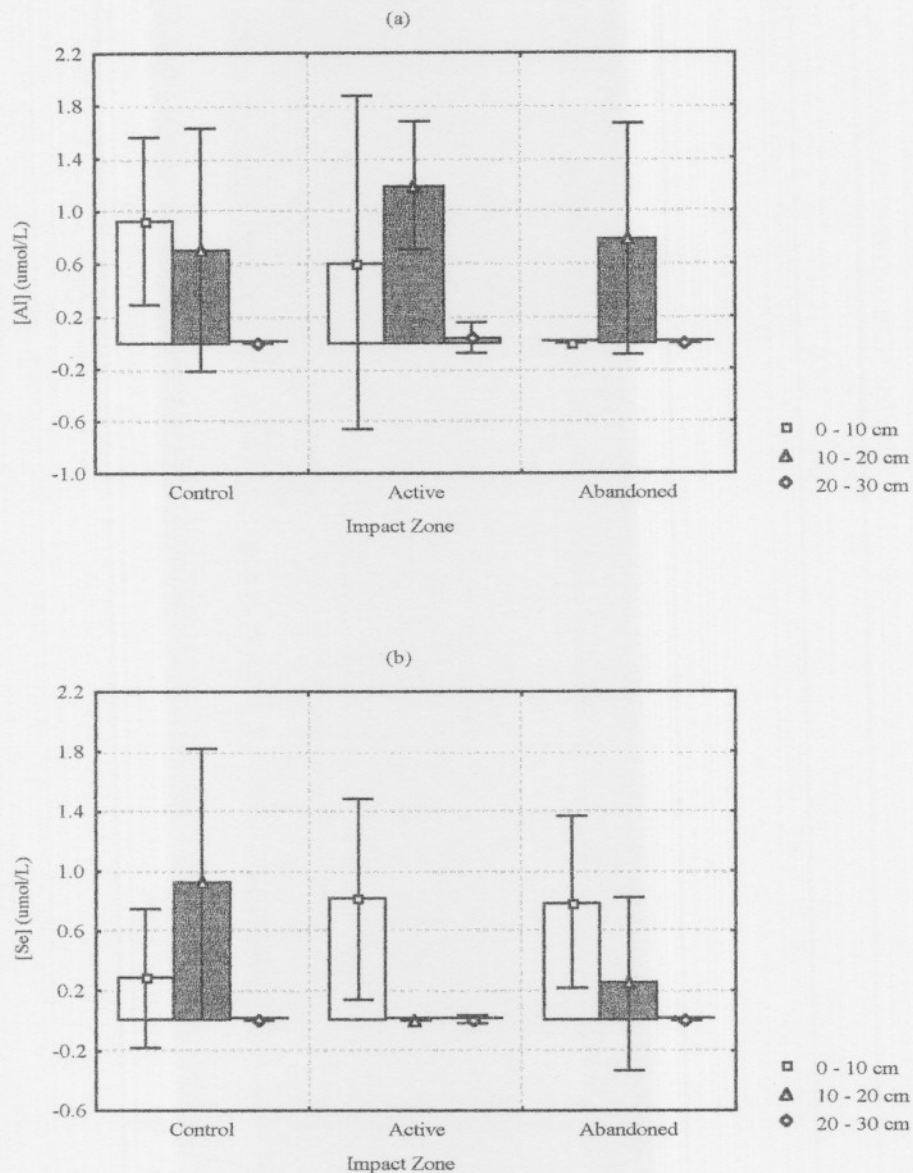


Figure 4.21: Comparison of substrate [Al] & [Se] at three depths among impact zones on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

4.3 Summary of factors affecting the substrate

The substrate variables that differed most among impact zones were extracted from the data set using a principal component analysis; substrate variables that did not show significant effects in any impact zone (i.e.: SO_4 , Cl, Zn, Al & Se) were omitted. Variables were also standardised as they were measured in different units, and data underwent a varimax normalised rotation, which maximises the variance of the normalised factor loadings.

In plots of loadings comparing the first three principal component axes (PCA), some separation of the impact zones from each other was evident (Fig. 4.22). Abandoned zones appeared separated from controls, particularly along PCA II, with active zones intermediate between the two, and overlapping

broadly. The majority of the active zones and most of the controls plotted to the right on PCA I (Figs. 4.22a & 4.22b), whereas most of the abandoned zones were separated towards the top along PCA II (Figs. 4.22a & 4.22c). PCA III was not useful in differentiating the impact zones from each other as there was extensive overlap along this axis (Figs. 4.22b & 4.22c).

The first three axes explained 58.965 % of the variance in the data and their eigenvalues were: PCA I: 4.694 (23.471 % of variance); PCA II: 3.824 (19.122 % of variance) & PCA III: 3.274 (16.372 % of variance).

The separation of impact zones along PCA I was most strongly influenced by (in decreasing order): substrate salinity; bicarbonate, Calcium and Potassium concentrations; and pH (Table 4.1), which all increased from left to right. PCA II was primarily influenced by the percentage of silt, and concentrations of Boron and Phosphorous (which increased from bottom to top, or left to right), and % sand, which increased from top to bottom (or right to left). PCA III was mainly influenced by substrate concentrations of Iron and Manganese (both increasing from bottom to top).

Table 4.1: Contributions of principal component scores (with factor loadings) of substrate variables to principal component axes I-III (varimax normalised), collectively explaining 59.0 % of the variance in the (standardised) data set, on PFA-dam A of Hendrina Power Station.

Variables that contributed most strongly to each axis are shown in bold.

Substrate Variable	PCA I	Factor Loading	PCA II	Factor Loading	PCA III	Factor Loading
% Moisture ($\log_e$)	-0.004	-0.078	0.121	0.518	-0.135	-0.489
pH ($\log_e$)	0.166	0.748	-0.030	-0.178	-0.029	-0.078
% Gravel	0.054	0.298	-0.143	-0.594	0.028	0.138
% Sand	-0.046	-0.129	-0.201	-0.764	-0.062	-0.161
% Silt	0.006	0.064	0.241	0.947	0.024	0.019
% Clay	0.042	0.168	0.059	0.205	0.050	0.156
Salinity ($\log_e$)	0.206	0.923	-0.028	-0.186	-0.018	-0.088
% Carbon ($\log_e$)	0.009	0.026	0.009	0.066	-0.120	-0.409
Ca ($\log_e$)	0.185	0.852	-0.073	-0.370	0.023	0.111
Mg ($\log_e$)	0.126	0.521	0.063	0.243	-0.164	-0.560
K ($\log_e$)	0.183	0.776	0.110	0.349	0.064	0.203
Na ($\log_e$)	0.154	0.634	0.098	0.362	-0.126	-0.442
P	-0.042	-0.253	0.191	0.748	0.094	0.262
NO ₃ ($\log_e$)	-0.014	-0.072	-0.007	0.011	-0.124	-0.418
NH ₄ ($\log_e$)	-0.023	-0.118	0.073	0.251	0.178	0.580
HCO ₃	0.195	0.873	0.002	-0.092	0.091	0.323
Fe ($\log_e$)	0.011	0.077	-0.022	-0.155	0.238	0.812
Mn ($\log_e$)	0.041	0.182	0.051	0.128	0.216	0.721
Cu ($\log_e$)	0.006	0.026	0.040	0.103	0.195	0.651
B ($\log_e$)	0.027	0.039	0.198	0.788	-0.050	-0.219

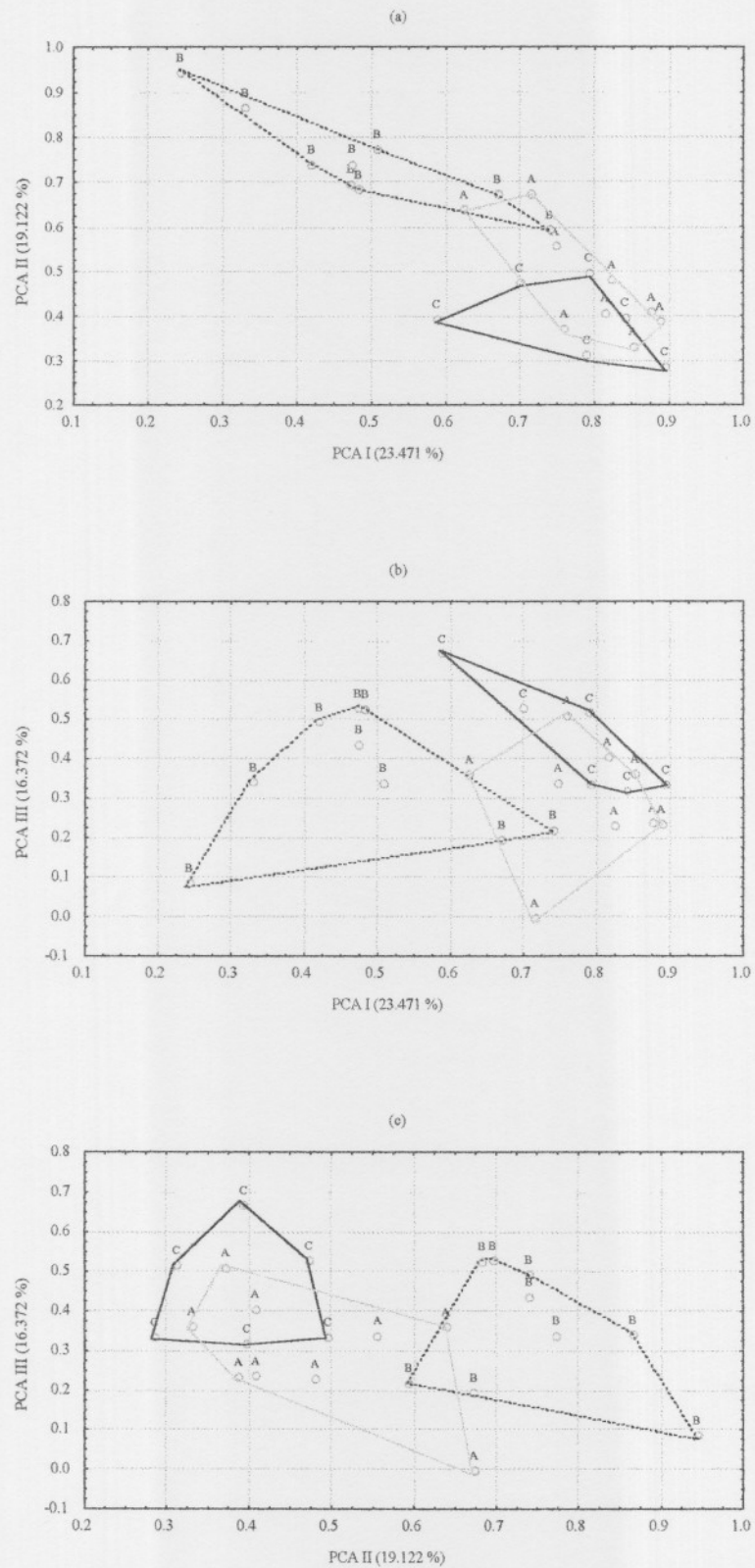


Figure 4.22: Separation of impact zones on PFA-dam A along Principal Component Axes: a) I & II; b) I & III; c) II & III. (C: Control zones, A: Active zones & B: Abandoned zones).

4.4 Discussion

Prior to *T. brantsii* impact (Fig. 4.1), the PFA-dam substrate had higher percentages of gravel and sand at the top of the soil profile, which suggested that they probably had their origin in the topsoil skin used to cover the ash during rehabilitation (Michael 1991, see also Section 2.1.4). The tendency of % silt to increase with depth reflected the increased proportion of the silt-sized, pulverised fuel-ash particles deeper in the soil profile. This is in agreement with other studies which also found that the majority of pulverised fuel-ash particles are silt-sized (Aitken *et al.* 1984, van Rensburg *et al.* 1998). Evaporative water loss from soil in this arid environment may have been slightly aided by the more air-permeable, coarser substrate of the 0-10 cm topsoil (the combined % of gravel and sand accounted for almost half the soil, 44.7 %).

Impact by gerbils on the substrate did not affect the decline in gravel with increasing depth (Fig. 4.2), but seemed to alter the distribution of gravel at the different depths, particularly at 20-30 cm. The increased gravel proportion at 20-30 cm in abandoned zones could likely be attributed to the collapse of burrow systems that were no longer maintained by gerbils. This could facilitate the mixing of gravel from the topsoil skin above the ash in with the deeper ash. The overall increased % gravel in abandoned zones could also indicate that some excavated (silt-sized) ash was lost through wind erosion (Thurlow 1937).

The absence of any significant depth changes in the % sand, in the active and abandoned zones (Fig. 4.3), suggests that digging activity by gerbils, or the collapse of tunnels once activity ceased, may have mixed the sand more evenly among the three depth categories. The overall increase of % sand in the abandoned zones could reflect a loss of fine silt particles, excavated onto the surface by gerbils, through wind erosion (Thurlow 1937), leading to the relative increase in the percentage of coarser particles.

Gerbil digging appeared to reduce the silt content of the substrate at both the 0-10 cm and 10-20 cm depths (Fig. 4.4). Substrate mixing as a result of burrow system construction was probably the most likely cause of this, especially on abandoned zones where the coarser sand and gravel particles were introduced deeper into the soil profile following tunnel collapse. It is also likely that much of the predominantly silt-sized ash particles were removed by wind from the substrate excavated to the surface by gerbils, thereby increasing relative percentages of sand and gravel at 0-10 cm.

No gerbil digging activity occurred on control zones, leaving the substrate in an unchanged condition (unmixed) following the rehabilitation work on the PFA-dam. Thus, the significantly elevated level of % clay in the control zones at 20-30 cm (Fig. 4.5) may be an artefact resulting from the introduction of sand and gravel at this depth in areas associated with gerbil activity (see Sections 4.1.1 & 4.1.2).

Substrate moisture content increased with depth (Fig. 4.6), whether gerbils were active in the impact zone or not, and this increased moisture content was associated with increased proportions of the finer substrate particles, particularly the silt-sized particles of the ash, which has a structure conducive to water retention (Aitken *et al.* 1984). The reduced moisture content in the top 10cm of the substrate of the abandoned zones corresponds with a relative decrease in the amount of silt and an increase in the percentage of coarse substrates (especially sand) which do not retain water well and allow faster water flow through them. This increased dryness could affect substrate chemistry and also any plants growing on these areas as it does in some natural ecosystems (Whitford & Kay 1999; Reichman & Seabloom 2002).

The higher pH and salinity found in the top 10 cm of control zone substrate on PFA-dam A (Fig. 4.7) was probably a result of the upward (evaporation driven) water-flow, moving soluble alkaline salts through the continuous soil profile of areas undisturbed by gerbil digging and concentrating them in the topsoil (Tivy 1990). On the scale of colonies (as opposed to simple burrow systems, see Section 3.1), gerbil digging activities could disrupt the continuity of the soil profile, and thus impair this upward water flow. The way ash particles are packed into the substrate structure is conducive to the retention of water (Aitken *et al.* 1984), and the digging of tunnels would allow the circulation of drying air below the surface, disrupting and interfering with the interstitial water flow of the ash. This could explain why the 0-10 cm depth category had reduced salinity and significantly lower pH in active zones (Fig. 4.8). Similarly, in abandoned zones, mixing of the substrate as a result of digging and the subsequent collapse of tunnels could also disrupt the upward movement of water, and account for the absence of any depth effects in the substrate conditions of pH and salinity.

The only apparent effect of gerbil activity on substrate % Carbon was in the topsoil of the active zones (Fig. 4.9), this possibly resulting from the increased amounts of organic matter (food remains, faeces, discarded vegetable matter) associated with gerbil presence. It seems unlikely, however, that the small amounts of organic material deposited in tunnels could be solely responsible for the increase in % C in this topsoil (see Section 3.2). Decaying plants, buried under excavated mounds (Huntly & Reichman 1994; Reichman & Seabloom 2002), and increased litter-fall (clipping) as a result of foraging activities (Golley *et al.* 1975; Hayward & Phillipson 1982) are probably the principal contributors to increased organic content of the topsoil.

In the absence of sufficient leaching (i.e., under conditions of high evaporation, where the depth to which rain penetrates is limited), Calcium, bicarbonates and Potassium accumulated in the upper part of the soil profile of control zones (Fig. 4.10). Calcium is usually present as insoluble carbonates or slightly soluble gypsum in arid substrates, and can form hard or soft nodules, or cemented horizons of varying thicknesses. Bicarbonates and Potassium are two of a variety of common soluble salts, which with others, are alkaline in reaction ($\text{pH} > 7$), and contribute to the higher pH of arid substrate (Tivy 1990).

Magnesium is characterised as a common soluble salt in arid soil (Tivy 1990), and its absence from the upper substrate of controls suggests that it did not originate in the topsoil, but it is likely to have come from the coal-source of the ash, given the higher concentrations in the deeper substrate (Fig. 4.10). Although the increased alkalinity at 0-10 cm (Section 4.2.1) could account for the low Phosphorous concentration, fixing this element in an unavailable mineral form (Tivy 1990), this also requires high levels of Sodium (in the form of carbonate salts) which are not observed in this substrate, leaving the ash as the probable source of substrate Phosphorous.

Prior to gerbil disturbance, nitrates and ammonia were not found to be concentrated at any particular depth (Fig. 4.11), but the sample data was variable and may have obscured any differences that were present. However, in the impact zone where gerbils were active, the concentration of NO_3 seemed reduced in the 10-20 cm depth category, the average depth of gerbil tunnels (~16cm, see Section 3.1), compared to the depth category below, but was not significantly different from the other two impact zones. Pulverised fuel ash is known to be N-deficient (Aitken *et al.* 1984; Piha *et al.* 1995; Shaw 1996; Pillman & Jusaitis 1997), and therefore, even a small increase in the Nitrogen compounds in each burrow in the colony may be sufficient to influence the data at impact zone level. It is possible, given the localised increases in $[\text{NO}_3]$ and $[\text{NH}_4]$ (see Section 3.2), that the influx of rainwater draining into tunnels, may have leached nitrates and ammonia deeper into the ash. Increased water infiltration through the coarser substrate in abandoned zones, leaching ammonia, could account for the reduced NH_4 concentration in the 0-10 cm depth category.

Gerbil digging activities, in disrupting the continuity of the substrate profile and mixing topsoil with underlying strata, could result in the observed lack of depth effects with regard to Calcium concentration in the active and abandoned impact zones (Fig. 4.12). Bicarbonate (HCO_3) levels are closely associated with both pH and salinity, and are similarly affected by water movement (Tivy 1990), namely that they are deposited in the topsoil as a result of the evaporation-driven flow of water through the substrate. Gerbil digging activities could increase the permeability of the substrate, either through enhanced drainage (active zones), or by mixing and increasing the substrate friability (abandoned zones, see Section 4.1), and thereby facilitate the leaching of soluble bicarbonates from the upper substrate. In this case, however, it seemed that the colony-scale effect on $[\text{HCO}_3]$ in these impact zones was more a result of the general infiltration of water through the substrate disrupted by digging, than by water draining through tunnels of burrow systems. The localised reduction of $[\text{HCO}_3]$ in tunnels (Section 3.2), in the 10-20 cm depth category, seemed to be occluded by the larger-scale reduction at 0-10 cm across the colony in the impact zones.

Control zones exemplify the substrate composition prior to gerbil impact, and although the active zones have mounds of excavated ash at burrow entrances, the topsoil layer remains unmixed with the ash layer below (Fig. 4.13). Thus, it appeared that Potassium originated in the topsoil as both the control and active impact zones had high concentrations in the 0-10 cm depth category. This distinction in $[\text{K}]$ could have been eliminated by substrate mixing in abandoned zones, when tunnels that were no longer maintained collapsed. The lower $[\text{K}]$ at 0-10 cm in abandoned zones, compared to the substrate concentrations before gerbils had an impact in this ecosystem (control zones), was probably a consequence

of leaching through the coarser substrate of the abandoned zones. Similarly, leaching of Sodium associated with greater water infiltration and reduced water retention of the coarser substrate in the abandoned zones may also have been responsible for the reduction in [Na] at 10-20 cm, compared to the depth category below.

The active and abandoned zones showed no concentration of Phosphorous at any particular depth (Fig. 4.14), possibly because of the mixing of substrates from different depths as a result of gerbil digging activities. The lower [P] at 10-20 cm in active and abandoned impact zones compared to controls may be a consequence of leaching at the colony-scale. Localised increases of [P] in the immediate vicinity of tunnels (see Section 3.2) seemed to be insignificant when compared to this larger-scale effect.

Magnesium in arid soils is fixed as an insoluble carbonate compound (Tivy 1990), and is thus relatively unaffected by water movement. If, as seems probable, the source of Magnesium is the ash below the topsoil, then the low [Mg] at 0-10 cm in active and control zones is a reflection of this, as they are considerably drier (see Section 4.1.5). The circulation of drying air through gerbil tunnels at 10-20 cm could slow the upward movement of Magnesium from deeper in the ash by encouraging the formation of insoluble carbonates. In abandoned zones, following the collapse of abandoned gerbil tunnels, physical mixing of the substrate was likely to have removed any distinction accorded by depth.

Both sulphates and Chlorine are common soluble salts in substrates (Tivy 1990) and their concentrations were comparable to those of other soluble salts in this substrate (NO_3 ; NH_4 ; HCO_3 ; K; Na; P; Mg). However, even after the data was log_e transformed and outliers were removed, the variability in the sample data remained (Fig. 4.15). It is possible that any significant differences, either with depth in impact zones, or among impact zones in each depth category, were obscured by this variability in the data.

Pulverised fuel ash is known to have high Boron concentrations (Aitken *et al.* 1984; Piha *et al.* 1995; Pillman & Jusaitis 1997; van Rensburg *et al.* 1998), and this is illustrated by the observed trend of increasing concentration with depth in the control zones (Fig. 4.16). Iron and Manganese, in the form of numerous oxide concretions, originated in the topsoil covering PFA-dam A (Morgenthal 2003), and the high concentrations observed at 0-10 cm are a reflection of this. Copper and Zinc form soluble salts (Tivy 1990), and although their concentrations were less than 1 $\mu\text{mol/l}$, it appeared that they may have originated from the topsoil and had subsequently been redistributed by limited leaching.

Gerbil digging activities thus did not change the overall tendency of Boron to increase with depth (Fig. 4.17), and as Boron is resistant to leaching (Tivy 1990), the increased friability of abandoned zone substrates (and thus enhanced water flow through it) was unlikely to account for the reduced [B]. However, the mixing of ash and topsoil, because of tunnel collapse after the cessation of gerbil digging activities (thereby reducing the relative proportion of ash which seems to be the source of B), was probably sufficient to reduce the concentration in the abandoned impact zones.

Iron and Manganese were introduced into the topsoil of the PFA-dam substrate during initial rehabilitation (Morgenthal 2003). The impact of digging by gerbils did not seem to have progressed far enough to have had an effect on the substrate in active zones as the topsoil layer had not yet collapsed into tunnels and mixed with the ash. Both [Fe] and [Mn] were therefore still high in the upper substrate (Fig. 4.18), and the process of leaching had only recently been affected by gerbil digging. The absence of any depth-related differences in [Fe] and [Mn] in abandoned zone substrates was probably because of the mixing topsoil and underlying ash, primarily through the collapse of tunnels when burrow systems were abandoned. The mixing of ash with the topsoil in abandoned zones would both reduce [Fe] at 0-10 cm and increase [Fe] at 20-30 cm, explaining the differences among active and abandoned zones in these two depth categories. The lack of digging in control zone substrates would restrict the leaching of Manganese from the topsoil. In active zones, leaching could be facilitated through tunnels dug by gerbils, and at these concentrations, this may result in the observed significant increase in the 10-20 cm depth category.

The concentration of Copper at 10-20 cm in the control zones (Fig. 4.16) seems to approximate the interface between ash and topsoil. This may have been as a result of the denser ash impeding the downwards infiltration of Copper salts from the coarser topsoil, which may have been disrupted by gerbil digging as there was no similar concentration in active or abandoned zone substrates (Fig. 4.19). However, as the only detectable statistical trend was dependent on highly variable data (even after log_e transformation), which could be from just one core sample, and which was not reflected in any of the remaining data, the significance of this result may be simply an artifice of the variability in the data.

Zinc concentration showed no deviation from the control values as a result of any digging activity by gerbils. But again, great variability may have masked any significant differences.

From control zone data, it appeared that [Al] & [Se] had their origin in the topsoil, as neither of these two elements were found at 20-30 cm (Fig. 4.20). The samples from active and abandoned zones seemed to support this observation (Fig. 4.21). However, variability in the data may have obscured any effects gerbil activity had on the heavy metals in the substrate of this ecosystem (standard deviations for both elements were extreme).

Mixing of the substrate was the primary difference which separated the controls from zones of gerbil impact, and the principal components extracted along PCA I were those particularly affected by digging. Each element or substrate condition was more concentrated in the upper soil profile of the control zones, and was reduced after gerbils began excavating burrows, probably because of the subsequent effects of water infiltration and the mixing of soil layers.

The main factor which separated out the abandoned zones (PCA II) appeared to be the reduced proportion of ash in their substrates, as exemplified by the reduced quantities of elements (P & B) and particles (silt) characteristic of the ash substratum. This appeared supported by the increased proportion of sand from the topsoil, as a consequence of the mixing of different substrate strata, following gerbil burrow system collapse.

Although sample variability obscured the data, which resulted in poor differentiation of the impact zones along PCA III, the extracted principal components (Fe & Mn) were important for defining variability in the data set as a whole. Both were elements associated with the topsoil (Morgenthal 2003), and their concentrations at levels in the soil profile, or lack thereof, emphasised that the consequence of gerbil actions on the substrate of the PFA-dams seemed to be mixing.

4.5 Conclusions

The impacts of gerbil digging activities on the substrate properties are substantial, affecting structure, broad-scale chemical parameters and the concentrations of many elements in the substrate. As with other studies (Golley *et al.* 1975; Mace *et al.* 1997; Whitford & Kay 1999; Reichman & Seabloom 2002), the primary effect of gerbil digging seems to be mixing, which in this case was an increase in the proportion of sand and a decrease in the proportion of silt. This mixing effect is supported by the observation that many of the principal components extracted were those elements particularly concentrated in the topsoil or deeper in the ash in control zones, and that gerbil digging activities removed this distinction. The resulting, more homogeneous, friable substrate had improved permeability in active and abandoned zones (water drainage through tunnels and infiltration through coarser substrates), which increases the effect of leaching, and consequently, the indirect gerbil-mediated impact on substrate chemistry.

Direct gerbil effects on substrate chemistry from the excretion of biological waste seemed too localised (see Section 3.2), and as gerbil colonies move over time (Korn & Korn 1989), there appears to be an insufficient period of time to form long-lived, nutrient-enriched areas of substrate, like mima-mounds.

On the PFA-dam, gerbil impacts on substrate seemed to promote pedogenesis, and increase the depth of the topsoil through mixing. In contrast to natural habitats, where digging brings soluble salts and nutrients to the surface from deeper in the soil profile (Whitford & Kay 1999), in this habitat, digging mixed the surface soil in with the underlying ash, increasing the availability of topsoil nutrients deeper in the profile. Ash excavation and mixing also benefit the substrate by alleviating the extreme chemical nature of the ash, making it less inimical to plants.

However, the excavation of ash, and its potential loss to wind erosion (Thurlow 1937), revives the problem that the topsoiling and revegetation efforts were supposed to alleviate in the first place, the containment of the ash, as ash pollution can reach almost 40 kg per night, per gerbil colony (see Section 3.4).

CHAPTER 5

RESULTS: IMPACTS OF GERBIL ACTIVITY ON THE PLANT COMMUNITY IN 1998

Burrowing small mammals have been shown to have substantial impacts on grassland plant communities in natural habitats, increasing productivity, and especially, increasing plant diversity in disturbed areas (Martinsen *et al.* 1990; Williams 1992; Stockrahm *et al.* 1993; Huntly & Reichman 1994; Whitford & Kay 1999). These impacts may be sufficient to cause the transition from one habitat type to another, such as a change from shrubland to grassland (Brown & Heske 1990).

Korn & Korn (1989) demonstrated that *Tatera brantsii* gerbils increased plant diversity, and favoured forb species, notably legumes, on their colonies. In the rehabilitated ash dam environment, greater plant diversity could give the habitat more resistance to change, and thus stability (Barbour *et al.* 1987), and the promotion of N-fixing plants could be particularly beneficial as ash is known to be deficient in Nitrogen (Aitken *et al.* 1984; Piha *et al.* 1995; Pillman & Jusaitis 1997; van Rensburg *et al.* 1998).

The impacts of *T. brantsii* in the *Lepidium bonariensis*-*Eragrostis trichophora* plant community variant of PFA-dam A were investigated to determine how they affected plant community variables, physiognomy and phenology.

5.1 Plant community composition and dominance

The *Lepidium bonariensis*-*Eragrostis trichophora* plant community was surveyed using two complimentary sampling techniques. Quadrats are more likely to sample the rarer species, being more intensive, and as they include a measure of area, allow densities to be calculated. Transects measure plant frequency in terms of 'presence', and give a better overview of the relationships between species as they cover larger areas of the plant community. Each technique was chosen for its suitability in sampling different aspects of the plant community (Barbour *et al.* 1987).

Table 5.1: Numbers of plant species, and the ratios of grasses:forbs & annuals:perennials in impact zones of the *Lepidium bonariensis*-*Eragrostis trichophora* plant community variant on PFA-dam A of Hendrina Power Station in 1998.

		Control	Active	Abandoned
Quadrats Data	Number of Species	15	22	18
	Grasses : Forbs	3:12 (1:4)	7:15 (1:2.1)	7:11 (1:1.6)
	Annuals : Perennials	10:4 (2.5:1)	9:9 (1:1)	9:7 (1.3:1)
Transect Data	Number of Species	11	17	14
	Grasses : Forbs	4:7 (1:1.75)	7:10 (1:1.4)	6:8 (1:1.3)
	Annuals : Perennials	5:5 (1:1)	6:9 (1:1.5)	8:6 (1.3:1)

Unidentified species (see Table 2.3), and species with variable categorisation, were excluded from the annual:perennial ratios.

Numbers of species, mainly grasses, were increased in areas of gerbil disturbance, more so for active than abandoned zones, and ratios of grasses:forbs and annuals:perennials were altered (Table 5.1). Perennials, predominantly grasses, seemed to be promoted in disturbed areas.

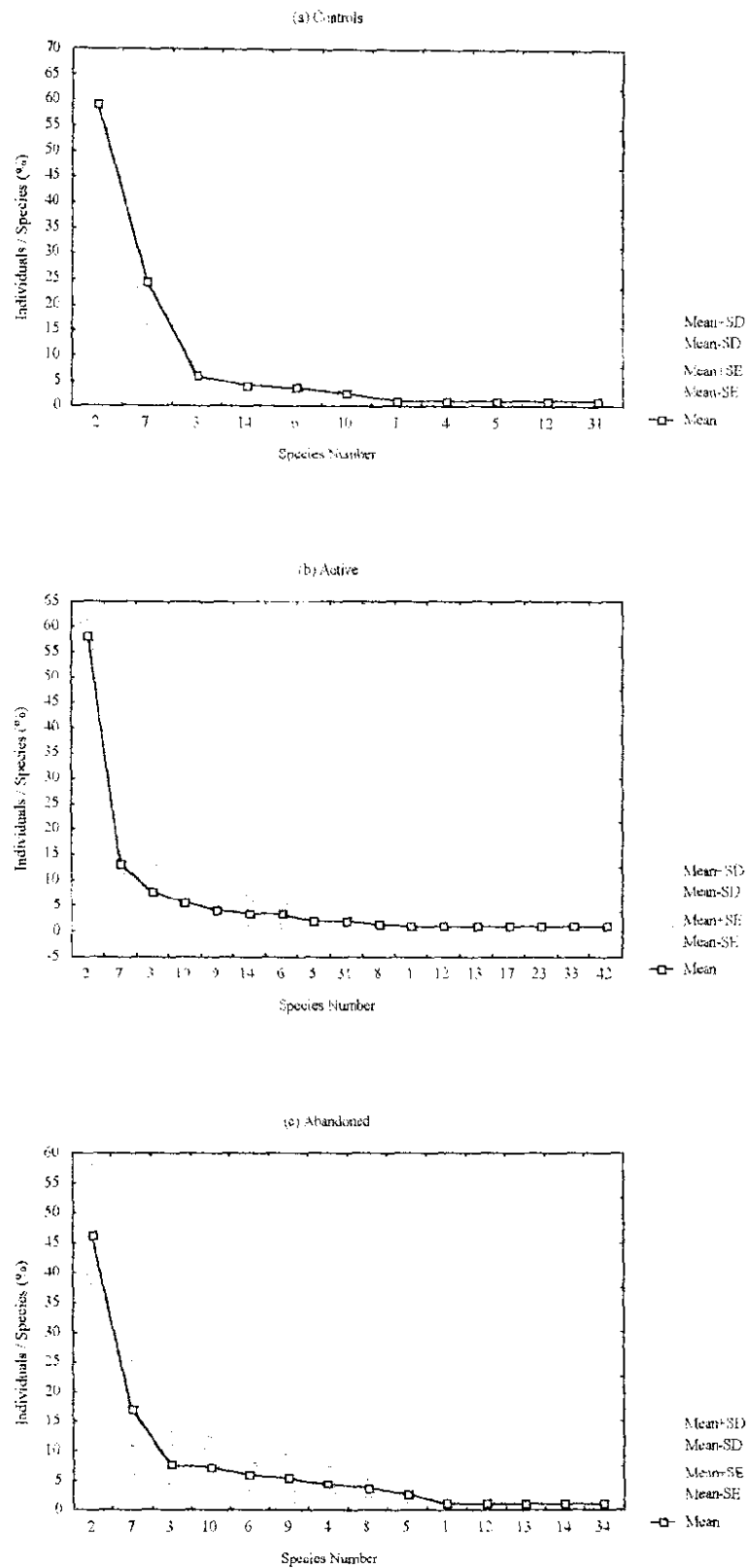


Figure 5.1: The % of individuals of plant species among impact zones in 1998 on PFA-dam A. a) Control, b) Active & c) Abandoned. Boxes: mean & ISE, vertical lines: 1SD. (Species names in Table 2.3).

Plant species dominance in impact zones was inferred from frequency (as %) of occurrence of each species (determined from transect data, which by sampling larger areas of the habitat, are more representative of the distributions of species; Fig. 5.1).

