A STUDY OF A CAPE MOUNTAIN STREAM ECOSYSTEM AND ITS RESPONSE TO FIRE

by

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To the "B" Team, Richard and Paula Britton

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DECLARATION

This thesis documents original research carried out in the Zoology Department, University of Cape Town, between 1986 and 1988, under the supervision of Dr Jennifer A. Day. The work presented in this thesis has not been submitted for a degree at any other university. Any assistance I have received is fully acknowledged.

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Signed by candidate

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D.L. BRITTON

20 July 1990

Date

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ABSTRACT

This thesis presents the findings of a two-year (1986-1988) study of a mountain stream draining a small catchment in the south-western Cape, South Africa. The catchment was deliberately burnt half-way through the study period. The study was undertaken because although fire is a major natural disturbance, and also a major tool in the management of mountain catchments in the region, the effects of fire on stream ecosystems was entirely unknown.

Stream water, inputs and retention of allochthonous detritus, and benthic macroinvertebrates were sampled at monthly intervals. Intensive sampling (2 - 6 hour intervals) was also carried out at extremes of discharge (during baseflow and storms) in order to gain a greater understanding of the major processes influencing stream chemistry.

Following the burn, statistically significant increases in the concentrations of nitrate, bicarbonate, chloride, potassium and polyphenols in stream water were recorded. Sodium concentrations were significantly lower in the post-burn year, while concentrations of ammonium, phosphate, calcium, magnesium and total dissolved solids were not significantly affected.

Ionic export was generally higher in the post-burn year. Apart from nitrate, however, it is likely that export values for the post-burn year lie within the natural range of year-to-year variation. Enhanced losses of nitrate are expected to decrease progressively with the recovery of the natural vegetation and the re-establishment of soil/plant nutrient cycles.

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Although the riparian vegetation was not directly affected by the fire, a heavy, aseasonal leaf-fall occurred shortly afterwards. The following summer, leaf-fall was less than half that of the pre-burn summer. Despite these alterations in the input regime, no statistically significant differences in standing stocks of benthic organic matter could be detected.

Temporal changes in the structure of the benthic macroinvertebrate community appear to associated with seasonal changes in the physical environment. The fire appeared to have little effect on the invertebrate fauna. It was concluded that the resistence of the natural riparian vegetation to fire greatly minimizes the potentially disturbing effects of fire on the stream environment.

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INTRODUCTION

Regions with mediterranean-type climates are found in five widely separated parts of the world, these being the Mediterranean Basin, southern California, central Chile, south-western and south-central Australia and the southern Cape of South Africa. The regions are characterized by cool, relatively humid winters, hot, dry summers and a distinctive flora adapted to these conditions (Kruger, 1979). The vegetation of each region consists of evergreen, sclerophyllous shrubs or trees, locally referred to as garrigue, macchia, phrygana (Mediterranean), chaparral (California), matorral (Chile), heath (Australia) and fynbos (South Africa) (Day, 1983).

The quartzitic mountain ranges of the south-western Cape of South Africa are vegetated by mountain fynbos, an exceptionally diverse flora distinguished by the presence of members of the plant families Proteaceae, Ericaceae and Restionaceae (Taylor, 1978). This flora grows on acidic, strongly leached soils where not only are nitrogen and phosphorus in short supply, but where one or more other nutrient elements (potassium, sulphur, copper, zinc, molybdenum) may also be limiting (Specht & Moll, 1983). Mountain fynbos is also found in upland plains and valleys where rainfall is sufficiently high to allow the development of moderately to highly leached acid soils on basic rock types such as granite or slates (Lambrechts, 1979).

Fire in fynbos

With the exception of Chile, fire represents the major disturbance factor in all mediterranean ecosystems (Keeley, 1986) and has undoubtedly played a major role in the evolution of plant life histories (Cowling, 1987). The reproductive effort of fynbos plants

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is usually geared for regeneration in the post-fire environment (Manders & Cunliffe, 1987) and some species, such as the so-called fire lilies (eg. *Cyrtanthus angustifolius*, *Watsonia pyrimidata*), require the stimulus of fire in order to flower and produce seed (Levyns, 1966; Le Maitre, 1984). Adaptations to fire are also exhibited by the fauna. For example, ground-nesting birds such as pipits, larks and gamebirds generally nest after the main fire season (Winterbottom, 1972), and several species of plover (*Vanellus* spp.), courser (*Cursorius* spp.) and pratincole (*Glareola* spp.) produce dark coloured eggs and heavily pigmented, downy chicks as an adaptation to nesting on blackened ground (Maclean & Kemp, 1973).

Natural fires in mountainous areas are caused by lightning and falling rocks, the latter being considerably less common than the former (Edwards, 1984). Over and above this, man has occupied the fynbos biome for the past 125,000 years, and it is likely that the vegetation of the biome has been subjected to some form of fire management for at least 100,000 years. Fire was used by early natives to attract game to young, post-fire herbage, in honey-hunting activities and in the 'farming' of geophytes (Deacon, 1983). The historical fire regime of the fynbos biome is not fully known, as few areas of the biome have good fire records. Conservative estimates of fire frequency prior to 1652, during pre-colonial times, are placed at 15 to 20 years or less (Edwards, 1984). After settlement in 1652, the early European farmers of the Cape learned the practice of veld burning from the nomadic Khoikhoi pastoralists (Bands, 1977), and this resulted in a marked increase in the frequency of burning (Edwards, 1984). In many areas, the veld was burnt as often as possible in order to provide fresh grazing for stock and as insurance against more destructive, accidental fires. A number of laws were passed against unpermitted burning during the 17th, 18th and 19th centuries, laws which carried severe penalties (including the death penalty) against offenders (Bands, 1977). These laws were passed not so much to conserve the veld, as to protect the grain and houses of the inhabitants against fire and to prevent the

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depletion of wood supplies. By 1865, on the recommendation of the Colonial Botanist, J.C. Brown, burning was being restricted on crown forest lands (Edwards, 1984).

Ironically, a direct consequence of the injudicious protection policy was the outbreak of extensive and highly destructive wildfires. In one instance, a wildfire swept through a tract of country some 640 km long and 24 to 240 km wide, causing loss of life and considerable damage to property and to the natural forests (Edwards, 1984). Despite this, the controversy between the Government and scientists, who viewed the burning of fynbos as highly detrimental, and farmers and landowners, who considered fire to be necessary to maintain grazing land and to reduce the risk of wildfire, continued up until the 1940's. In 1945, Wicht presented an extensive report which pointed out the natural occurrence of fire in the fynbos biome and the adaptations to fire exhibited by the indigenous flora. Subsequent research confirmed the necessity of fire in maintaining fynbos diversity, as well as in reducing the risk of wildfire, and controlled burning was accepted as part of catchment and conservation management for farming areas and proclaimed mountain catchment areas (the latter managed, since 1970, by the Forestry Branch of the Department of Environment Affairs). There is still a certain amount of uncertainty over the optimal frequency and timing of burns for different fynbos communities, although it is generally accepted that fynbos is adapted to fire intervals of between 10 and 30 years (van Wilgen, 1987). Burning at intervals of less than 10 years may have deleterious effects on the flora, in that many seed-producing shrubs cannot mature and produce seed between fires (van Wilgen, 1987). Conversely, protecting the vegetation from fire for more than 30 years results in senescence, a reduction in total live biomass, increased risk of wildfire due to litter build-up (van Wilgen, 1981), poor regeneration of mature plants and poor seed germination (Bond, 1980). Prescribed burning of fynbos-dominated catchments in the south-western Cape is presently carried out at 12 to 15 year intervals. The formulation of this management policy was based on the premise that if the burning cycle ensures the survival of the slowest

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maturing plant, survival of the full range of plant species will also be ensured (Bands, 1987[a]).

Rivers and streams of the south-western Cape

South Africa is poorly supplied with water. Only 20% of the country receives more than 800 mm of rain per year, and most of this area is mountainous (Bands, 1987[b]). Water draining mountain catchments of the south-western Cape is therefore a valuable commodity which is already extensively exploited. The impending crisis facing the country as the demand for water outstrips supply has led to recognition of the need to manage this limiting resource wisely. Judicious management of a natural system, however, requires an understanding of the processes and interactions taking place in that system in its undisturbed state as well as an understanding of how the system will react to manipulation.

As far as the rivers and streams of the south-western Cape are concerned, it is only in recent years that the pioneering work of Harrison & Elsworth (1958) on the Great Berg River has been expanded by work on the Berg River (Coetzer, 1978; Bath, 1989) the Breede River (Coetzer, 1986), the Eerste River (King, 1981, 1982, 1983; Petitjean, 1987), the Palmiet River (Byren & Davies, 1989) and Langrivier (King *et al.* 1987[a], 1987[b], 1988), and our knowledge of these systems is still not sufficient for detailed environmental management plans to be constructed (King, 1988). On the basis of these studies, it is known that the upper reaches of the rivers are generally steep, fast-flowing mountain streams shaded by evergreen forests of Afromontane origin. The streams are acid and poorly buffered. Most nutrients and other minerals are present at exceedingly low concentrations, and sediment loads are similarly very low. The colour of the water is variable, but is often 'peaty' due to the presence of humic substances. The food web in these streams, as in canopied headwater streams worldwide, is based primarily on inputs of allochthonous detritus, primary productivity being very low due to low nutrient and light levels and the scouring effects of periodic spates. The aquatic macroinvertebrate fauna appears to be largely endemic. Insect species that occur throughout several zones of these rivers grow most slowly in, and emerge as the smallest adults from, the pristine headwaters. This reflects the very low levels of secondary productivity. The lower reaches of the rivers pass through land disturbed in a variety of ways, resulting in altered flow regimes and reduced water quality. As a consequence, the natural downstream changes in the riverine biota are exaggerated, with the headwaters supporting a largely endemic, clean-water biota and the lower reaches supporting more widespread and hardy forms. The rivers are divided into those with clear, "white", slightly acid waters such as the Olifants, Berg, Eerste and Breede Rivers, and those with dark, very acid waters such as the Palmiet and Storms Rivers (Harrison & Agnew, 1962; Noble & Hemens, 1978). Generally, the white rivers are longer with well-developed zones (mountain stream, foothills, lower river and estuary) whilst the dark rivers change abruptly from mountain stream to estuary, reflecting their origins in coastal hills and their proximity to the sea (King & Day, 1979). In addition, there are a number of very short rivers, such as the Rooiels, which descend steeply through undisturbed fynbos, but nothing is known about them. All of the larger rivers in the fynbos biome are now regulated by dams, and are losing an increasing proportion of their flow because of water extraction.

<u>Linkages between terrestrial and aquatic ecosystems</u>

It is well known that the character of streams are an expression of the land they drain. Hynes (1975) concluded that in every aspect, the valley rules the stream. Geology determines slope, soil-type and availability of ions; these and the climate determine the vegetation, which in turn affects the quality and quantity of organic matter in the system. This exerts a major influence on the release of water, particles and dissolved salts from the

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catchment, which in turn control aquatic ecosystem processes. Undisturbed terrestrial ecosystems develop "tight" nutrient cycles as they mature, and thus lose only small amounts of the available nutrient capital to drainage waters (Likens & Bormann, 1974). Because of the strong linkages between terrestrial and aquatic systems, a major disturbance, such as fire, in the surrounding catchment may be expected to cause a major disturbance in the stream environment, manifested by changes in the quality and quantity of stream water and alterations in the regime of allochthonous inputs. If the stream environment is disturbed in this way, it may further be hypothesized that the relatively slow turnover times of the benthic fauna render it highly sensitive to changes in the stream environment, and the faunal community will thus be altered by the occurrence of a fire.

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The deliberate burning of Swartboskloof, a small, fynbos-dominated catchment in the south-western Cape, provided an opportunity for these hypotheses to be tested. The Swartboskloof catchment, situated in the Jonkershoek Valley approximately 60 km east of Cape Town, was identified by the Fynbos Biome Project as a primary site for the study of fynbos ecosystems. The Project, one of several National Scientific Programmes administered by the Council for Scientific and Industrial Research (CSIR), was initiated in 1977 with the aim of gaining a predictive knowledge of the structure and functioning of fynbos ecosystems for management and conservation purposes. The first phase of the Project, which included the review and synthesis of current knowledge about fynbos ecosystems, and broad surveys of climate, vegetation, fauna and land use patterns, was completed by the mid 1980's. The burning of Swartboskloof in 1987, as part of the normal management of the area, constituted the second phase of the Project, that of testing hypotheses derived in the first phase on the outcome of a late-summer prescribed burn on a mountain fynbos ecosystem.

Prior to the burn, 30 multidisciplinary research projects were initiated at Swartboskloof (Table 1). Unfortunately, 5 of these projects were either never fully initiated or

Table 1 RESEARCH PROJECTS UNDERTAKEN AT SWARTBOSKLOOF

Project	Organization
Climatic studies	Jonkershoek Forestry Research Centre (JFRC), Stellenbosch
Streamflow	JFRC
Catchment nutrient studies	JFRC
* Physical properties of soil	JFRC
Soil wettability and repellancy	JFRC
* Soil temperature studies	Dept Environmental and Geographical Science, University of Cape Town
* Information content of fynbos spectral characteristics	Dept Environment Affairs, Cape Town
* Nitrification in topsoils	Dept Microbiology and Virology, University of Stellenbosch
The Swartboskloof stream ecosystem	Freshwater Research Unit, University of Cape Town
* Response of selected fynbos species to post-fire nutrient additions	JFRC
Seed biology dispersal and regeneration modes in the Proteaceae	JFRC
Biology and post-fire responses of geophytes	JFRC
Influence of fire on forest/fynbos boundaries	JFRC
Phenological study of eight fynbos species	JFRC
Study of the root systems of eight fynbos species	JFRC
Plant-water relations	South African Forestry Research Institute (SAFRI) and JFRC
Effect of flower harvesting on the population biology of *Protea neriifolia*	JFRC
Autecology of *Heliophila cuneata*	JFRC
Water uptake and photosynthesis in fynbos species	JFRC
Autecological study of three Bruniaceae species	JFRC
Effects of fire on pathogenic plant fungi	Plant Protection Research Unit, Stellenbosch
Avian responses to fire	Percy FitzPatrick Institute of African Ornithology
* Insects - herbivore feeding patterns	Zoology Dept, University of Cape Town
Insect pollination of *Erica* species	Dept Entomology, University of Stellenbosch
The impact of Argentine ants on fynbos ecology	JFRC
Soil invertebrate studies	JFRC
Small mammal-plant interactions	JFRC
Response of small mammal populations to fire	Dept Nature Conservation, University of Stellenbosch
Effects of fire on small carnivore populations	Dept Nature Conservation, University of Stellenbosch
Influence of fire on the herpetofauna	Jonkershoek Nature Conservation Station, Stellenbosch

* Project never fully initiated, or discontinued prior to the fire

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discontinued prior to the burning of the catchment. Furthermore, other studies which would have contributed greatly to our understanding of nutrient cycling processes in fynbos ecosystems failed to receive funding. Since the effects of the prescribed burn on nutrient loads leaving the catchment were a major research objective, freshwater ecologists associated with the project considered it of great importance that subsurface hydrological outflow of nutrients be assessed. Motivations were thus made for the drilling of boreholes in Swartboskloof in order to assess groundwater chemistry and flow within the catchment before and after the fire. For the same reason, it was also strongly recommended that atmospheric losses of nutrients in smoke be quantified by collecting smoke samples during the course of the burn. Neither of these studies was financed, however, and thus quantification of nutrient export from the catchment is restricted in this thesis to losses via surface runoff.

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The Swartboskloof Programme was initiated and run largely by terrestrial ecologists. Since changes in the biomass and composition of terrestrial vegetation are immediately obvious after a fire, such projects require only a relatively short pre-burn monitoring period. Conversely, research into the effects of catchment disturbances on stream chemistry or stream communities, for example, require an extensive pre-impact data record in order to establish the degree of natural variation within the system. Without such records, it is difficult to determine with certainty when variations in stream chemistry or invertebrate numbers exceed the normal range, thereby indicating that the system has been disturbed. As the present study was initiated only one year prior to the burning of Swartboskloof, it was recognized from the outset that the lack of a long-term, pre-impact data base would be one of the major limitations of the study. Nevertheless, because it was highly unlikely that a catchment would be deliberately burnt purely for research into freshwater systems, the burning of Swartboskloof provided the best opportunity to date for research of this nature.

To circumvent the problem of a short pre-burn data set, it was originally intended that the

Langrivier catchment be used as a control against which the effects of fire on the Swartboskloof stream ecosystem could be determined. Langrivier is a 246 ha, fynbos-dominated catchment situated in the Jonkershoek Valley approximately 1.5 km north-east of Swartboskloof, and has been the focus of several studies conducted by the Freshwater Research Unit at the University of Cape Town (King *et al.*, 1987[a]; 1987[b]; 1988). Unfortunately, however, Langrivier burnt in a wildfire in October 1987, effectively restricting its use as a control to the first six months after the Swartboskloof burn. Although as much data as possible has been used from the Langrivier catchment, this unforseen event clearly represents an additional limitation of the present study.

Swartboskloof is a fan-shaped catchment, 373 ha in area and 285 to 1200 m in altitude, which forms part of the greater Jonkershoek catchment in the Hottentots-Holland mountains. The head of the Swartboskloof catchment forms the widest part of the "fan", and it narrows with a decrease in altitude. Slopes range from less than 5° to 45°, with the steep slopes averaging 30° (McDonald, 1985). About 2 % of the area consists of inaccessible, almost vertical cliffs (McDonald, 1985). Loose boulder screes, consisting of sandstone boulders, are found on the higher slopes immediately below the steep cliffs. In parts, the screes have stabilized and support evergreen forests of Afromontane origin. Forest communities are also found along the length of the main drainage lines and streams in the catchment. Dominant riparian trees are *Brabejum stellatifolium*, *Cunonia capensis*, *Ilex mitis*, *Maytenus acuminata* and *Rapanea melanophloeos* (McDonald, 1985). The open slopes of the catchment are vegetated by sclerophyllous shrubland (fynbos) (McDonald, 1985).

The streams in Swartboskloof follow fault lines in the strata. The main Swartboskloof stream, which flows from south-west to north-east, is perennial and seasonally fed by four smaller streams. Jubilee Creek, which rises outside the study area and flows along the eastern side of the catchment, is also perennial but without seasonal tributaries. The two

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concentration of dissolved solids in stream and river water (Edwards, 1973; O'Connor, 1976), yet certain ions may demonstrate variable responses to changes in discharge during storm events (Walling & Foster, 1975), suggesting that this is only one of the controls which influence solute concentrations in streams. The results of this part of the study are presented in Paper II. Paper III describes inputs to, and retention of allochthonous detritus by the Swartboskloof stream, and the effects of fire on these aspects of stream ecology. Finally, Paper IV investigates the functional organization of the benthic macroinvertebrate fauna of the Swartboskloof stream, and describes the effects of fire on the faunal community in light of earlier findings on changes in stream chemistry and standing stocks of benthic organic matter after the fire.

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REFERENCES

Bands D.P. (1977).
Prescribed burning in Cape fynbos catchments. In: H.A. Mooney & C.E. Conrad (tech. coordinators), Proceedings of the symposium on the environmental consequences of fire and fuel management in mediterranean ecosystems, Palo Alto, California. USDA For. Serv. Gen. Tech. Rep. WO3-3: 245-256.

Bands, D.P. (1987[a]).
Management of fynbos mountain catchments. S. Afr. Inst. For. Handbook: 509-521.

Bands, D.P. (1987[b]).
Jonkershoek Forestry Research Centre, Pamphlet 384. 12 pp.

Bath, A.J. (1989).
Phosphorus transport in the Berg River, Western Cape. Unpublished PhD thesis, University of Cape Town. 525 pp.

Bond, W.J. (1980).
Fire and senescent fynbos in the Swartberg, southern Cape. S. Afr. For. J., 114: 68-71.

Byren, B.A. & B.R. Davies. (1989).
The effect of stream regulation on the physico-chemical properties of the Palmiet River, South Africa. Regulated Rivers: Research and Management 3: 107-121.

Coetzer, A.H. (1978).
The invertebrate fauna and biotic index value of water quality of the Great Berg River, western Cape. J. Limn. Soc. Sthn. Afr. 4: 1-7.

Coetzer, A.H. (1986).
Benthic invertebrate communities and the biological assessment of the water quality of the Breede River during 1975 and 1976. Bontebok 5: 42-51.

Cowling, R.M. (1987).
Fire and its role in coexistence and speciation in Gondwanaland shrublands. S. Afr. J. Sci. 83: 106-112.

University of Cape Town

Day, J.A. (1983).
Preface. In: J.A. Day (Ed.), Mineral nutrients in mediterranean ecosystems, pp. 1-10. S. Afr. Nat. Sci. Prog. Report 71. CSIR, Pretoria.

Deacon, H.J. (1983).
The peopling of the fynbos region. In: H.J. Deacon, Q.B. Hendey & J.J.N. Lambrechts (Eds.), Fynbos palaeoecology: a preliminary synthesis, pp.183-204. S. Afr. Nat. Sci. Prog. Report 75. CSIR, Pretoria.

Edwards, A.M.C. (1973).
The variation of dissolved constituents with discharge in some Norfolk rivers. J. Hydrol. 18: 219-242

Edwards, D. (1984).
Fire regimes in the biomes of South Africa. In: P. de V. Booysen & N.M. Tainton (Eds.), Ecological effects of fire in South African ecosystems, pp. 19-37. Springer-Verlag.

Harrison, A.D. (1958).
Hydrobiological studies on the Great Berg River, western Cape Province. Part II: Quantitative studies on sandy bottoms, notes on tributaries and further information on the fauna, arranged systematically. Trans. R. Soc. S. Afr. 35: 227-276.

Harrison, A.D. & J.D. Agnew. (1962).
The distribution of invertebrates endemic to acid streams in the western and southern Cape Province. Ann. Cape Prov. Museums 2: 273-291.

Harrison, A.D. & J.F. Elsworth. (1958).
Hydrobiological studies on the Great Berg River, western Cape Province. Trans. R. Soc. S. Afr. 35: 125-276.

Hynes, H.B.N. (1975).
The stream and its valley. Int. Ver. Angew. Limnol. Verh. 19: 1-15.

University of Cape Town

Keeley, J.E. (1986).
Resilience of mediterranean shrub communities to fires. In: B. Dell, A.J.M. Hopkins & B.B. Lamont (Eds.), Resilience in Mediterranean-type ecosystems, pp. 95-112. W. Junk.

King, J.M. (1981).
The distribution of invertebrate communities in a small South African river. Hydrobiol. 83: 43-65.

King, J.M. (1982).
An ecological study of the macro-invertebrate fauna of the Eerste River, western Cape Province, South Africa. Unpublished PhD thesis, Zoology Department, University of Cape Town. 222 pp.

King, J.M. (1983).
Abundance, biomass and diversity of benthic macro-invertebrates in a western Cape river, South Africa. Trans. R. Soc. S. Afr. 45: 11-34.

King. J.M. (1988).
Conclusions and recommendations for future research. In: J.M. King (Ed.), Hydrology and Hydrobiology in the fynbos biome, pp. 50-52. Nat. Prog. Ecosystem Research, Occasional Report 26. CSIR, Pretoria. 60 pp.

King, J.M. & J.A. Day. (1979).
Hydrology and Hydrobiology. In: J.Day, W.R. Siegfried, G.N. Louw & M.L. Jarman (Eds.), Fynbos ecology: a preliminary synthesis, pp. 27-42. S. Afr. Nat. Sci. Prog. Report 40. CSIR, Pretoria.

King, J.M., M-P. Henshall-Howard, J.A. Day & B.R. Davies. (1987[a]).
Leaf-pack dynamics in a southern African mountain stream. Freshwater Biol. 18: 325-340.

King, J.M., J.A. Day, B.R. Davies & M-P. Henshall-Howard. (1987[b]).
Particulate organic matter in a mountain stream in the south-western Cape, South Africa. Hydrobiol. 154: 165-187.

University of Cape Town

King, J.M., J.A. Day, P.R. Hurley, M-P. Henshall-Howard & B.R. Davies. (1988).
Macroinvertebrate communities and environment in a southern African mountain stream. Can. J. Fish. aquat. Sci. 45: 2168-2181.

Kruger, F.J. (1979).
Introduction. In: J. Day, W.R. Siegfried, G.N. Louw & M.L. Jarman (Eds.), Fynbos ecology: a preliminary synthesis, pp. 1-6. S. Afr. Nat. Sci. Prog. Report 40. CSIR, Pretoria.

Lambrechts, J.J.N. (1979).
Geology, geomorphology and soils. In: J. Day, W.R. Siegfried, G.N Louw & M.L. Jarman (Eds.), Fynbos ecology: a preliminary synthesis, pp. 16-26. S. Afr. Nat. Sci. Prog. Report 40. CSIR, Pretoria.

Le Maitre, D.C. (1984).
A short note on seed predation in *Watsonia pyrimidata* (Andr.) Stapf. in relation to season of burn. J. S. Afr. Bot. 50: 407-415.

Levyns, M.R. (1966).
Haemanthus canaliculatus, a new fire-lily from the Western Province. J. S. Afr. Bot. 32: 73-75.

Likens, G.E. & F.H. Bormann. (1974).
Linkages between terrestrial and aquatic ecosystems. BioScience 24: 447-456.

Maclean, G.L. & A.C. Kemp. (1973).
Neonatal plumage patterns of Three-banded and Temminck's Coursers and their bearing on Courser genera. Ostrich 44: 80-81.

Manders, P.T. & R.N. Cunliffe. (1987).
Fynbos plant life histories, population dynamics and species interactions in relation to fire: an overview. In: R.M. Cowling, D.C. le Maitre, B. Mackenzie, R.P. Prys-Jones & B.W. van Wilgen (Eds.), Disturbance and the dynamics of fynbos biome communities, pp. 15-23. S. Afr. Nat. Sci. Prog. Report 135. CSIR, Pretoria.

University of Cape Town

McDonald, D.J. (1985).
The plant communities of Swartboschkloof, Jonkershoek. S. Afr. Nat. Sci. Prog. Report 104. CSIR, Pretoria. 54 pp.

Noble, R.G. & J. Hemens. (1978).
Inland water ecosystems in South Africa - a review of research needs. S. Afr. Nat. Sci. Prog. Report 34. CSIR, Pretoria.

O'Connor, D.J. (1976).
The concentration of dissolved solids and river flow. Water Resour. Res. 12: 279-294.

Petitjean, M.O.G. (1987).
Eerste River catchment management report. Freshwater Research Unit, University of Cape Town.

Specht, R.L. & E.J. Moll. (1983).
Mediterranean-type heathlands and sclerophyllous shrublands of the world: an overview. In: F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis (Eds.), Mediterranean-type ecosystems: the role of nutrients, pp.41-65. Springer-Verlag.