Four species seemed dominant in control zones (Fig. 5.1a), yielding a cumulative total of 93.5% of individual plants of the community. They were three grass species making up 89.5% (ie: *Pennisetum clandestinum*, sp.#2 [59%]; *Eragrostis curvula*, sp.#7 [24.5%] & *Cynodon dactylon*, sp.#3 [6%]) and one forb species (*Conyza bonariensis*, sp.#14 [4%]).

In active zones, the apparent dominance by grasses was reduced to 82.7% of individuals of the community (ie: *P. clandestinum*, sp.#2 [58%]; *E. curvula*, sp.#7 [13%]; *C. dactylon*, sp.#3 [7.7%] & *Hyparrhenia hirta*, sp.#9 [4%]), and that of forbs was increased to 12.7% (namely *Cyperus esculentus*, sp.#10 [5.7%]; *C. bonariensis*, sp.#14 [3.5%] & *Lepidium bonariensis*, sp.#12 [3.5%]). These seven common species represented a total of 95.4% of individuals in the plant community (Fig. 5.1b).

When abandoned by gerbils, the percentage contribution of dominant grasses seemed further reduced to 76.3% (*P. clandestinum*, sp.#2 [46.3%]; *E. curvula*, sp.#7 [17%]; *C. dactylon*, sp.#3 [7.7%] & *H. hirta*, sp.#9 [5.3%]). Dominant forbs (*C. esculentus*, sp.#10 [7.3%] & *Chamaecrista biensis*, sp.#4 [4.3%]) contributed 11.6% to the total contribution of 87.9% by dominant plants to the community (Fig. 5.1c).

5.2 Ecological status of grasses

The grass species of the control zones (Table 5.2) were dominated by exotics (*Pennisetum clandestinum*, sp.#2) and two (quadrate data) or three (transect data) increaser II species (*Eragrostis plana*, sp.#1; *Cynodon dactylon*, sp.#3 & *Eragrostis curvula*, sp.#7). Increaser II species are typical pioneer and sub-climax grasses, and are prevalent following grassland disturbances (van Oudsthoorn 1991), in this case the processes associated with the ecological rehabilitation practices at Hendrina Power Station (see Section 2.1.6).

Table 5.2: Ecological status of the *Lepidium bonariensis*-*Eragrostis trichophora* plant community variant in the three impact zones of PFA-dam A of Hendrina Power Station in 1998, as indicated by the percentage of grass species in each category.

	Ecological Status	Control	Active	Abandoned
Quadrate Data	Exotic	33.3 %	14.3 %	14.3 %
	Increaser I	0 %	14.3 %	14.3 %
	Increaser II	66.7 %	57.1 %	71.4 %
	Increaser III	0 %	14.3 %	0 %
	Decreaser	0 %	0 %	0 %
Transect Data	Exotic	25 %	14.3 %	16.7 %
	Increaser I	0 %	14.3 %	16.7 %
	Increaser II	75 %	57.1 %	66.6 %
	Increaser III	0 %	0 %	0 %
	Decreaser	0 %	14.3 %	0 %

In active zones, the numbers of increaser II species were increased to four in quadrats and transects (ie: *E. plana*, sp.#1; *C. dactylon*, sp.#3; *E. curvula*, sp.#7 & *Setaria pallide-fusca*, sp.#17). The exotic component (*P. clandestinum*, sp.#2) was reduced, but this was offset by the presence of an

unpalatable increaser I species (*Hyparrhenia hirta*, sp.#9), and either an increaser III species (*Sporobolus africanus*, sp.#30) in quadrats, or a decreaser species (*Themeda triandra*, sp.#42) in transects. In this impact zone, the activities of gerbils appeared to increase the diversity of grasses in the community, promoting the more competitive indigenous climax grasses.

Abandoned zones supported four (transects) or five (quadrats) increaser II species (*E. plana*, sp.#1; *C. dactylon*, sp.#3; *E. curvula*, sp.#7; *Aristida congesta*, sp.#34 & *Pogonarthria squarrosa*, sp.#37), with the remainder of the grass community consisting of equal amounts of exotics (*P. clandestinum*, sp.#1) and increaser I species (*H. hirta*, sp.#9). Cessation of gerbil activity in this environment seemed to result in the disappearance of increaser III and decreaser species and a greater proportion of increaser II species.

5.3 Plant Diversity Indices

Species Richness

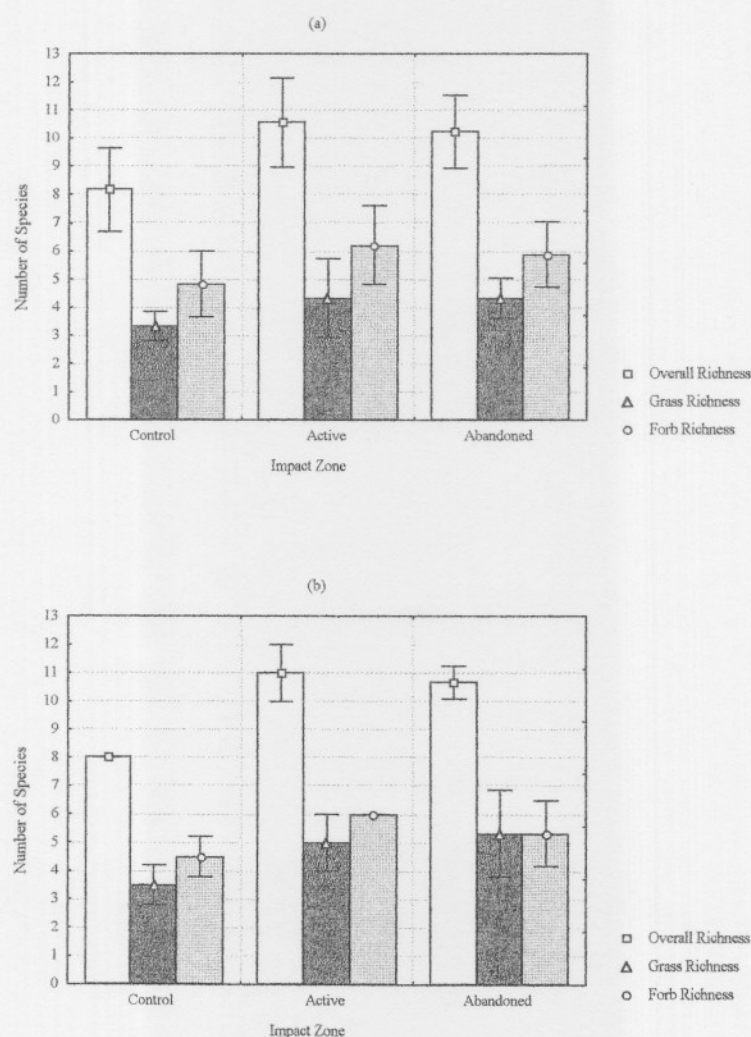


Figure 5.2: Differences in plant community species richness among impact zones in 1998 on PFA-dam A. a) quadrats & b) transects. Bars denote mean values, vertical lines represent 1SD.

Quadrat data indicated that the active and abandoned zones had significantly greater overall

species richness ($F_{2,21}:5.348$, $P < 0.05$) than control zones (Fig. 5.2a). Similarly, transect data showed that control zones had a significantly lower species richness ($F_{2,5}:11.445$, $P < 0.05$) than active and abandoned zones (Fig. 5.2b). No significant differences among impact zones were found for grass or forb richness.

Despite that the numbers of both grass and forb species were increased in areas of gerbil activity (see Section 5.1), neither of these increases were significant. However, the combination of their effects seemed sufficient to produce a significant increase in overall plant species richness.

Species Evenness

Analysis of quadrat data (Fig 5.3a) indicated that overall plant evenness appeared significantly lower in active zones than in abandoned zones ($F_{2,21}:3.692$, $P < 0.05$), but neither of these differed significantly from controls. However, as quadrats sampled only small areas of the community, localised differences (patchiness) may have influenced the data, and for these community variables, transect data was considered more reliable.

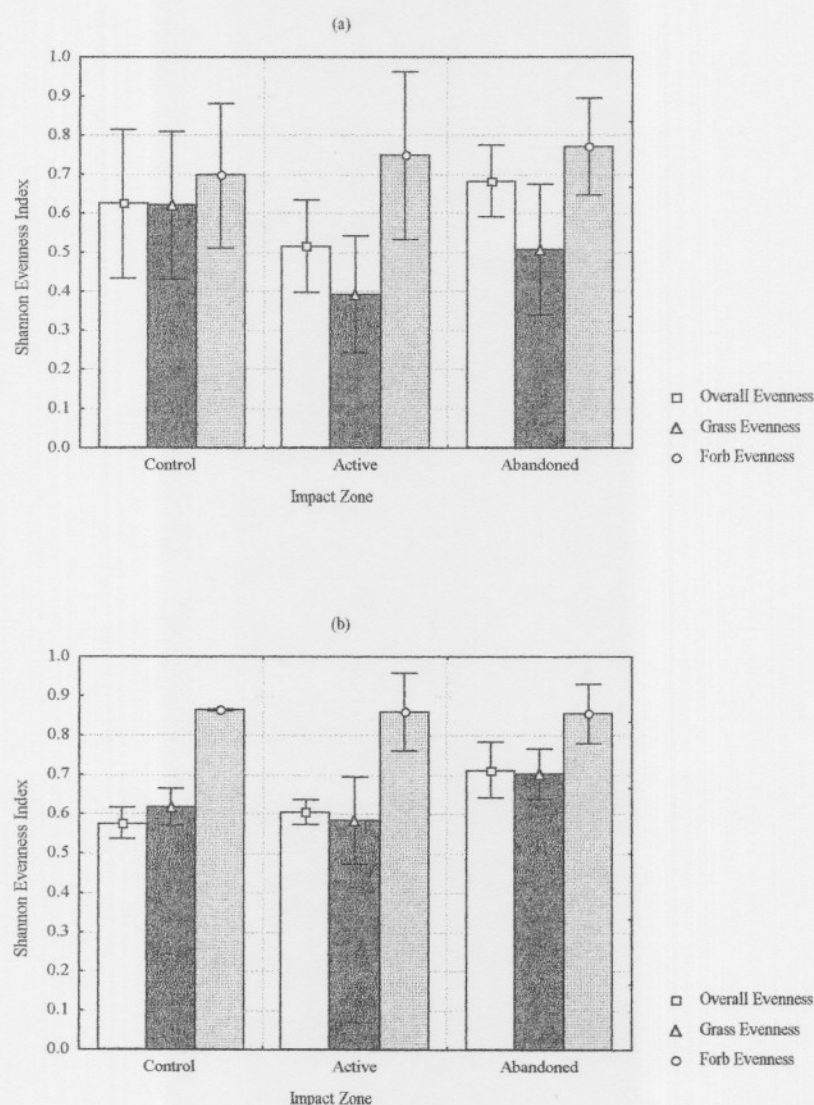


Figure 5.3: Differences in plant community species evenness among impact zones in 1998 on PFA-dam A. a) quadrats & b) transects. Bars denote mean values, vertical lines represent 1SD.

Individually, neither grass nor forb evenness differed significantly among impact zones, which suggests that only the combination of these two effects were sufficient to alter the overall index. Analysis of transect data (Fig 5.3b) revealed no significant differences in overall, grass or forb evenness among impact zones.

Species Diversity

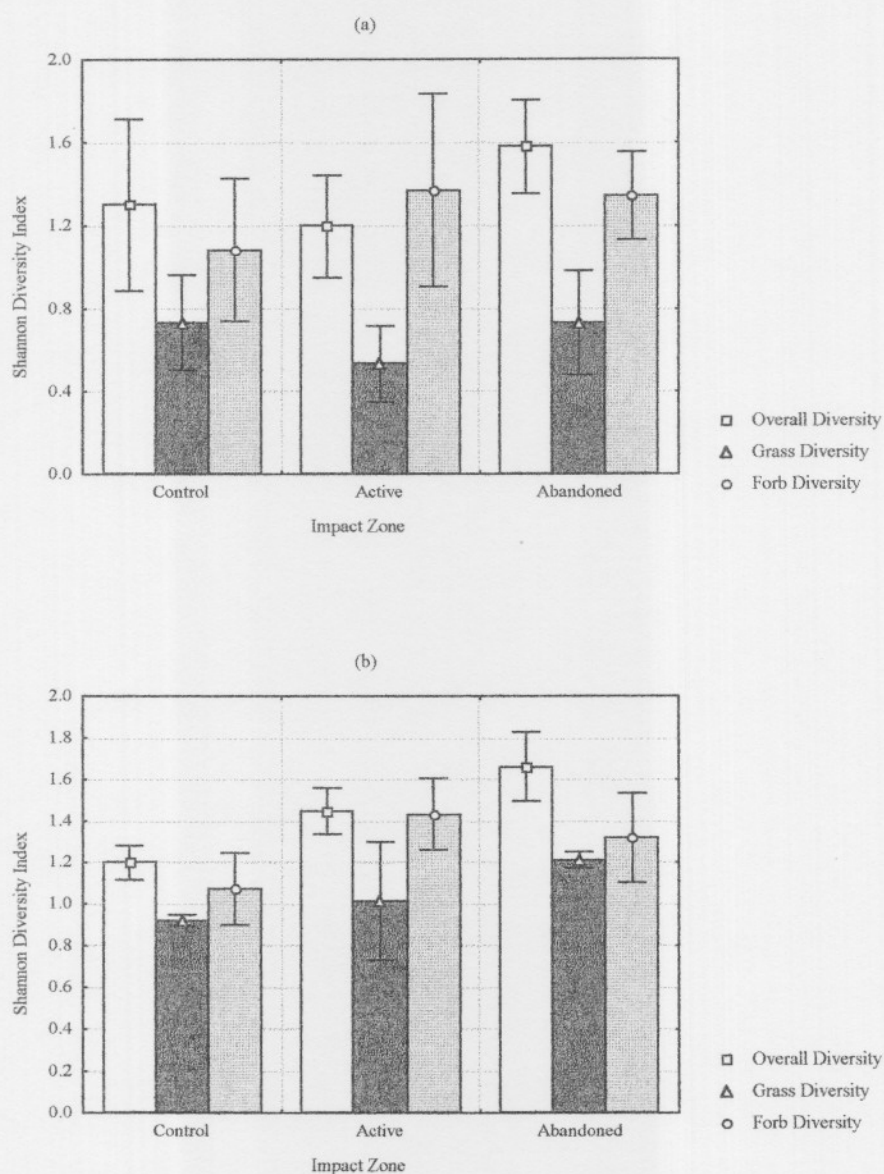


Figure 5.4: Differences in plant community species diversity among impact zones in 1998 on PFA-dam A. a) quadrats & b) transects. Bars denote mean values, vertical lines represent 1SD.

Quadrat data indicated that overall plant diversity (Fig. 5.4a) was significantly higher in abandoned zones than in active zones ($F_{2,21}:4.168$, $P < 0.05$), but neither of these differed significantly from controls, which showed intermediate diversity. Conversely, transect data (Fig. 5.4b) indicated that

abandoned zones had a significantly greater overall plant diversity than control zones ($F_{2,5}:7.476$, $P < 0.05$), but neither of these differed significantly from the active zones. The results from transect data were preferred, and thus indicated a tendency of elevated overall plant diversity in abandoned impact zones.

Neither grass or forb diversity indices differed significantly among impact zones for quadrat or transect data. It thus appeared that only the combination of these two diversity indices into the overall value was sufficient to alter plant species diversity.

5.4 Plant biomass

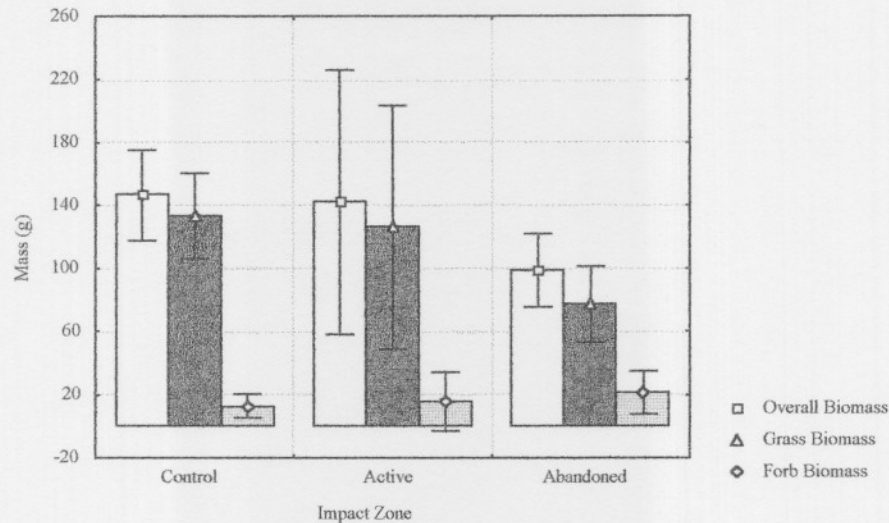


Figure 5.5: Differences in plant community biomass among impact zones in 1998 on PFA-dam A. (From quadrat data.) Bars denote mean values, vertical lines represent 1SD.

Overall biomass and forb biomass (data $\log_e$ transformed) did not differ significantly among impact zones (Fig. 5.5), but despite variability in the data, grass biomass appeared significantly reduced in abandoned zones compared to controls ($F_{2,21}:4.674$, $P < 0.05$), based on data from quadrats.

The percentage contributions of some species to overall biomass were different among impact zones. The biomass of *Eragrostis curvula* (Fig. 5.6a) was significantly lower in the active zones compared to controls ($F_{2,21}:3.684$, $P < 0.05$). *Chamaecrista biensis* (Fig. 5.6b) contributed a significantly greater percentage to the biomass in abandoned zones than in both active and control zones ($F_{2,17}:6.618$, $P < 0.01$). The biomass of *Schkuhria pinnata* (Fig. 5.6c) differed significantly among impact zones ($H_{2,20}:10.913$, $P < 0.01$), being lower in active zones than both abandoned zones ($Z:-3.182$, $P < 0.01$) and controls ($Z:-2.067$, $P < 0.05$).

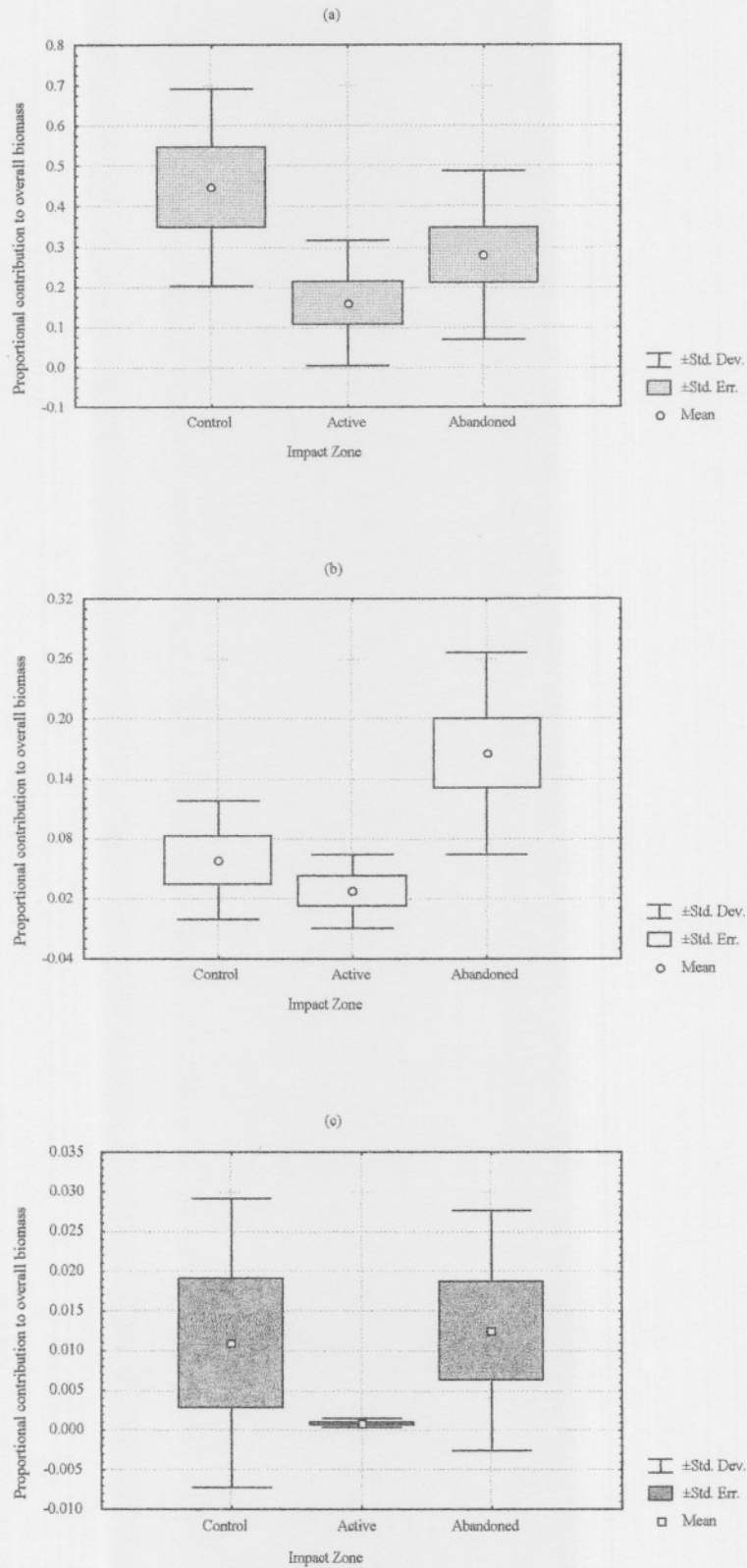


Figure 5.6: Differences in percentage contributions of species to overall biomass among impact zones in 1998. a) *E. curvula*, b) *C. biensis* & c) *S. pinnata*. Boxes denote mean & 1SE, vertical lines denote 1SD.

5.5 Plant Canopy Cover

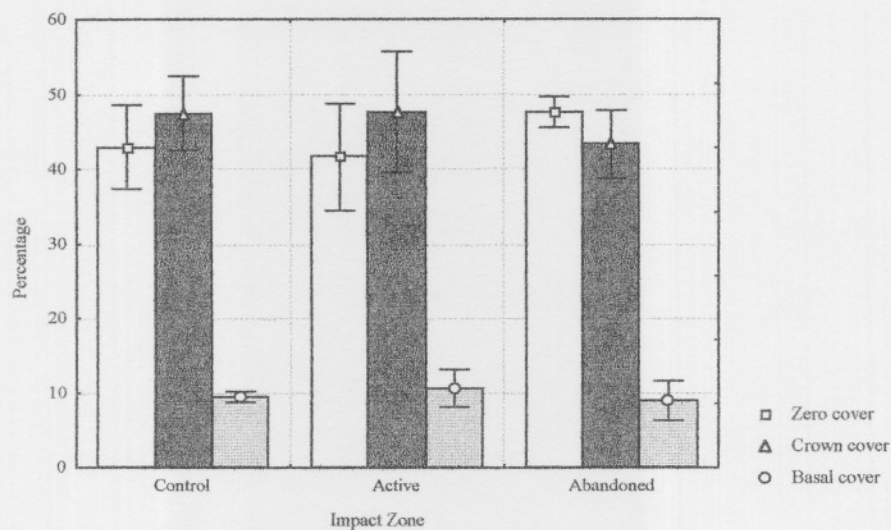


Figure 5.7: The percentages in each of three cover categories (i.e.: Zero; Crown & Basal cover) among impact zones in 1998 on PFA-dam A. (From transect data.) Bars denote mean values, vertical lines represent 1SD.

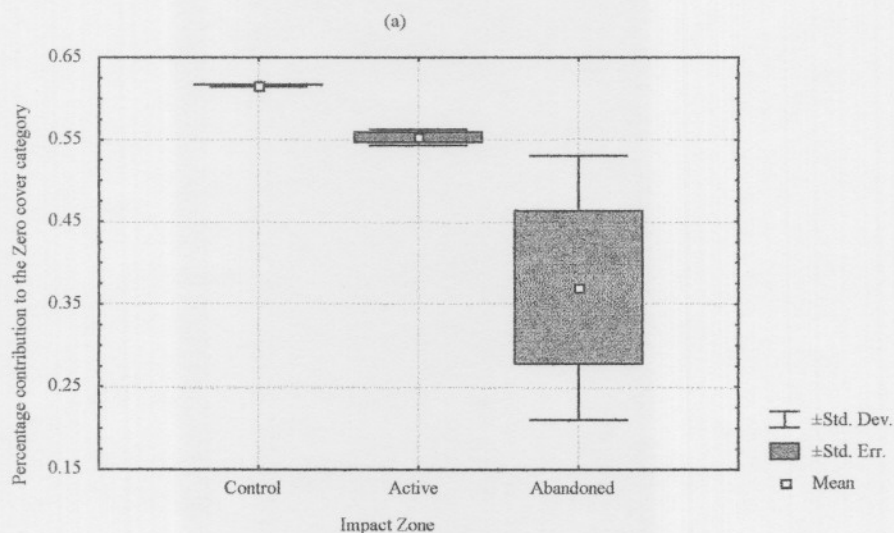


Figure 5.8a: Significant *P. clandestinum* contributions to the zero cover category among impact zones in 1998 on PFA-dam A. (From transect samples.) Boxes denote mean & 1SE, vertical lines represent 1SD.

No significant differences in any of the three overall cover categories (based on transect data) was found among controls and areas of gerbil impact (Fig. 5.7). However, in the zero cover category, the amount of space between plants of *Pennisetum clandestinum* (Fig. 5.8a) differed significantly among impact zones ($H_{2,8}: 6.250$, $P < 0.05$), where plants were significantly closer together in abandoned zones

than in active zones (that is, less of plants of this species were associated with zero cover in abandoned impact zones, $Z:1.964$, $P < 0.05$). There were too few *P. clandestinum* individuals associated with zero cover on control zones for accurate statistical comparison with this impact zone. Also in the zero cover category, for *Schkuhria pinnata* (Fig. 5.8b), the amount of space between plants was increased in abandoned zones compared to active zones (a greater proportion of plants of this species was associated with zero cover, $t_{df4}:-2.928$, $P < 0.05$). No individuals of *S. pinnata* were sampled in this cover category in control zones.

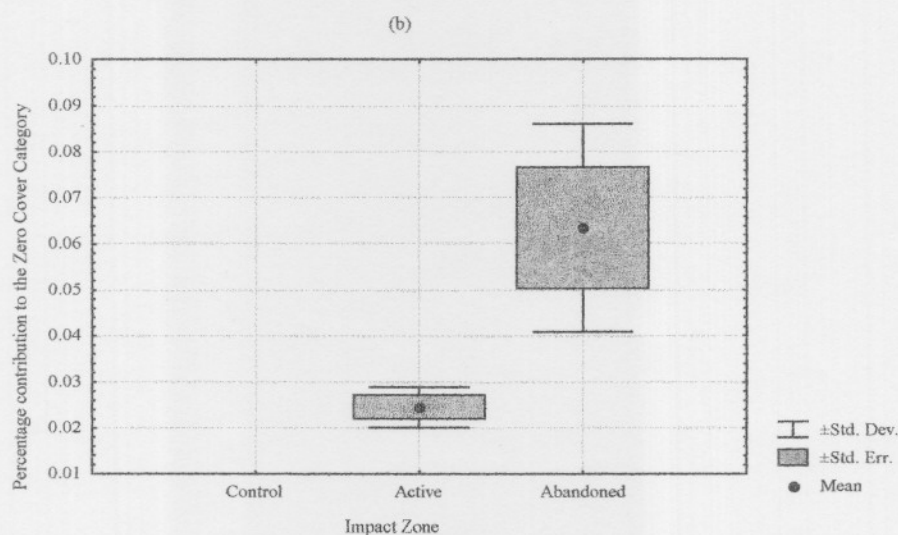


Figure 5.8b: Significant *S. pinnata* contributions to the zero cover category among impact zones in 1998 on PFA-dam A, (there was no data for this species in controls). (From transect samples.) Boxes denote mean values & 1SE, vertical lines represent 1SD.

5.6 Plant Density

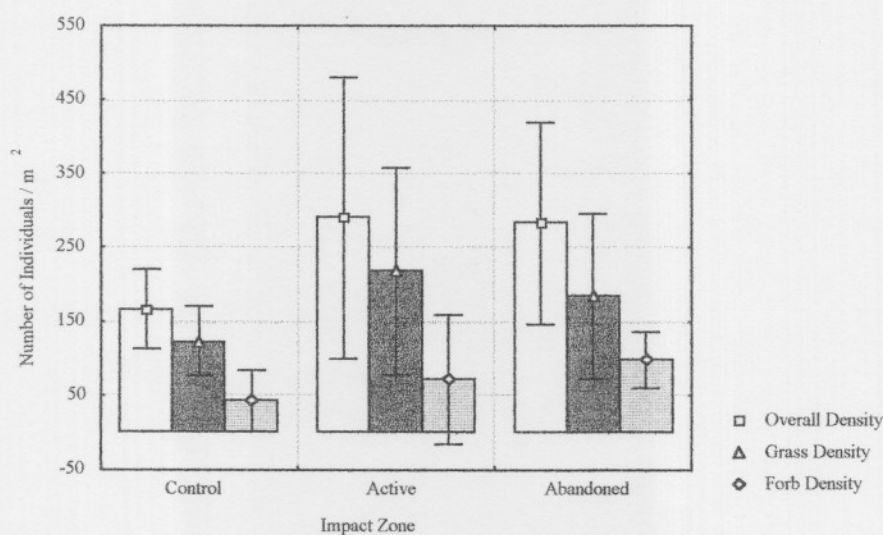


Figure 5.9: Differences in plant community density (per m^2) among impact zones in 1998 on PFA-dam A. (From quadrat data.) Bars denote mean values, vertical lines represent 1SD.

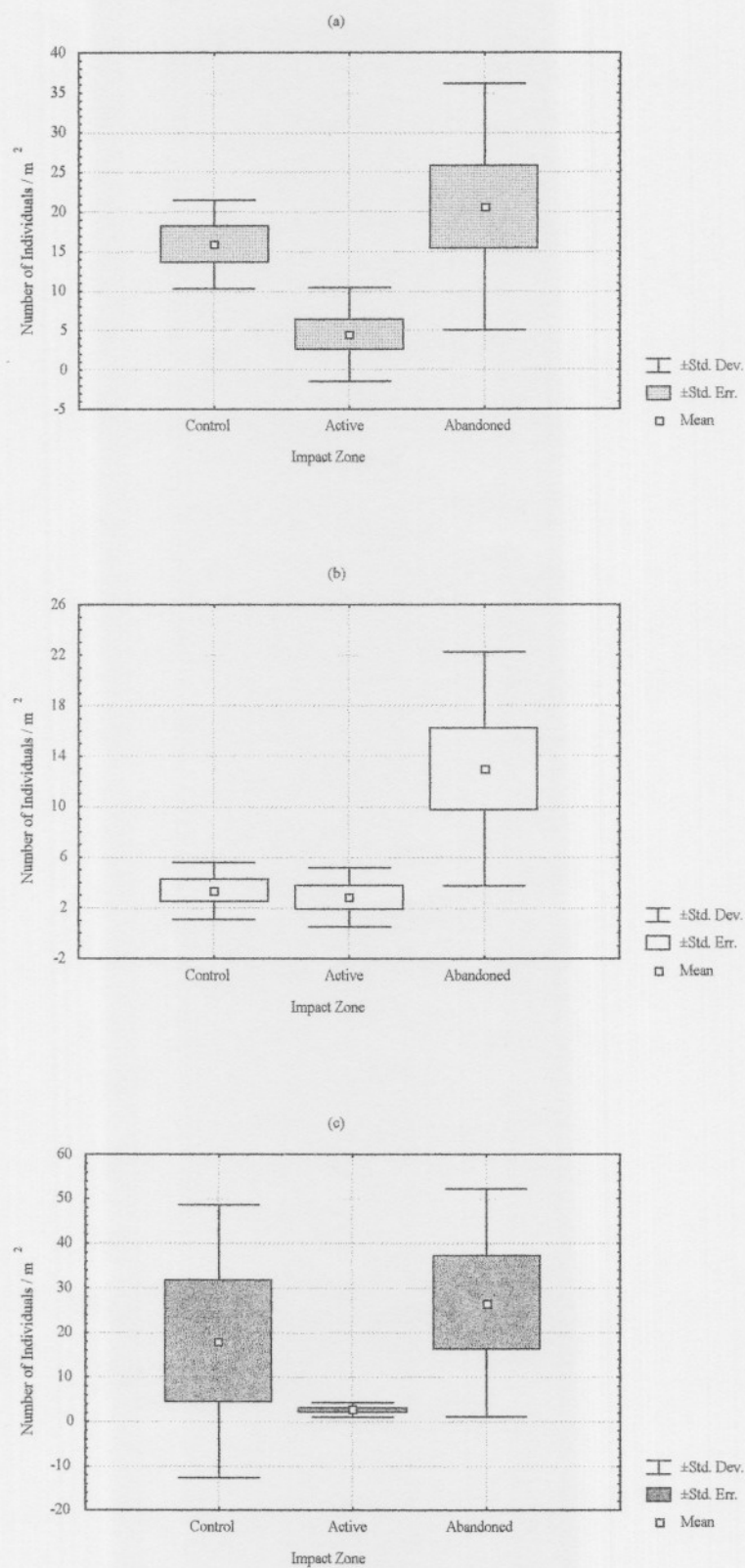


Figure 5.10: Differences in % contributions of species to the density/m² index among impact zones (1998) on PFA-dam A. a) *E. curvula*, b) *C. biensis* & c) *S. pinnata*. Boxes: mean & 1SE, vertical lines: 1SD.

Forb density (from quadrature data, $\log_e$ transformed to reduce variability) was significantly higher on abandoned zones compared to controls ($F_{2,21}:4.278$, $P < 0.05$), but was not significantly different from active zones, possibly because of variability in the data. Overall and grass densities were not significantly altered by gerbil activities (Fig. 5.9).