Taylor, H.C. (1978).
Capensis. In: M.J.A. Werger (Ed.), Biogeography and ecology of southern Africa, pp. 171-229. W. Junk.

van Wilgen, B.W. (1981).
Some effects of fire frequency on fynbos plant community structure at Jonkershoek, Stellenbosch. S. Afr. For. J., 118: 42-55.

van Wilgen, B.W. (1987).
Fire regimes in the fynbos biome. In: R.M. Cowling, D.C. le Maitre, B. Mackenzie, R.P. Prys-Jones & B.W. van Wilgen (Eds.), Disturbance and the dynamics of fynbos biome communities, pp. 6-14. S. Afr. Nat. Sci. Prog. Report 135. CSIR, Pretoria.

Walling, D.E. & I.D.L. Foster. (1975).
Variations in the natural chemical concentration of river water during flood flows, and the lag effect: some further comments. J. Hydrol. 26: 237-244.

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Wicht, C.L. (1945).
Report of the committee on the preservation of the vegetation of the south-western Cape. Special publication of the Royal Society of South Africa, Cape Town, pp.1-56.

Winterbottom, J.M. (1972).
The ecological distribution of birds in southern Africa. Monogr. Percy FitzPatrick Inst. Afr. Ornith. 1: 1-81.

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FIRE AND THE CHEMISTRY OF A SOUTH AFRICAN MOUNTAIN STREAM

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ABSTRACT

The short-term effects of a late-summer prescribed burn on the chemistry of a south-western Cape mountain stream were investigated. Nitrate concentrations in stream water were significantly higher during the post-burn year. Increased concentrations of Cl^-, HCO_3^-, polyphenols and K^+ and decreased Na^+ concentrations were also recorded. Stream pH and concentrations of NH_4^+-N, PO_4^{3-}-P, Ca^{2+}, Mg^{2+} and total dissolved solids were not significantly affected by the burn. Ionic export from the catchment was generally greater in the post-burn year. Apart from NO_3^--N, however, values probably lie within the natural range of year-to-year variation. It is predicted that enhanced losses of NO_3^--N will decrease progressively with the recovery of the vegetation and the re-establishment of soil/plant nutrient cycles. Atmospheric losses of nutrients in smoke were unquantified, but may be of more significance to site productivity than losses through surface runoff, which, in the case of N, appear to be compensated by precipitation inputs.

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INTRODUCTION

The management of mountain catchment areas in South Africa is aimed at yielding the maximum quantity of water of the highest possible quality, whilst retaining optimal plant cover and variety of species (Department of Water Affairs, 1986). In the south-western Cape, where south-easterly winds and dry summer and autumn periods provide a highly favourable climate for fire (Edwards, 1984), prescribed burning is recognised as being an effective tool in achieving such objectives.

Manipulation of plant biomass has been shown worldwide to have a marked effect on water yield from catchments (see review by Bosch & Hewlett, 1982), with greatest yield changes reported from catchments situated in high-rainfall areas. Studies on the effects of prescribed burning on water yield from mountain catchments in the south-western Cape have produced inconsistent results, which nonetheless suggest some potential for increasing water yield, especially in well-managed areas of pristine vegetation (Lindley *et al.*, 1988).

The indigenous vegetation of the region, mountain fynbos, is sclerophyllous and characterized by the presence of members of the plant families Proteaceae, Ericaceae and Restionaceae. Observations of fynbos ecosystems indicate that the flora is fire-adapted, and that periodic fires are necessary to maintain the complete range of species (Bands, 1977). While the fire regime under which such vegetation evolved is not fully known, it is generally accepted that fynbos is adapted to fire intervals of between 10 and 30 years (van Wilgen, 1987). Prescribed burning of fynbos-dominated catchments in the south-western Cape is presently carried out at 12-15 year intervals. Management aimed at achieving objectives set for nature conservation appears equally effective in achieving the objectives of water conservation (Bands, 1987), although there are still many gaps in our understanding of the functioning of fynbos ecosystems, and little is known about the effects of fire on site productivity and the quality of drainage waters.

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Fire exerts a profound effect on the nutrient status of ecosystems. Burning mobilizes nutrients and may bring about substantial losses through volatilization and through subsequent leaching of soluble cations present in ash. Mountain fynbos is associated with strongly leached, nutrient-poor soils (Specht & Moll, 1983) derived from infertile parent material. Despite the fact that periodic fires play an important role in releasing nutrients from the litter layer (Mitchell, 1987), frequent destruction of litter may have severe repercussions on site productivity. Evidence of veld degradation and soil erosion as a result of deliberate fires can be detected on many mountain slopes in the Western Cape (Bands, 1977). In addition to such adverse effects on site productivity, substantial increases in net nutrient loss from mountain catchments could also lead to a deterioration in the quality of surface water intended for municipal use.

Although fire-induced nutrient losses to the atmosphere have received relatively little attention, the effects of fire on water quality and nutrient losses to drainage waters have been well documented for pine- and spruce-dominated catchments in the United States and Canada. The findings have been somewhat conflicting. Prescribed fire was found to have no significant effect on water quality or export of dissolved solids from catchments in the Piedmont of South Carolina (Douglass & van Lear, 1983). Johnson & Needham (1966) and McColl & Grigal (1975) did not report on ionic export, but concluded that wildfire had no effect on ionic concentrations in stream water. Conversely, Tiedemann *et al.* (1978) and Schindler *et al.* (1980) reported significant increases in both concentration and export of ions from catchments following wildfire. Recent work in Australia (Mackay & Robinson, 1987) describes similar increases in ionic concentration and export from *Eucalyptus*-dominated catchments in response to fire. In South Africa, the results of a study carried out in the south-western Cape (van Wyk, 1982) suggest that prescribed burning has a limited effect on water quality and nutrient budgets, as enhanced nutrient release was not found to persist beyond the first winter after burning. Further research is warranted, however, since this study failed to detect nitrogen or phosphorus in water samples either before or after prescribed burns.

The effects of fire on water quality clearly vary greatly. Inconsistencies arise from differences in the climates, topography, geomorphology, soil types and vegetation associated with the different study catchments, in addition to variation in the severity (wildfire versus controlled) and timing of the burns themselves and the intervals between previous fire events. The aim of the present study was to determine how fire affects stream chemistry and, by implication, nutrient export via surface runoff from a fynbos-dominated mountain catchment in the south-western Cape. The fire was a prescribed burn and was carried out in late summer, when most fires of 'natural' origin in the south-western Cape occur (Kruger, 1977).

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THE STUDY AREA.

The study catchment, Swartboskloof, is situated in the Jonkershoek Valley (34°00'S, 18°57'E) approximately 60 km east of Cape Town (Fig. 1). The valley forms part of a State-owned Mountain Catchment Area, managed by the Forestry Branch of the Department of Environment Affairs, and represents a source of both potable and irrigation water.

The climate of the region is mediterranean, with cool, wet winters and warm, dry summers. Rain falls throughout the year, although around 60 % of the annual total falls during the four winter months of June to September. A single raingauge in the Swartboskloof catchment, situated at point X in Fig. 1, gave a mean annual rainfall of 1530 mm over the period 1976-1986 (South African Forestry Research Institute - SAFRI - unpublished data). Measurements of rainfall obtained from five raingauges established more recently throughout the catchment indicate that, as might be expected, precipitation increases with

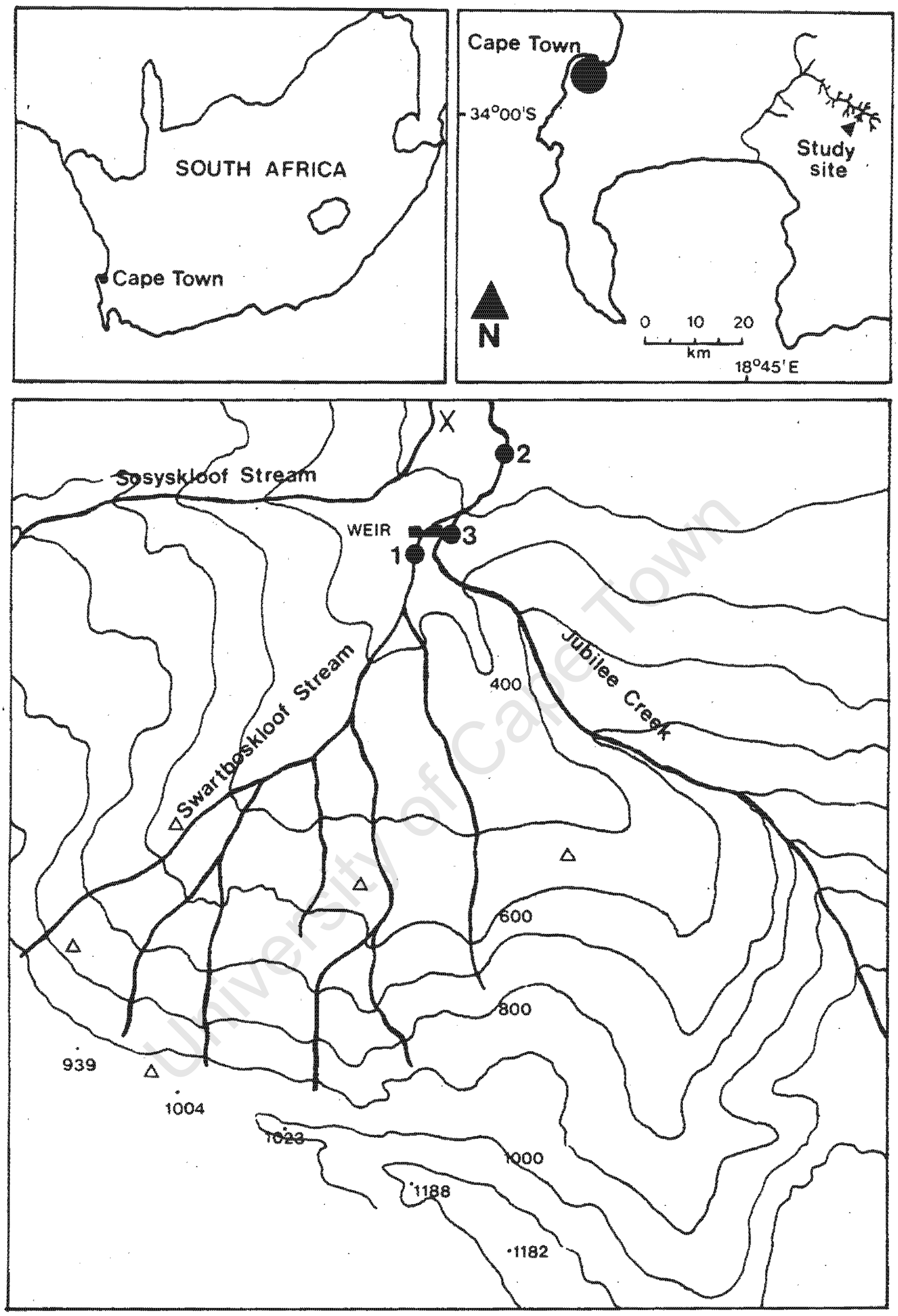

Fig. 1: Outline map of the study area. Circles indicate positions of the sampling sites, triangles represent raingauges. Oldest established raingauge represented by a cross. Contours in metres.

altitude, and therefore Swartboskloof receives considerably more rain than indicated by the single gauge. Rainfall during 1986 and 1987 at Swartboskloof, based on the average of the five raingauges, amounted to 2801.4 and 2725.9 mm respectively (SAFRI, unpublished data). Air temperature data were obtained over a 36 year period (1936-1972) from a weather station situated at the entrance to the Jonkershoek Valley, approximately 3 km from the study catchment. Temperatures range from a mean summer (December to February) maximum of 23.1 °C to a mean summer minimum of 17.3 °C and a mean winter (June to August) maximum of 14.2 °C to a mean winter minimum of 9.8 °C (van Lill, 1976).

The Swartboskloof catchment is 373 ha in area, ranges from 320 to 1200 m in altitude and has a north-easterly aspect. The geology of the catchment has been most recently described by Sohnge (1988). Briefly, quartzitic sandstones of the Table Mountain Group lie unconformably upon porphyritic Cape Granite. The sandstone forms a wall of sheer cliffs around the undulating lower slopes of the catchment where fluvial erosion, sapping and creep have progressively broken down the overlying sheet of sandstone to expose the granite floor. The soils are acid with low buffering capacity (Fry, 1987).

The vegetation of the catchment has been described in detail by McDonald (1985) and consists of sclerophyllous shrubland on open slopes and evergreen forests of Afromontane origin on sandstone boulder screes and along boulder-lined watercourses. The riparian vegetation forms an almost closed canopy over the main Swartboskloof stream and its tributaries, and extends outwards from between 10 and 20 m on either stream bank.

The streams which drain the catchment are tributaries of the Eerste River. The Swartboskloof stream, flowing from south-west to north-east, is perennial and seasonally fed by four smaller streams. Streamflow varies from 340 to 15,900 $m^3\ d^{-1}$ (SAFRI, unpublished data). Jubilee Creek, which rises outside the study area and flows along the eastern side of the catchment, is also perennial but without seasonal tributaries. The two

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streams join at the lower end of the catchment before flowing into the Eerste River. Between 400 and 720 m elevation, mean bank slopes surrounding the Swartboskloof stream and Jubilee Creek are 14.7 and 51.1 % respectively.