The densities of some species differed significantly among impact zones, namely, the grass *Eragrostis curvula* ($H_{2,24}:9.447$, $P < 0.01$, Fig. 5.10a), and the forbs *Chamaecrista biensis* ($H_{2,20}:9.364$, $P < 0.01$, Fig. 5.10b) and *Schkuhria pinnata* ($H_{2,20}:8.765$, $P < 0.05$, Fig. 5.10c). The density of *E. curvula* was reduced on active zones when compared to both controls ($Z:-2.593$, $P < 0.01$) and abandoned zones ($Z:-2.605$, $P < 0.01$), *C. biensis* density was significantly lower on both controls ($Z:-2.453$, $P < 0.05$) and in active zones ($Z:-2.582$, $P < 0.01$) compared to abandoned zones, and the density of *S. pinnata* was higher in abandoned zones than in active zones ($Z:3.182$, $P < 0.01$).

6.5 Plant phenology

Seedlings

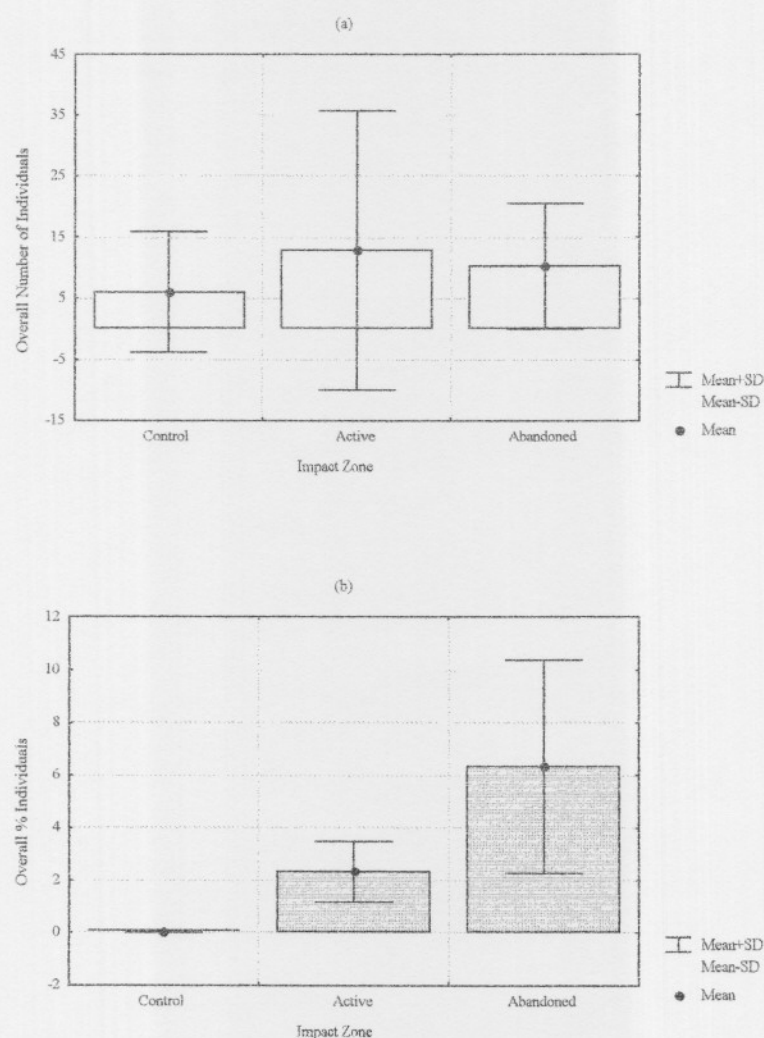


Figure 5.11: Differences in seedling density (per m²) and frequency (%) among impact zones in 1998 on PFA-dam A. a) quadrats & b) transects. Bars denote mean values, vertical lines represent 1SD.

Although there was no significant difference in seedling density (determined from quadrat samples, Fig. 5.11a) among gerbil impact zones, the frequency (determined from transect samples, Fig. 5.11b) of seedlings was higher in abandoned zones than in active zones ($Z:1.964$, $P < 0.05$). Too few seedlings were recorded in control zones to permit statistical comparison. The proportion seedlings of *Eragrostis curvula* (Fig. 5.12) contributed to the overall seedling frequency was significantly greater in abandoned zones than in active zones ($t_{df4}:4.429$, $P < 0.05$).

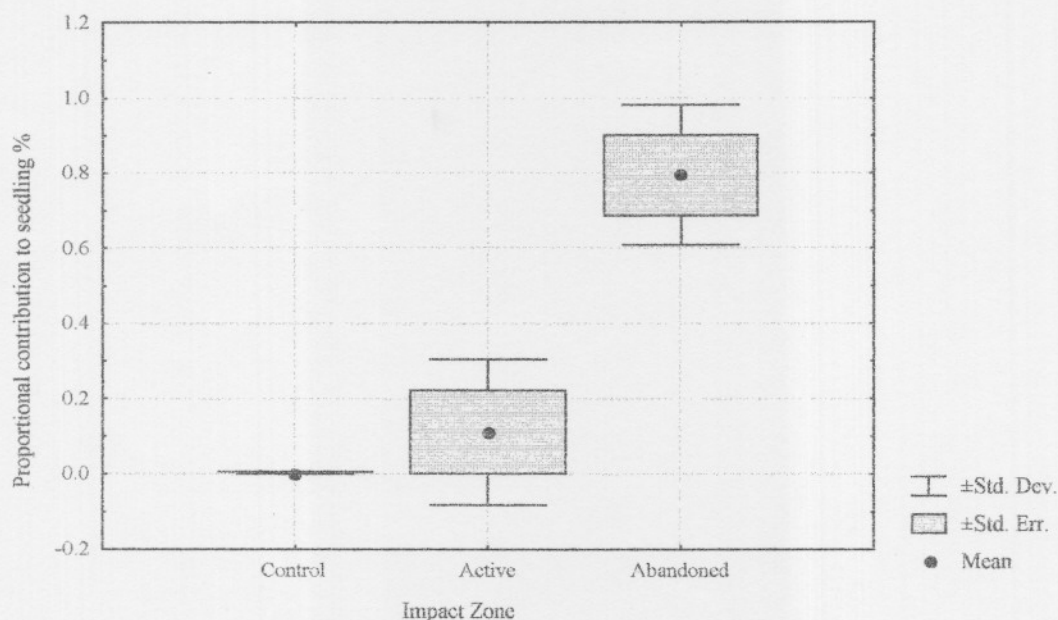


Figure 5.12: Differences in the proportional contribution of *E. curvula* seedlings to overall percentages among impact zones in 1998 on PFA-dam A. (From transect data.) Boxes denote mean values & 1SE, vertical lines represent 1SD.

Non-Flowering mature plants

There were no significant differences in overall non-flowering mature plant density (quadrats, Fig. 5.13a) or frequency (transects, Fig. 5.13b) among gerbil impact zones. The density (quadrat data) of non-flowering mature *E. curvula* ($H_{2,24}:12.850$, $P < 0.01$, Fig. 5.14a) differed significantly among impact zones, where it was significantly lower in active zones than in both control ($Z:-3.064$, $P < 0.01$) and abandoned ($Z:-2.517$, $P < 0.05$) zones. Non-flowering mature *Conyza bonariensis* (Fig. 5.14b) density (based on quadrat data) was higher on controls than in active ($Z_{(adj)}:2.137$, $P < 0.05$) zones. Too few individuals of this species were recorded in abandoned zones to allow statistical comparison.

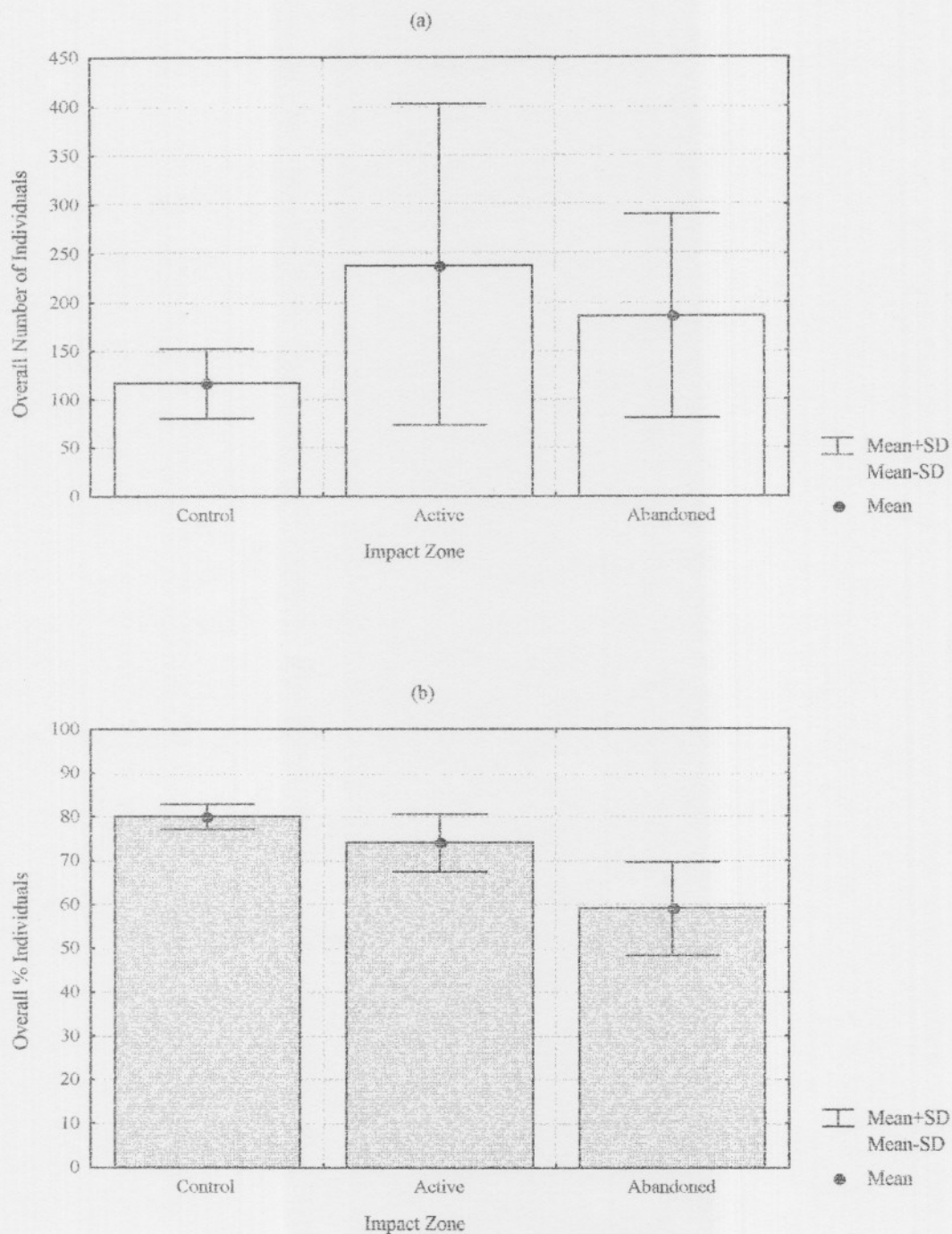


Figure 5.13: Differences in non-flowering mature plant density (per m²) and frequency (%) among impact zones in 1998 on PFA-dam A. a) quadrats & b) transects. Bars denote mean values, vertical lines represent 1SD.

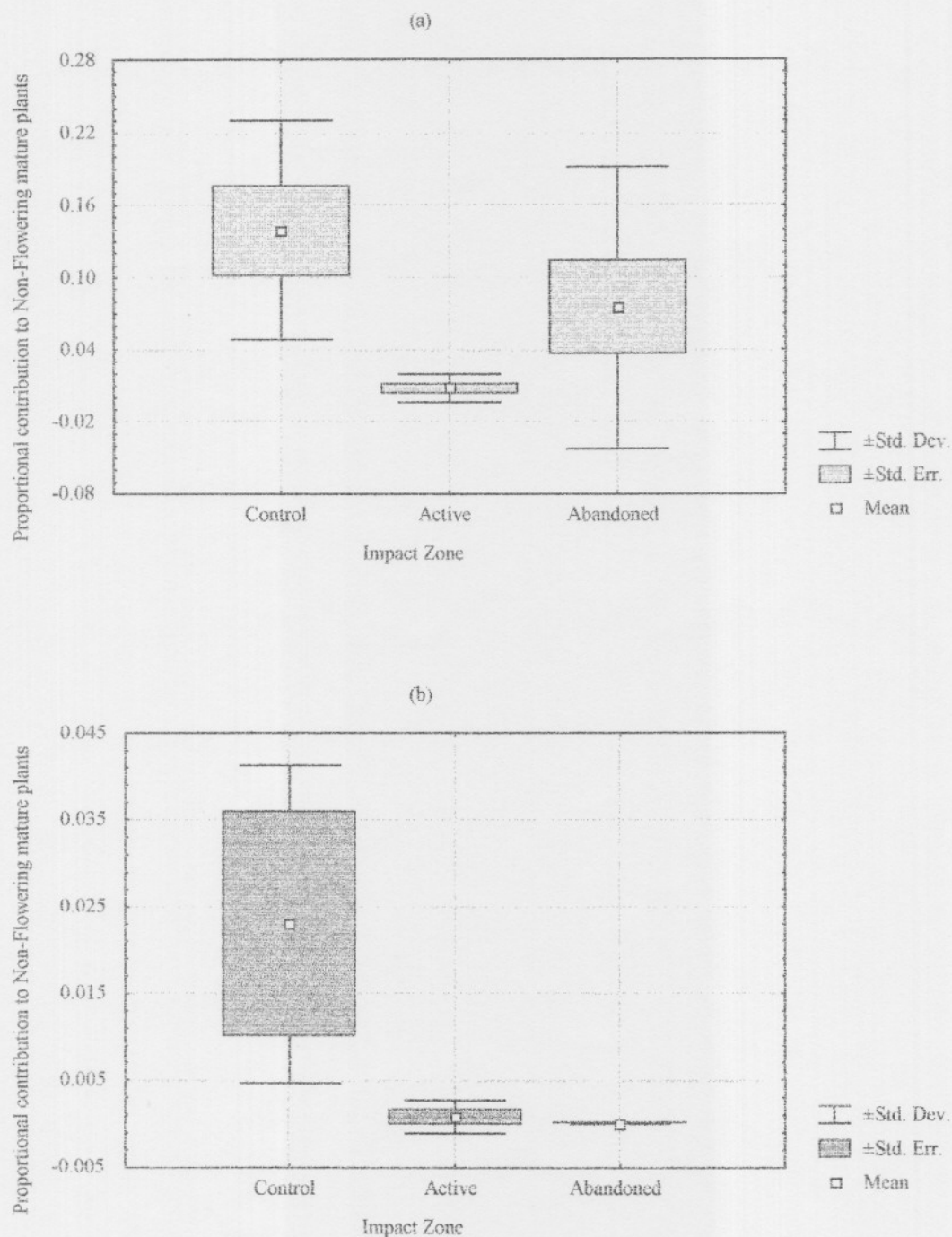


Figure 5.14: Differences in the proportional contributions of species to the overall non-flowering mature plant density/m² index, among impact zones in 1998 on PFA-dam A. a) *E. curvula* & b) *C. bonariensis*. (From quadrata data). Boxes denote mean values & 1SE, vertical lines represent 1SD.

Mature plants in Flower

Overall density (quadrata data) of flowering plants appeared significantly different among impact zones ($H_{2,24}:9.157$, $P < 0.01$, Fig. 5.15a), and seemed lower in abandoned zones than in control zones

(Z : -3.064, $P < 0.01$) despite variability in the sample data. The overall frequency (transect data) of flowering plants did not differ significantly among gerbil impact zones (Fig. 5.15b). The density (quadrant data) of flowering *Tagetes minuta* (Fig. 6.16) was significantly lower in active zones than in controls ($Z_{(adj)}$: -2.069, $P < 0.05$). No individuals of this species were flowering in abandoned zones.

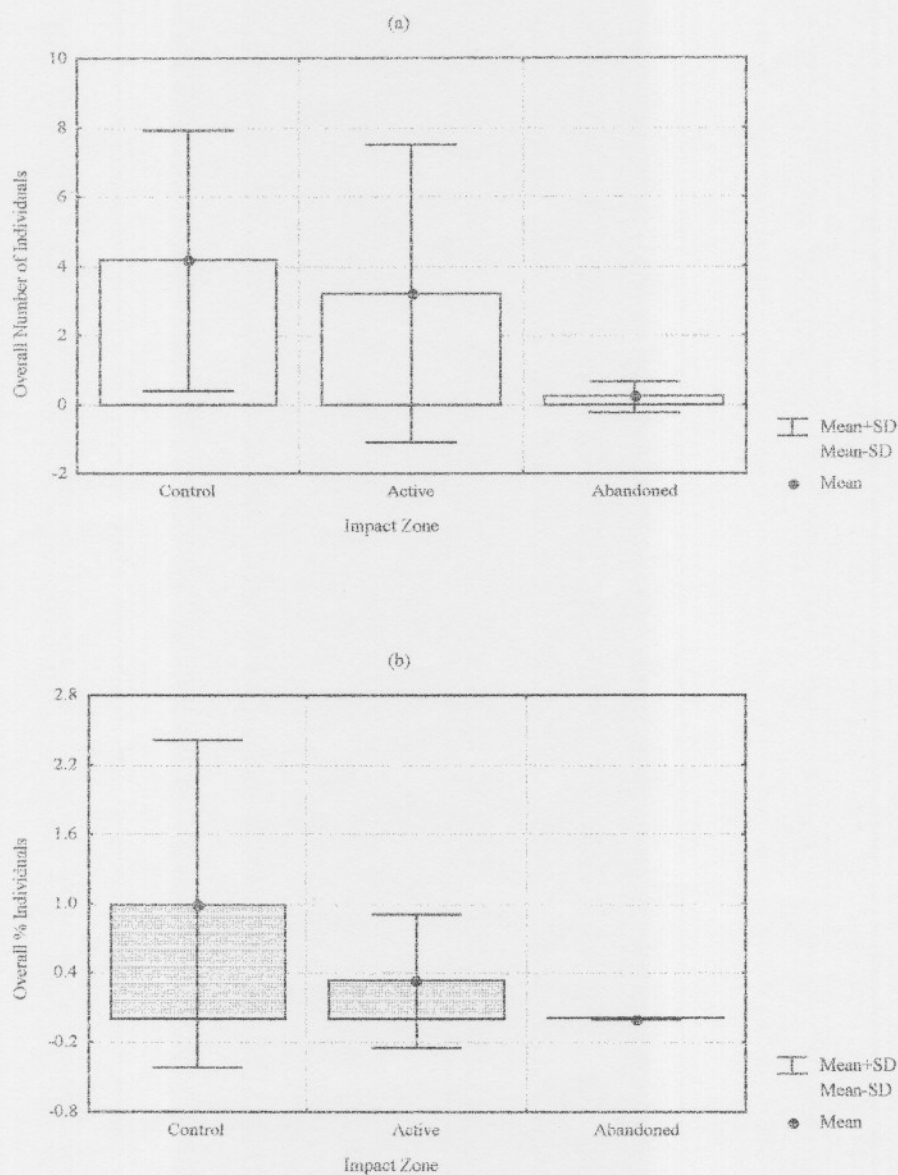


Figure 5.15: Differences in flowering mature plant density (per m^2) and frequency (%) among impact zones in 1998 on PFA-dam A. a) quadrats & b) transects. Bars denote mean values, vertical lines represent 1SD.

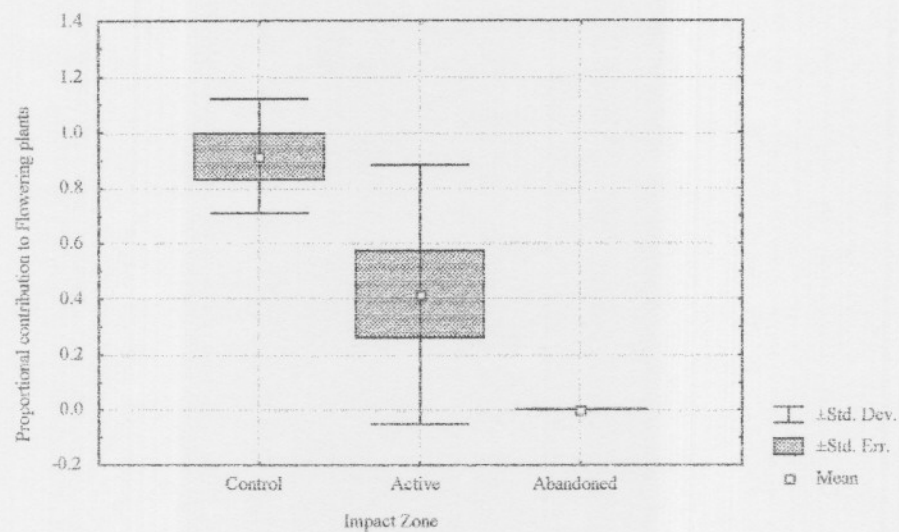


Figure 5.16: Differences in the proportional contribution of *T. minuta* to overall density/m² of flowering plants among impact zones in 1998 on PFA-dam A. (From quadrat data.) Boxes denote mean values & 1SE, vertical lines represent 1SD.

Mature plants with seed

The overall densities (quadrat data, Fig. 5.17a) and frequencies (transect data, Fig. 5.17b) of plants with seed did not appear significantly different among areas of gerbil activity (active & abandoned zones) and control zones. However, variability in data from the samples may have masked significant differences.

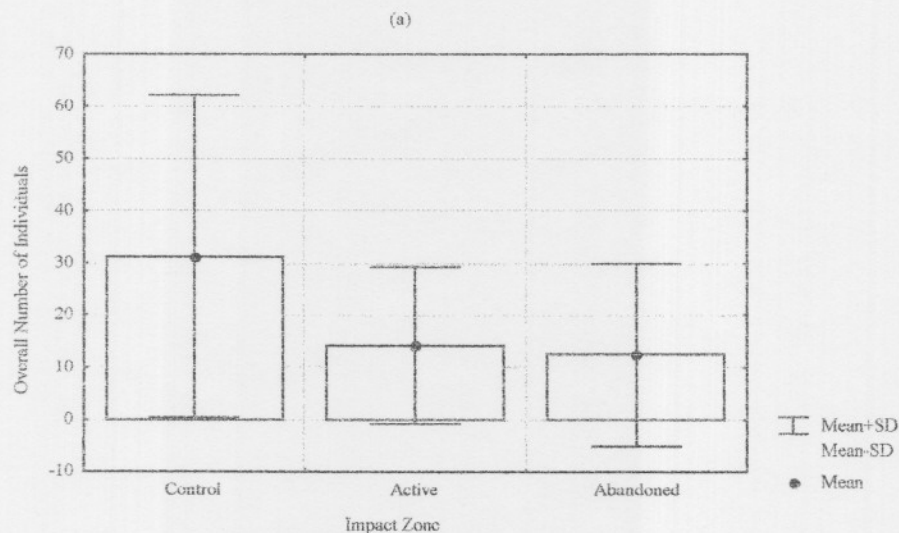


Figure 5.17a: Differences in the density (per m²) of mature plants with seed among impact zones in 1998 on PFA-dam A. (From quadrat data.) Bars denote mean values, vertical lines represent 1SD.

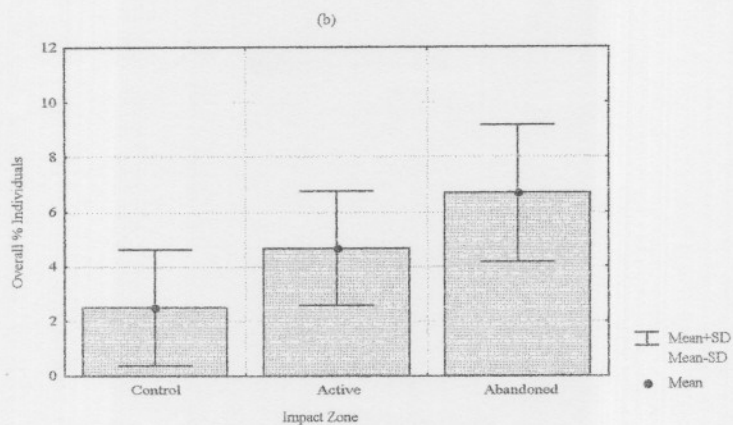


Figure 5.17b: Differences in the frequency (%) of mature plants with seed among impact zones in 1998 on PFA-dam A. (From transect data.) Bars denote mean values, vertical lines represent 1SD.

Mature plants with chaff

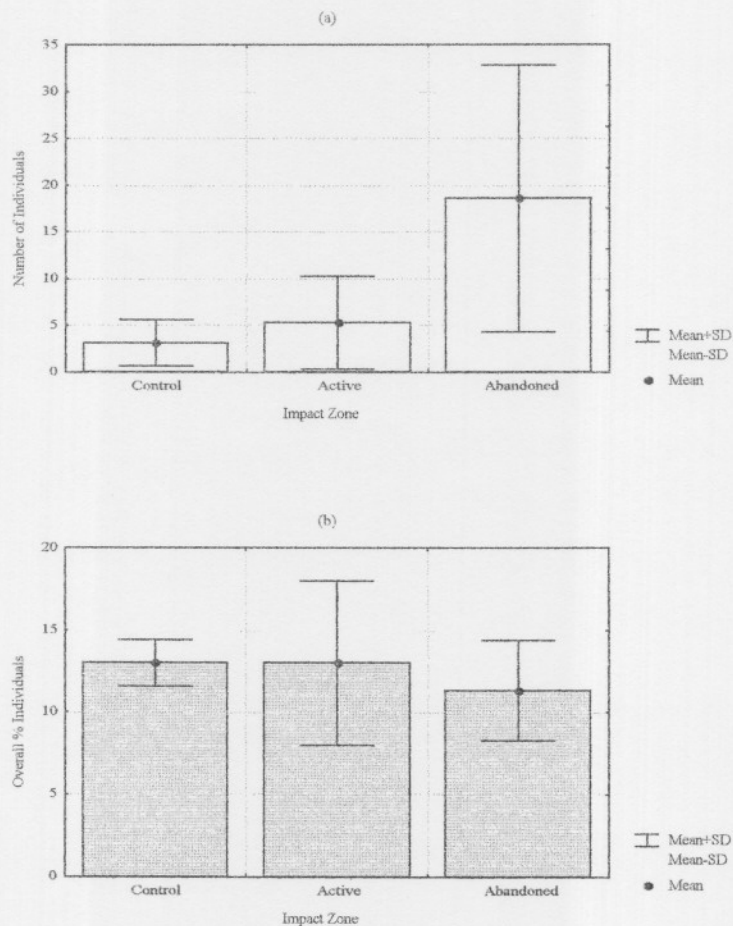


Figure 5.18: Differences in the density (per m²) and frequency (%) of mature plants with chaff among impact zones in 1998 on PFA-dam A. a) quadrats & b) transects. Bars: mean values, vertical lines: 1SD.

Despite variability in the sample data, the overall density (quadrant data) of plants with chaff appeared to differ significantly among impact zones ($H_{2,24}:9.602$, $P < 0.01$, Fig. 5.18a), where it seemed higher on abandoned zones than on control ($Z:2.652$, $P < 0.01$) or active ($Z:2.517$, $P < 0.05$) zones. There was no significant difference in overall frequency (transect data) of plants with chaff across the three site types (Fig. 5.18b)

Dead plants

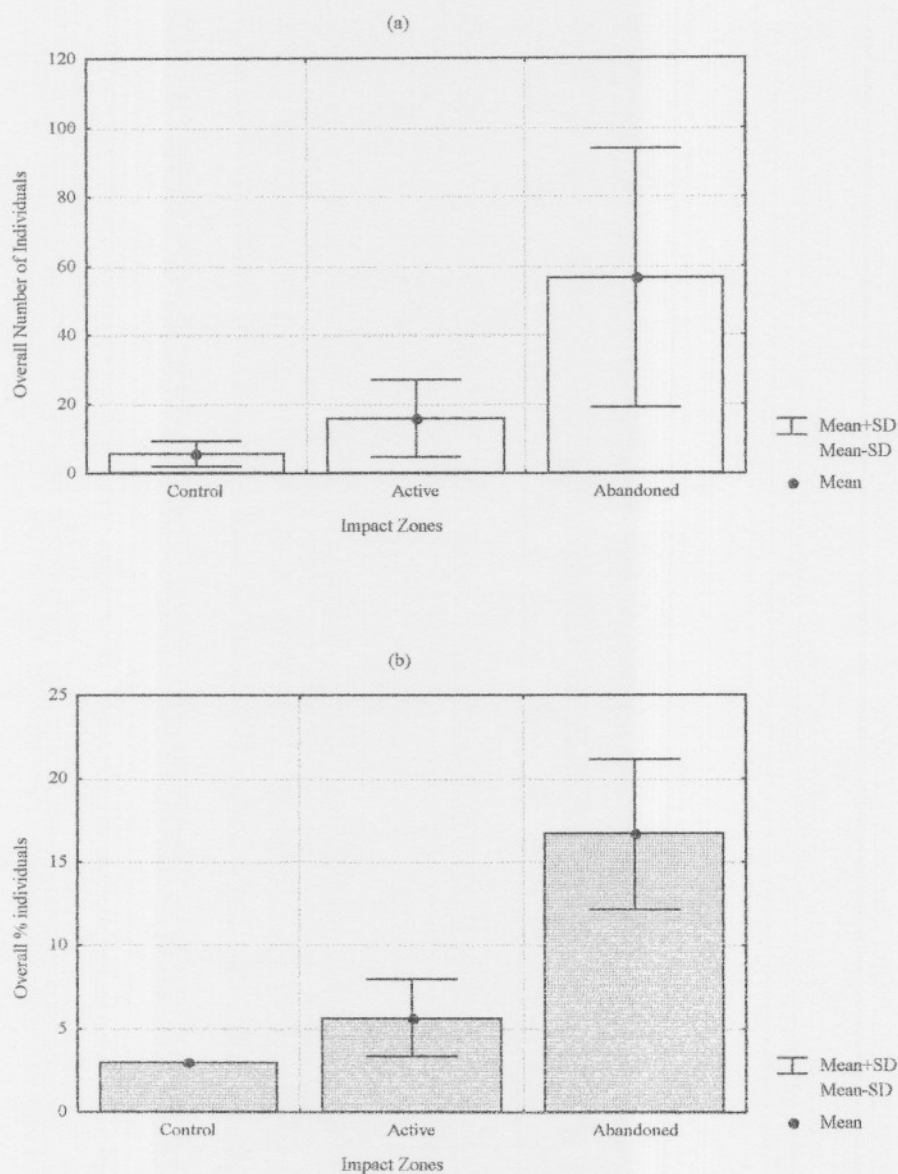


Figure 5.19: Differences in the density (per m²) and frequency (%) of dead plants among impact zones in 1998 on PFA-dam A. a) quadrats & b) transects. Bars denote mean values, vertical lines represent 1SD.

Dead plant density (quadrant data, Fig. 5.19a) was significantly different among impact zones ($H_{2,24}:14.799$, $P < 0.001$). Abandoned zones had higher overall densities of dead plants than both active ($Z:2.869$, $P < 0.01$) and control zones ($Z:3.064$, $P < 0.01$), and active zones had significantly more dead plants than controls ($Z:2.239$, $P < 0.05$). The overall frequency (transect data, Fig. 5.19b) of dead plants

also differed significantly among impact zones ($F_{2,5}:13.711$, $P < 0.01$), and proved to be higher in abandoned zones than in control and active zones. The density (quadrant data) of dead *Chamaecrista biensis* (Fig. 5.20) appeared to differ significantly among impact zones ($H_{2,20}:7.805$, $P < 0.05$). Active zones seemed to have lower densities of dead *C. biensis* than control ($Z_{(adj)}:-1.964$, $P < 0.05$) or abandoned zones ($Z:-2.840$, $P < 0.01$). However, variability in the sample data may have yielded a significant result when none was present.

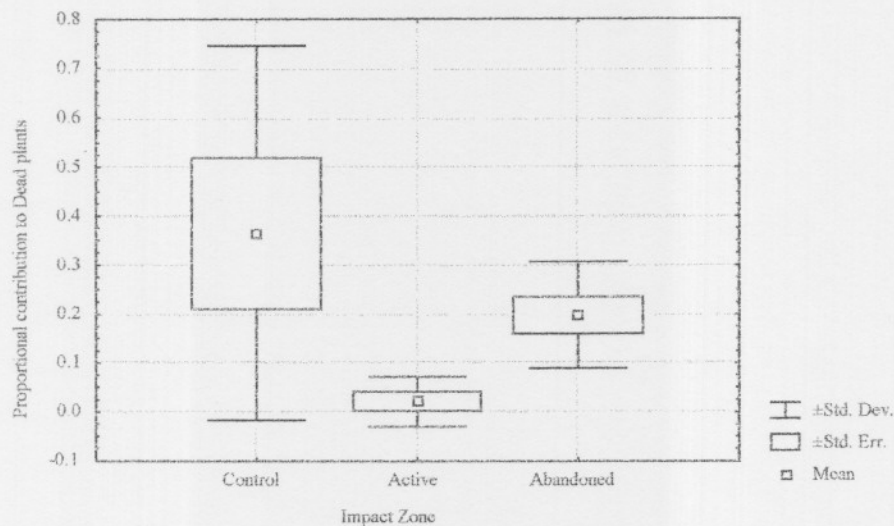


Figure 5.20: Differences in the proportional contribution of *C. biensis* to overall density/m² of dead plants among impact zones in 1998 on PFA-dam A. (From quadrant data.) Boxes denote mean values & 1SE, vertical lines represent 1SD.

5.8 Summary of the factors affecting the *Lepidium bonariensis*-*Eragrostis trichophora* plant community variant on PFA-dam A in 1998

The plant community characteristics that differed most among impact zones were determined from principal component analyses of quadrant data; plant community variables that did not show any significant differences among impact zones were omitted (i.e.: grass & forb diversity, evenness & richness; overall & forb biomass; overall & grass density; seedling density; non-flowering mature plant density and mature plants with seed density). Variables were standardised as they were measured in different units, and data underwent a varimax normalisation.

From the plots of loadings (Fig. 5.21) comparing the first three PCAs, the abandoned and control zones tended to plot apart on PCA II, and to a lesser extent on PCA I, though some overlap was evident. The active zones, however, overlapped considerably with both control and abandoned zones along all three axes. Almost all the abandoned zones and most of the active zones plotted to the right on PCA I (Fig. 5.21 a & b), whereas the majority of the control zones were separated out towards the top (or right) of PCA II (Fig. 5.21 a & c). Impact zones were not well separated along PCA III (Fig. 5.21 b & c).