On 17 March 1987, the entire catchment was deliberately burned in an operation lasting approximately 30 hours. Relative humidities during the burn ranged from 37-99 %, air temperatures from 11.5-25.0 °C and wind speed from 0-23 km hr^{-1} (SAFRI, unpublished data). The fire was considered to be of low to moderate intensity (D. Versfeld, SAFRI, *pers comm.*). Virtually all the vegetation on the slopes of the catchment was burnt. Riparian vegetation was burnt at the edges along the length of the streams, although the major canopy remained unaffected. Prior to this, Swartboskloof had been protected from fire for 29 years.

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METHODS

Sampling sites

Fig. 1 shows the position of the three sampling sites established in the Swartboskloof catchment. Site 1 was situated immediately above a gauging weir on the main Swartboskloof stream. Sampling at this site commenced in January 1986. In March 1986, Site 2 was established approximately 150 m below the confluence of the Swartboskloof stream with Jubilee Creek. Site 3, established in August 1986, was situated on Jubilee Creek above its confluence with the Swartboskloof stream. Monthly sampling at the three sites was carried out until the burn in March 1987. After this, sampling was increased to two-weekly intervals until the end of June 1987, then maintained at monthly intervals until March 1988, providing one full year of post-burn data. The results of additional intensive sampling during two pre-burn and two post-burn spates will be reported elsewhere.

Field

Streamflow was measured continuously at Site 1 by means of a compound 90° V-notch weir and data logger constructed and installed by SAFRI. At sites 2 and 3 (ungauged), discharge at the time of sampling was determined using the velocity-area method described by Herschy (1985). Current velocity was measured with an Ott flow meter. Runoff (in mm) from the gauged part of the catchment was calculated by dividing total streamflow (m^3) by the gauged area of the catchment (190 ha). A network of raingauges, installed by SAFRI throughout the catchment, provided daily and monthly measurements of rainfall.

Conductivity was measured with a Crison CDTM-523 conductivity meter, accurate to 0.1 $\mu S\ cm^{-1}$, and pH with a Lilliput pH meter accurate to 0.1 pH units.

Water samples were filtered through Whatman GF/F filters and collected in 250 ml polyethene containers pre-cleaned in 5 % Extran^R solution (phosphate-free) and double-distilled water. Samples intended for NH_4^+-N determination were collected in pre-cleaned glass pill-vials. All samples - with the exception of those intended for the determination of total dissolved solids (TDS) - were frozen in the field. Samples were stored at -20 °C in darkness for up to 3 months prior to analysis.

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Laboratory

Nitrate-nitrogen, NH_4^+-N and PO_4^{3-}-P were measured with a Technicon Auto-Analyser following the methods described by Mostert (1983). Calcium and Mg^{2+} were measured on

SPECIES	METHOD	PRECISION
NO_3^- -N	Technicon Auto-Analyser (following Mostert, 1983)	Standard deviation of the mean is $\pm$ 0.26 at the level of 15 ug at. NO_3^--N ℓ^{-1}
NH_4^+-N	Technicon Auto-Analyser (following Mostert, 1983)	Standard deviation of the mean is $\pm$ 0.06 at the level of 2.5 ug at. NH_4^+-N ℓ^{-1}
PO_4^{3-} -P	Technicon Auto-Analyser (following Mostert, 1983)	Standard deviation of the mean is $\pm$ 0.04 at the level of 1.5 ug at. P ℓ^{-1}
Na^+ & K^+	IL 243 Flame Photometer	Typical within-instrument, between day relative standard deviations for the same input solution one approximately 0.5% for Na and 1% for K.
Cl^+	Volumetric method (Golterman et al., 1978)	Precision estimated at 0.5 mg ℓ^{-1} from 0-50 mg ℓ^{-1}
Total alkalinity	Acidimetric method (Golterman et al., 1978)	Precision estimated at 2-10% at total alkalinity between 1 and 0.1 mmol ℓ^{-1}

TABLE (i) Estimates of the precision of analytical methods used.

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a Perkin-Elmer atomic absorption spectrophotometer. Sodium and K^+ were measured on an IL 243 flame photometer.

Chloride determinations were made using the volumetric method described by Golterman *et al.* (1978) in which Cl^- is titrated with $Hg(NO_3)_2$ at a pH of 3.1. Total and phenolphthalein alkalinity were determined using the acidimetric method (Golterman *et al.*, 1978) with methyl-orange and phenolphthalein end-point indicators respectively. Estimates of precision for each method are given in Table (i).

Soluble polyphenolic compounds were measured as per Box (1983) using Folin-Ciocalteu phenol reagent. Total dissolved solids were measured by evaporating one litre of filtered sample to dryness in a pre-weighed glass beaker.

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Statistical analysis

Regression analysis (Zar, 1984) was used to determine relationships between rainfall and runoff data and between ionic concentration and discharge. Comparisons of slopes and elevations of regression lines were carried out using Student's t tests (Zar, 1984). Where no consistent relationship between ionic concentration and discharge could be determined, pre- and post-burn ionic concentrations were compared by means of the Mann-Whitney test (Zar, 1984). In all cases, significance was accepted at the 5 % level ($P < 0.05$).

RESULTS

Hydrology

Mean rainfall over the year preceding the burn (17 March 1986 to 16 March 1987) for the gauged part of the catchment (see Fig. 1) was 2,919 mm. Total runoff over this period was 1,213 mm. Mean rainfall for the post-burn year (17 March 1987 to 16 March 1988) was 2,468 mm, and total runoff 1,175 mm. Water yield from the catchment for the pre- and post-burn years was thus 41.6 and 47.6 % of rainfall respectively.

For each year, a strong positive correlation existed between monthly rainfall and monthly runoff (Fig. 2). The slopes and intercepts of the two regression lines did not differ significantly. It should be noted, however, that only 164 mm of rain in April 1987 was necessary to recharge soil-moisture levels, depleted over the summer months, resulting in a strong response to heavy rainfall during May and June of that year. A similar response in June of the pre-burn year was observed only after the catchment had received 619 mm during April and May. Accruals to the soil moisture store after burning are favoured by reductions in interception and transpiration losses (Bosch *et al.*, 1984).

A control catchment was used to evaluate further the effects of fire on streamflow. Weekly runoff from Swartboskloof was compared with runoff from Langrivier, a 246 ha, fynbos-dominated sub-catchment of the Eerste River, protected from fire since 1943. Langrivier is situated in the Jonkershoek Valley approximately 1.5 km north-east of Swartboskloof, and has a south-westerly aspect. The catchment has been described in detail by King *et al*, (1987). The use of this catchment as a control, however, was restricted to the first six months following the Swartboskloof burn, as Langrivier burnt on 6 October 1987 in a wildfire. Flow measurements for Langrivier were supplied by SAFRI.

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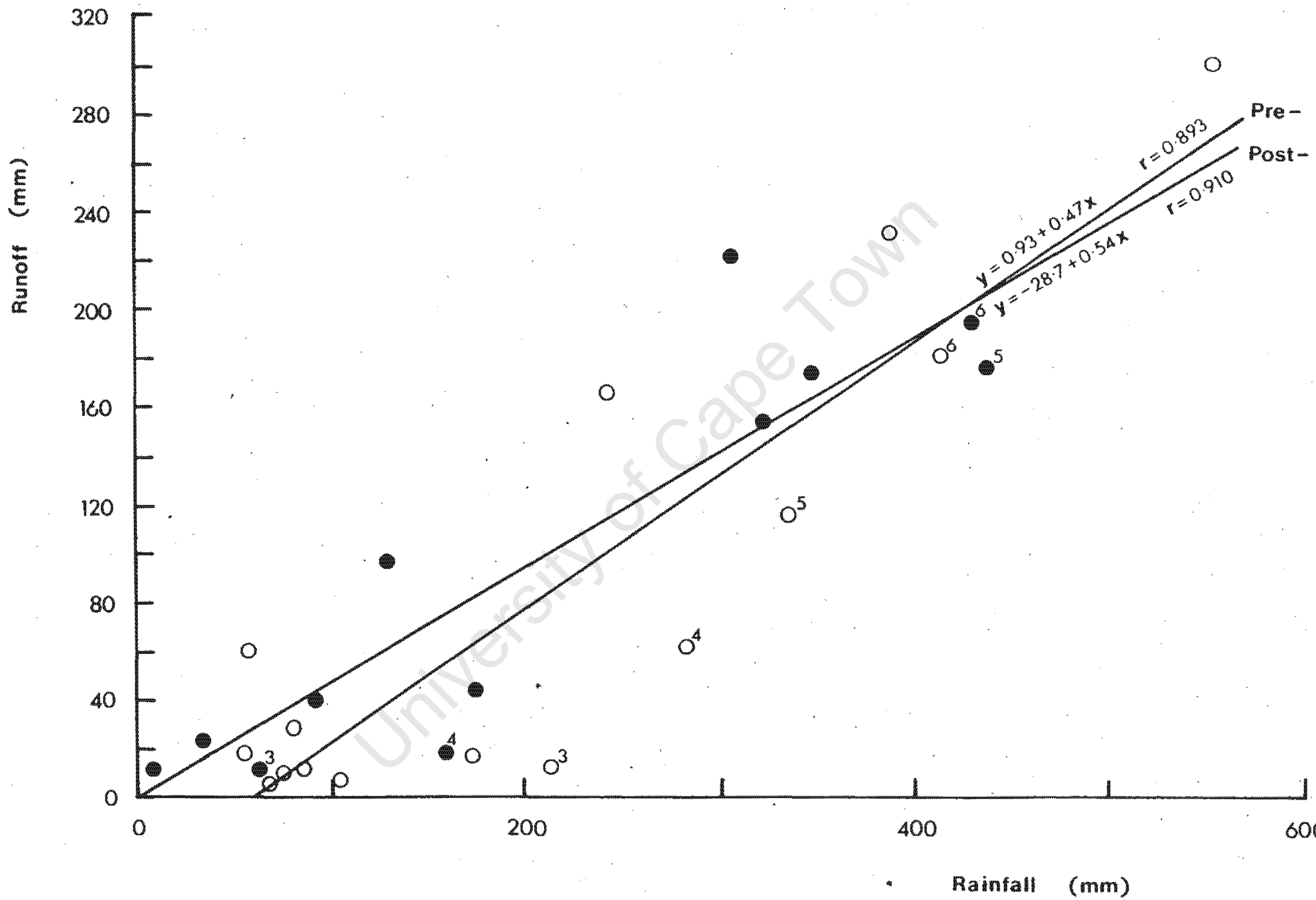

Fig. 2: Monthly runoff from Swartboskloof plotted against monthly rainfall. Open circles represent pre-burn values, solid circles represent post-burn values. 3, 4, 5 and 6 indicate values for the months of March, April, May and June respectively for the pre- and post-burn years.

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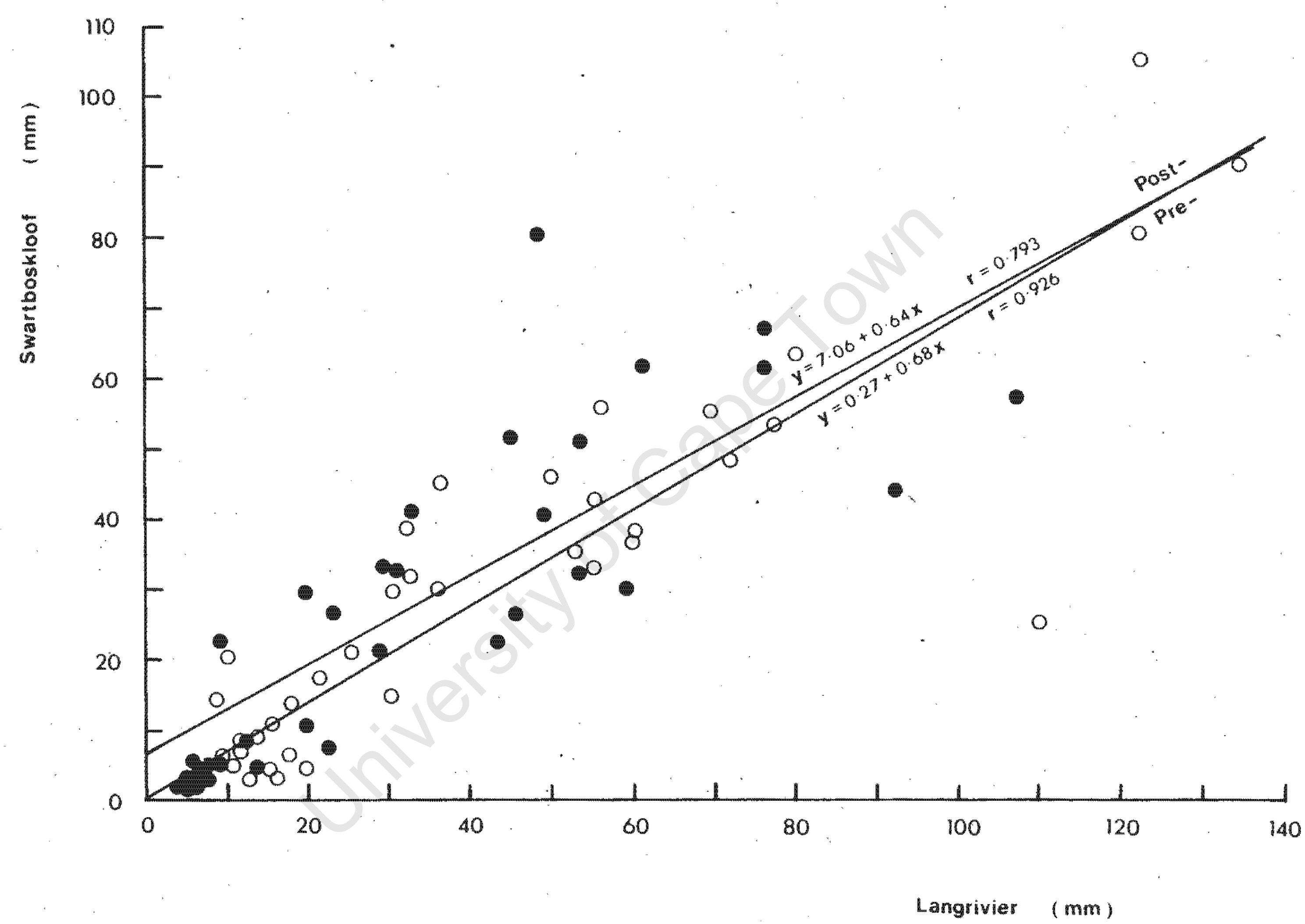

Fig. 3: Weekly runoff from Swartboskloof plotted against weekly runoff from Langrivier. Open circles represent pre-burn values, solid circles represent post-burn values.

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Weekly runoff from Swartboskloof was positively correlated with runoff from Langrivier for the pre-burn sampling period (Fig. 3). Outlying points may be attributed to differences in rainfall (due to aspect) and dissimilarities in the physical characteristics of the individual catchments which influence their hydrologies. A positive correlation also existed for the six month post-burn period, although neither the slope nor intercept of this regression differed significantly from the pre-burn regression line.

Pre-burn chemistry

The streams draining the Swartboskloof catchment are acidic and very low in dissolved substances (Table 1). Conductivity ranged from 20.2 to 30.8 $\mu S\ cm^{-1}$ for the three sites, and TDS from 17.0 to 33.1 mg l^{-1}. Nitrate-nitrogen and PO_4^{3-}-P were present at extremely low concentrations, varying between 0.3 to 29.9 and 0.6 to 10.9 $\mu g\ l^{-1}$ respectively. Ammonium concentrations were erratic at all sites, and varied between 5.3 and 65.7 $\mu g\ l^{-1}$ NH_4^+-N. The major cations (Na^+, Mg^{2+}, Ca^{2+}, K^+) were measured at sites 1 and 2 only, and were also present at very low concentrations. Stream water was poorly buffered at all sites; OH^- and CO_3^{2-} ions were not detected in any of the samples, and HCO_3^- concentrations never exceeded 9.0 mg l^{-1}. The highest concentrations of most dissolved substances and highest pHs were generally recorded at site 1 on the main Swartboskloof stream. In Jubilee Creek (site 3), stream water was almost always higher in NO_3^--N than it was at the other two sites, but lower in pH and mineral solute content. The steeper slopes surrounding Jubilee Creek encourage lateral movement of water above the mineral soil, resulting in heavy leaching of NO_3-N concentrated in the top soil horizons by biological activity, and proportionally less leaching of the lower soil horizons. Concentrations of dissolved substances at site 2 tended to be intermediate between sites 1

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Table 1 Pre- and post-burn water chemistry data for sites 1, 2 and 3. Discharge (at time of sampling) in $m^3\ s^{-1}$; TDS, HCO_3, Cl, polyphenols, Na, K, Ca, Mg in mg ℓ^{-1}; NO_3-N, NH_4-N, PO_4-P in $\mu g\ \ell^{-1}$. Conductivity in μScm^{-1}.

VARIABLE	SITE	PERIOD	n	$\overline{x}$	sd	min	med	max
Discharge	1	Pre-	14	0.05	0.05	0.007	0.028	0.148
		Post-	16	0.06	0.05	0.007	0.043	0.177
	2	Pre-	12	0.15	0.13	0.028	0.092	0.365
		Post-	16	0.16	0.14	0.027	0.104	0.463
	3	Pre-	7	0.07	0.06	0.015	0.036	0.177
		Post-	16	0.10	0.09	0.015	0.075	0.314
TDS	1	Pre-	12	26.70	3.47	20.5	26.7	33.1
		Post-	16	29.34	4.19	24.3	27.5	36.8
	2	Pre-	11	23.07	2.56	18.5	25.0	27.8
		Post-	15	24.51	2.28	21.2	24.4	29.5
	3	Pre-	7	20.94	3.50	17.0	21.3	26.8
		Post-	15	22.07	2.72	18.1	21.6	28.7
Cond.	1	Pre-	13	25.80	2.47	22.1	25.0	30.8
		Post-	16	28.95	5.65	20.2	29.1	39.9
	2	Pre-	12	24.73	2.90	19.8	24.5	28.9
		Post-	15	25.52	3.58	18.1	24.6	30.5
	3	Pre-	6	22.35	2.00	20.2	22.4	25.4
		Post-	15	24.48	4.11	19.1	23.3	30.5
pH	1	Pre-	13	5.31		4.6	5.6	6.6
		Post-	16	5.61		4.9	6.0	6.5
	2	Pre-	10	5.06		4.3	5.7	6.5
		Post-	16	5.17		4.3	5.5	6.0
	3	Pre-	6	4.86		4.7	4.8	5.2
		Post-	16	4.25		3.3	4.7	5.8

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Table 1 - continued

VARIABLE	SITE	PERIOD	n	$\bar{x}$	sd	min	med	max
HCO_3^-	1	Pre-	14	5.03	1.71	2.94	4.84	9.00
		Post-	16	5.94	1.62	3.84	5.31	9.24
	2	Pre-	12	2.34	1.32	0.78	2.21	4.80
		Post-	16	3.00	1.20	0.00	3.09	4.98
	3	Pre-	7	1.62	0.90	0.00	1.75	2.76
		Post-	16	2.04	0.54	1.68	1.83	3.60
Cl^-	1	Pre-	14	7.27	0.69	6.56	7.10	9.09
		Post-	16	8.09	1.07	6.82	7.83	10.31
	2	Pre-	12	7.57	0.71	6.72	7.43	9.44
		Post	16	7.88	1.03	6.28	7.81	9.53
	3	Pre-	7	7.35	0.61	6.46	7.64	7.89
		Post-	16	7.53	0.92	6.07	7.50	9.22
Phenols	1	Pre-	14	0.10	0.06	0.01	0.09	0.18
		Post-	16	0.14	0.12	0.04	0.08	0.41
	2	Pre-	11	0.09	0.04	0.04	0.08	0.17
		Post-	16	0.17	0.10	0.07	0.13	0.37
	3	Pre-	7	0.10	0.04	0.05	0.09	0.19
		Post-	16	0.20	0.18	0.08	0.13	0.81
NO_3^--N	1	Pre-	14	7.7	8.1	0.3	4.8	25.8
		Post-	16	15.6	16.5	0.4	8.0	50.3
	2	Pre-	12	13.2	8.9	4.9	10.9	34.9
		Post-	16	19.5	16.0	2.9	18.1	47.5
	3	Pre-	7	16.1	5.7	9.8	14.4	26.5
		Post-	16	20.5	13.4	3.2	19.2	40.0

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Table 1 - continued

VARIABLE	SITE	PERIOD	n	$\bar{x}$	sd	min	med	max
NH_4^+-N	1	Pre-	12	18.1	15.6	5.3	15.1	65.7
		Post-	16	26.9	23.2	7.1	21.3	88.6
	2	Pre-	10	16.4	5.3	8.7	18.3	24.9
		Post-	15	21.6	17.0	6.0	18.5	69.0
	3	Pre-	5	23.4	12.5	13.3	16.1	41.9
		Post-	15	30.0	23.1	5.6	23.2	97.3
PO_4^{3-}-P	1	Pre-	14	3.8	0.1	0.9	3.1	8.4
		Post-	16	3.4	2.0	1.2	3.1	9.6
	2	Pre-	12	2.9	1.7	0.9	3.1	7.1
		Post-	16	2.7	1.8	0.9	2.3	6.8
	3	Pre-	7	2.4	1.6	0.6	1.9	10.9
		Post-	16	3.1	3.0	0.6	2.5	13.3
Na^+	1	Pre-	14	5.32	0.69	4.14	5.52	6.90
		Post-	14	4.83	1.13	2.76	4.60	6.21
	2	Pre-	12	3.91	0.61	2.76	4.14	4.83
		Post-	15	4.09	0.20	3.68	4.14	4.37
K^+	1	Pre-	14	0.35	0.11	0.23	0.35	0.59
		Post-	14	0.40	0.11	0.23	0.39	0.70
	2	Pre-	12	0.21	0.08	0.12	0.27	0.27
		Post-	15	0.35	0.20	0.20	0.27	1.05
Ca^{2+}	1	Pre-	14	0.60	0.17	0.38	0.56	0.99
		Post-	15	0.52	0.12	0.40	0.46	0.80
	2	Pre-	12	0.30	0.05	0.22	0.29	0.36
		Post-	15	0.30	0.04	0.21	0.30	0.35

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Table 1 - continued

VARIABLE	SITE	PERIOD	n	$\overline{x}$	sd	min	med	max
Mg^{2+}	1	Pre-	14	0.46	0.04	0.39	0.46	0.53
		Post-	15	0.44	0.04	0.34	0.44	0.48
	2	Pre-	12	0.43	0.07	0.37	0.41	0.61
		Post-	15	0.41	0.05	0.34	0.41	0.53

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and 3; stream water from Jubilee Creek serving to dilute the higher concentrations in the main Swartboskloof stream.

Although TDS concentrations at all sites were generally higher during the summer months when discharge was low, there were few statistically significant relationships between the concentration of individual ions and discharge. At sites 1 and 2, a positive, linear relationship existed between NO_3^--N concentration and discharge (Fig. 4). A similar, but non-significant relationship between these two variables was also found at site 3. A significant relationship between conductivity and discharge ($y = 22.2 + 16.75\ x$, $r = 0.768$) was found at site 2 only. At site 1, significant relationships existed between discharge (x) and the following variables: HCO_3^- ($y = 2.07\ x^{-0.23}$, $r^2 = 0.67$), Ca^{2+} ($y = 0.29\ x^{-0.19}$, $r^2 = 0.61$), Na^+ ($y = 3.97\ x^{-0.08}$, $r^2 = 0.527$) and polyphenols ($y = 0.02\ x^{-0.38}$, $r^2 = 0.33$). Chloride concentration was significantly related to discharge at site 3 ($y = 7.94 - 9.01\ x$, $r = 0.913$). Other ions measured at each of the sites showed either a weak, negative relationship or no relationship with discharge.

Post-burn chemistry

Higher conductivities and elevated levels of TDS, Cl^- and polyphenols were recorded at all three sites during the first seven weeks after the fire. In early May 1987, at site 3, the stream water, which was usually colourless, was stained light-brown, reflecting the higher (0.81 mg l^{-1}) polyphenol content. Short-lived flushes of NH_4^+-N occurred at sites 1 and 2 immediately after the burn (Fig. 5). A post-fire flush of NO_3^--N, unrelated to discharge, was also recorded at site 1 one week after the fire.

At all three sites, NO_3^--N concentrations were higher during the months of May to October than during the corresponding pre-burn sampling period, and again showed a positive relationship with discharge (Fig. 4). Mean post-burn NO_3^--N concentrations at sites 1 and

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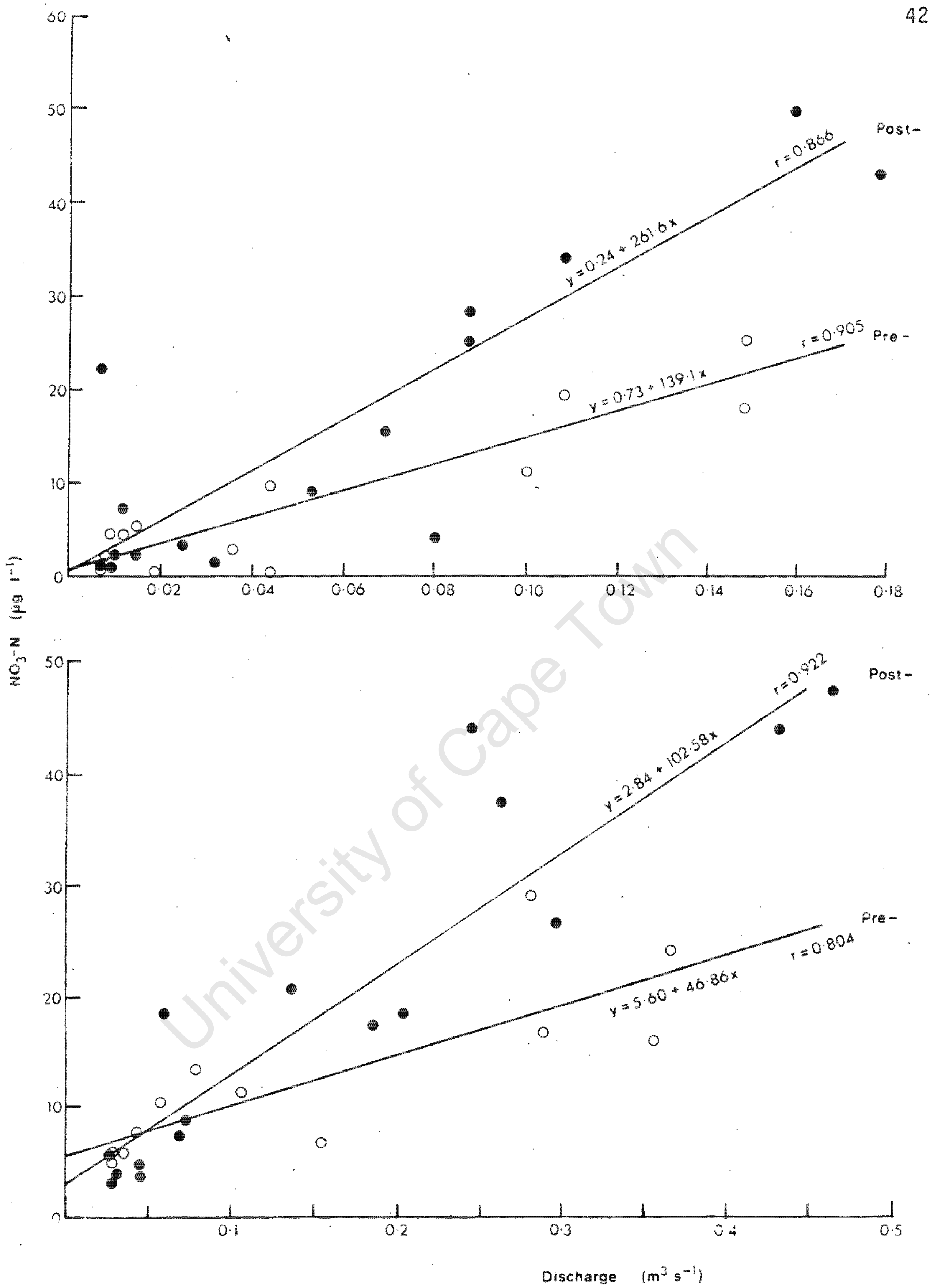

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Fig. 4: Nitrate concentrations plotted against discharge at sites 1 and 2. Open circles represent pre-burn values, solid circles represent post-burn values.