The first three axes explained 73.774 % of the variance in the data, with eigenvalues of: PCA I: 2.918 (36.476 % of variance); PCA II: 1.778 (22.228 % of variance) & PCA III: 1.206 (15.070 % of variance).

The separation of impact zones was most strongly influenced by plant community species diversity and evenness which increased to the right along PCA I (Table 5.3). PCA II was mainly influenced by plant community species richness, and the densities of mature plants with chaff, which increased from bottom to top (or left to right). PCA III was most powerfully influenced by grass biomass (which increased from top to bottom) and the density of dead plants (which increased from bottom to top).

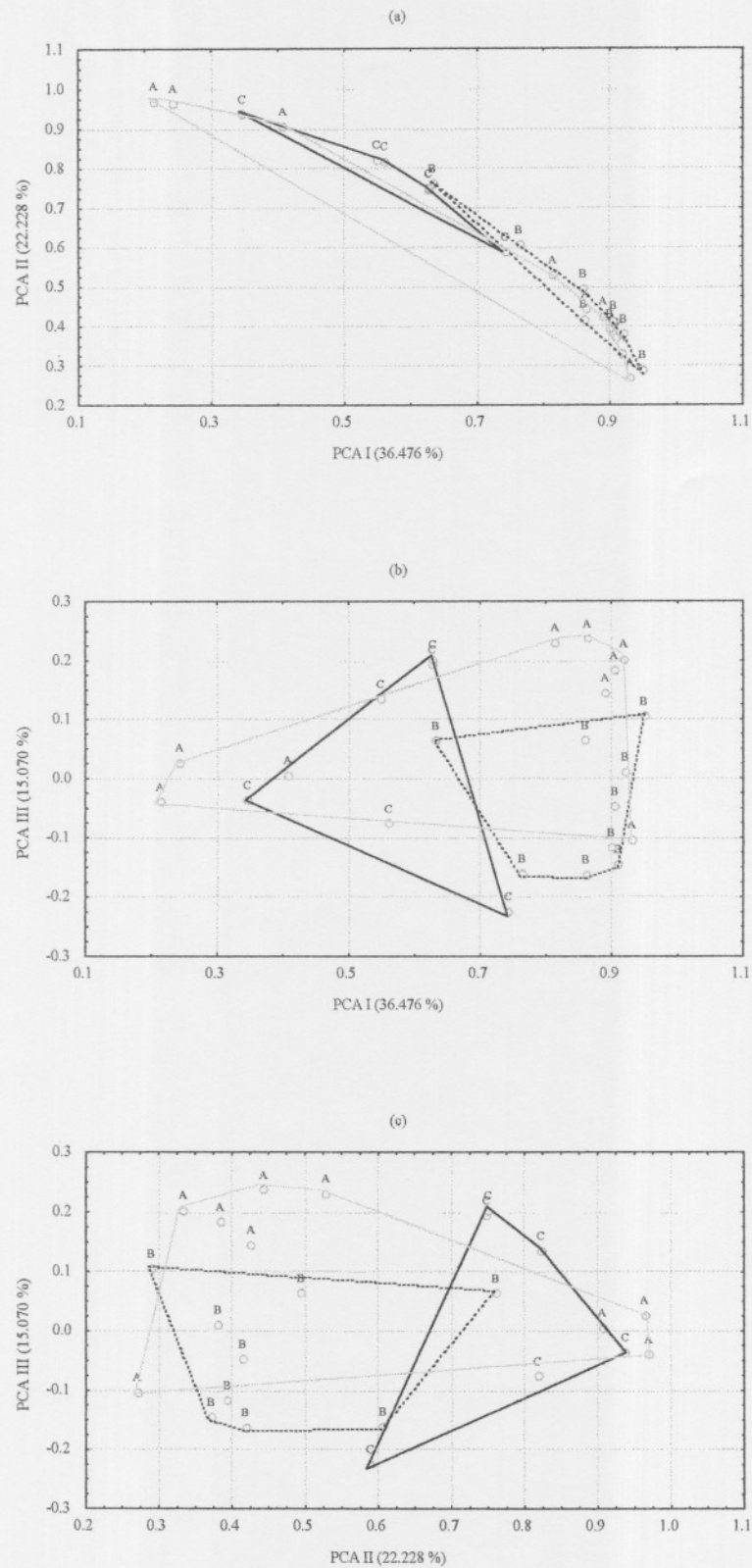


Figure 5.21: Separation of impact zones of PFA-dam A along Principal Component Axes: a) I & II; b) I & III; c) II & III. (From quadrate data.) (C: Control zones, A: Active zones & B: Abandoned zones).

Table 5.3: Contributions of principal component scores (with factor loadings) of plant community variables to principal component axes I-III (varimax normalised) in 1998, collectively explaining 73.8 % of the variance in the (standardised) data set, on PFA-dam A of Hendrina Power Station.

Variables that contributed most strongly to each axis are shown in bold.

Plant Community Variable	PCA I	Factor Loading	PCA II	Factor Loading	PCA III	Factor Loading
Overall Species Diversity	0.436	0.958	0.001	0.063	-0.044	0.195
Overall Species Evenness	0.444	0.953	-0.139	-0.180	-0.037	0.144
Overall Species Richness	-0.092	-0.128	0.454	0.780	-0.010	0.149
Grass Biomass (log _e)	0.067	-0.134	0.172	0.066	-0.502	-0.810
Forb Density (log _e)	0.106	0.433	0.068	0.284	0.284	0.633
Flowering plant Density	0.098	0.119	-0.326	-0.592	-0.066	-0.224
Mature plants with Chaff Density	0.234	0.446	0.493	0.778	-0.278	-0.124
Dead plant Density	-0.118	0.038	0.045	0.290	0.465	0.817

5.9 Discussion

Numerical dominance by grass species (Fig. 5.1) in control zones may have been because these species were introduced into the PFA-dam environment during revegetation efforts, either as sods (*P. clandestinum*) or as part of the seed mixtures used (*E. curvula* & *C. dactylon*), (see Section 2.1.6).

In areas where gerbil impact was current and ongoing (active zones), the increased numbers of plant species may have resulted, in part, from gerbils scratching and digging into the hard topsoil crust. This disrupts established root systems, particularly of dominant grasses, reducing competition for resources, and provides additional germination sites for seedlings of both local, non-dominant species, and plants from regional species pools (Dean & Milton 1991a, b).

The number of species in abandoned zones was elevated relative to controls, but to a lesser extent than in active zones. The coarser substrate (as a consequence of mixing following tunnel collapse) would promote the establishment of seedlings, as the impenetrability of the hard crust had been broken, but fewer may have survived, owing to improved drainage and thus drier substrate (Reichman & Seabloom 2002), resulting from the reduced proportion of the water-retaining, silt-sized particles (see Section 4.1.3). However, most of the new species introduced into the community as a result of gerbil activities were ruderal forbs and increaser II grasses (see Section 5.2) that are typical of ecological retrogression.

Both active and abandoned zones were characterised by a reduced representation of the sub-dominant *E. curvula*, possibly because the tussocks of this grass were buried under substrates excavated by gerbils. The stoloniferous *P. clandestinum* would probably be less affected by the loss of some of its aboveground modules, and although dominance by this species was not changed by the activities of gerbils, the proportional representation of this grass was reduced in the abandoned zones. The reduction of dominance by individuals of few species was notable in abandoned zones, where individuals seemed more evenly distributed among the species comprising the community.

The impacts of gerbil-mediated disturbances in this plant community variant did not alter the initial ecological status of the grass community, which remained at a sub-climax stage dominated by increaser II species. However, the presence of gerbils (active impact zones) may have produced circumstances which were equivalent to over-grazed conditions, as the appearance of unpalatable increaser III species are indicative of a mature grassland affected by overgrazing (van Oudtshoorn 1991). After the impact zones were abandoned, the plant community reverted to a sub-climax stage, but with a greater diversity of grasses, and a reduced proportion of exotics.

Dean & Milton (1991b) have shown that substrate disruptions (excavated mounds, hollows & scratches), in areas occupied by gerbils, provide open places where moisture and seeds of species new to the area, as well as competitively-inferior annual forbs, could accumulate and germinate without competition from dominant, established plants. Inter-specific plant competition may also be reduced by

the excavation of burrow systems by gerbils which would disrupt the root systems of established plants and bury their above-ground foliage under excavated substrates (Milton & Dean 1991).

In the abandoned zones, the reduced competition between plants (following the impacts of gerbil presence), and the coarser, mixed substrate, may have facilitated the establishment of seeds, and thus the recruitment of plants from regional species pools (Martinsen *et al.* 1990; Olff & Ritchie 1998), thereby increasing species richness (Fig. 5.2).

It seemed that initial activity (active zones) by gerbils did not significantly alter the evenness of the plant community relative to controls (Fig. 5.3), and that species evenness remained unchanged after the cessation of gerbil activity (abandoned zones). Despite that there was no significant difference among controls and areas of gerbil impact, zones abandoned by gerbils seemed to have a more even distribution of individuals across species present than zones occupied by gerbils, implying that the presence of gerbils may have promoted a temporary uneven distribution of plant individuals among the species present.

The occurrence of dominant species (see Section 5.1), particularly grasses, was more likely to have been reduced by the disruption of root systems as a result of gerbil burrowing (Milton & Dean 1991). This would benefit competitively-inferior species and facilitate the recruitment of more individuals of the rarer plants from regional species pools (Martinsen *et al.* 1990; Olff & Ritchie 1998).

Where gerbil activity was current (active zones), no significant impact on the species diversity of the *Lepidium bonariensis*-*Eragrostis trichophora* community variant was detected (Fig. 5.4). The open patches may have created substrate disturbances (scratches, burrow entrances and excavated soil mounds) that have been shown to promote the successful germination and establishment of both grass and forb species (Dean & Milton 1991b), but this was not sufficient to increase the diversity in 1998. It was possible, however, that any increase in diversity was offset by reduced plant survival as a result of feeding by gerbils on newly established seedlings.

The increased species richness of abandoned zones (see above) seemed responsible for the increase in diversity in these areas, possibly because the cessation of gerbil activities allowed plants better chances of establishment. The coarser substrate of this impact zone (see Section 4.1), could facilitate the colonisation of plants from regional species pools (Olff & Ritchie 1998) by allowing the seeds of wind- and animal-dispersed species, to lodge in the soil. Plants would also benefit from reduced competition with dominant species, as prior burrowing by gerbils would have been more likely to disrupt the root systems of these established, common species (Milton & Dean 1991).

The reduced biomass of *E. curvula* in active zones reflects the reduced dominance of this grass (see Section 5.1), and was probably brought about by tussock death due to burial under excavated substrates (Fig. 5.6). However, as overall grass biomass was unchanged (Fig. 5.5), the biomass of introduced grass species possibly compensated for the loss. The reduction in *S. pinnata* biomass was likely to have been because of reduced density (see Section 5.6), but selective feeding by gerbils may also have contributed to this loss.

The reduction of overall grass biomass in abandoned zones (Fig. 5.5) can probably be attributed to the coarser, and thus drier, substrates of these areas (see Section 4.1.5) limiting growth, and thus productivity. However, the reduction in grass species dominance seemed more likely to effect the observed reduction in grass biomass as there were less high-mass individuals. This was, however, accompanied by an increase in species richness (see Section 5.3), which included the recruitment of a number of ruderal forb species in these areas of substrate disturbance. Although most of these forbs represented species of low biomass, *C. biensis*, a woody species which contributed a significantly greater percentage to overall biomass in abandoned zones, may have offset the reduction of grass biomass in the overall biomass index.

Although gerbil activity did not significantly alter the overall percentages of cover in each category (Fig. 5.7), in the zero cover category, the proportion the grass *P. clandestinum* contributed to the overall percentage was reduced after abandonment by gerbils (Fig. 5.8). Individuals of this species were closer together following digging into the substrate crust, possibly because the friable substrate was more easily penetrated by roots and stolons, allowing this grass to form more closely-knit mats. This is an advantage in terms of erosion prevention (Jaaback & Muzzell 1971), and the resulting topsoil loss.

In zones abandoned by gerbils, the increase in the space between *S. pinnata* individuals may have

been because of drier substrates (see section 4.1.5) impeding plant growth, resulting in a smaller canopy and thus reduced cover provided by the plant.

The presence of gerbils (active zones) did not significantly change the community density indices from controls (Fig. 5.9). However, the density of *E. curvula* was repressed in active zones, which correlates with both the reduced dominance and biomass previously found for this species (see Sections 5.1 & 5.4). The probable reason is that individuals of this particular tussock grass were killed by being completely buried under substrates excavated by gerbils.

Following abandonment by gerbils, overall plant density and grass density were not significantly different from controls. The increase in forb density could have been because of the combined effects of more friable soil allowing better establishment of plants and the reduction of competitiveness of numerically dominant species (Dean & Milton 1991a). The densities of both forb species which showed significant differences among the impact zones reflected this trend. Mean *C. biensis* densities were increased from 3.3 / m² in controls and 2.8 / m² in active zones to 13.0 / m² in abandoned zones, and the mean density of *S. pinnata* increased from 18.0 / m² in controls and 2.7 / m² active zones to 26.7 / m² in abandoned zones (Fig. 5.10).

At the end of the growing season in 1998, the highest frequency of seedlings (Fig. 5.11) was recorded in the abandoned zones, largely due to a substantial increase in *E. curvula* seedlings (Fig. 5.12). Here, the friable substrate resulting from the mixing of substrates after the collapse of gerbil tunnels, may have been conducive to seedling establishment. In contrast with active zones, where palatable seedlings, especially grasses (Hulme 1994; Clements & Young 1996), germinating in disturbed substrate, were probably consumed, the survival of seedlings would be greater in abandoned zones.

At the end of the growth season in 1998, the non-flowering mature plants (mostly grasses) occurred in similar densities and frequencies in areas impacted on by gerbils and areas not subject to such impacts (Fig. 5.13). Gerbil activities did not therefore alter the overall distribution of non-flowering mature plants of the plant community. However, the densities of non-flowering mature plants of two species seemed to be affected by gerbil impacts (Fig. 5.14). In areas occupied by gerbils, the apparently lower density of non-flowering mature *E. curvula* was possibly due to burial under excavated substrates. The reduced species dominance, biomass and density already shown (Sections 5.1, 5.4 & 5.6) appear to reflect that gerbil activities have the most impact on this stage of the *E. curvula* life cycle. The reduced densities of the non-flowering mature forb, *C. bonariensis*, found in areas where gerbils were active may have been due to feeding.

The lower overall density of flowering plants in abandoned zones at the end of the growth season may be attributable to the drier substrate there (see Section 4.1.5) which may have resulted in the hastening of plant life cycles, as plants on control and active zones still remained at this stage (fig. 5.15). This applied particularly to flowering *T. minuta*, the only species common to all three impact zones which showed differences in flowering mature plant density (Fig. 5.16). A steady decline in the number of flowering plants was apparent from controls (4.0 / m²) to active zones (2.8 / m²) to abandoned zones (0 / m²).

Gerbil activity did not change the distribution of mature plants with seed across the impact zones (Fig. 5.17).

A greater overall density of plants had reached the chaff stage of their life cycles at the end of the growing season in 1998 in the abandoned zones (Fig. 5.18). This was possibly because the drier substrate of the abandoned zones had hastened the completion of plant life cycles, whereas in active and control zones, far fewer plants had entered the chaff stage.

The greater dryness of abandoned site substrates (see Section 4.1.5) was probably the cause of the overall greater density of dead plants, as well as the overall higher frequency of dead plants found there (Fig. 5.19). The overall species density of *C. biensis* was lower in active zones (see Section 5.6), and this was reflected by the reduced proportion of dead plants found there (Fig. 5.20).

Following the cessation of gerbil activity (abandoned zones), the plant community of PFA-dam A in 1998 was different in several aspects compared to that prior to gerbil impact (control zones). This was indicated by the separation of these two impact zones along the first two principal component axes, and

seemed because of the increased densities of mature plants with chaff and higher species richness and diversity of abandoned zones. Overall community evenness was also extracted as important in separating the impact zones but variability in the data masked exactly how this community variable affected the plant community.

Although not useful in separating the impact zones, PCA III did extract components which differentiated the abandoned zones, namely increased dead plant density and reduced grass biomass. As both of these were important in defining variability in the data, the difference between abandoned and control zones was highlighted.

These characteristics seem to point to the influence of the friable substrate of abandoned zones on the plant community (Chapter 4), which, through its dryness, may have caused the hastening of plant life cycles compared to active and control zones, and through its coarseness, facilitated the establishment of plant species, thereby increasing the diversity of the community.

Active zones overlapped extensively with both the control and abandoned zones on all three axes, reflecting this intermediate stage in the process of gerbil impact. This stage appeared to have characteristics of both the “before” and “after” conditions of the effect of gerbil impact, representing the transition between the two.

5.10 Conclusions

Gerbil impacts on the plant community in 1998 are extensive, affecting plant community parameters, physiognomy and phenology (the timing of stages of plant life cycles). Perhaps the most significant change brought about by gerbil activities in the *Lepidium bonariensis-Eragrostis trichophora* plant community variant is the increase in species richness, where the plant community after gerbil impact has almost half again the number of species it was originally composed of in controls. This is in general agreement with the effects of burrowing small mammals recorded by other authors in natural habitats (Martinsen *et al.* 1990; Dean & Milton 1991a; Milton & Dean 1991; English & Bowers 1994; Huntly & Reichman 1994; Olff & Ritchie 1998). Dominance of the community by few grass species was reduced by the activities of gerbils, but despite the increase in species richness, the plant community was still composed of only 43 species (see Table 2.3), and this may explain why increases in the diversity index were not significant, as a similar study in a natural grassland identified 72 plant species (Korn & Korn 1989).

The effects of *Tatera brantsii* in this industrial habitat appear similar to those found by Korn & Korn (1989) in a natural grassland habitat, and may benefit the rehabilitation effort by promoting greater biodiversity. However, the current levels of impact (assessed from grass ecological status), at these densities of gerbils (37.098 / ha; Vermaak 2000), seem to delay and impede the processes of succession by maintaining it at a sub-climax stage, and this may have negative longer-term effects.

CHAPTER 6

RESULTS: IMPACTS OF GERBIL ACTIVITY ON THE PLANT COMMUNITY IN 1999

A second survey of the plant *Lepidium bonariensis-Eragrostis trichophora* community variant was undertaken in 1999 to establish whether the changes brought about by the activities of *Tatera brantsii* in 1998 persisted in the following year. The lower rainfall in 1999 (see Section 2.1.1) may have affected plant community characteristics and gerbil activities may therefore have a more extensive impact in this habitat.

6.1 Plant community composition and dominance

Table 6.1: Numbers of plant species, and the ratios of grasses:forbs & annuals:perennials in impact zones of the *Lepidium bonariensis-Eragrostis trichophora* plant community variant on PFA-dam A of Hendrina Power Station in 1999.

		Control	Active	Abandoned
Quadrat Data	Number of Species	14	25	22
	Grasses : Forbs	5:9 (1:1.8)	8:17 (1:2.12)	9:13 (1:1.4)
	Annuals : Perennials	7:7 (1:1)	10:14 (1:1.4)	10:12 (1:1.2)
Transect Data	Number of Species	13	11	12
	Grasses : Forbs	6:7 (1:1.17)	5:6 (1:1.2)	6:6 (1:1)
	Annuals : Perennials	7:6 (1.17:1)	7:4 (1.75:1)	7:5 (1.4:1)

Unidentified species (see Table 2.3), and species with variable categorisation, were excluded from the annual:perennial ratios.

Areas undisturbed by gerbil activity (controls, Fig. 6.1a) were dominated (assessed from frequency) by grasses (cumulative total of 85.4 %) with three perennial grass species making up 70.4 % of individuals (ie: *Pennisetum clandestinum*, sp.#2 [46 %]; *Eragrostis curvula*, sp.#7 [19.7%] & *Cynodon dactylon*, sp.#3 [4.7 %]). Two forb species were numerically dominant and constituted 15 % of the individuals of the community (ie: *Chamaecrista biensis*, sp.#4 [10 %] & *Cyperus esculentus*, sp.#10 [5 %]).

In the active zones (Fig. 6.1b), dominance by these few species was altered, with the contribution of grass species increased to 73.8 % (*P. clandestinum*, sp.#2 [50.3 %]; *Hyparrhenia hirta*, sp.#9 [12 %] & *C. dactylon*, sp.#3 [11.5 %]). Dominant forbs contributed 14 % (ie: *C. biensis*, sp.#4 [8 %] & *Tagetes minuta*, sp.#6 [6 %]) to the total of 87.8 %. Here, the presence of gerbils seemed to stimulate dominance by a few plant species as dominant plants contributed a slightly greater percentage to the individuals of the plant community.

The total contribution of dominant plants to the plant community in abandoned zones was reduced to 73.1 % (Fig. 6.1c). Grasses contributed 44.7 % to this total (*P. clandestinum*, sp.#2 [38 %] & *Eragrostis plana*, sp.#1 [6.7 %]) and that of forbs was 28.4 % (*C. biensis*, sp.#4 [12 %]; *Cyperus usitatus*, sp.#19 [9.7 %] & *T. minuta*, sp.#6 [6.7 %]).

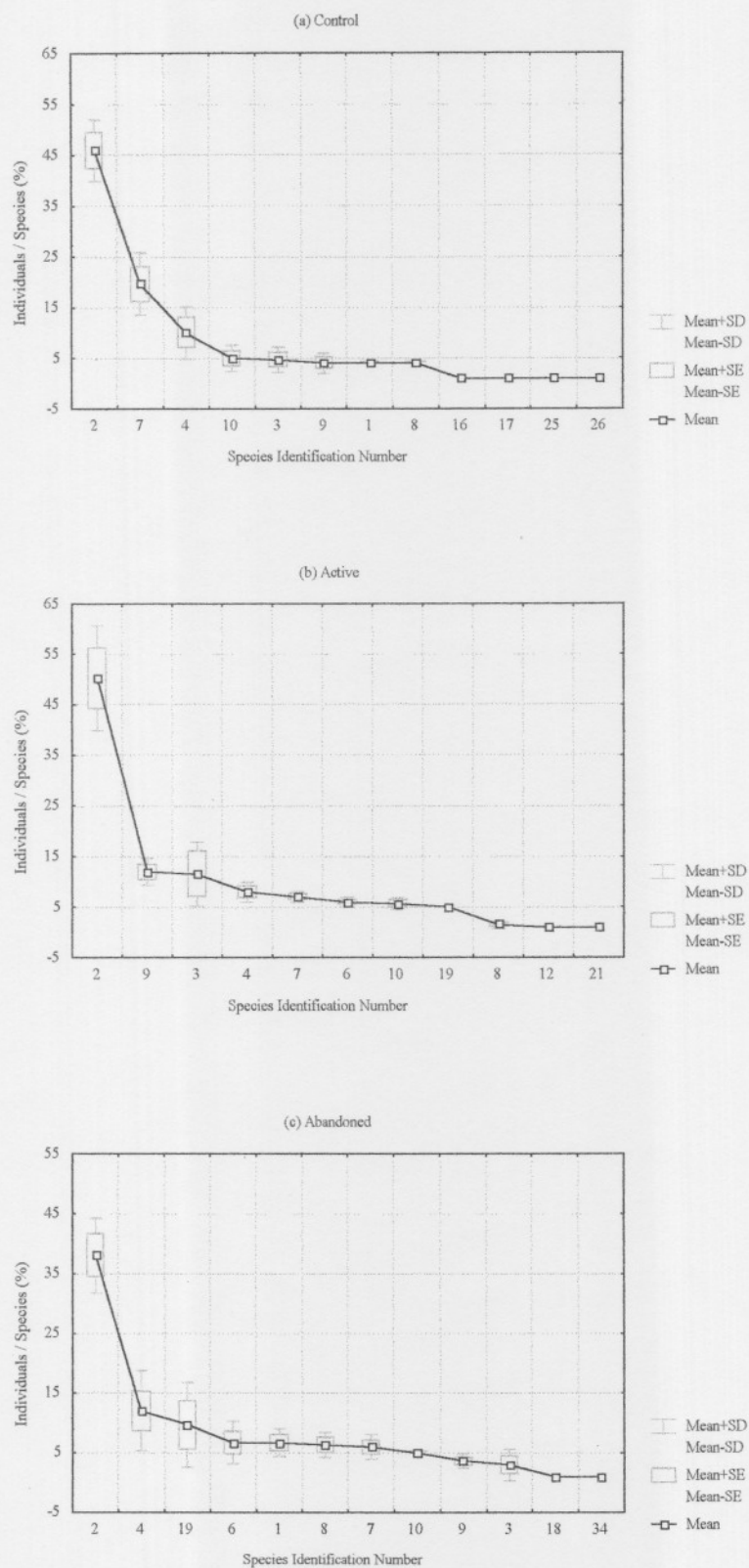


Figure 6.1: The % of individuals of plant species among impact zones in 1999 on PFA-dam A. a) Control, b) Active & c) Abandoned. Boxes: mean & ISE, vertical lines: 1SD. (For species names, see Table 2.3).

6.2 Ecological status of grasses

Grass species in control zones (Table 6.2) comprised one exotic species (*Pennisetum clandestinum*, sp.#2), one increaser I species (*Hyparrhenia hirta*, sp.#9), and three (quadrate data) or four (transect data) increaser II species (*Eragrostis plana*, sp.#1; *Cynodon dactylon*, sp.#3; *Eragrostis curvula*, sp.#7 & *Setaria pallide-fusca*, sp.#17).

Areas where gerbil impact was current and ongoing (active zones) were characterised (based on quadrate data) by reduced proportions of exotics (*P. clandestinum*, sp.#2) and increaser I species (*H. hirta*, sp.#9), and greater numbers of increaser II species (*E. plana*, sp.#1; *C. dactylon*, sp.#3; *E. curvula*, sp.#7; *Setaria pallide-fusca*, sp.#17 & *Eragrostis echinocloidea*, sp.#21). Gerbil activities also resulted in the introduction of a decrease species (*Panicum coloratum*, sp.#29). However, transect data indicated that the proportions of exotics and increaser I species were increased, with a concomitant reduction in the dominance of increaser II species, where the number of increaser II species were reduced to three.

Increaser II species increased to six (quadrate data) or four (transect data) species in abandoned zones (*E. plana*, sp.#1; *C. dactylon*, sp.#3; *E. curvula*, sp.#7; *S. pallide-fusca*, sp.#17; *Aristida congesta*, sp.#34 & *Pogonarthria squarrosa*, sp.#37). Quadrate data indicated that increaser I (*H. hirta*, sp.#9), exotic (*P. clandestinum*, sp.#2) and decrease species (*P. coloratum*, sp.#29) each contributed equal proportions to the grasses of the community, whereas transect data showed that increaser I and exotic species contributed the same percentages to the ecological status of the community, similar to the control zones.

Table 6.2: Ecological status of the *Lepidium bonariensis*-*Eragrostis trichophora* plant community variant in the three impact zones of PFA-dam A of Hendrina Power Station in 1999, as indicated by the percentage of grass species in each category.

	Ecological Status	Control	Active	Abandoned
Quadrate Data	Exotic	20 %	12.5 %	11.1 %
	Increaser I	20 %	12.5 %	11.1 %
	Increaser II	60 %	62.5 %	66.7 %
	Increaser III	0 %	0 %	0 %
	Decreaser	0 %	12.5 %	11.1 %
Transect Data	Exotic	16.7 %	20 %	16.7 %
	Increaser I	16.7 %	20 %	16.7 %
	Increaser II	66.6 %	60 %	66.6 %
	Increaser III	0 %	0 %	0 %
	Decreaser	0 %	0 %	0 %

6.3 Plant Diversity Indices

Species Richness

From quadrate data (Fig. 6.2a) it was seen that both active and abandoned zones had significantly greater overall species richness ($F_{2,24}:12.728$, $P < 0.001$) and grass species richness ($F_{2,24}:14.640$, $P < 0.001$) than control zones. In addition, active zones also had greater forb species richness ($F_{2,24}:4.959$, $P < 0.05$) than controls. However, no significant differences among impact zones for the species richness indices (ie: total, grass or forb species richness) were found following analysis of transect data (Fig. 6.2b).

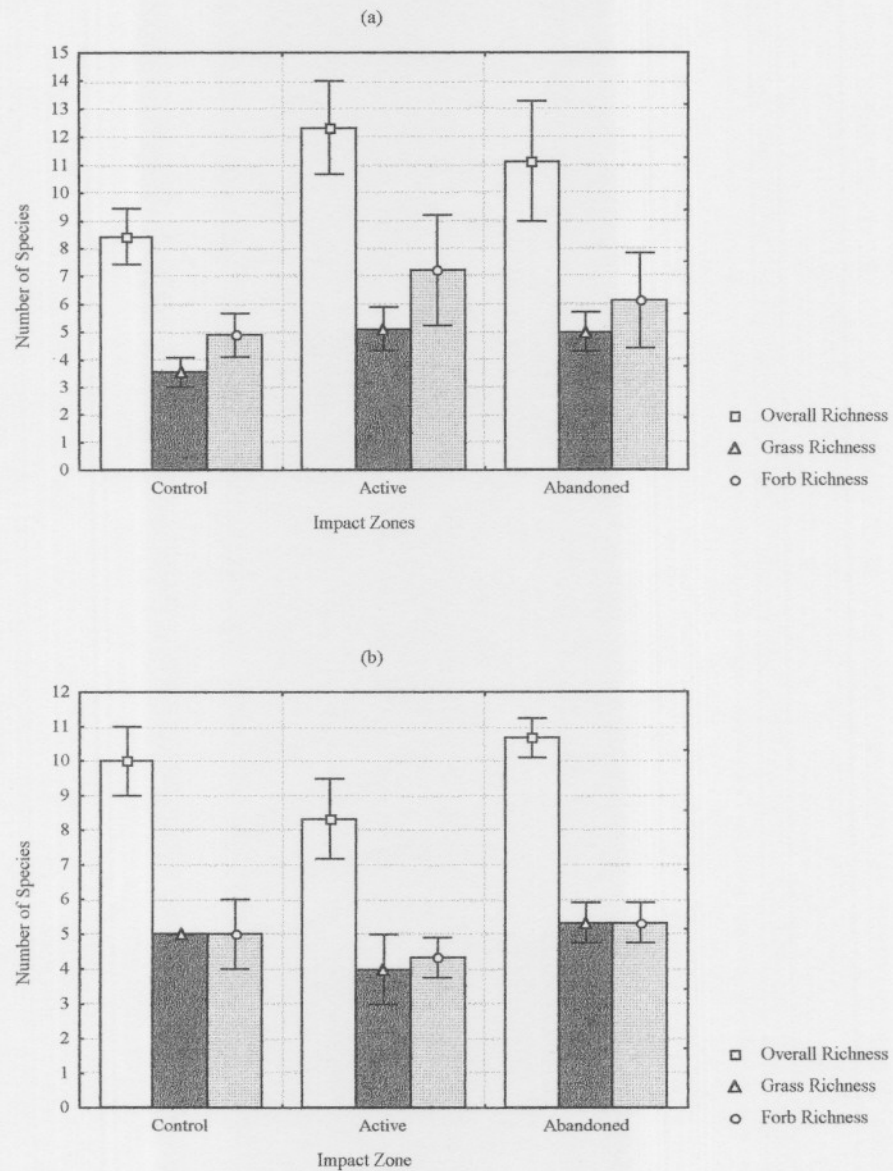


Figure 6.2: Differences in plant community species richness among impact zones in 1999 on PFA-dam A. a) quadrats & b) transects. Bars denote mean values, vertical lines represent 1SD.

Species Evenness

There were no significant differences among impact zones in overall community evenness, grass evenness or forb evenness following analysis of either quadrat (Fig. 6.3a) or transect (Fig. 6.3b) data.

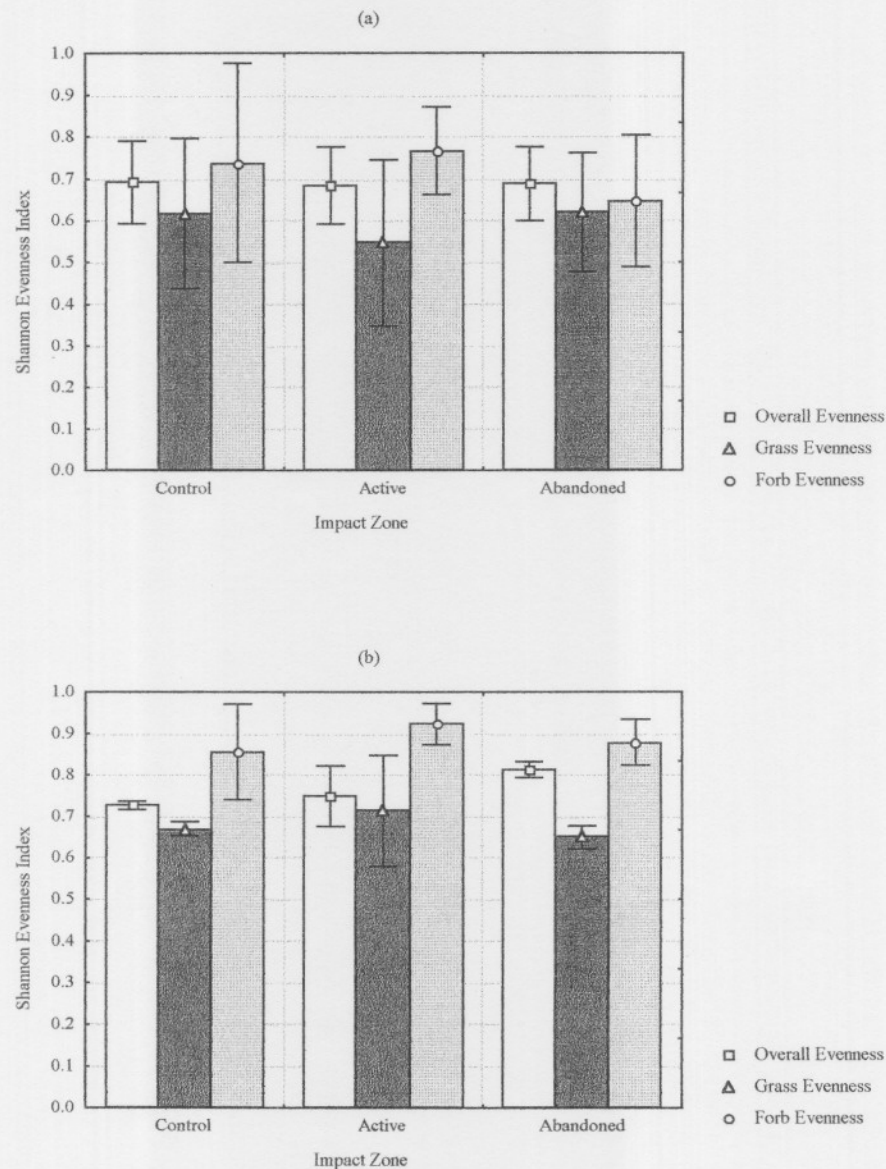


Figure 6.3: Differences in plant community species evenness among impact zones in 1999 on PFA-dam A. a) quadrats & b) transects. Bars denote mean values, vertical lines represent 1SD.

Species Diversity

There were no significant differences among impact zones in overall plant diversity, grass diversity and forb diversity, based on analysis of the data from both quadrats (Fig. 6.4a) and transects (Fig. 6.4b).

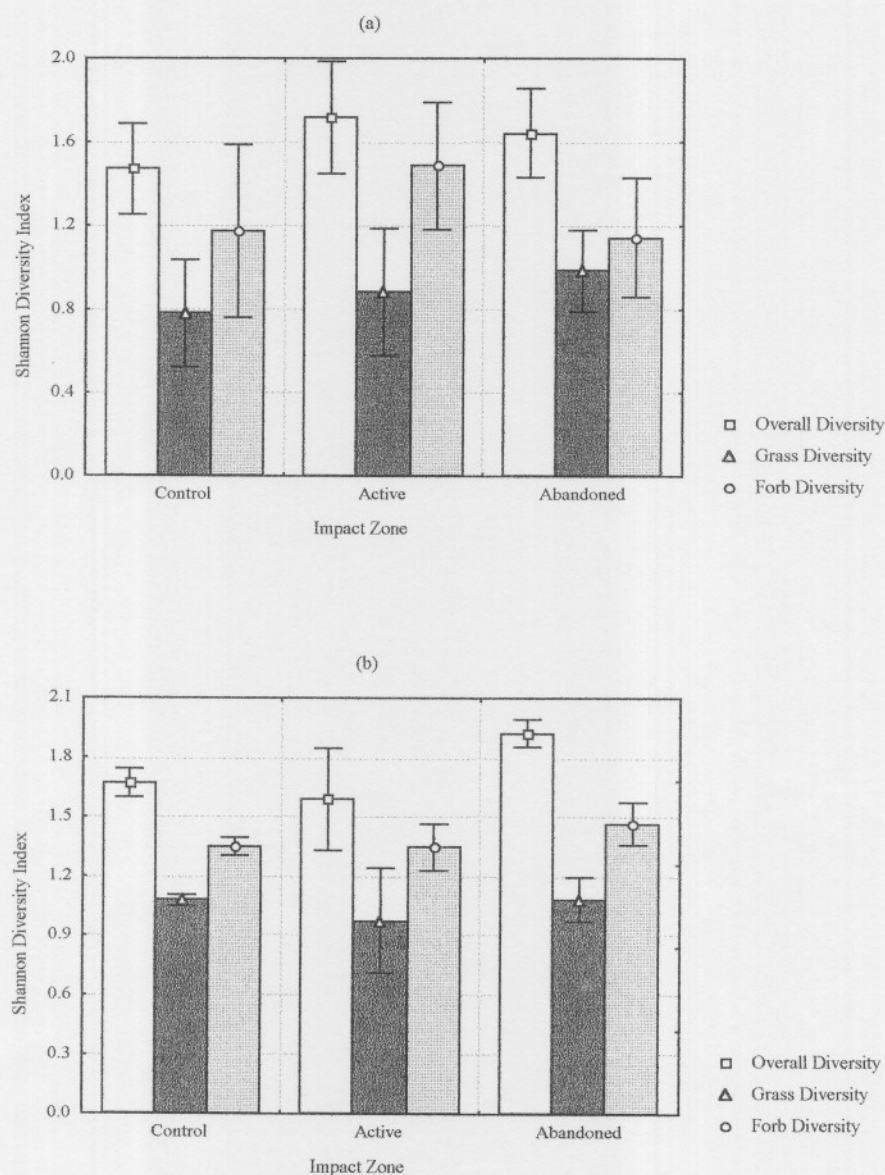


Figure 6.4: Differences in plant community species diversity among impact zones in 1999 on PFA-dam A. a) quadrats & b) transects. Bars denote mean values, vertical lines represent 1SD.

6.4 Plant Biomass

Although total plant biomass, grass biomass and forb biomass (quadrant data) did not differ significantly among impact zones (Fig. 6.5), the biomass of some species was affected by gerbil activity.

Pennisetum clandestinum biomass ($F_{2,24}:3.505$, $P < 0.05$, Fig. 6.6a) was greater in active zones than in abandoned zones, but neither differed from control site samples. *Tagetes minuta* biomass ($H_{2,27}:9.915$, $P < 0.01$, Fig. 6.6b) was higher in both active ($Z:2.870$, $P < 0.01$) and abandoned ($Z:2.517$, $P < 0.05$) zones than in controls. The biomass of *Schkuhria pinnata* ($H_{2,25}:7.801$, $P < 0.05$, Fig. 6.6c) was greater in abandoned zones than in both active ($Z:2.502$, $P < 0.05$) and control zones ($Z:2.021$, $P < 0.05$). *Cyperus esculentus* biomass ($H_{2,24}:13.683$, $P < 0.01$, Fig. 6.6d) of both active ($Z:3.272$, $P < 0.01$) and

abandoned zones ($Z:1.967$, $P < 0.05$) was higher than controls, and in addition, active zones had greater biomass than abandoned zones ($Z:2.382$, $P < 0.05$).

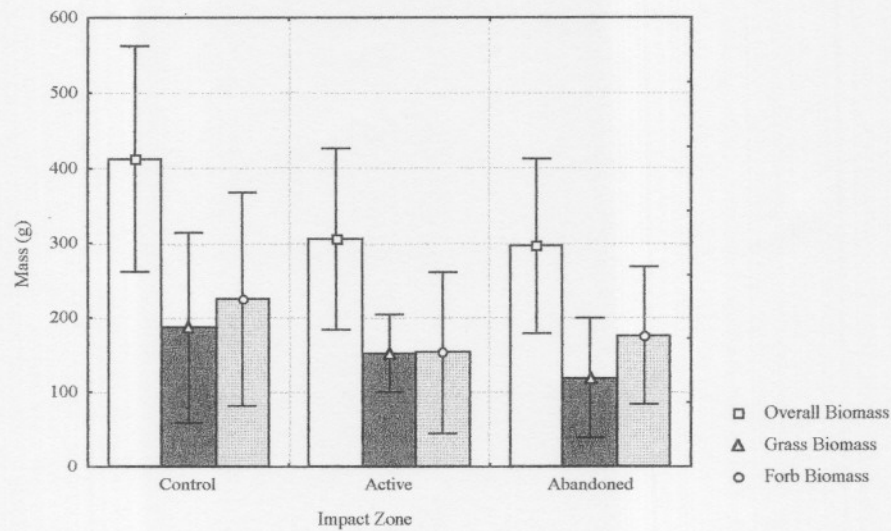


Figure 6.5: Differences in plant community biomass among impact zones in 1999 on PFA-dam A. (From quadrat data.) Bars denote mean values, vertical lines represent 1SD.

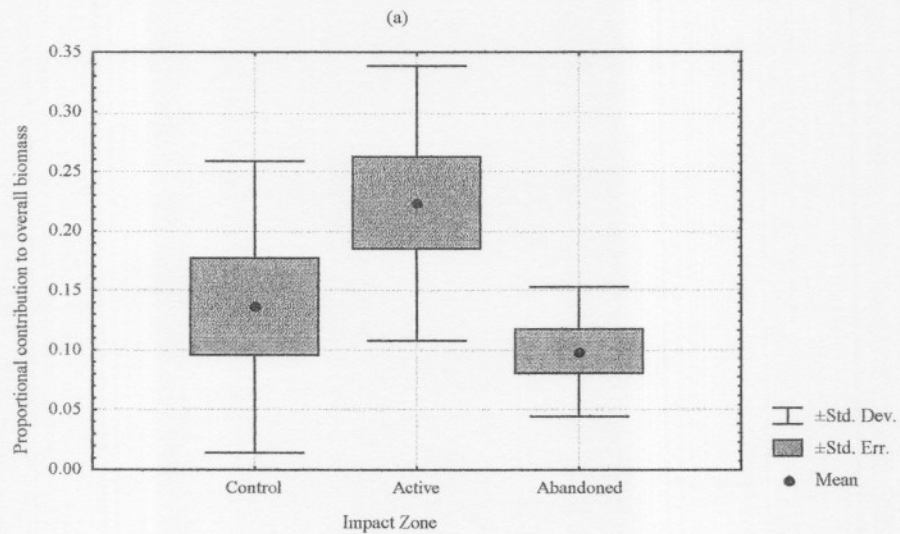


Figure 6.6a: Differences in proportional contributions of *P. clandestinum* to biomass among impact zones in 1999 on PFA-dam A. Bars denote mean values, vertical lines represent 1SD.

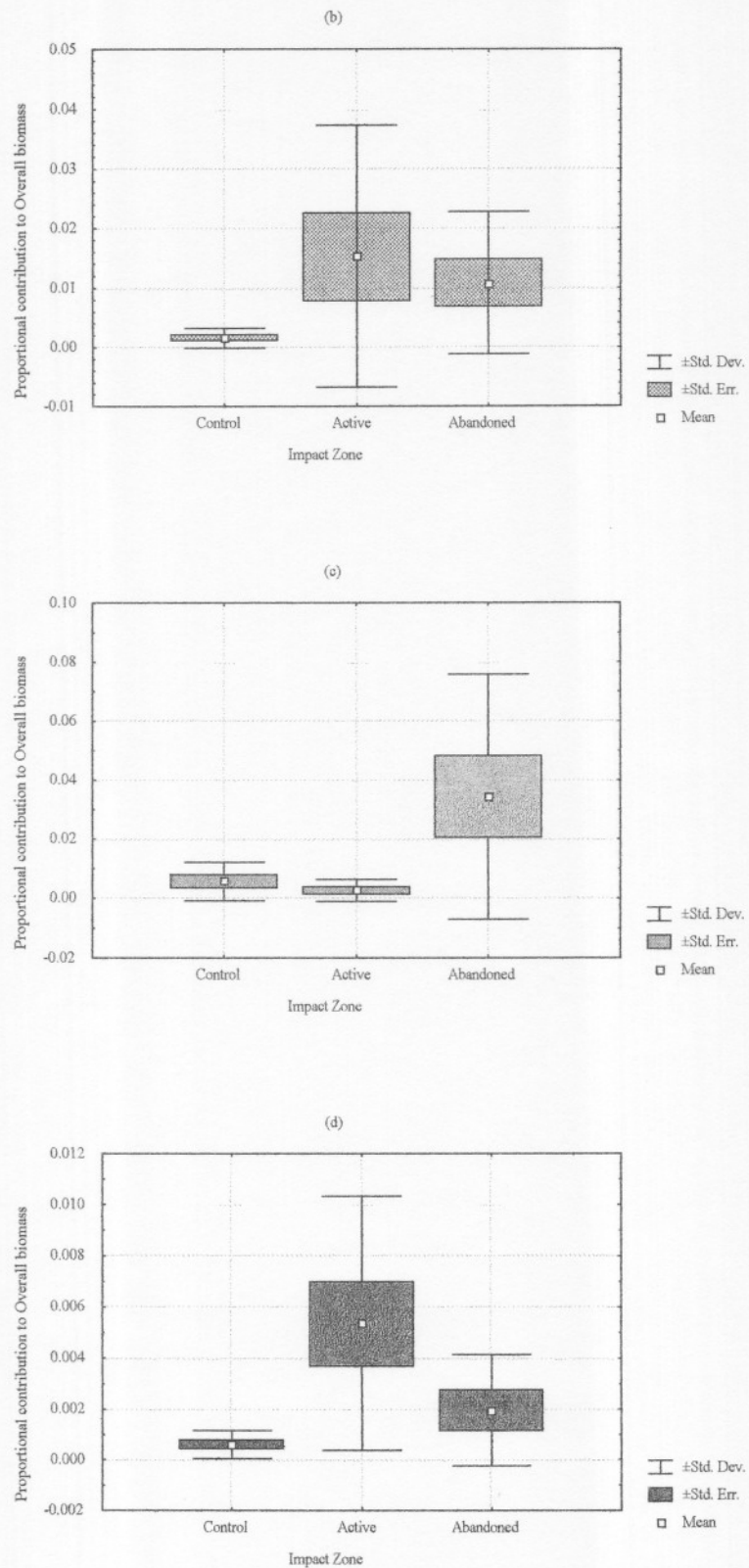


Figure 6.6: Differences in % contributions of species to biomass among impact zones in 1999 on PFA-dam A. b) *T. minuta*, c) *S. pinnata* & d) *C. esculentus*. Boxes: mean & 1SE, vertical lines: 1SD.

6.5 Plant Canopy Cover

The percentage of plants (from transect data) in the zero cover category differed significantly among gerbil impact zones ($F_{2,6}:6.084$, $P < 0.05$), where there was a greater amount of space among plants (i.e.: more plants within the zero cover category) in abandoned zones compared to controls (Fig. 6.7). The percentage of plants in the crown cover category did not differ significantly among impact zones. Controls had a higher percentage basal cover ($F_{2,6}:28.091$, $P < 0.001$) than either active or abandoned zones.

Hyparrhenia hirta contributed a significantly lesser proportion ($F_{2,6}:5.365$, $P < 0.05$) to the overall percentage of plants in the zero cover category in active zones (i.e.: less individuals were associated with zero cover) than in control and abandoned zones (Fig. 6.8).

In the crown cover category, *Eragrostis curvula* contributed a greater proportion to the overall percentage in control zones than in active or abandoned zones ($F_{2,6}:10.425$, $P < 0.05$, Fig. 6.9).

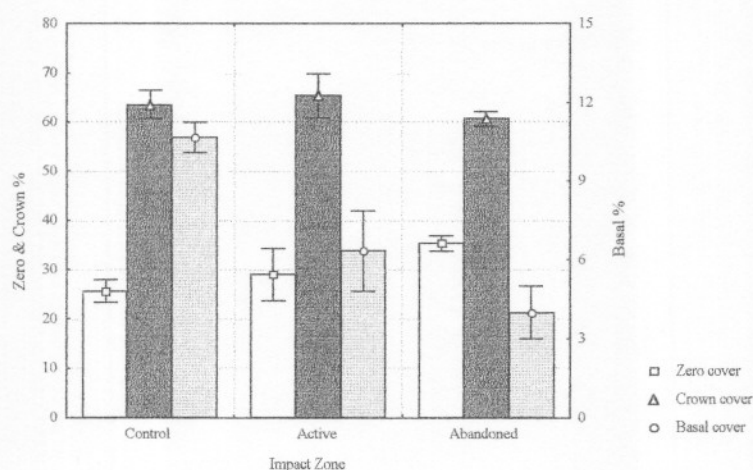


Figure 6.7: The percentages in each of three cover categories (i.e.: Zero; Crown & Basal cover) among impact zones in 1999 on PFA-dam A. (From transect data.) Bars denote mean values, vertical lines represent 1SD.

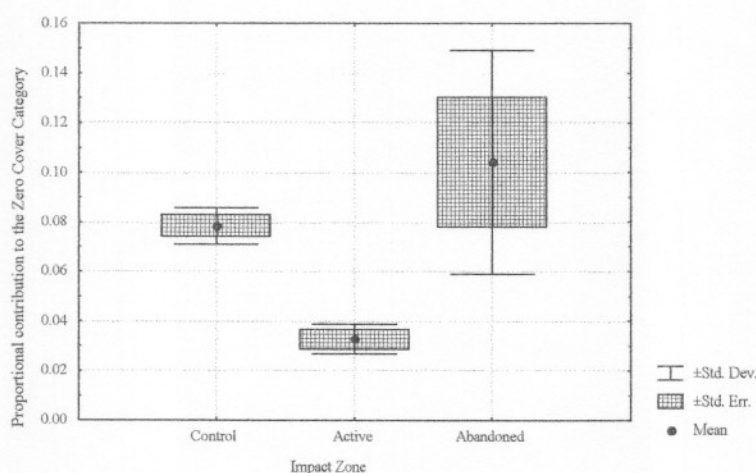


Figure 6.8: Significant *H. hirta* contribution to the zero cover category among impact zones in 1999 on PFA-dam A. (Based on transect samples.) Boxes denote mean & 1 SE, vertical lines represent 1SD.

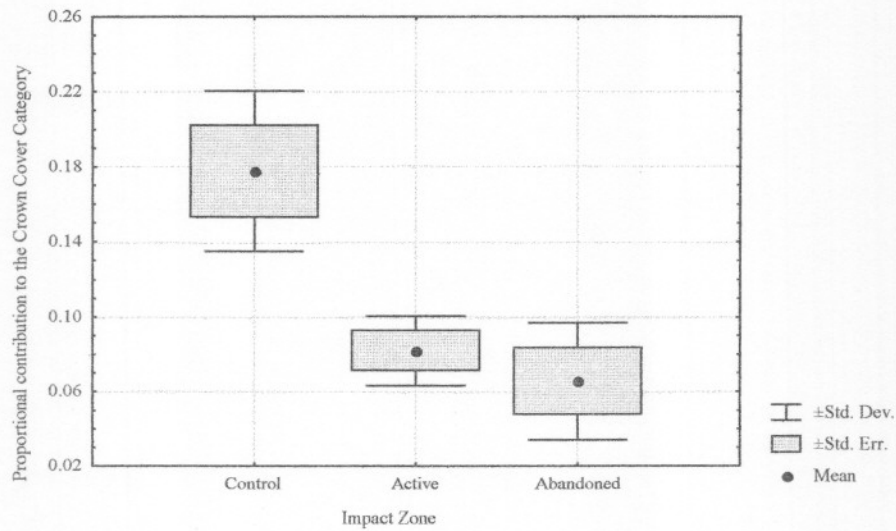


Figure 6.9: Significant *E. curvula* contribution to the crown cover category among impact zones in 1999 on PFA-dam A. (Based on transect samples.) Boxes denote mean & 1SE, vertical lines represent 1SD.

6.6 Plant Density

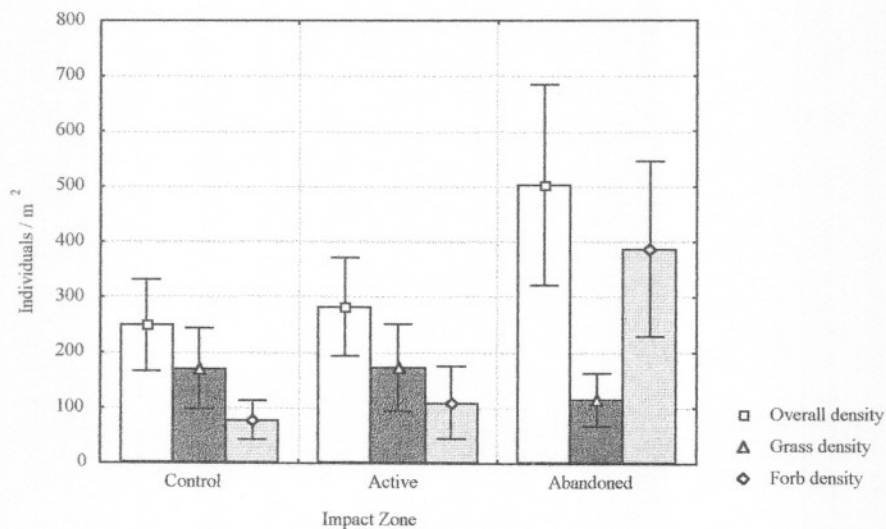


Figure 6.10: Differences in plant community density (per m²) among impact zones in 1999 on PFA-dam A. (From quadrat data.) Bars denote mean values, vertical lines represent 1SD.

The overall plant density (data log_e transformed) for the community was elevated on abandoned zones ($F_{2,24}:9.081$, $P < 0.01$) compared to both control zones and active zones (Fig. 6. 10). Grass density did not differ among impact zones but forb density was also high on abandoned zones ($F_{2,24}:27.081$, $P < 0.001$).

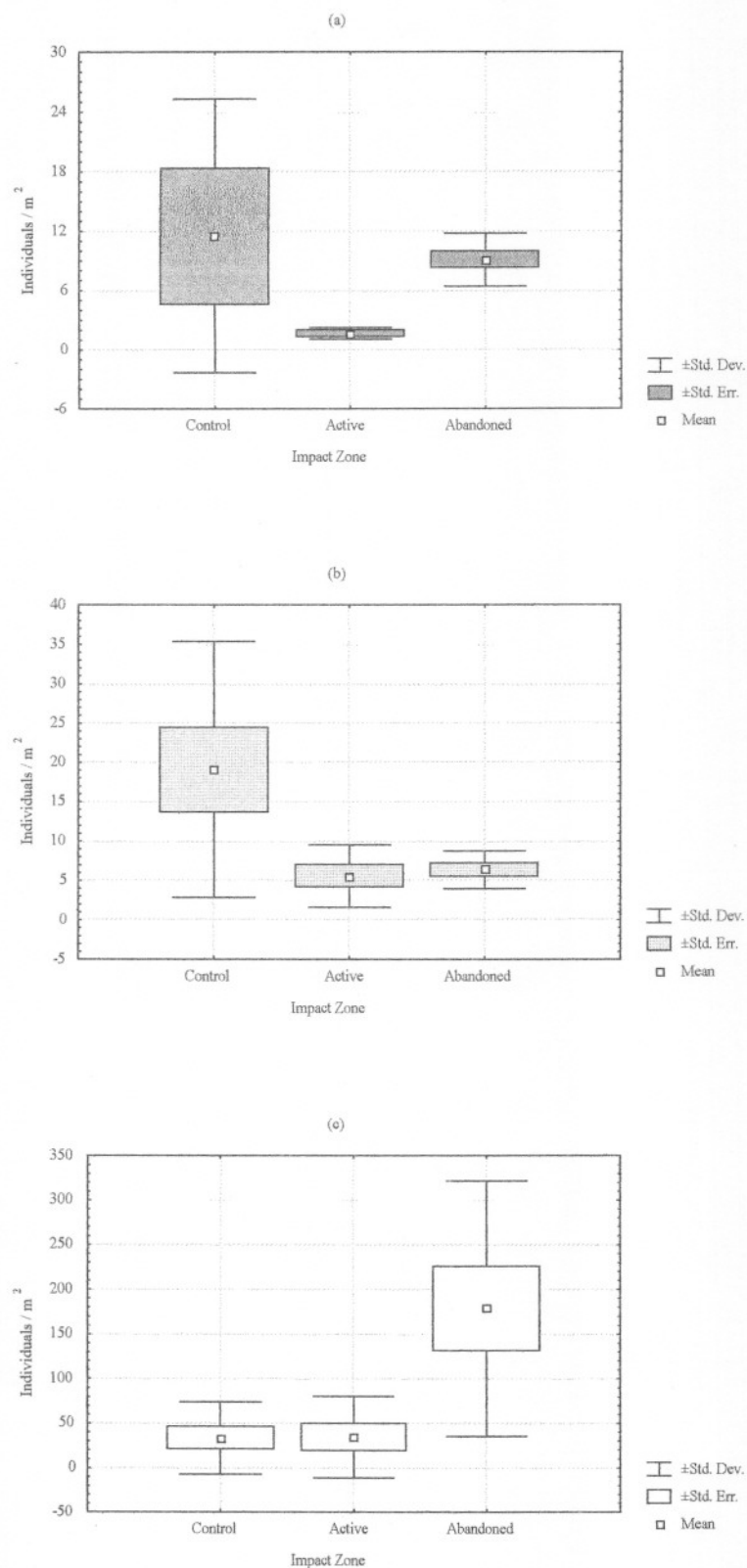


Figure 6.11: Differences in % contributions of species the density / m² index among impact zones in 1999 on PFA-dam A. a) *E. plana*, b) *E. curvula* & c) *C. biensis*. Boxes: mean & 1SE, vertical lines: 1SD.

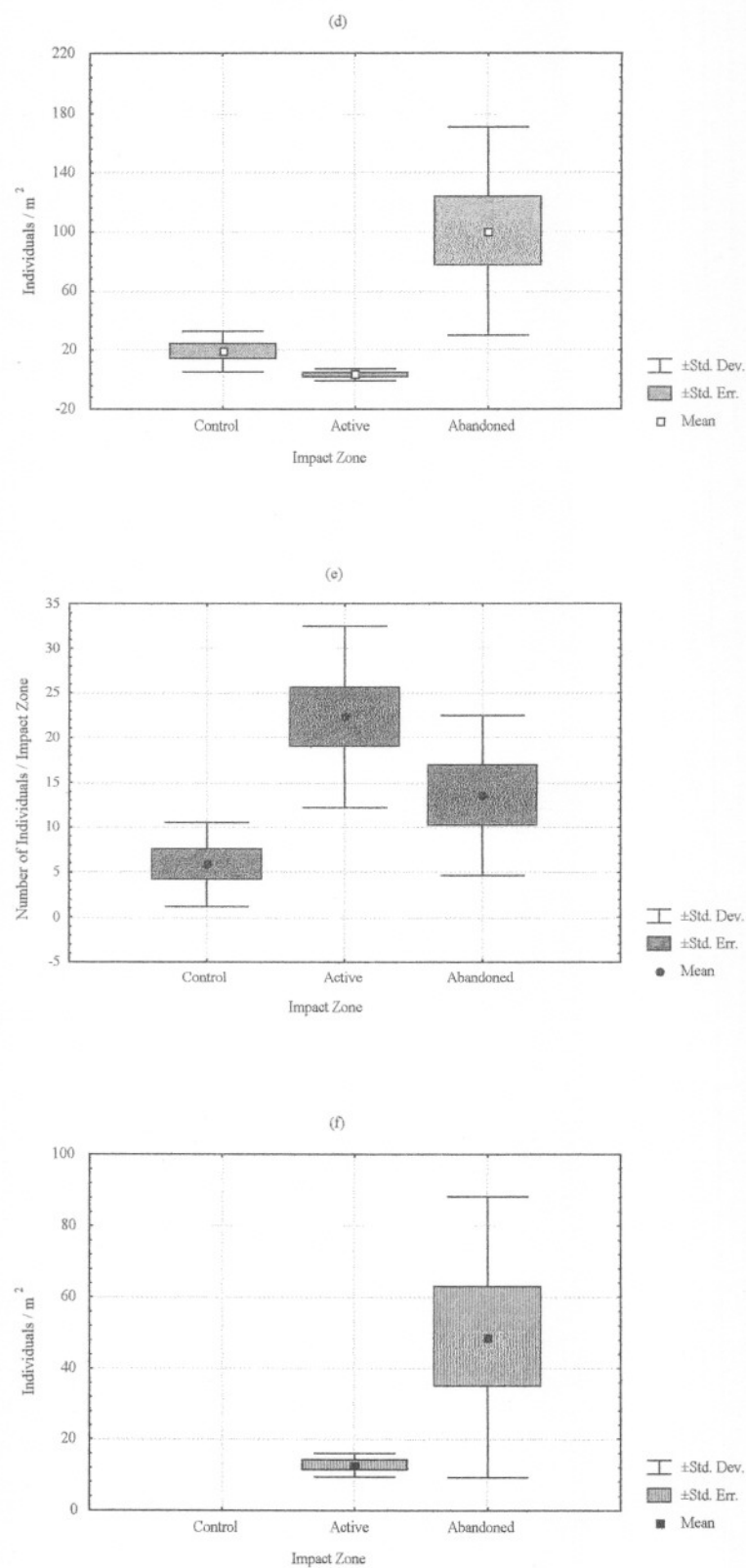


Figure 6.11: Differences in % contributions of species the density / m² index among impact zones in 1999 on PFA-dam A. d) *S. pinnata*, e) *C. esculentus* & f) *C. usitatus*. Boxes: mean & 1SE, vertical lines: 1SD.

The density of two grass species differed significantly among impact zones, namely *Eragrostis plana* ($H_{2,16}:6.990$, $P < 0.05$) and *Eragrostis curvula* ($H_{2,24}:8.718$, $P < 0.05$). Active zones appeared to have lower densities of *E. plana* than abandoned zones ($Z:-2.496$, $P < 0.05$), neither active nor abandoned zones differed from control zones (Fig. 6.11a), but any differences may have been masked by variability in the control data. The density of *E. curvula* on control zones was higher than on both active ($Z:2.502$, $P < 0.05$) and abandoned zones ($Z:2.434$, $P < 0.05$, Fig. 6.11b), this may also be an artefact of the highly variable data.

Several forb species also differed in densities among impact zones. *Chamaecrista biensis* ($H_{2,27}:9.004$, $P < 0.05$, Fig. 6.11c), *Schkuhria pinnata* ($H_{2,25}:14.030$, $P < 0.001$, Fig. 6.11d) & *Cyperus esculentus* ($F_{2,21}:8.330$, $P < 0.01$, Fig. 6.11e). *C. biensis* appeared to have greater density in abandoned zones than in both active ($Z:2.605$, $P < 0.01$) and control zones ($Z:2.517$, $P < 0.05$), but again this may be because of data variability. Abandoned zones seemed to have greater densities of *S. pinnata* than both active ($Z:3.224$, $P < 0.01$) and control zones ($Z:2.406$, $P < 0.05$), but data was quite variable, and active zones had lower *S. pinnata* densities than control zones ($Z:-2.205$, $P < 0.05$). Active zones also seemed to have greater densities of *C. esculentus* than control zones, but this was based on variability in the data. In addition, the forb *Cyperus usitatus*, not sampled on control zones, had lower densities on active zones when compared to abandoned zones ($Z:-2.196$, $P < 0.05$, Fig. 6.11f), but this too may be due to variability in the data.

6.7 Plant Phenology

Seedlings

Seedling density, based on quadrat data, was higher on abandoned zones than on either the control or active zones ($F_{2,24}:8.533$, $P < 0.01$, Fig. 6.12a). However, seedling frequency, based on transect data, did not differ among impact zones (Fig. 6.12b).

The proportional contribution to the overall density of seedlings of some species differed significantly among impact zones, namely those of *Hyparrhenia hirta* ($H_{2,22}:9.468$, $P < 0.01$, Fig. 6.14a), *Chamaecrista biensis* ($F_{2,24}:10.494$, $P < 0.001$, Fig. 6.14b) and *Acanthospermum glabratum* ($H_{2,10}:6.212$, $P < 0.05$, Fig. 6.14c). *H. hirta* seedlings were denser on active zones than on both control ($Z:2.400$, $P < 0.05$) and abandoned zones ($Z:2.694$, $P < 0.01$) but control and abandoned zones were not significantly different, and had higher frequencies of occurrence in active zones ($F_{2,6}:13.940$, $P < 0.01$, Fig. 6.13). Abandoned zones had a greater density of *C. biensis* seedlings than both active and control zones. Control zones supported greater densities of seedlings of *A. glabratum* than both active ($Z_{(adj)}:1.961$, $P < 0.05$) and abandoned zones ($Z_{(adj)}:1.972$, $P < 0.05$).

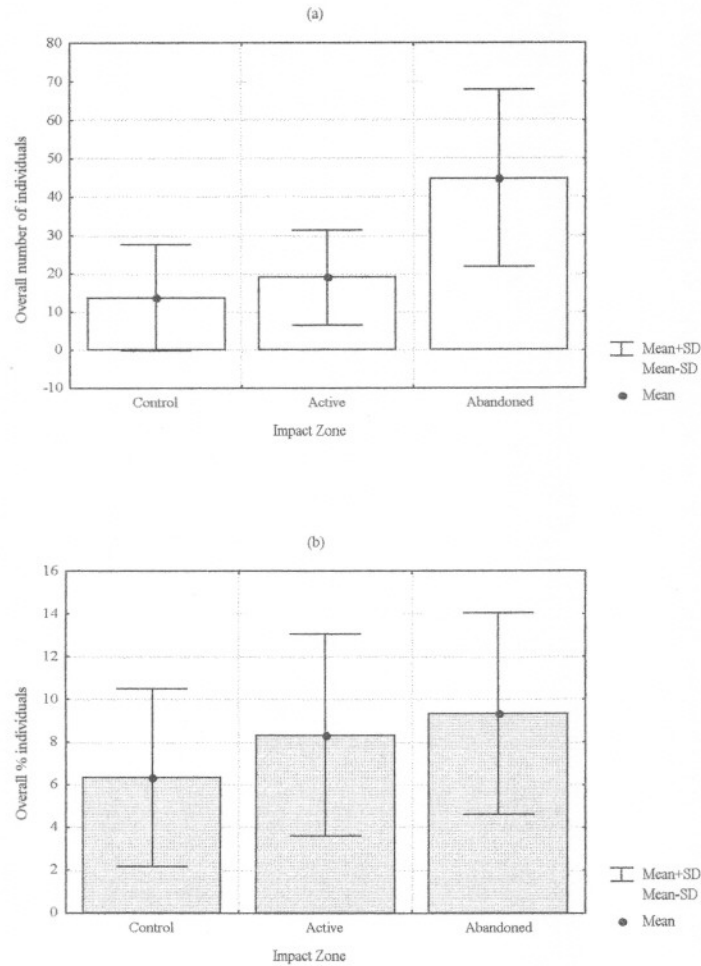


Figure 6.12: Differences in seedling density (per m^2) and frequency (%) among impact zones in 1999 on PFA-dam A. a) quadrats & b) transects. Bars denote mean values, vertical lines represent 1SD.

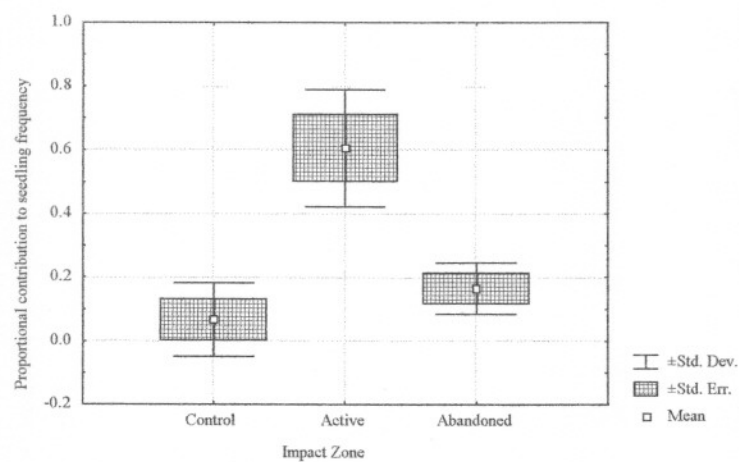


Figure 6.13: Differences in the proportional contribution of *H. hirta* seedlings to overall % among impact zones in 1999 on PFA-dam A. (From transect data.) Boxes: mean & 1SE, vertical lines: 1SD.