2 from May to October were 103 and 81 % higher, respectively, than the corresponding pre-burn period, although parallel increases in mean post-burn discharge (at the time of sampling) were just 5 and 9 % higher. Pre- and post-burn regressions between NO_3^--N concentration and discharge were compared for sites 1 and 2. The slopes differed significantly at both sites, indicating increased NO_3^--N concentrations during the post-burn year at a given discharge. Although a significant post-burn relationship between NO_3^--N concentration and discharge was recorded at site 3, pre- and post-burn samples were not compared, as the pre-burn relationship was not significant.

Phosphate concentrations in stream water at sites 1 and 2 were generally lower during the post-burn year. Potassium levels peaked in early May at site 1 (0.18 mg l^{-1}) and in early June at site 2 (0.27 mg l^{-1}).

Bicarbonate concentrations increased slightly three weeks after the fire at all three sites. Sites 1, 2 and 3 showed peaks of 9.24, 4.98 and 3.6 mg l^{-1} respectively. These increases corresponded with the first post-burn rain event in which the catchment received 15 mm of rain over two days. Bicarbonate concentrations at site 1 were again significantly related to discharge ($y = 3.03\ x^{-0.19}$, $r^2 = 0.746$) as were Ca^{2+} concentrations ($y = 0.34\ x^{-0.12}$, $r^2 = 0.431$). There was no significant difference between the slopes and intercepts of pre- and post-burn regressions for Ca^{2+} concentration and discharge, although the intercepts of the HCO_3^- regressions differed significantly, indicating that concentrations in the post-burn year were significantly higher.

The results of comparisons of pre- and post-burn ionic concentrations using the Mann-Whitney test are presented in Table 2. Although NH_4^+-N concentrations during the post-burn year were slightly higher at all three sites, differences between pre- and post-burn concentrations over the whole year were not significant. A significant increase in Cl^- concentration was recorded at site 1 during the post-burn year. Sodium concentrations were

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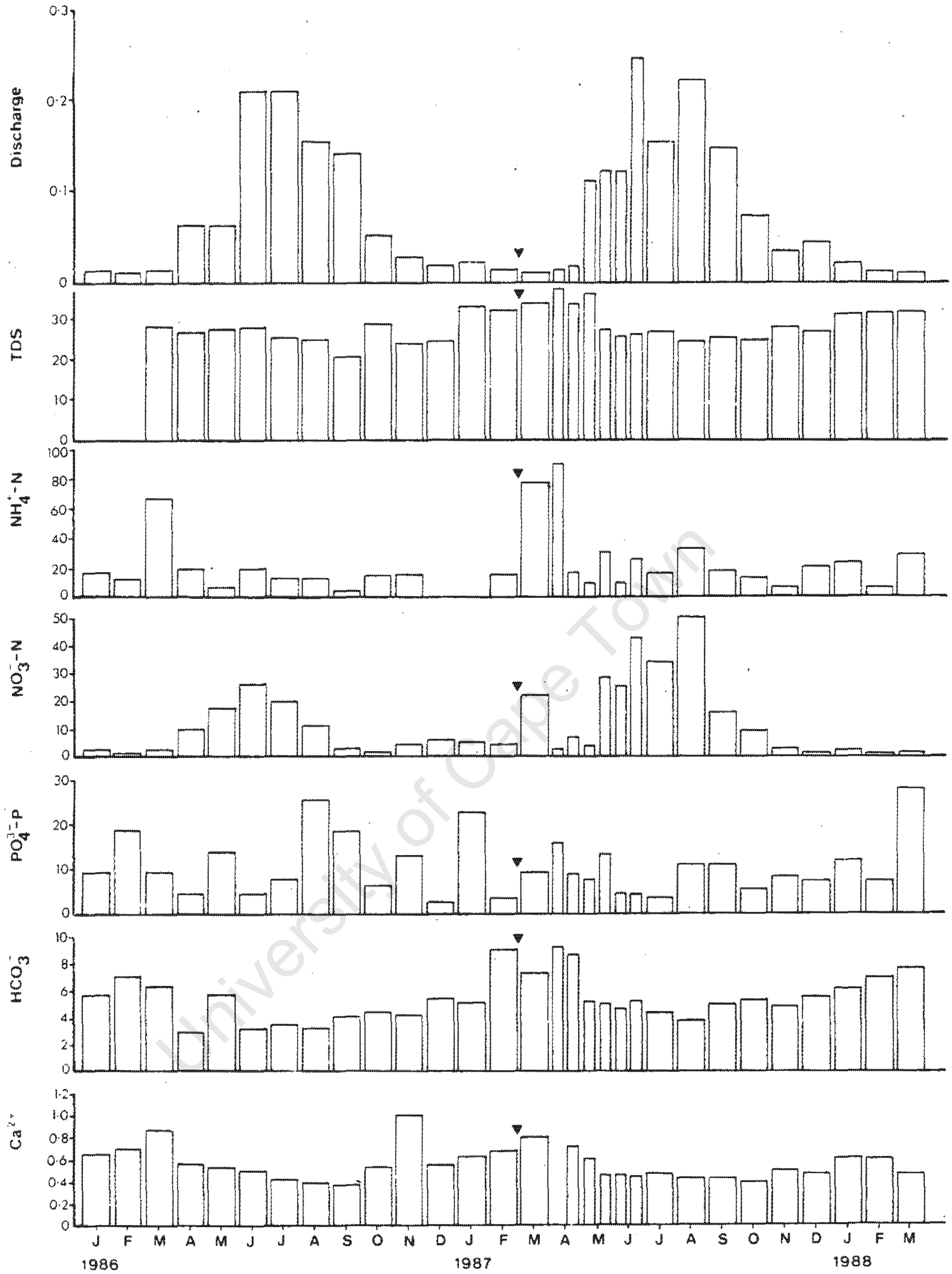

Fig. 5: Instantaneous discharge and concentrations of six variables in stream water at site 1 over the entire sampling period. Discharge in $m^3\ s^{-1}$; TDS, HCO_3 and Ca in mg l^{-1}; NH_4-N, NO_3-N and PO_4-P in µg l^{-1}. Arrows indicate the timing of the prescribed burn.

Table 2 Comparison of pre- and post-burn ionic concentrations using the Mann-Whitney test. 'ns' indicates concentrations in the post-burn year do not differ significantly from pre-burn concentrations. Arrows indicate increased or decreased concentrations in the post-burn year.

	SITE		
VARIABLE	1	2	3
TDS	ns	ns	ns
pH	ns	ns	ns
NH_4-N	ns	ns	ns
PO_4-P	ns	ns	ns
HCO_3	–	▲	ns
Phenols	ns	▲	▲
Cl	▲	ns	ns
Na	▼	ns	–
K	ns	▲	–
Ca	–	ns	–
Mg	ns	ns	–

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significantly lower in the post-burn year. Increases in HCO_3^-, polyphenol and K^+ concentrations were recorded at site 2 over the post-burn year, and at site 3 there was a significant increase in polyphenol concentration.

DISCUSSION

Effects of the precribed burn on water yield

Increased nutrient outputs from disturbed catchments may be masked by large increases in hydrologic output (see, for example, Tiedemann *et al.*, 1978) but, as Lindley *et al.* (1988) point out, major changes in streamflow are relatively easy to detect. Comparison of pre- and post-burn rainfall-runoff relationships for the Swartboskloof catchment and comparison of runoff data with data for the control catchment, Langrivier, revealed little evidence of any major increase in hydrological output after the fire, and it can therefore be concluded that the prescribed burn had no demonstrable effect on water yield. To a large extent, this finding may be attributed to the rapid growth of post-fire vegetation, which increases transpiration and interception losses, and the fact that the riparian vegetation was not destroyed by the fire. Riggs (1965) notes that the clearing of land along stream channels seems to have a greater effect on discharge than clearing over the catchment generally. Work carried out by Nanni (1972) in a small catchment in the Natal Drakensberg has effectively demonstrated an increase in daily runoff of approximately 12 litres for every meter of streambank cleared of riparian vegetation. Such increases are expected to be greater in the south-western Cape mountain catchments, as transpiration losses in the Natal Drakensberg - where summers are wet and winters cool and dry - are generally much lower than in the south-western Cape, where summers are hot and dry and winters wet (Nanni, 1972).

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In concluding that the prescribed burn had no appreciable effect on water yield from the gauged part of the catchment, it is assumed that water yield from the ungauged parts was similarly unaffected, and that any increases in nutrient export must therefore be the result of increases in chemical concentration.

Effects of the prescribed burn on water chemistry

The effects of disturbance on water chemistry are usually determined using the 'paired catchment' approach, where comparisons are made between the chemistry of the disturbed catchment and that of a physiographically similar and undisturbed 'control'. In the present study, this approach was not feasible due to insufficient chemistry data for the Langrivier catchment, and it was therefore necessary to employ alternative methods. The first method used was similar in principle to the paired catchment approach, and involved the comparison of pre- and post-burn relationships between ionic concentration (expected to be affected by fire) and discharge (proved not to be affected). Where no significant relationships could be detected, the Mann-Whitney test has been used to compare pre- and post-burn ionic concentrations.

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In freshwater lotic systems, discharge is considered to be one of the most significant factors influencing the concentration of dissolved solids (Edwards, 1973; O'Connor, 1976), and relationships between these variables have been well documented (Toler, 1965; Johnson *et al.*, 1969; Edwards, 1973; Glover & Johnson, 1974; O'Connor, 1976; Bond, 1979; Lewis & Grant, 1979; Cornish, 1982; Rieger *et al.*, 1982; Keller *et al.*, 1986). In the present study, although TDS concentrations were generally higher in summer and lower in winter at all three sites, sampling at monthly intervals revealed few statistically significant relationships between the concentration of individual ions and discharge. Assuming, as a regression equation does, that the relationship between ionic concentration and discharge is constant, such a finding may be ascribed to inaccurate flow measurements at ungauged sites, to analytical error (many chemical analyses were performed close to their limits of detection and sensitivity) or to the fact that samples were collected at discharges which ranged over only two orders of magnitude (as opposed to five orders as in some rivers in the U.S., where there may be well-defined dilution patterns of dissolved load - Edwards, 1973). Intensive sampling of stream water during storm events, however, confirmed that the relationship between solute concentration and discharge is far more complex than that assumed by the fixed coefficients of a regression equation (Britton *et al.*, in prep.). For example, some ions (eg. PO_4^{3-}, H^+), may exhibit lags of several hours between discharge peaks and concentration peaks (or troughs), others (eg. Cl^-, NH_4^+) may exhibit hysteretic relationships between concentration and discharge, and many concentration-discharge relationships appear to be strongly influenced by antecedent conditions in the surrounding catchment. Relationships between solute concentration and discharge for all but the most mobile of ions may thus pass undetected when samples are collected at monthly intervals. In the light of these findings, it may therefore be incorrect to assume that because correlation coefficients are not significant, relationships between the concentrations of some ions in stream water and discharge do not exist. Comparison of pre- and post-burn ionic concentrations by means of the Mann-Whitney test is nevertheless considered viable here, as the range of discharges over which sampling was carried out was similar for the pre- and post-burn years, and in all but one case (July 1987), samples were collected on the falling limb of the hydrograph.

The ionic species which displayed a consistent relationship with discharge over the pre- and post-burn sampling periods were NO_3^- (at all sites) and HCO_3^- and Ca^{2+} (at site 1). That NO_3^- concentrations showed a significant, positive correlation with discharge is consistent with reports by Johnson *et al.* (1969) and Edwards (1973). Comparison of the slopes of pre- and post-burn regressions revealed significant differences at site 1 and 2. Nitrate

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concentrations thus appeared to increase significantly during the post-burn year. Tiedemann *et al.* (1978), Schindler *et al.* (1980) and Mackay & Robinson (1987) all reported substantial increases in NO_3^- concentration in stream water following wildfires. Increased NO_3^- concentrations are indicative of disturbance within a catchment (Pierce *et al.*, 1970; Swank & Douglass, 1975; Vitousek *et al.*, 1979) and reflect an interruption in established soil/plant nutrient cycles. Increases in stream NO_3^--N levels after fire have been ascribed to enhanced nitrification and reduced demand for NO_3^--N by vegetation (Tiedemann *et al.*, 1978). Nitrate is one of the most mobile ions in soil-water systems, and when uptake by vegetation is reduced, excess NO_3^- moves with moisture through the soil to drainage waters and is lost from the system.