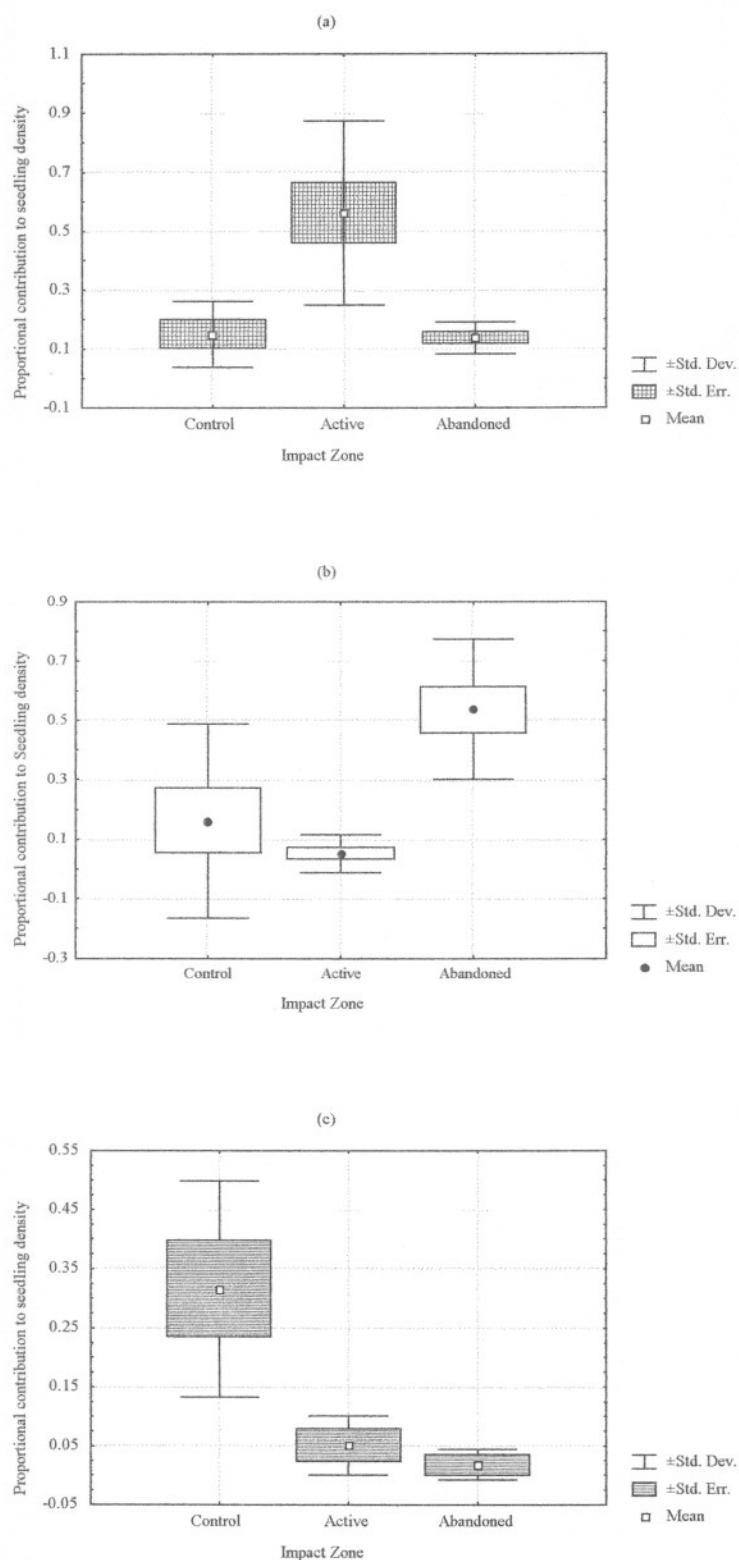


Figure 6.14: Differences in the proportional contributions of species to the overall seedling density / m^2 index, among impact zones in 1999 on PFA-dam A. a) *H. hirta*, b) *C. biensis* & c) *A. glabratum*. (From quadrat data.) Boxes denote mean & 1SE, vertical lines represent 1SD.

Non-Flowering mature plants

Overall non-flowering mature plant density and frequency did not differ significantly between the control zones and areas of gerbil impact (Fig. 6.15).

However, for many species, non-flowering mature plant density differed among impact zones. Grass species which differed significantly were: *Eragrostis plana* ($H_{2,16}:6.146$, $P < 0.05$, Fig. 6.16a); *Pennisetum clandestinum* ($H_{2,27}:9.051$, $P < 0.05$, Fig. 6.16b); *Eragrostis curvula* ($H_{2,24}:14.413$, $P < 0.001$, Fig. 6.16c) & *H. hirta* ($H_{2,22}:8.380$, $P < 0.05$, Fig. 6.16d), and forbs were: *Schkuhria pinnata* ($H_{2,25}:6.579$, $P < 0.05$, Fig. 6.16e); *Cyperus esculentus* ($F_{2,21}:4.034$, $P < 0.05$, Fig. 6.16f)

The variability in non-flowering *E. plana* density data in control zones impaired further non-parametric testing with the U-test but it appeared that density was reduced in active and abandoned zones compared to controls (Fig. 6.16a). Non-flowering *P. clandestinum* had a lower density in abandoned zones than both control ($Z:-2.870$, $P < 0.01$) and active zones ($Z:-2.208$, $P < 0.05$). Control zones supported a greater density of non-flowering *E. curvula* than both active ($Z:3.368$, $P < 0.001$) and abandoned zones ($Z:2.805$, $P < 0.01$). Similarly, non-flowering *H. hirta* had a greater density in controls than in active ($Z:2.067$, $P < 0.05$) or abandoned zones ($Z:1.976$, $P < 0.05$). However, for both of these grasses, the control site data was highly variable and may have produced a significant effect when there was none. Active zones had lower non-flowering *S. pinnata* densities ($Z:-2.598$, $P < 0.01$) than abandoned zones, and non-flowering *C. esculentus* density was higher in active zones than in controls.

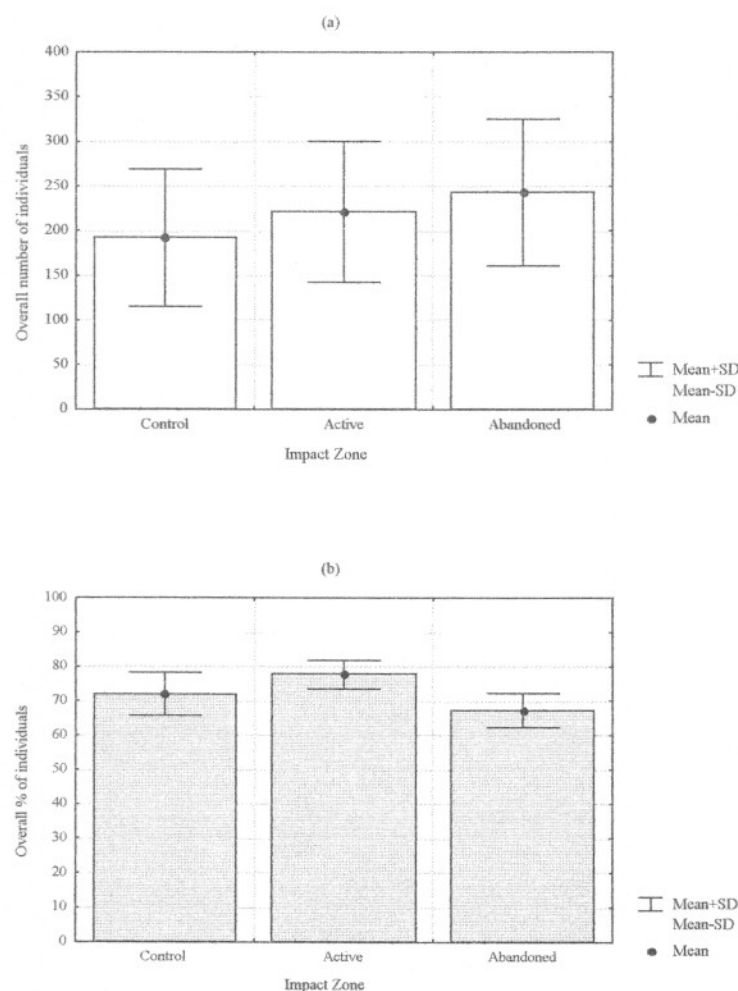


Figure 6.15: Differences in non-flowering mature plant density (per m²) and frequency (%) among impact zones in 1999 on PFA-dam A. a) quadrats & b) transects. Bars: mean values, vertical lines: 1SD.

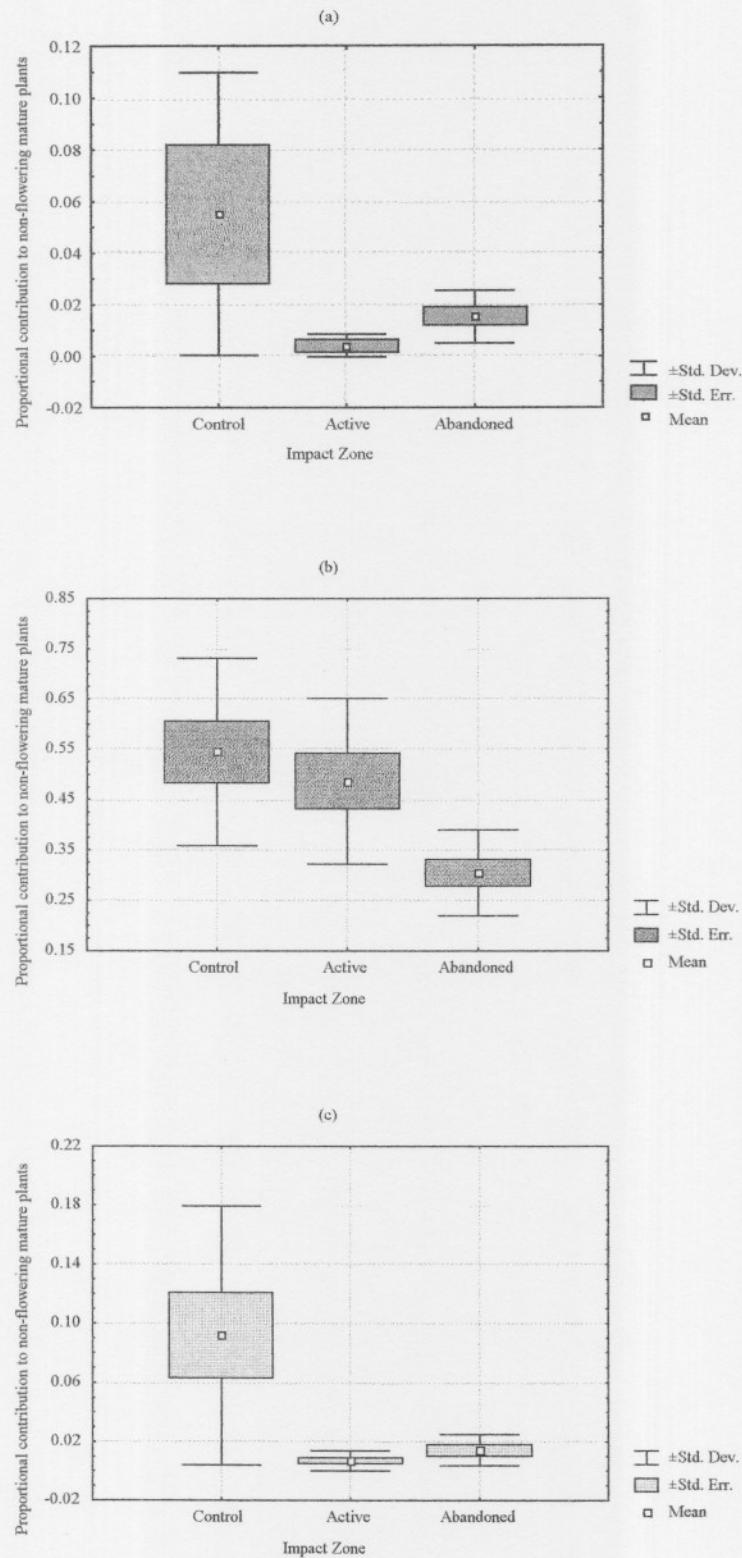


Figure 6.16: Differences in the proportional contributions of species to the overall non-flowering mature plant density / m² index, among impact zones in 1999 on PFA-dam A. a) *E. plana*, b) *P. clandestinum* & c) *E. curvula*. (From quadrat data.) Boxes denote mean & 1SE, vertical lines represent 1SD.

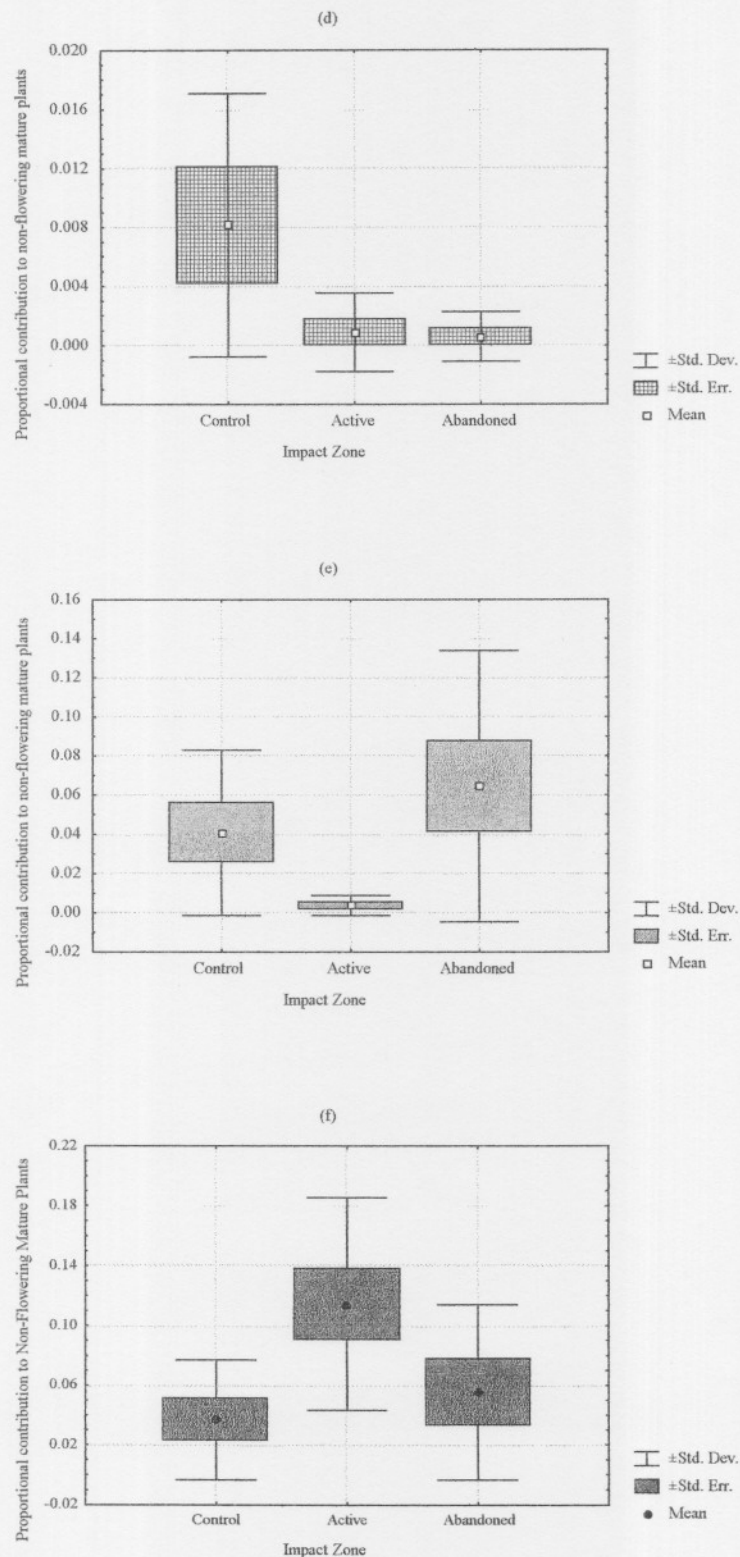


Figure 6.16: Differences in the proportional contributions of species to the overall non-flowering mature plant density / m^2 index, among impact zones in 1999 on PFA-dam A. d) *H. hirta*, e) *S. pinnata* & f) *C. esculentus*. (From quadrat data.) Boxes denote mean & 1SE, vertical lines represent 1SD.

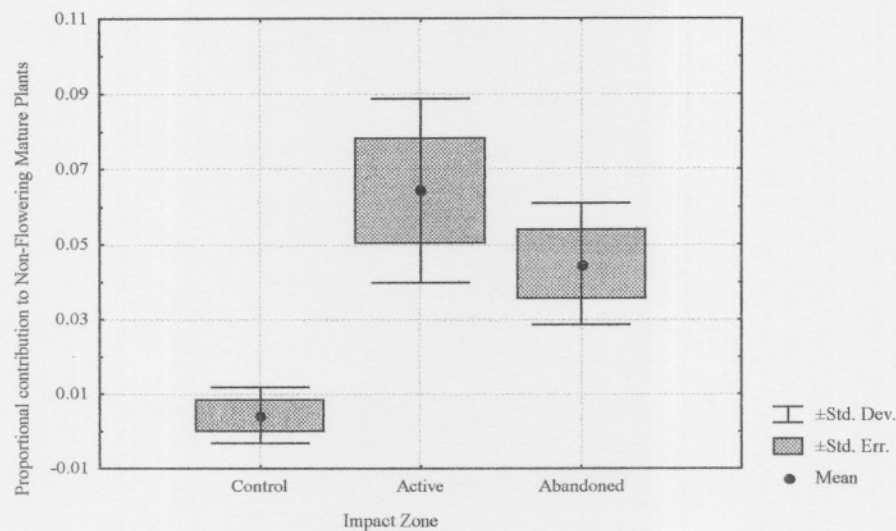


Figure 6.17: Differences in the proportional contribution of *T. minuta* to overall frequency (%) of non-flowering mature plants among impact zones in 1999 on PFA-dam A. (From transect data.) Boxes denote mean & 1SE, vertical lines represent 1SD.

The proportion *Tagetes minuta* contributed to overall non-flowering mature plant frequency was greater in active zones than in control zones ($F_{2,6}:9.170$, $P < 0.05$, Fig. 6.17).

Mature plants in Flower

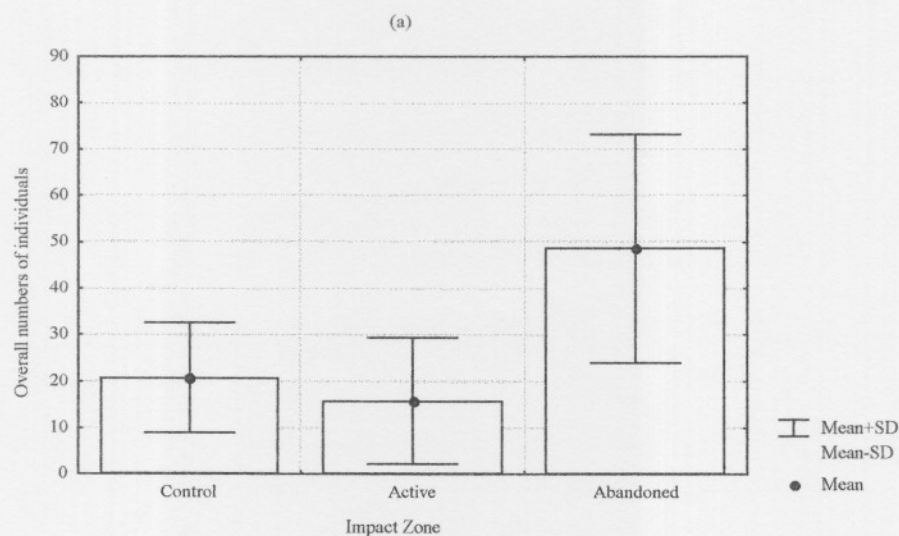


Figure 6.18a: Differences in flowering plant density (per m^2) among impact zones on PFA-dam A. in 1999 (From quadrat samples) Bars denote mean values, vertical lines represent 1SD.

Based on quadrat data, the overall density of flowering plants was significantly higher in abandoned zones than in control or active zones ($F_{2,24}:9.076$, $P < 0.01$, Fig. 6.18a). Transect data,

however, did not indicate any significant differences in the frequency of flowering plants, possibly due to the considerable variability in the active zone data (Fig. 6.18b).

The density of flowering *S. pinnata* was lower in active zones compared to both controls and abandoned zones ($F_{2,22}:6.685$, $P < 0.01$, Fig. 6.19), and *S. pinnata* also contributed a significantly greater proportion ($F_{2,5}:10.485$, $P < 0.05$, Fig. 6.20) to the flowering plant frequency in abandoned zones than in control or active zones.

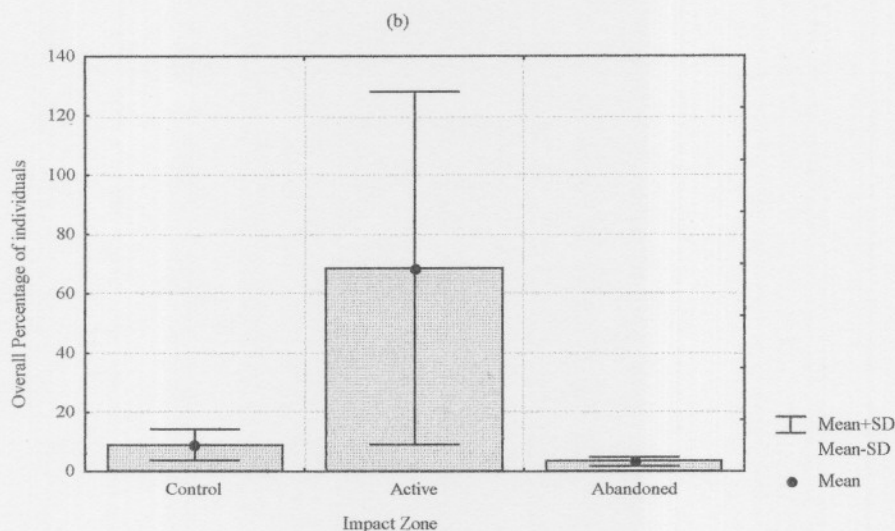


Figure 6.18b: Differences in flowering plant frequency (%) among impact zones on PFA-dam A in 1999. (From transect samples). Bars denote mean values, vertical lines represent 1SD.

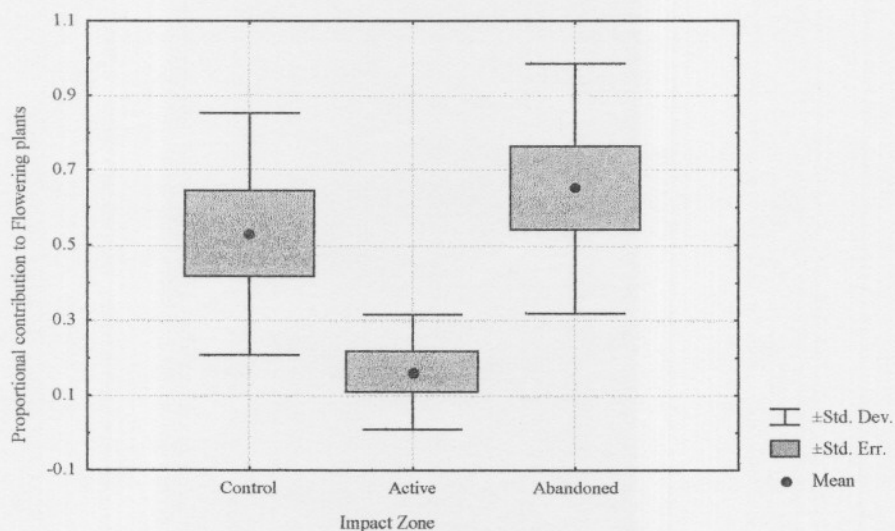


Figure 6.19: Differences in the proportional contributions of *S. pinnata* to the overall flowering plant density / m^2 index, among impact zones on PFA-dam A in 1999. (From quadrat data.) Boxes denote mean & 1SE, vertical lines represent 1SD.

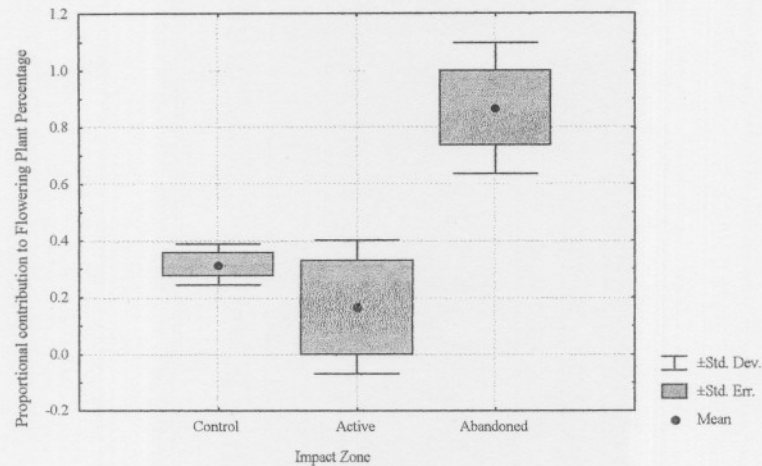


Figure 6.20: Differences in the proportional contribution of *S. pinnata* to overall frequency (%) of flowering plants among impact zones on PFA-dam A in 1999. (From transect data.) Boxes denote mean & 1SE, vertical lines represent 1SD.

Mature plants with seed

Based on quadrature data, overall density of plants with seed differed among impact zones ($H_{2,27}:7.850$, $P < 0.05$, Fig. 6.21a), where abandoned zones supported higher densities than active zones ($Z:2.428$, $P < 0.05$) or controls ($Z:2.208$, $P < 0.05$). Despite variability in control site data limiting analysis, the frequency (based on transect data) of plants with seed was higher in abandoned zones than in active zones ($t_{df4}:4.243$, $P < 0.05$, Fig. 6.21b). Active zones had reduced densities of *C. biensis* with seed than control or abandoned zones ($F_{2,24}:10.122$, $P < 0.001$, Fig. 6.22). The proportion *H. hirta* with seed contributed to the overall frequency differed among impact zones ($H_{2,9}:6.543$, $P < 0.05$, Fig. 6.23). Abandoned zones had reduced proportions of *H. hirta* with seed than both active ($Z:-1.964$, $P < 0.05$) and control zones ($Z:-1.964$, $P < 0.05$).

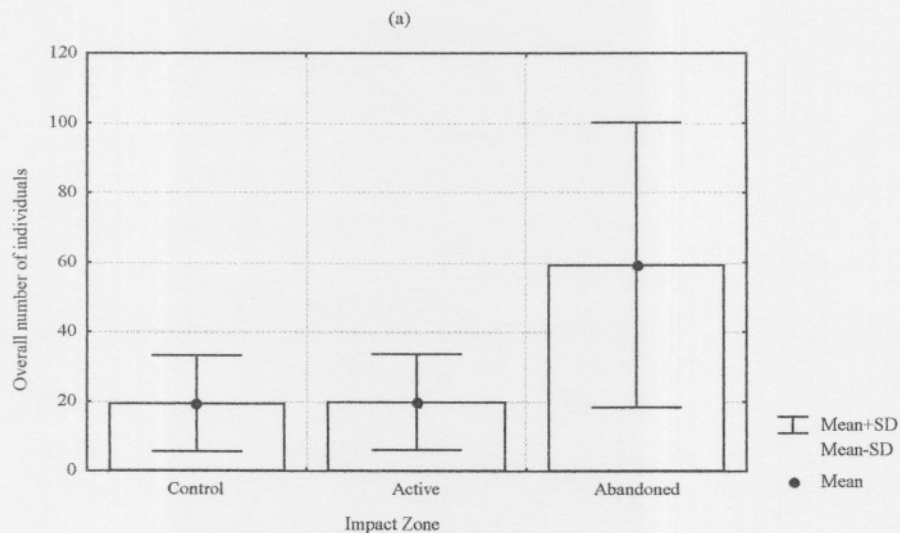


Figure 6.21a: Differences in the density (per m^2) of mature plants in seed among impact zones on PFA-dam A in 1999. (From quadrature samples) Bars denote mean values, vertical lines represent 1SD.

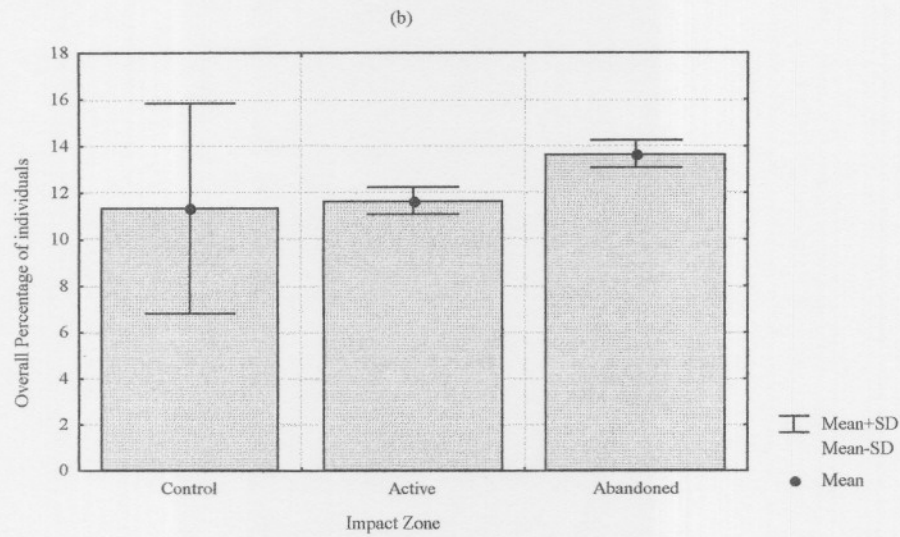


Figure 6.21b: Differences in the frequency (%) of mature plants in seed among impact zones on PFA-dam A in 1999. (From transect samples). Bars denote mean values, vertical lines represent 1SD.

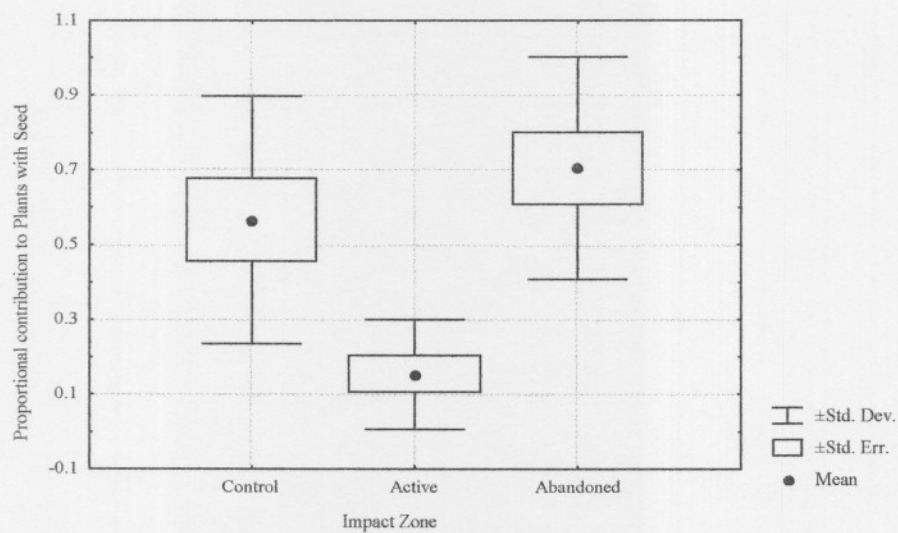


Figure 6.22: Differences in the proportional contributions of *C. biensis* to the overall mature plant with seed density / m² index, among impact zones on PFA-dam A in 1999. (From quadrat data.) Boxes denote mean & 1SE, vertical lines represent 1SD.

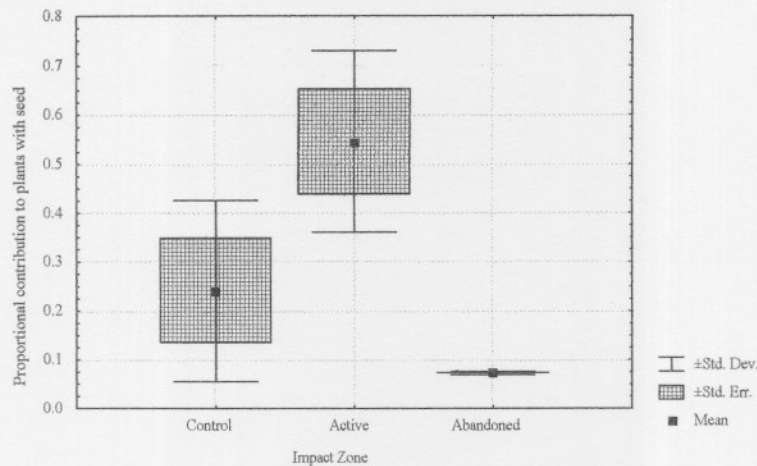


Figure 6.23: Differences in the proportional contribution of *H. hirta* to overall frequency (%) of mature plants with seed among impact zones on PFA-dam A in 1999. (From transect data.) Boxes denote mean & 1SE, vertical lines represent 1SD.

Mature plants with chaff

Despite the considerable variability in abandoned zone data, the density (quadrates data) of plants with chaff differed among impact zones ($H_{2,27}:16.644$, $P < 0.001$, Fig. 6.24a). Overall density was lower in active zones ($Z:-3.135$, $P < 0.01$) and control zones ($Z:-3.400$, $P < 0.001$) compared to abandoned zones, but active zones and controls did not differ from each other. No plants with chaff were recorded in active zones and the control and abandoned impact zones did not differ significantly from each other with regard to frequency (transect data) of occurrence (Fig. 6.24b), perhaps because the great variability in abandoned zone data masked any differences.