The five-month period of enhanced NO_3^--N concentrations in Swartboskloof stream water compares favourably with the findings of Stock & Lewis (1986[a]) who reported a 9 month post-fire increase in available soil NO_3^--N in a coastal fynbos system. Stock & Lewis (1986[a]) also reported a post-fire flush of NH_4^+-N at the soil surface resulting from the deposition of partially combusted plant material and the physical and chemical breakdown of organic matter in the upper soil layers. This increase was short-lived and rapidly disappeared due to nitrification. Similar short-lived post-fire peaks of NH_4^+-N in stream water were observed in the present study at sites 1 and 2.

Bicarbonate concentrations during the post-burn year were significantly higher at two of the three sites. Bicarbonate is an end product of respiration in undisturbed catchments and a product of oxide conversion following fire (Tiedemann *et al.*, 1979). Short-lived increases in HCO_3^- levels have been reported by Tiedemann *et al.* (1978) and attributed to ash deposition in the stream. It is probable that the comparatively long-term increases observed in the Swartboskloof study occurred as a result of the leaching of ash deposited throughout the catchment.

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Significant increases in Cl^- (site 1) and polyphenol (sites 2 and 3) concentrations during the post-burn year were also identified. At site 2, mean K^+ concentrations increased by 80 % during the post-burn year. Potassium levels were not affected at site 1, so it is likely that the observed increases at the lower site were due to increased concentrations in Jubilee Creek, although data for site 3 are not available to support this. Apart from K^+ at site 2, post-burn cation concentrations in stream water did not differ significantly from pre-burn concentrations. Johnson & Needham (1966) proposed that dissolved major cations from ash may be adsorbed onto soil particles rather than being washed directly into streams. Additionally, in contrast to the highly mobile NO_3^- ion, the PO_4^{3-} ion reacts vigorously with the soil and thus very little passes through the soil profile into drainage waters (Bailey, 1968). The uptake of water-soluble elements by unburned buffer strips bordering stream channels has also been reported to limit nutrient loss following fires (Richter *et al.*, 1982). The decrease in Na^+ concentration at site 1 during the post-burn year is hard to explain, especially in view of the fact that Cl^- concentrations were significantly higher at this site after the burn. It is assumed that Na^+ is derived mainly from the solution of chlorides.

pH values were slightly, but not significantly lower throughout the post-burn year at site 3, and pH was similarly unaffected at the other two sites. After the fire, H^+ concentration was found to correlate positively with polyphenol levels at site 3, suggesting that post-burn concentrations of humic substances at this site were at high enough concentrations to influence stream pH. Polyphenol concentrations were, in turn, closely associated with leaf-fall from riparian trees. Exposure of the riparian canopy to high temperatures during the course of the burn resulted in a heavy post-burn leaf-fall (Britton, 1990) which lasted approximately two months and appeared to be the cause of high polyphenol concentrations in stream water at all three sites. Polyphenol concentrations at sites 2 and 3 were higher than at site 1, and this may have been due to heavier leaf-falls along Jubilee Creek in

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comparison with falls along the main Swartboskloof stream. This cannot be confirmed, however, as litter-fall data are available for site 1 only.

Effects of the prescribed burn on nutrient export

In the present study, financial constraints restricted the number of samples that could be collected. As a consequence, the small data set imposes limitations on the accuracy of quantitative estimates of total ionic export during the pre- and post-burn years. A rough estimate of ionic export from the gauged part of the catchment may be obtained by multiplying mean ionic concentration at site 1 by total runoff and dividing by drainage area (190 ha.). Values for ionic export during the pre- and post-burn years are presented in Table 3.

Export of most ions from the gauged part of the catchment was greater in the post-burn year, although these results, as well as the results for pre- and post-burn ionic concentrations, must be interpreted with caution. Large differences in input and output of nutrients may occur from year to year, according to variations in the hydrologic cycle and ionic concentrations for precipitation and stream water (Likens *et al.*, 1971). Without an extensive pre-burn data record of stream chemistry, or control catchment data for comparison, it is not possible to determine with certainty whether small increases in either ionic concentration or ionic export are directly attributable to the fire or simply lie within the natural range of year-to-year variation. Increases in the export of individual ions from the gauged part of the catchment, relative to pre-burn values, rarely exceeded 40 %, and it is probable that these increases lie within the normal ranges of the catchment in its undisturbed state. In the case of NO_3^--N, however, where concentrations were found to increase significantly at two sites during the post-burn year, and where export from the gauged part of the catchment was 100 % higher than the pre-burn year, it is very likely that

Table 3 Export in kg ha^{-1} yr^{-1} from the gauged part of the Swartboskloof catchment for the pre- and post-burn years (March 1986 to February 1987 and March 1987 to February 1988).

VARIABLE	PRE-BURN	POST-BURN	% DIFFERENCE
Runoff (m^3)	2,304,186	2 232,830	-3.1
TDS	323.8	344.8	+6.5
Cl^-	88.17	95.07	+7.8
Na^+	64.52	56.76	-12.0
HCO_3^-	61.00	69.81	+14.4
Ca^{2+}	7.28	6.11	-16.1
Mg^{2+}	5.58	5.17	- 7.3
K^+	4.24	4.70	+10.8
Phenols	1.21	1.65	+36.4
NH_4^+-N	0.22	0.32	+45.5
NO_3^--N	0.09	0.18	+100.0
PO_4^{3-}-P	0.05	0.04	-20.0

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increased losses occurred as a result of the fire. Because the sampling period did not extend further than the first post-burn year, it is not possible to comment on NO_3^--N losses beyond this period; however, the potential for movement of NO_3^--N from the soil to drainage waters will be progressively reduced with the recovery of post-fire vegetation and the re-establishment of soil/plant nutrient cycles.

Consequences for site productivity

In the post-burn year, increases in the concentration of NO_3^--N, HCO_3^-, Cl^-, K^+ and polyphenols in stream water were recorded at one or more of the sites. Apart from NO_3^--N and K^+, it is unlikely that enhanced losses of these species will have a major impact on the productivity of mountain fynbos ecosystems, especially in the quantities measured.

It is probable that the productivity of fynbos ecosystems is most significantly affected by the availability of N and P (Groves, 1983; Specht & Moll, 1983). The results of the present study suggest that while P export in the form of PO_4^{3-} was not enhanced during the post-burn year, N losses in the form of NO_3^- increased after the burn due to significant increases in ionic concentration in stream water. Export of NO_3^--N in the post-burn year was estimated to be 0.18 kg N ha^{-1}, an increase of 100 % over the pre-burn year. Annual precipitation inputs of NO_3^--N to the study area have been estimated at between 0.5 and 0.95 kg N ha^{-1} (Bohm, 1985; Stock & Lewis, 1986[b]; Britton - unpublished data), so that enhanced NO_3^--N losses from the burnt catchment in stream water will be offset by precipitation inputs. Care must be taken, however, when drawing conclusions about the overall effects of fire on site productivity, since atmospheric losses of nutrients in smoke were not quantified, and may represent a substantial net loss to the system. Debano & Conrad (1978), working in a Californian chaparral ecosystem, reported N losses of

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146 kg ha^{-1} during the course of a prescribed burn due to volatilization of nitrogen in the plants, litter and upper soil layers.

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University of Cape Town

REFERENCES

Bailey, G.W., 1968.
Role of soils and sediment in water pollution control. Part 1: Reactions of nitrogenous and phosphatic compounds with soils and geologic strata. U.S.D.I. Federal Water Pollution Control Administration, Southeast Water Laboratory.

Bands, D.P., 1977.
Prescribed burning in Cape fynbos catchments. In: H.A. Mooney & C.E. Conrad (tech. coordinators), Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems, Palo Alto, California. U.S.D.A. For. Serv. Gen. Tech. Rep. WO-3: 245-256.

Bands, D.P., 1987.
Management of fynbos mountain catchments. South African Institute of Forestry Handbook: 509-521.

Bohm, M., 1985.
Rain acidity in Stellenbosch. S. Afr. J. Sci. 81: 652-654.

Bond, H.W., 1979.
Nutrient concentration patterns in a stream draining a montane ecosystem in Utah. Ecology 60: 1184-1196.

Bosch, J.M. & J.D. Hewlett, 1982.
A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. J. Hydrol. 55: 3-23.

Bosch, J.M., R.E. Schulze and F.J. Kruger, 1984.
The effect of fire on water yield. In: P. de V. Booysen & N.M. Tainton (eds.) Ecological Effects of Fire in South African Ecosystems. Springer-Verlag, Ecological Studies Series, 48: 327-348.

Box, J.D., 1983.
Investigation of the Folin-Ciocalteu phenol reagent for the determination of polyphenolic substances in natural waters. Wat. Res. 17: 511-525.

University of Cape Town

Britton, D.L., 1990.
Fire and the dynamics of allochthonous detritus in a South African mountain stream. Freshwat. Biol. 24: 347-360.

Britton, D.L., J.A Day & M-P Henshall-Howard, (in prep.)
Hydrochemical response during storm events in a South African mountain catchment: The influence of antecedent conditions and catchment disturbance.

Cornish, P.M., 1982.
The variation of dissolved ion concentration with discharge in some New South Wales streams. Proceedings of the First National Symposium on Forest Hydrology, Melbourne. Institution of Engineers and Australian Forestry Council, 82/6: 67-71.

Debano, L.F. & C.E. Conrad, 1978.
The effect of fire on nutrients in a chaparral ecosystem. Ecology 59: 489-497.

Department of Water Affairs, 1986.
Management of the water resources of the Republic of South Africa. Department of Water Affairs, Pretoria.

Douglass, J.E. & D.H. Van Lear, 1983.
Prescribed burning and water quality of ephemeral streams in the Piedmont of South Carolina. For. Sci. 29: 181-189.

Edwards, A.M.C., 1973.
The variation of dissolved constituents with discharge in some Norfolk rivers. J. Hydrol. 18: 219-242.

Edwards, D., 1984.
Fire regimes in the biomes of South Africa. In: P. de V. Booysen & N.M. Tainton (eds.), Ecological Effects of Fire in South African Ecosystems. Springer-Verlag, Ecological Studies Series 48: 20-37.

Fry, M.St.J., 1987.
A detailed characterization of soils under different fynbos-climate-geology conditions in the south-western Cape. M.Sc. thesis, University of Stellenbosch.

University of Cape Town

Glover, B.J. & P. Johnson, 1974.
Variations in the natural chemical concentration of river water during flood flows, and the lag effect. J. Hydrol. 22: 303-316.

Golterman, H.L., R.S. Clymo & M.A.M. Ohnstad, 1978.
Methods for physical and chemical analysis of fresh waters. International Biological Programme Handbooks, 8, (2nd ed.) Blackwell Scientific Publications.

Groves, R.H., 1983.
Nutrient Cycling in Australian Heath and South African Fynbos. In: F.J Kruger, D.T. Mitchell & J.U.M. Jarvis (eds.), Mediterranean-type Ecosystems - The Role of Nutrients. Springer-Verlag, Ecological Studies Series, 43: 179-191.

Herschy, W.R., 1985.
Streamflow measurement. Elsevier Applied Science Publishers Ltd., Barking, Essex.

Johnson, C.M. & P.R. Needham, 1966.
Ionic composition of Sagehan Creek, California, following an adjacent fire. Ecology, 47: 636-639.

Johnson, N.M., G.E. Likens, F.H. Bormann, D.W. Fisher & R.S. Pierce, 1969.
A working model for the variation in stream water chemistry at the Hubbard Brook Experimental Forest, New Hampshire. Wat. Resour. Res. 5: 1353-1363.

Keller, H.M., F. Forster & P. Weibel, 1986.
Factors affecting stream water quality: Results of a 15 year monitoring study in the Swiss prealps. Proceedings of the Symposium on Monitoring to Detect Changes in Water Quality Series, Budapest. IAHS Publ. 157: 215-225.

King, J.M., M-P Henshall-Howard, J.A. Day & B.R. Davies, 1987.
Leaf-pack dynamics in a southern African mountain stream. Freshwat. Biol. 18: 325-340.

Kruger, F.J., 1977.
Ecology of Cape Fynbos in relation to fire. In: H.A. Mooney & C.E. Conrad (tech. coordinators), Proceedings of the Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems, Palo Alto, California. U.S.D.A. For. Serv. Gen. Tech. Rep. WO-3: 75-84.

University of Cape Town

Lewis, W.M. Jr. & M.C. Grant, 1979.
Relationships between stream discharge and yield of dissolved substances from a Colorado mountain watershed. Soil Sci. 128: 353-363.

Likens, G.E., F.H. Bormann, R.S. Pierce & D.W. Fisher, 1971.
Nutrient-hydrologic cycle interaction in small forested watershed-ecosystems. In: P. Duvigneaud (ed.), Proceedings of the Symposium on Productivity of Forest Ecosystems, (Ecology and Conservation, 4), Brussels: 553-563.

Lindley, A.J., J.M. Bosch & D.B. van Wyk, 1988.
Changes in water yield after fire in fynbos catchments. Water S.A. 14: 7-12.

Mackay, S.M. & G. Robinson, 1987.
Effects of wildfire and logging on streamwater chemistry and cation exports of small forested catchments in southeastern New South Wales, Australia. Hydrol. Processes 1: 359-384.