The density of *S. pinnata* with chaff differed among impact zones ($H_{2,25}:9.028$, $P < 0.05$, Fig. 6.25), and was higher in abandoned zones than in active ($Z:2.261$, $P < 0.05$) and control zones ($Z:2.261$, $P < 0.05$).

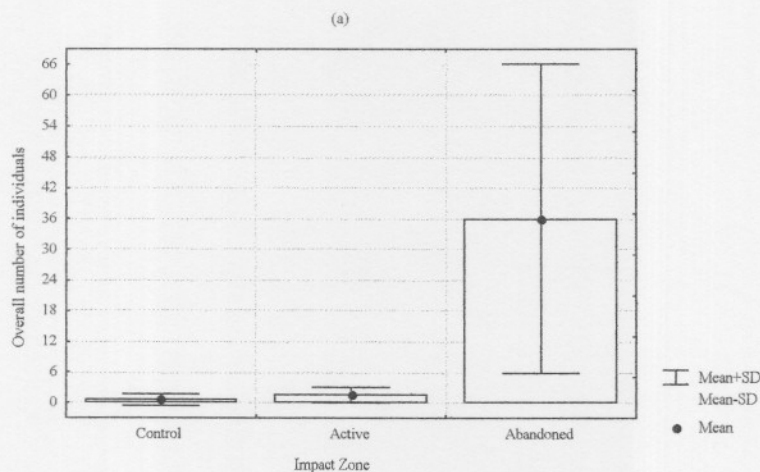


Figure 6.24a: Differences in the density (per m^2) of mature plants in chaff among impact zones on PFA-dam A in 1999. (From quadrates samples) Bars denote mean values, vertical lines represent 1SD.

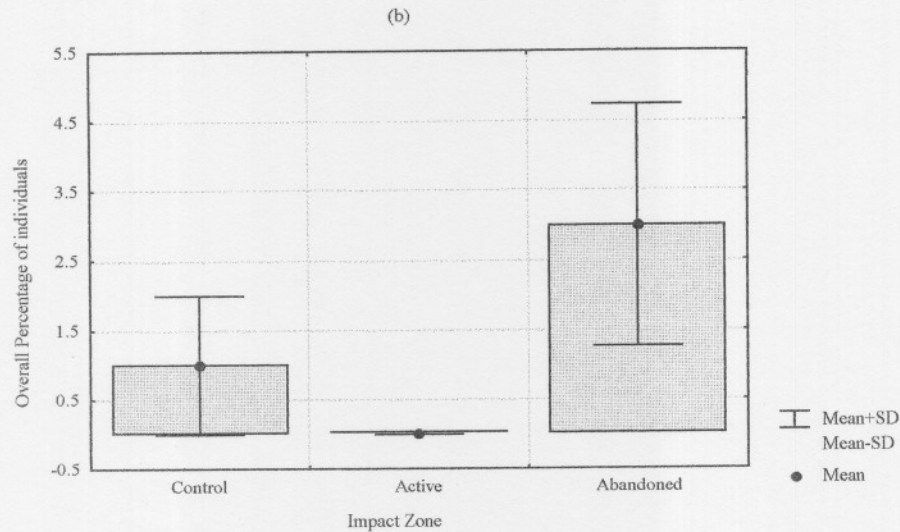


Figure 6.24b: Differences in the frequency (%) of mature plants in chaff among impact zones on PFA-dam A in 1999. (From transect samples) Bars denote mean values, vertical lines represent 1SD.

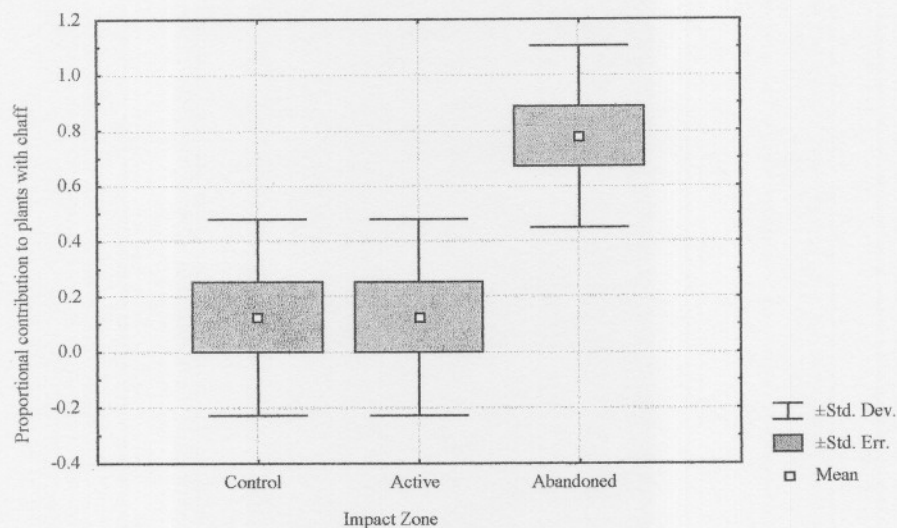


Figure 6.25: Differences in the proportional contributions of *S. pinnata* to the overall mature plant with chaff density / m² index, among impact zones on PFA-dam A in 1999. (From quadrat data.) Boxes denote mean & 1SE, vertical lines represent 1SD.

Dead plants

Overall dead plant density differed among impact zones ($H_{2,27}:17.383$, $P < 0.001$, Fig. 6.26a) and was higher on abandoned zones than control ($Z:3.576$, $P < 0.001$) or active zones ($Z:2.782$, $P < 0.01$). Active zones also had greater densities of dead plants than control zones ($Z:2.296$, $P < 0.05$). The overall frequency of dead plants also differed among impact zones ($F_{2,6}:9.000$, $P < 0.05$, Fig. 6.26b), being higher in abandoned zones than in control or active zones.

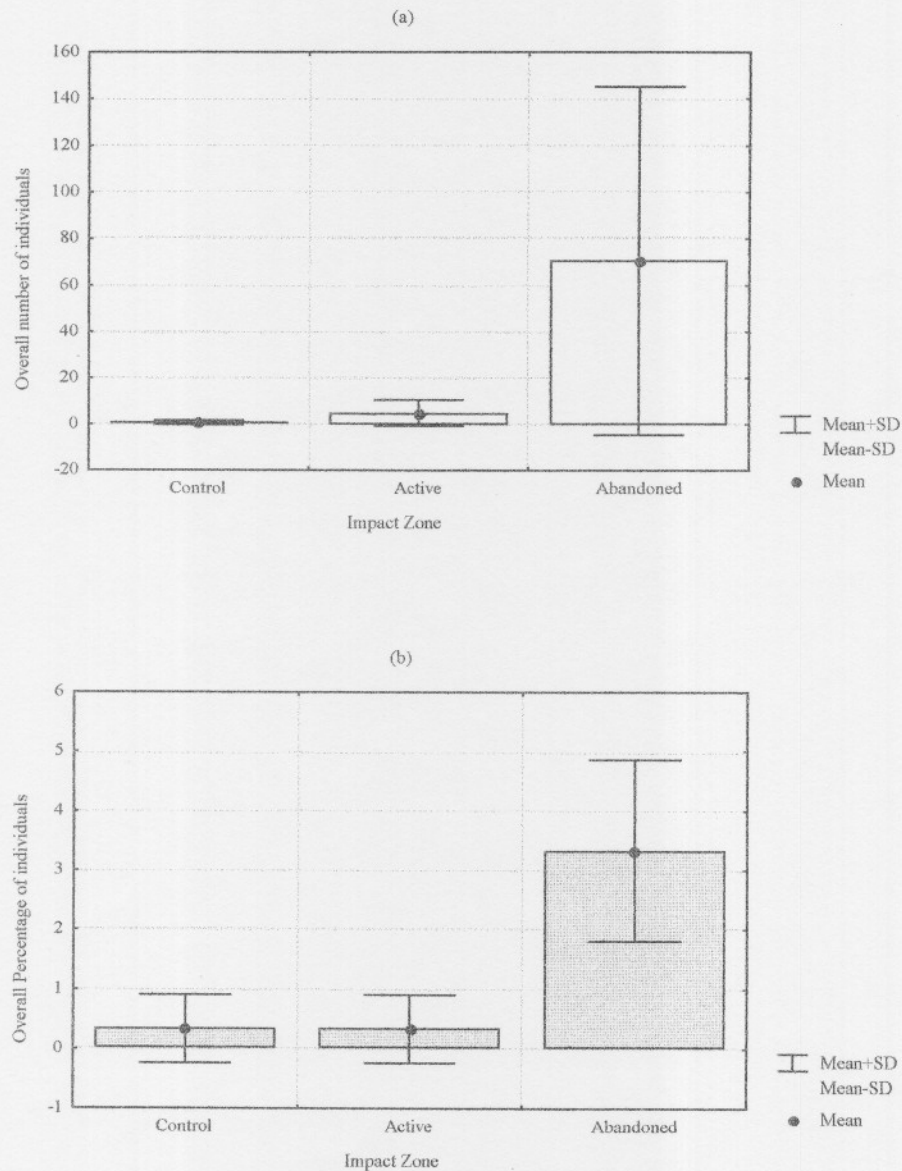


Figure 6.26: Differences in the density (per m²) and frequency (%) of dead plants among impact zones on PFA-dam A in 1999. a) quadrats & b) transects. Bars denote mean values, vertical lines represent 1SD.

6.8 Summary of the factors affecting the *Lepidium bonariensis*-*Eragrostis trichophora* plant community variant on PFA-dam A in 1999

The most influential characteristics of the plant community in separating the active and abandoned zones from the control zones were determined from principal component analyses of quadrat data; plant community variables that did not show any significant differences among impact zones were omitted (i.e.: overall, grass & forb diversity and evenness indices; overall, grass & forb biomass; grass density and non-flowering mature plant density). Variables were also standardised as they were measured in different units and data was varimax normalised.

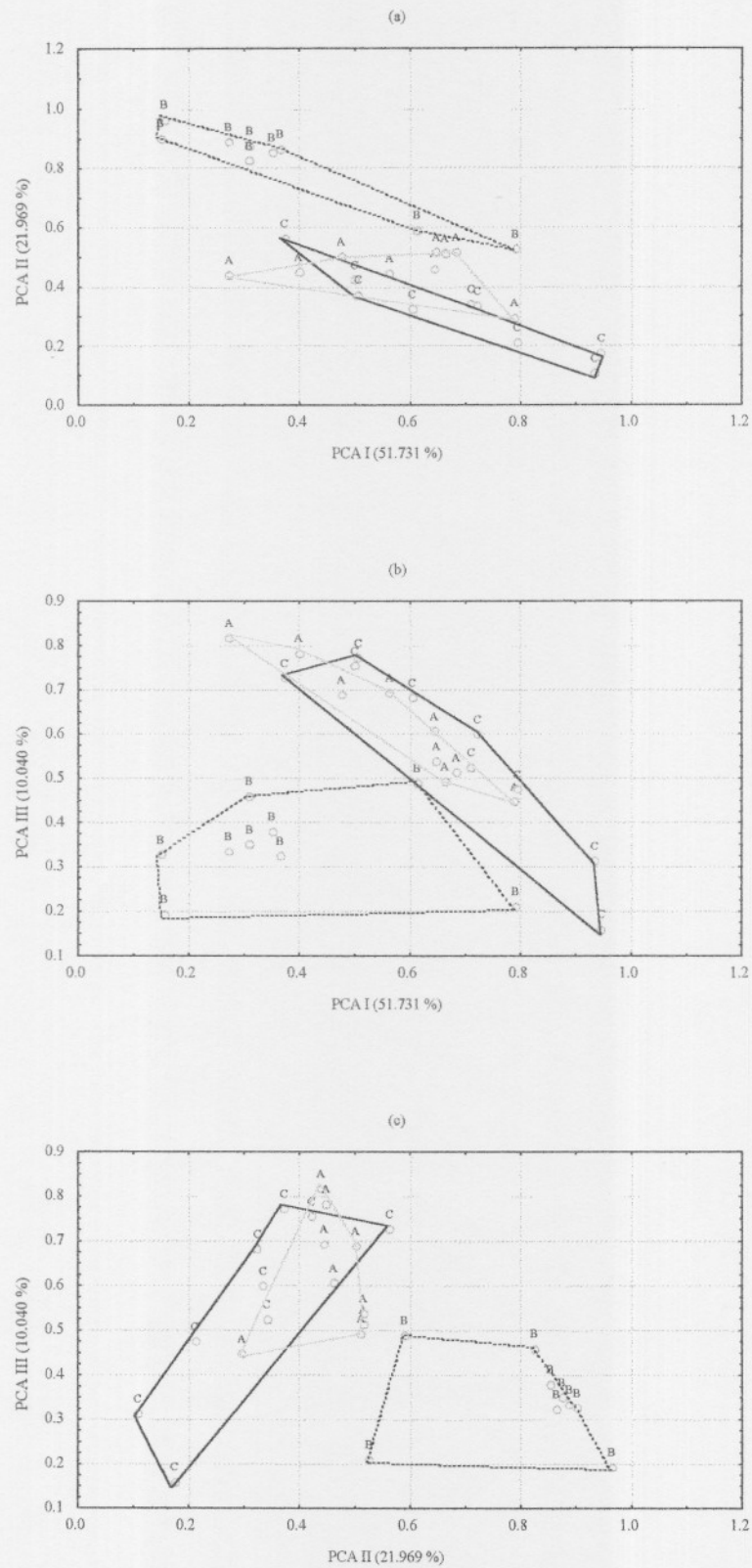


Figure 6.27: Separation of impact zones along Principal Component Axes: a) I & II; b) I & III; c) II & III. (From quadrat data.) (C: Control zones, A: Active zones & B: Abandoned zones).

Plots of loadings of the first three PCAs showed some separation of the impact zones from each other (Fig. 6.27). Abandoned zones tended to plot apart from controls, particularly along PCA II, but there was some overlap. Active zones overlapped considerably with controls on all three axes, but separation from abandoned zones was evident along PCA II.

Many of the control zones plotted to the right along PCA I (Fig. 6.27 a & b), but the overlap of impact zones on this axis impaired its use in differentiating them. However, along PCA II (Fig. 6.27 a & c), most abandoned zones plotted apart from active and control zones, towards the top (or right). PCA III (Fig. 6.27 b & c) shows considerable overlap of the impact zones, even though it extracted some active and control zones towards the top as important in differentiating, and thus separating, the data.

Eigenvalues for the data were: PCA I: 5.173 (51.731 % of variance); PCA II: 2.197 (21.969 % of variance) & PCA III: 1.004 (10.040 % of variance), where the first three axes explained 83.740 % of the variance in the data.

PCA I was most strongly influenced by overall and forb density, and the densities of mature plants with seed and dead plants, all of which increased from left to right (Table 6.3). PCA II separated impact zones, primarily, according to plant community species richness, grass and forb species richness, which increased from bottom to top (or left to right). PCA III was powerfully influenced by the densities of flowering plants and mature plants with chaff, both of which increased from bottom to top.

Table 6.3: Contributions of principal component scores (with factor loadings) of plant community variables to principal component axes I-III (varimax normalised) in 1999, collectively explaining 83.7 % of the variance in the (standardised) data set on PFA-dam A of Hendrina Power Station.

Variables that contributed most strongly to each axis are shown in bold.

Plant Community Variable	PCA I	Factor Loading	PCA II	Factor Loading	PCA III	Factor Loading
Overall Species Richness	-0.010	0.034	0.445	0.979	-0.081	0.182
Grass Richness	0.242	0.488	0.353	0.702	-0.273	0.044
Forb Richness	-0.144	-0.221	0.380	0.876	0.044	0.210
Overall Species Density	0.260	0.848	-0.004	0.103	-0.012	0.434
Forb Density	0.141	0.741	-0.035	0.130	0.157	0.637
Seedling Density	0.086	0.533	0.038	0.250	0.126	0.523
Flowering Plant Density	-0.207	0.204	-0.107	0.134	0.526	0.915
Mature Plants with Chaff Density	-0.167	0.229	-0.050	0.219	0.450	0.840
Mature Plants with Seed Density	0.414	0.890	0.004	-0.050	-0.275	0.231
Dead Plant Density	0.243	0.790	-0.081	-0.068	0.009	0.387

6.9 Discussion

Quadrat data indicated that the number of species, especially of forbs, was increased by gerbil activities, more so in active zones (Table 6.1). Perennials, predominantly grasses, were also increased. Transect data, however, showed the opposite trend, where the number of species and perennials were reduced. These conflicting results probably arise from the differing capabilities of the two sampling techniques used. The quadrat technique is more likely to sample rarer species as it works on a more fine-grained scale, and is thus more useful in describing the composition of the plant community. However, this technique is also sensitive to localised differences, and may yield results that are not characteristic of the plant community as a whole. The transect technique samples the commoner species as it measures frequency of occurrence, and is designed to detect trends in the relations among species (Barbour *et al.* 1987), such as dominance by species (Fig. 6.1).

The composition of the plant community, determined from quadrat data (Table 6.1), was changed by gerbil impact. The number of species was increased, particularly of forbs and perennials, and more so in areas where gerbils were active than in areas abandoned by gerbils. Scratching and digging by gerbils in active zones could produce micro-sites where dispersed seeds of plants from regional species

pools could lodge and germinate (Dean & Milton 1991b; Olff & Ritchie 1998), and similarly, the coarser, broken substrate of abandoned zones may have facilitated the germination of seeds.

The dominance by grasses was considerably reduced after gerbils abandoned the area, largely because of the reduced contribution of a single species (*P. clandestinum*). Plant individuals became more evenly spread across species comprising the community as a result of gerbil activities.

Based on the ecological status of grasses in the control zones, these areas were undergoing succession as the community consisted of a greater number of sub-climax increaser II species, with an ecological trajectory towards a potentially underutilised climax state (as indicated by the presence of an increaser I grass). This was the expected outcome following the ecological rehabilitation of the PFA-dam at Hendrina power station (see Section 2.1.6). Gerbil activity (active zones) stimulated an increase in grass species, including a palatable decreaser climax grass, indicating that while still at the sub-climax stage, the community had become more diverse. Following abandonment, the main result of gerbil impact on the ecological status of this plant community variant seemed to be the encouragement of secondary succession as the impact promoted grass species indicative of a pioneer or sub-climax stage (van Oudtshoorn 1991). Transect data showed no change in ecological status from controls after impacts by gerbils had ceased, and quadrat data showed only a slight net gain of increaser II species for the community relative to controls. Overall the ecological status was not changed very much by the activities of gerbils, and secondary succession was only slightly promoted.

In active zones (Fig. 6.2), where gerbil disturbance was current and ongoing, substrate disruptions (namely excavated mounds, scratches, and diggings by gerbils into the crust) probably aided the establishment of new species (Dean & Milton 1991b). These open spaces provide sites where new species of plants from regional species pools can become established without competition from pre-existing plants (Olff & Ritchie 1998), and gerbil burrowing would also disrupt pre-existing root systems, further reducing competition from already established plants (Dean & Milton 1991a).

In impact zones abandoned by gerbils (Fig. 6.2), prior disruption of the topsoil crust by digging and burrowing, followed by the collapse of subterranean tunnels, and subsequent mixing of the substrate resulted in the coarser texture of the substrate (see Section 4.1), which may have been conducive to the establishment of plant species, particularly grasses.

Gerbil activities, either current (active zones) or past (abandoned zones) thus did not significantly change the evenness indices of this plant community variant (Fig. 6.3). The influx of individuals of new species in areas affected by gerbil impact appeared to be too few per species to effect change in the evenness indices. The reduction in dominance of a few species (see Section 6.1) was also not extensive enough to alter the evenness indices of the community.

Despite the increase in the number of species, gerbil activities proved insufficient to significantly alter the overall plant diversity, grass diversity or forb diversity indices from their original values in control zones (Fig. 6.4). This was possibly because individuals of new species introduced to the plant community were too few (low evenness) to affect the species diversity indices.

The biomass of the nut sedge *C. esculentus* was increased by gerbil impacts (Fig. 6.6d), especially where their activities were current (active zones), as this early successional forb species favours areas of disturbed soil, such as those brought about by gerbil burrowing (de Moor 1969). The increased biomass of *T. minuta* seems to be a reflection of the increased dominance of this forb in areas of gerbil impact (see Section 6.1), and it may possibly also indicate that *T. minuta* is less palatable than other forbs promoted by gerbil disturbance (Dean & Milton 1991b), thereby escaping predation by gerbils.

The reduced biomass of the grass *P. clandestinum* in abandoned zones (Fig. 6.6a) reflected the reduction in dominance of this species (see Section 6.1), possibly because the friable substrate of abandoned zones is drier. Increased *S. pinnata* biomass (Fig. 6.6c), after the area was abandoned by gerbils, may indicate the relaxation of grazing pressure, or possibly that *S. pinnata* is more tolerant of drier, coarser substrates, as density of this species was also increased (see Section 6.6).

The percentage of area covered by foliage (crown cover) remained similar among impact zones, whereas the percentage of space between plants (zero cover) increased and the percentage area covered by

plant stems (basal cover) decreased following gerbil activity (Fig. 6.7). Thus gerbil activities opened up the vegetation, creating more space in the grass sward.

The increased amount of space between plants in abandoned zones may be an effect of the drier substrate limiting foliage growth. It could also reflect a change in dominance among species of the plant community (see Section 6.1), where, because of the increased numbers of forb species, plant canopies of species were comparatively smaller. The decreased amount of space between *H. hirta* individuals of active zones (in the zero cover category) may have resulted from the increased dominance of this species in terms of frequency of occurrence (see Section 6.1).

The proportional contribution to plant community crown cover of the grass species *E. curvula* was decreased by gerbil activity, possibly representing the destruction of individuals by burial under excavated substrates, as both dominance and density were reduced in areas of gerbil impact (see Sections 6.1 & 6.6).

A decrease in the percentage of the larger stem-diameter grasses, and the increase in percentage of small diameter forbs could account for the lower basal cover index found. Gerbil activities seemed to promote forb individuals over grasses in this plant community variant (see Section 6.6).

In areas where gerbil activity was current and ongoing (active zones), the increased densities of *C. esculentus* may have been brought about by the disturbance caused by gerbil burrowing, as this species is known to establish well in disrupted substrates (de Moor 1969).

The friable substrate of abandoned zones, resulting from the mixing of soil horizons following tunnel collapse, and the reduced competition from dominant species because of gerbil activities, probably facilitated the establishment of ruderal forbs (annual weeds), which increase following disturbance (Dean & Milton 1991a, b). Each forb species with sufficient numbers of individuals to be sampled in more than one impact zone, reflect this increase in forb density in abandoned zones. This is a complete turnaround from the initial situation in control zones, where the density of grasses was higher. The increase in total density was probably as a result of the increase in forb density (Fig. 6.10).

The greater density of seedlings (Fig. 6.12) observed in abandoned zones may reflect increased seedling establishment in the loose substrates caused by the collapse of gerbil burrow systems (Dean & Milton 1991b), or that seedlings escaped predation by gerbils (unlike seedlings germinating in active zones). The forb *C. biensis* also had increased seedling density in this impact zone. The grass *H. hirta* had a greater density, as well as a higher frequency, of seedlings in zones where gerbils were active, but this could be a reflection of the increased dominance of this plant species (see Section 6.1). Seedling density of *A. glabratum* was diminished in areas of gerbil impact, possibly having been out competed, or their numbers simply diluted by the increased numbers of new species on active and abandoned zones.

Analysis of the samples taken during the middle of the growth season in 1999, indicated that gerbil activities did not significantly alter the overall densities or frequencies of non-flowering mature plants from the control zones (Fig. 6.15). However, the non-flowering mature plant densities of many individual species were changed by gerbil impact. The non-flowering mature plant densities of some common grass species were reduced by gerbil activities, namely: *E. curvula*, *H. hirta*, *P. clandestinum* and possibly also *E. plana*. This was more apparent from abandoned site data than from active zones, and is likely to have been attributable to the increased forb density in abandoned zones (see Section 6.6) making up greater proportions of the samples. The possible burial of tussocks under substrate excavated by gerbil digging would account for the reduction of non-flowering mature *E. curvula*, *H. hirta* and *E. plana* densities on active zones. *P. clandestinum*, being stoloniferous, could be less affected by burial, thus accounting for their higher recorded density here (Fig. 6.16b).

Non-flowering mature densities of *S. pinnata* were reduced by the presence of gerbils (active zones), and this could possibly be attributable to selective feeding as the biomass and overall density of this species were also reduced in active zones (Fig. 6.16e). The disruption of the substrate by gerbils that encouraged increased biomass and species densities of *C. esculentus* (de Moor 1969; see Sections 6.4 & 6.6) seems to be reflected by increased numbers of individuals at this non-flowering mature life-cycle stage.

T. minuta may have contributed a higher proportion of non-flowering mature plants to the overall frequency of non-flowering mature plants in active zones, possibly because it is an unpalatable species.

The increased density of flowering plants (Fig. 6.18) in the middle of the 1999 growth season in

abandoned zones could be as a response to the coarser, and thus drier, substrate of abandoned zones hastening plant life-cycles. Flowering plant frequency seemed higher in active zones, but the variability in the percentage flowering plant data on active zones (mean: 68.7 %, SD: ± 59.5 %) obscured any statistically detectable differences with abandoned (mean: 3.3 %, SD: ± 1.5 %) or control zones (mean: 9.0 %, SD: ± 5.3 %).

The lower flowering *S. pinnata* density in active zones reflects that this species does not tolerate direct gerbil impact, as this species also shows reduced biomass and density. The increased proportional contribution to the frequency of flowering plants by *S. pinnata* in abandoned zones was possibly because of the increased number of individuals established in the abandoned zones (see Section 6.6).

In the middle of the growth season, the overall density of plants with seed (Fig. 6.21) was highest in areas abandoned by gerbils, and the frequency was also slightly elevated on abandoned zones. Perhaps this life-cycle stage was reached sooner by plants in abandoned zones due to the drier substrate. The reduced dominance of *C. biensis* in active zones is reflected here by the decreased density of *C. biensis* with seed, possibly indicating that most *C. biensis* individuals were at this life-cycle stage. Conversely, the increased dominance of *H. hirta* (see Section 6.1) in active zones may be reflected here by the higher proportion of *H. hirta* with seed.

These middle-of-season samples showed higher overall densities of plants with chaff (Fig. 6.24) in abandoned zones, life cycles of plants probably having been accelerated as a response to the drier soil (Section 4.1). In abandoned zones, greater numbers of *S. pinnata* plants were in the chaff stage of their life-cycles, again probably as a result of the drier soil (Fig. 6.25).

Gerbil activities increased the overall densities and percentages of dead plants (Fig. 6.26), more on abandoned zones than on active zones. On active zones, burial under excavated substrate, and the drier substrate on abandoned zones, were the probable causes of this.

The increased numbers of plant individuals, especially forbs, where *T. brantsii* had an impact was one of the principal ways that defined variability in the data, and thus separation of impact zones. The consequences of gerbil activities were more distinguishable from the initial state before the impact, than where impacts were currently being effected.

The areas resulting from gerbil impact (abandoned zones) were distinguished from controls and areas where gerbils were active, particularly by their increased species richness. Increases in both density and species richness probably resulted from the disturbance of the substrate by gerbil diggings, which facilitated the recruitment of plant individuals.

In these mid-season samples, the flowering, seed, chaff and dead stages of plant life-cycles were already significant in abandoned zones, hinting that their drier substrate may be accelerating these life-cycles. Topsoil is mixed in with the ash in abandoned zones, which consequently have more friable substrates (see Section 4.1), and while the recruitment of new species from regional species pools (Dean & Milton 1991b) may be facilitated by the disruptions to the substrate in active zones, it is not as coarse, and thus as dry, as that of abandoned zones.

6.10 Conclusions

In 1999, in the middle of the growth season, *T. brantsii* impacts in the *Lepidium bonariensis*-*Eragrostis trichophora* plant community variant were apparent, and it was observed that they affected physiognomy, phenology and community parameters. In abandoned zones, cover was reduced, and gerbil impact appeared to have already begun to effect change in the composition and phenology of the plant community. Dominance by a few grass species was reduced and many more species had been introduced into the community. The effects of gerbils in this industrial habitat seemed similar to the effects of small mammals in natural habitats (Korn & Korn 1989; Martinsen *et al.* 1990; Dean & Milton 1991b; Huntly & Reichman 1994; Olff & Ritchie 1998).

The results of this second year survey seem to correlate well with those found in 1998, but this is examined further in the next section.

6.11 Comparison of the *Lepidium bonariensis*-*Eragrostis trichophora* plant community variant on PFA-dam A of Hendrina Power Station between 1998 and 1999

6.11.1 Diversity, Evenness and Richness

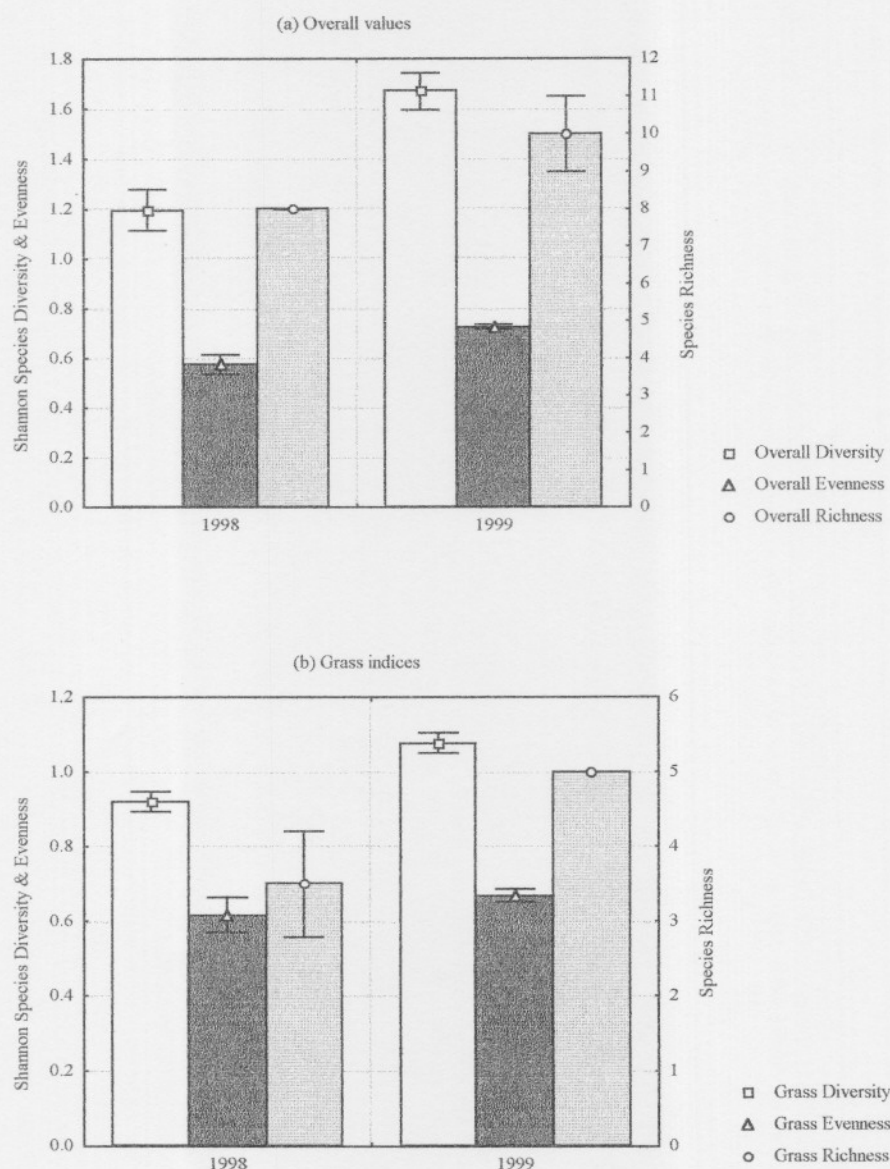


Figure 6.28: Comparative diversity, evenness and richness indices on PFA-dam A from transect samples of control zones between 1998 and 1999. a) overall plant community & b) grasses. Bars denote mean values, vertical lines represent 1SD.

No significant differences in diversity, evenness or richness indices between 1998 and 1999 were noted for the quadrat samples.

The general plant community differed in overall frequency (from transects) of diversity and evenness (Fig. 6.28a), as well as grass species diversity and richness percentages (Fig. 6.28b). The 1998 samples had lower overall diversity ($t_{df} = -6.780$, $P < 0.01$, means: 1998: 1.198 ± 0.083 ; 1999:

1.670±0.073) and evenness indices ($t_{df3}:-6.782$, $P < 0.01$, means: 1998: 0.576±0.040; 1999: 0.726±0.010). Grass species were more diverse in 1999 ($t_{df3}:6.419$, $P < 0.01$, means: 1998: 0.921±0.027; 1999: 1.079±0.027) and had greater species richness ($t_{df3}:4.025$, $P < 0.05$, means: 1998: 3.500±0.707; 1999: 5.000±0.000) than the 1998 samples.

6.11.2 Plant density

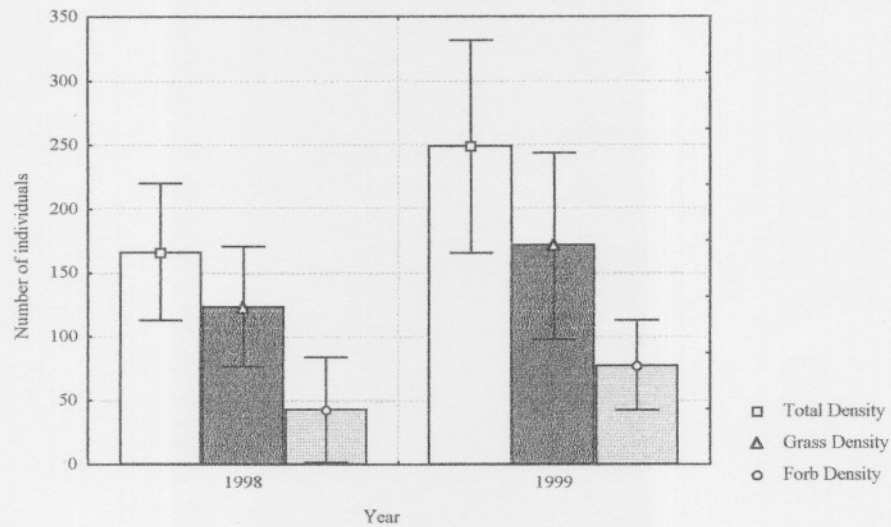


Figure 6.29: Comparative species densities from quadrature samples of control zones of PFA-dam A between 1998 and 1999. Bars denote mean values, vertical lines represent 1SD.

Densities in 1999 (Fig. 6.29), although higher than in 1998, were not significantly different.

6.11.3 Plant biomass

Overall plant biomass (data log_e transformed, Fig. 6.30) on control zones was reduced in 1998 compared to 1999 ($t_{df13}:-5.576$, $P < 0.001$, means: 1998: 4.970±0.194; 1999: 5.955±0.398). Grass biomass did not differ between the two years in this plant community variant. Forb biomass was lower in 1998 than in 1999 ($t_{df13}:-8.370$, $P < 0.001$, means: 1998: 2.415±0.600; 1999: 5.228±0.660).

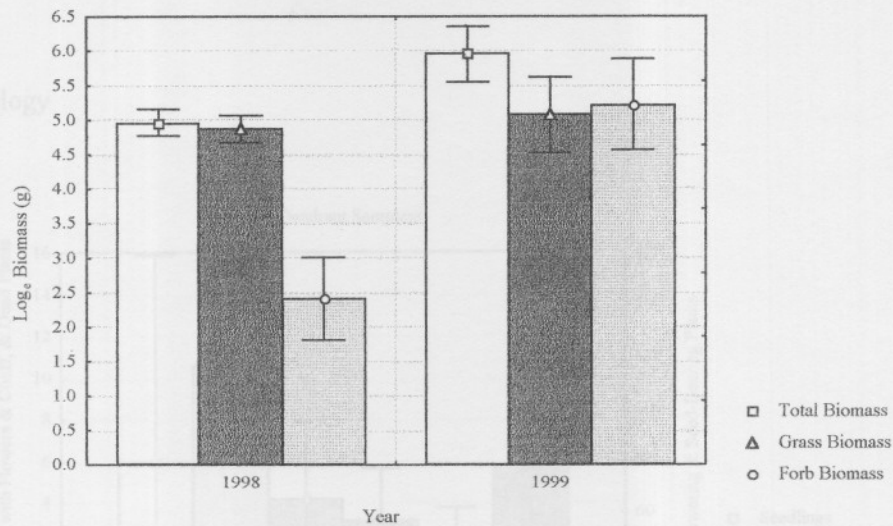


Figure 6.30: Comparative biomass indices from quadrat samples of control zones on PFA-dam A between 1998 and 1999. Bars denote mean values, vertical lines represent 1SD.

6.11.4 Plant canopy cover

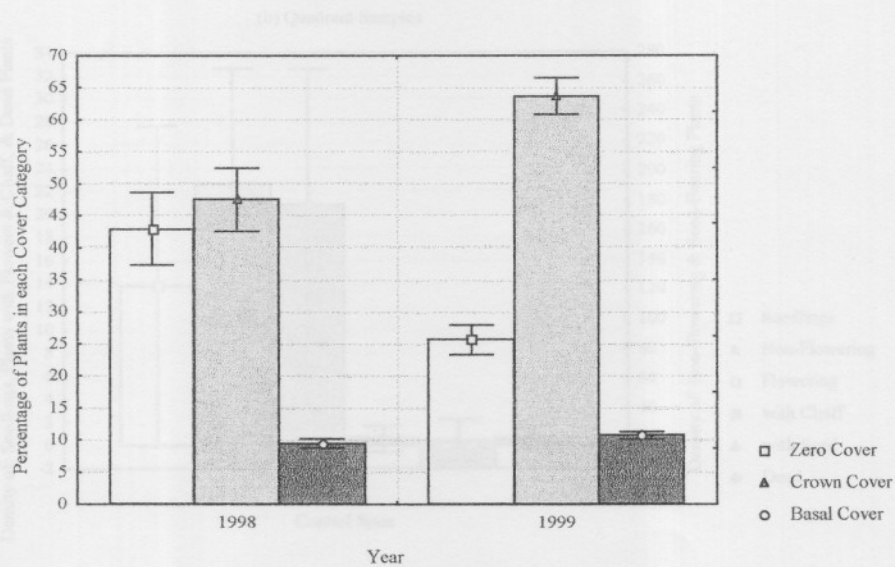


Figure 6.31: The percentages in each of three cover categories (i.e.: Zero; Crown & Basal cover) on PFA-dam A between 1998 and 1999. (From transect data.) Bars denote mean values, vertical lines represent 1SD.

In 1998 there were significantly greater percentages of plants in the zero cover category ($t_{df3}: 5.035$, $P < 0.05$, means: 1998: 43.000 ± 5.657 ; 1999: 25.667 ± 2.309), and lower percentages in the crown cover category ($t_{df3}: -4.781$, $P < 0.05$, means: 1998: 47.500 ± 4.950 ; 1999: 63.667 ± 2.887 ; Fig. 6.31).

6.11.5 Plant phenology

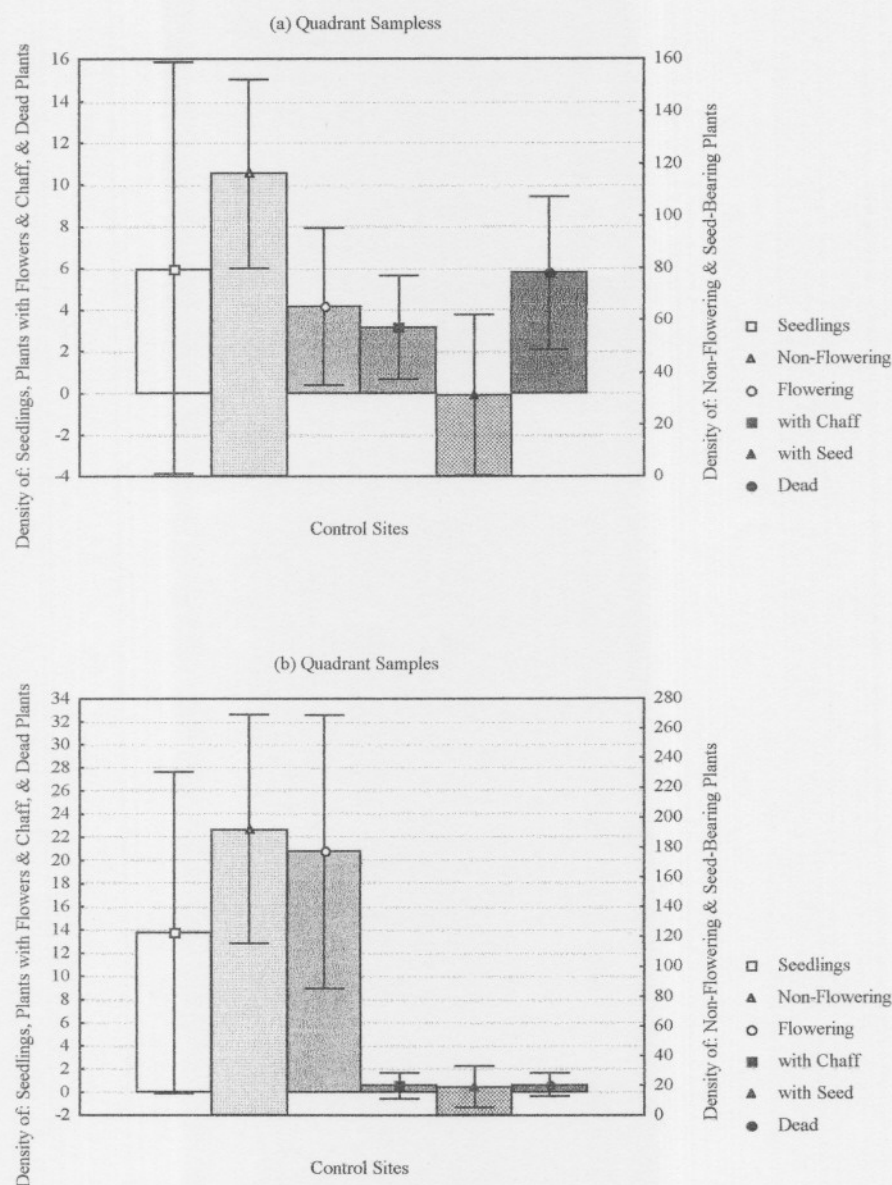


Figure 6.32: Comparative plant phenology from quadrat samples of control zones on PFA-dam A between 1998 and 1999. Bars denote mean values, vertical lines represent 1SD.

Analysis of the phenological state of the plant community variant showed that although the number of seedlings and mature plants bearing seed did not differ significantly between the two years, the other aspects did.

In 1998, a greater proportion of plants sampled were found to exhibit a phenological state characteristic of the latter stages of a plant's life cycle. There were more plants with chaff ($t_{df13}: 2.788$, $P < 0.05$, means: 1998: 3.167 ± 2.483 ; 1999: 0.556 ± 1.130) and more dead plants ($Z: 3.005$, $P < 0.01$, means: 1998: 5.750 ± 3.657 ; 1999: 0.667 ± 1.000) in 1998 (Fig. 6.32a). Conversely in 1999 more plants were at the middle stages of plant life-cycles and 1998 samples showed lower densities of mature non-flowering ($t_{df13}: -2.242$, $P < 0.05$, means: 1998: 116.250 ± 36.116 ; 1999: 192.278 ± 76.892) and flowering ($t_{df13}: -3.299$,

$P < 0.01$, means: 1998: 4.167 ± 3.764 ; 1999: 20.778 ± 11.809) plants (Fig. 6.32b).

The percentage of dead plants (assessed from transect samples but not illustrated) was also greater in 1998 than in 1999 ($t_{df3}: 6.197$, $P < 0.01$, means: 1998: 3.000 ± 0.000 ; 1999: 0.333 ± 0.577).

6.11.6 Discussion and Conclusions

The general plant community characteristics were very similar for the two consecutive years (Fig. 6.28). Quadrats had equivalent overall species, grass and forb diversities, the evenness of species was not changed from the previous year and species richness was likewise similar. With regard to transects, the increases in the indices seem largely attributable to grass species, which are dominant in the community, especially in the middle of the growth season compared to the end.

Densities in 1999 (Fig. 6.29), although higher than in 1998, were not significantly different.

The plant biomass index was greater in 1999 (Fig. 6.30). This was probably because the 1999 samples included more robust plants, as sampling took place earlier in the growth season in 1999 and therefore would not include end-of-season dieback, like the 1998 samples.

As the 1998 samples were taken towards the end of the growth season, and the substrate was therefore drier, it was not surprising to find that the conditions of the ash dam environment were such that space between plants (zero cover) was promoted instead of larger canopies (crown cover; Fig. 6.31). The limiting effect of dry conditions would be less of a restriction in the middle of the growth season, when the 1999 samples were taken, explaining the increased percentage of crown cover provided by plants and thus the reduced amount of space between plants.

The greater proportion of plants in the latter stages of their life cycles in the *Lepidium bonariensis-Eragrostis trichophora* plant community variant in 1998 on PFA-dam A (Fig. 6.32), and the converse increased proportion of plants in the middle stages of their life cycles in 1999, was probably due to sampling the plant community at different points in the growth season, as overall densities (see Section 6.11.2) did not differ between the two years.

These results in 1999 were congruous with those found in 1998 in this plant community variant, and although the sub-dominant species composition was slightly different, the principal dominant species remained unaltered.

The differences between 1998 and 1999 were slight, and arose mainly from sampling at different points in the growth season.

Thus the overall effect of gerbil impact was similar for both years, species richness was increased and dominance by few grass species was reduced. The coarser, drier substrate of abandoned zones seemed to accelerate plant life-cycles, reduce biomass and encourage the establishment of ruderal forbs after gerbils moved away.

CHAPTER 7

CONCLUSIONS

7.1 Effects on substrate

Highveld Gerbils on the PFA-dams at Hendrina Power station excavated vast quantities of ash, but this “ecosystem engineering” (Reichman & Seabloom 2002) by *Tatera brantsii* was transient, because colonies moved over time as they depleted local resources (Korn & Korn 1989). Direct, nutrient-enrichment effects (increased nitrates, organic Carbon & Phosphorous) by gerbils had insufficient time to accumulate, and, unlike the more permanent burrows of other fossorial small mammals, these burrows were soon abandoned and collapsed, mixing soil horizons. The resulting, more friable substrate, facilitates water infiltration (Whitford & Kay 1999), but it also more permeable to air, drying out more easily. In addition, many of the water-retaining, silt-sized ash particles (Aitken *et al.* 1984), excavated by gerbils are blown away by the wind (Thurlow 1937).

Water infiltration and mixing were the principal ways that the substrate chemistry of the PFA-dam was altered, and distinctive concentrations of pH, salinity and elements associated with the topsoil or the ash, were erased as a consequence of gerbil digging. The resulting substrate is more homogeneous, and this may benefit plants in that the potentially toxic components of the substrate are spread throughout the area of disturbance, rather than concentrated in a particular area.

7.2 Effects on plants

The main effect by gerbils on the plant community of PFA-dam A was an increase in the number of species, which was similar to the effect that many burrowing small mammals have in natural habitats (Martinsen *et al.* 1990; Dean & Milton 1991b; Stockrham *et al.* 1993; Huntly & Reichman 1994).

Biomass, and thus cover, was slightly reduced by gerbil impact, and plant life-cycles seemed hastened in the drier, abandoned areas. Density, especially of forbs, was increased, and dominance by small numbers of grass species was diminished. The sub-dominant species composition was slightly different, but the principal dominant species remained unaltered

7.3 Answers to questions posed at start of the study

It appears as if gerbil impacts are significant in the rehabilitated PFA-dam ecosystem. They seem to benefit the area studied by facilitating pedogenesis, increasing the depth of the substrate useable by plants, and ameliorating some of the extreme chemical conditions of the ash.

The plant community was slightly more diverse, following gerbil impact, and consisted of many more species that originally sampled in controls.

However, the density of gerbils was high (Vermaak 2000), and as a consequence, their burrowing impact could have been disproportionate. Considerable quantities of ash were brought to the surface, complicating the rehabilitation effort, and possibly requiring further expenditure in the future.

This density of gerbils also seemed to slow the process of succession on the PFA-dam, resulting in a longer period before the ecosystem could reach a sustainable climax state.

Most of the results found in this study are in accordance with those found for *T. brantsii* in savanna by Korn & Korn (1989). Dominance by grasses was reduced, and their biomass was lower at the end of the growth season. The number of forb species was increased, but legumes did not appear to be favoured. Diversity was slightly higher at the end of the growth season, but evenness was not changed by gerbil activities.

Species richness, was however, significantly increased by gerbil activities, even though many new species were annual forbs of a ruderal nature.

7.4 Recommendations and possibilities for future research

Lower densities of *Tatera brantsii* may be beneficial to the ecological rehabilitation effort of PFA-dams at Hendrina power station.

They appear to assist the development of the topsoil, mixing horizons and distributing nutrients more evenly.

They also seem to promote a more diverse plant community which is not dominated by tussocks of grass, and therefore vulnerable to erosion. Stoloniferous grass species are less affected by burial under excavated substrates and help stabilise the soil.

To achieve a lower stable population of *T. brantsii* it is recommended that perches for raptors be installed across the PFA-dams, thereby allowing the birds a different hunting strategem, which may be more effective. The more numerous rodent species are likely to be hunted first, and as *T. brantsii* is numerically dominant on the plateaux of the PFA-dams, its population should be reduced.

Perhaps the gerbil population could be reduced to the point where gerbil impact will aid the rehabilitation effort, rather than overwhelm it.

CHAPTER 8

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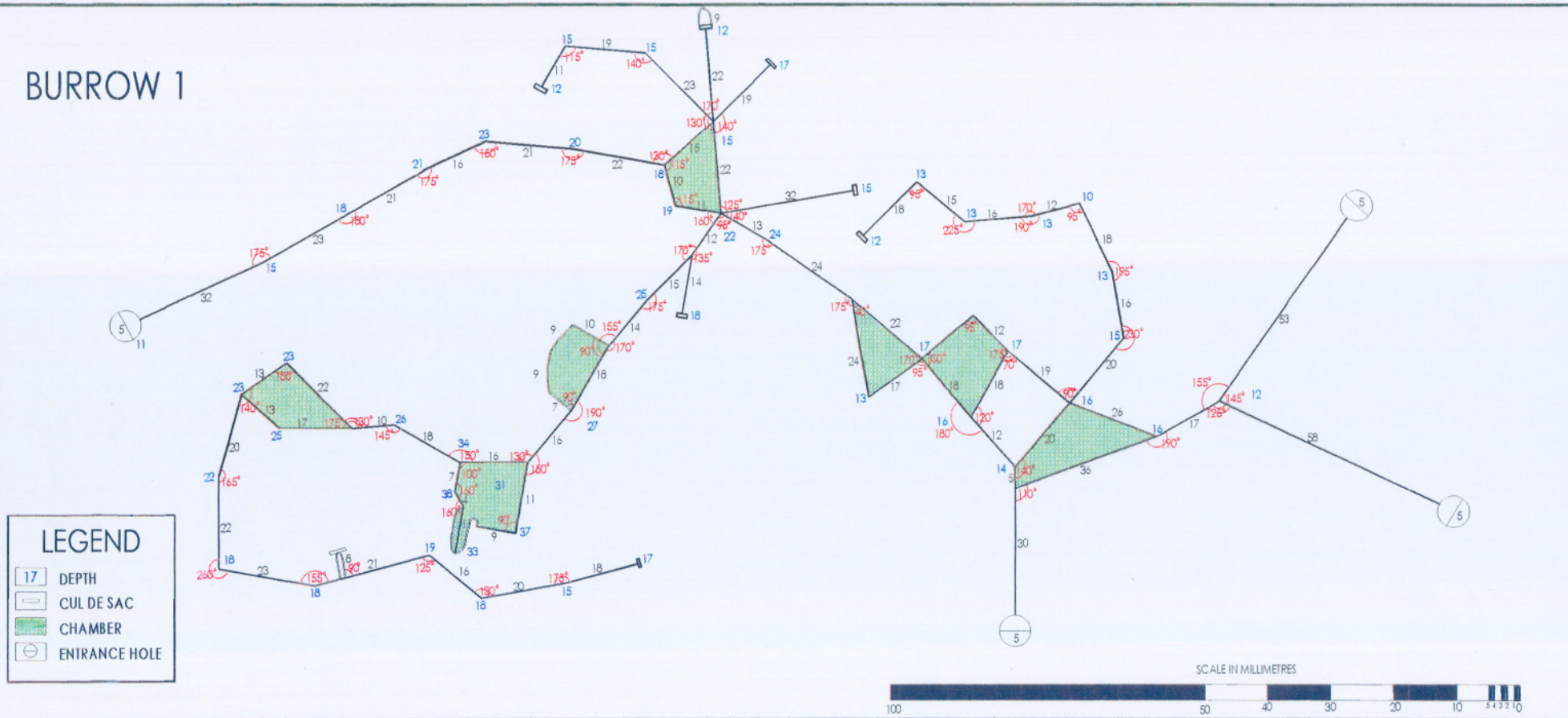
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APPENDIX 1

Burrow System Maps

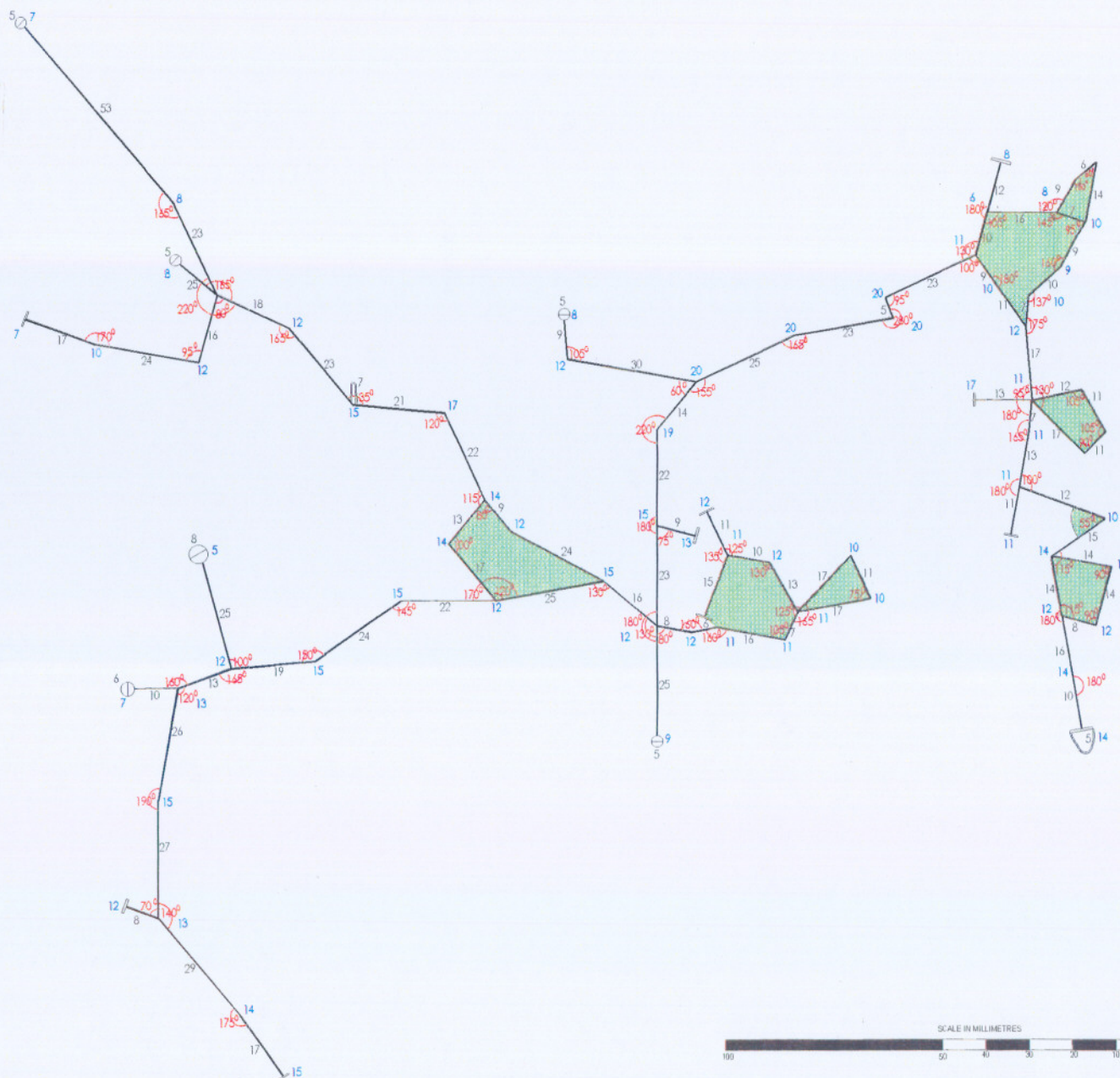
BURROW 1



BURROW 2



BURROW 3



LEGEND

- 12 DEPTH
- CUL DE SAC
- CHAMBER
- ENTRANCE HOLE

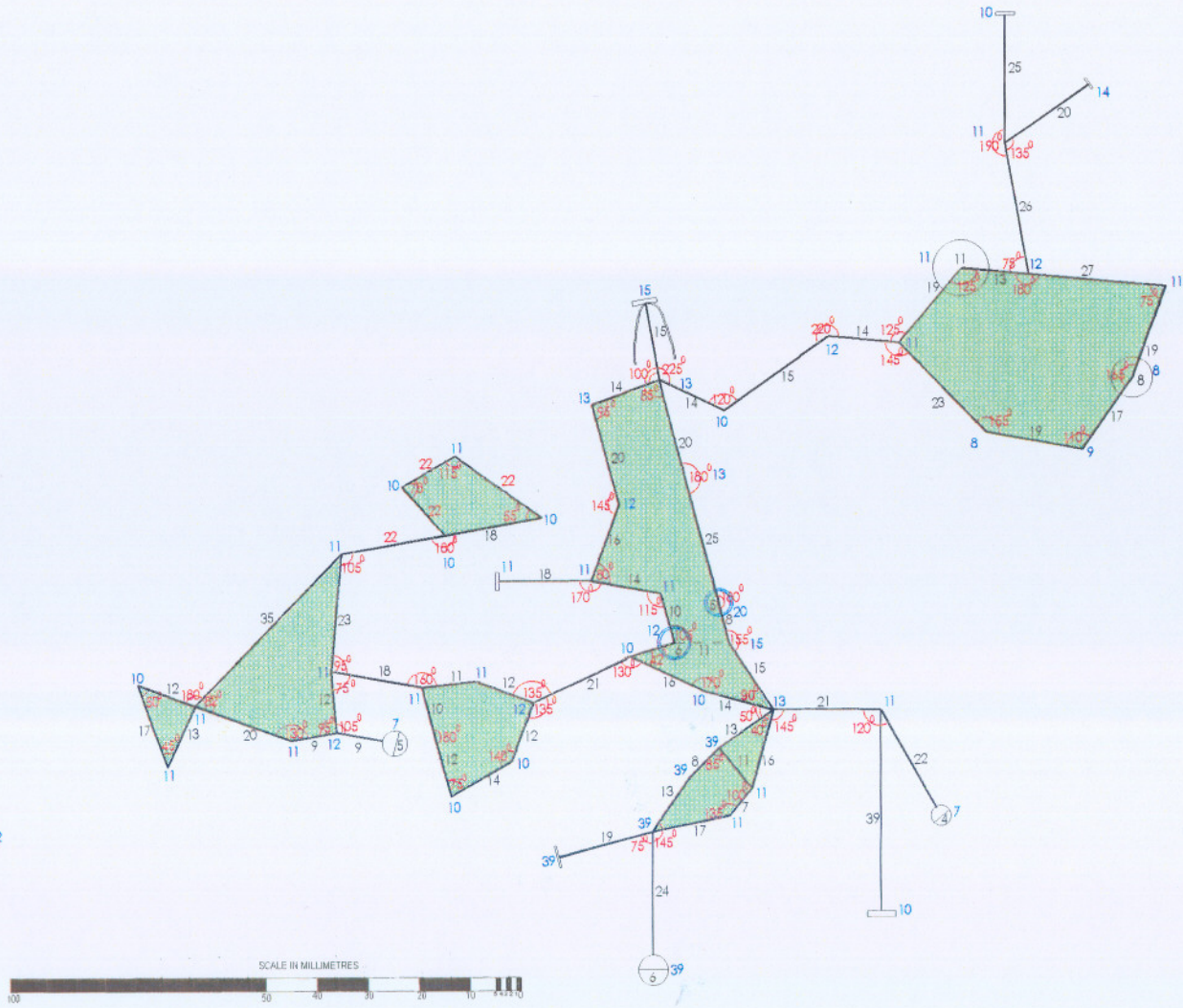
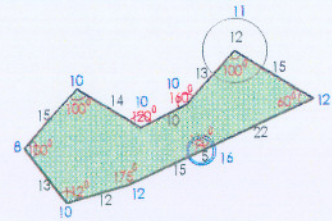
SCALE IN MILLIMETRES

100 50 40 30 20 10 0

BURROW 4 (UPPER LEVEL)

LEGEND

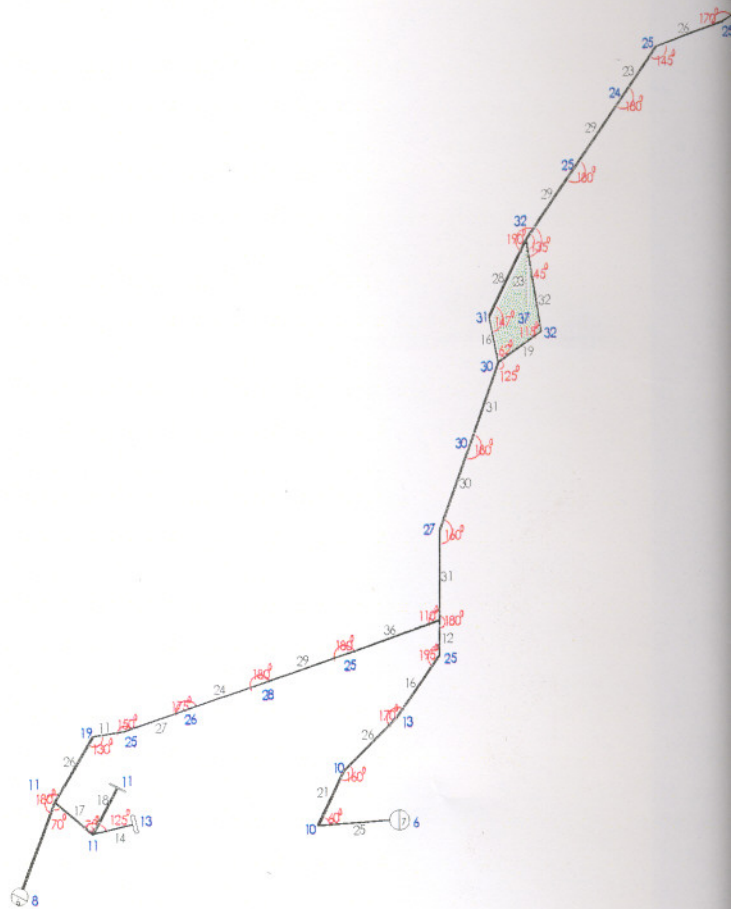
- 10 DEPTH
- CUL DE SAC
- CHAMBER
- ENTRANCE HOLE
- ACCESS HOLE

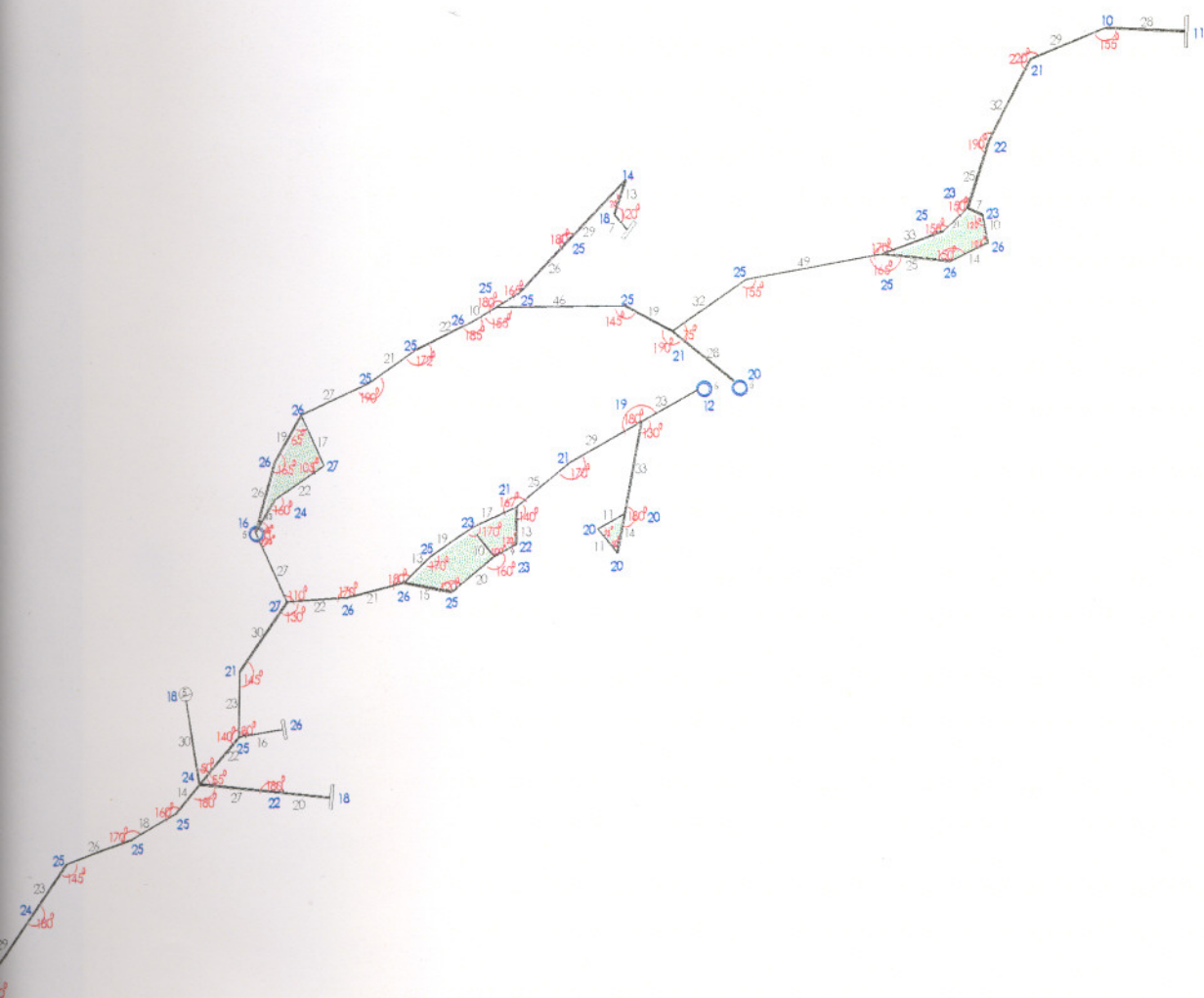


BURROW 4 (LOWER LEVEL)

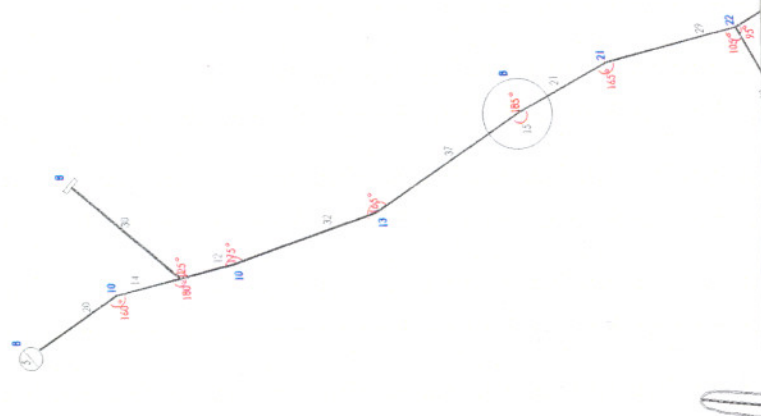
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-  DEPTH
-  CUL DE SAC
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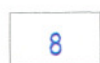




BURROW 5



LEGEND



DEPTH



CUL DE SAC



CHAMBER



ENTRANCE HOLE