McColl, J.G. & D.F. Grigal, 1975.
Forest fire: Effects on phosphorus movement to lakes. Science 188: 1109-1111.

McDonald, D.J., 1985.
The plant communities of Swartboschkloof, Jonkershoek. South African National Scientific Programmes Rep. 104. Foundation for Research Development, Pretoria.

Mitchell, D.T., 1987.
Fire and fynbos ecosystem nutrient dynamics. In: R.M. Cowling, D.C. Le Maitre, B. McKenzie, R.P. Prys-Jones & B.W. van Wilgen (eds.), Disturbance and the Dynamics of Fynbos Biome Communities. South African National Scientific Programmes, Rep. 135: 69-73. Foundation for Research Development, Pretoria.

Mostert, S.A., 1983.
Procedures used in South Africa for the automatic photometric determination of micronutrients in seawater. S. Afr. J. Mar. Sci. 1: 189-198.

Nanni, U.W., 1972.
Water-use by riparian vegetation at Cathedral Peak. S. Afr. For. J. 80: 1-10.

University of Cape Town

O'Connor, D.J., 1976.
The concentration of dissolved solids and river flow. Water Resour. Res. 12: 279-294.

Pierce, R.S., J.W. Hornbeck, G.E. Likens & F.H. Bormann, 1970.
Effect of elimination of vegetation on stream water quality and quantity. In: Proceedings of the International Symposium on the Results of Research on Representative and Experimental Basins, Wellington, New Zealand. IASH - Unesco: 311-328.

Richter, D.D., C.W. Ralston & W.R. Harms, 1982.
Prescribed fire: Effects on water quality and forest nutrient cycling. Science, 215: 661-663.

Rieger, W.A., L.J. Olive & J.S. Burgess, 1982.
The behaviour of sediment concentrations and solute concentrations in small forested catchments. In: Proceedings of the First National Symposium on Forest Hydrology, Melbourne. Institution of Engineers and Australian Forestry Council, 82/6: 79-83.

Riggs, H.C., 1965.
Effect of land use on the low flow of streams in Rappahannock County, Virginia. U.S. Geol. Surv. Prof. Paper 525-C: 196-198.

Schindler, D.W., R.W. Newbury, K.G. Beaty, J. Prokopowich, T. Ruszczynski & J.A. Dalton, 1980.
Effects of a windstorm and forest fire on chemical losses from forested watersheds and on the quality of receiving streams. Can. J. Fish. aquat. Sci. 37: 328-334.

Sohnge, A.P.G., 1988.
The geology of Swartboskloof. Unpublished Report, Dept. of Geology, University of Stellenbosch.

Specht, R.L. & E.J. Moll, 1983.
Mediterranean-type heathlands and sclerophyllous shrublands of the world: An overview. In: F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis (eds.), Mediterranean-type Ecosystems - the Role of Nutrients. Springer-Verlag, Ecological Studies Series, 43: 41-65.

University of Cape Town

Stock, W.D. & O.A.M. Lewis, 1986[a].
Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. J. Ecol. 74: 317-328.

Stock, W.D. & O.A.M. Lewis, 1986[b].
Atmospheric input of nitrogen to a coastal fynbos ecosystem of the south-western Cape Province, South Africa. S. Afr. J. Bot. 52: 273-276.

Swank, W.T. & J.E. Douglass, 1975.
Nutrient flux in undisturbed and manipulated forest ecosystems in the Southern Appalachian Mountains. In: Proceedings of the Conference of the International Association of Hydrological Sciences, Tokyo. IAHS Publ. 117: 445-456.

Tiedemann, A.R., J.D. Helvey & T.D. Anderson, 1978.
Stream chemistry and watershed nutrient economy following wildfire and fertilization in Eastern Washington. J. envir. Qual. 7: 580-588.

Tiedemann, A.R., C.E. Conrad, J.H. Dieterich, J.W. Hornbeck, W.F. Megahan, L.A. Viereck & D.D. Wade, 1979.
Effects of fire on water - A state of knowledge review. USDA For. Serv. Gen. Tech. Rep. WO-10.

Toler, L.G., 1965.
Relation between chemical quality and water discharge in Spring Creek, Southwestern Georgia. U.S. Geol. Surv. Prof. Paper 525-C: 209-213.

van Lill, W.S., 1976.
'n Klimaat beskrywing van die Jonkershoek Bosnavorsingstasie met die doel om klimaatverandering wat stroom afvoer kan beinvloed, opte spoor. M.Sc. Thesis, University of Stellenbosch.

van Wilgen, B.W., 1987.
Fire regimes in the fynbos biome. In: R.M. Cowling, D.C. le Maitre, B. Mackenzie, R.P. Prys-Jones & B.W. van Wilgen (eds.), Disturbance and the Dynamics of Fynbos Biome Communities. South African National Scientific Programmes Report 135: 6-14. Foundation for Research Development, Pretoria.

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van Wyk, D.B., 1982.
Influence of prescribed burning on nutrient budgets of mountain fynbos catchments in the SW Cape, Republic of South Africa. In: C.E. Conrad and W.C. Oechel (eds.), Proceedings of the Symposium on Dynamics and Management of Mediterranean-type Ecosystems, San Diego State University, California, 390-396.

Vitousek, P.M., J.R. Gosz, C.C. Grier, J.M. Melillo, W.A. Reiners & R.L. Todd, 1979.
Nitrate losses from disturbed ecosystems. Science 204: 469-474.

White, F. 1978.
The Afromontane region. In: M.J.A. Werger & J.C. Van Bruggen (eds.), Biogeography and Ecology of Southern Africa. Monogr. Biol. 3. W. Junk, The Hague. pp. 463-513.

Zar, J.H., 1984.
Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, New Jersey.

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HYDROCHEMICAL RESPONSE DURING STORM EVENTS IN A SOUTH AFRICAN MOUNTAIN CATCHMENT: THE INFLUENCE OF ANTECEDENT CONDITIONS AND CATCHMENT DISTURBANCE

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ABSTRACT

The influence of different antecedent conditions on hydrochemical response during storm events was investigated in a small, south-western Cape mountain catchment. Winter and summer storms (four in total) were sampled both before and after the catchment was deliberately burnt. During winter storms, discharge responded rapidly to rainfall, and direct runoff represented the major component of streamflow. Marked lags were observed between rainfall and discharge peaks during the summer storms, and streamflow was dominated by delayed interflow. Chloride, PO_4^{3-}-P and NO_3^--N exhibited variable response to discharge according to seasonal variations in soil-moisture levels, whereas the response of HCO_3^-, H^+ and NH_4^+-N was not influenced by season. The movement of ions appears to be affected more by geochemical processes operating within the soil than by plant-uptake dynamics, as the prescribed burn appeared to have little effect on relationships between ionic concentration and discharge. The findings of the study highlight the complexity of relationships between solute concentration and discharge, and have implications for the use of rating curves in the estimation of solute concentration and load.

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INTRODUCTION

In a recent paper, McDiffett *et al.* (1989) reported that relatively little attention has been paid to relationships between discharge and element concentration in stream water. This statement is unfounded. Such relationships have been the primary focus of a large number of studies worldwide (eg. Toler, 1965; Pinder & Jones, 1969; Edwards, 1973; Walling & Foster, 1975; Lewis & Grant, 1979; Cornish, 1982; Johnson & East, 1982; Rieger *et al.* 1982; Hart *et al.* 1988; Muraoka & Hirata, 1988) and have been used extensively by hydrologists in order to gain an understanding of the hydrological pathways operating during storm events (eg. Pinder & Jones, 1969; Nakamura, 1971; Glover & Johnson, 1974; Jenkins, 1989).

On the basis of this work it is clear that distinct relationships exist between discharge and the concentration of dissolved solids in stream water. Nevertheless, certain ionic species such as NO_3^- and K^+ may demonstrate variable responses to changes in discharge, exhibiting, for example, increased concentrations during certain storm events and decreased concentrations during others (Walling & Foster, 1975). This behaviour suggests that discharge is only one of the controls which influence variations in solute concentrations in streams, and that a full understanding of the 'chemograph' during flood flows hinges on a complete picture of the processes occurring over the entire drainage basin (Walling & Foster, 1975). Cornish (1982) recognized that antecedent conditions may affect relationships between ionic concentration and discharge, and suggested further research into this area.

The output of dissolved solids from a catchment is strongly influenced by the frequency and intensity of rainfall (Trudgill, 1977). Since rainfall naturally occurs in events of varying frequency and intensity, there may be marked differences in both the residence times of water in the catchment between rainfall events and the rates of flow through the catchment

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during rain events and, hence, marked differences in solutional losses during storms. Furthermore, the uptake of nutrients by plants, a compensatory mechanism whereby nutrients are returned to surface layers, may also be subject to considerable seasonal variation (Groves, 1983). Since stream chemistry is largely influenced by processes occurring in the surrounding catchment, we might expect the relationship between discharge and the concentration of plant nutrients in stream water to vary seasonally.

The primary aim of our study was to investigate the influence of different antecedent conditions on hydrochemical responses during storm events. Because the south-western Cape of South Africa has a mediterranean climate, the study area is ideally suited to such an investigation. Although rainfall occurs throughout the year, frequencies and intensities are predictably high during winter (June to August) and low during summer (December to February). Furthermore, high air temperatures during the summer, together with longer sun hours and lower relative humidity, result in increased evapotranspiration which will increase the variability of soil-moisture levels and runoff throughout the year. With the knowledge that the study catchment was to be deliberately burnt in March 1987, we also aimed to investigate the influence of fire on the relationship between nutrient concentration and discharge during storm events. Virtually all the vegetation on the slopes of the catchment was burnt during the course of the prescribed burn, although the riparian vegetation was burnt at the edges only, and the canopy remained intact.

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THE STUDY AREA

The study catchment, Swartboskloof, has been described in detail by Britton (in press). Briefly, Swartboskloof is a fan-shaped catchment, 373 ha in area, located in the Jonkershoek Valley (34°00'S, 18°57'E) approximately 60 km east of Cape Town. The catchment ranges from 320 to 1200 m in altitude and has a north-easterly aspect.

The geology and soils of Swartboskloof have been described by Fry (1987). Peninsula Formation quartzites of the Table Mountain Group rest unconformably on Cape Granite, which forms the undulating floor of the Swartboskloof valley. Scree slopes consisting of quartzite stones and boulders are common and are the result of weathering and erosion of the Peninsula Formation quartzite cliffs which ring the valley. The scree slopes cover much of the granite inlier and can vary in depth. Cape Granite is exposed in the central sector as clusters of corestones and large boulders. The soils are acid with low base saturation, and the cation exchange complex is dominated by exchangeable hydrogen and aluminium. The soil catena tends toward Mispah, Glenrosa, Nomanci and Magwa soil forms.

The climate of the region is mediterranean, with warm, dry summers and cool, wet winters. Rainfall occurs throughout the year, although around 60 % of the annual total falls in the four winter months of June to September. The driest months are generally from January to March. Annual rainfall during 1986 and 1987 at Swartboskloof, based on the average of five raingauges established throughout the catchment, amounted to 2801.4 and 2725.9 mm respectively (South African Forestry Research Institute - SAFRI - unpublished data). Air temperatures at the entrance to the Jonkershoek Valley range from a mean summer (December to February) maximum of 23.1 ^{o}C to a mean summer minimum of 17.3 ^{o}C, and a mean winter (June to August) maximum of 14.2 ^{o}C to a mean winter minimum of 9.8 ^{o}C (van Lill, 1976).

The indigenous vegetation of the catchment, mountain fynbos, is fire-adapted and characterized by the presence of members of the plant families Proteaceae, Ericaceae and Restionaceae. Mountain fynbos is found on the open slopes of the catchment, whilst sandstone boulder screes and boulder-lined watercourses are vegetated by remnant Afromontane forest (White, 1978). Prior to the prescribed burn on 17 March 1987, the catchment had been protected from fire since 1958.

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The streams which drain the catchment are tributaries of the Eerste River. The Swartboskloof stream, flowing from south-west to north-east, is perennial and seasonally fed by four smaller streams. Streamflow varies from 340 to 15,900 $m^3\ d^{-1}$ (SAFRI, unpublished data). Jubilee Creek, which flows along the eastern side of the catchment, is also perennial, but without seasonal tributaries. The two streams join at the lower end of the catchment before flowing into the Eerste River. Between 400 and 720 m elevation, mean bank slopes surrounding the Swartboskloof stream and Jubilee Creek are 14.7 and 51.1 % respectively.

METHODS

Although the main Swartboskloof stream is gauged 90 m above its confluence with Jubilee Creek, this site was not accessible by vehicle and impractical for frequent manual sampling. Sampling was therefore carried out at a site 150 m below the confluence of the two main streams at a point where a bridge crosses the stream (Fig. 1). Stream water and rainwater were sampled manually at this site during the course of four storms, two in winter (August 3 - 6, 1986; August 9 - 12, 1987) and two in summer (Jan 21 - 24, 1987; April 13 - 15, 1987). (Although strictly speaking, April is classified as 'autumn', summer-like conditions of rainfall and temperature prevailed prior to the April storm, thus April is referred to here as 'summer'). The August 1986 and January 1987 storms represent pre-burn events. Sampling intervals varied between storms, depending upon rainfall intensity and duration, but were generally at 4 - 6 hr intervals until rain had stopped, peak discharge had been observed and discharge was falling. Thereafter, one sample was generally taken after a further 12 hrs, and a final sample taken 48 hrs later. The amount of rain falling between each sampling event was measured by means of a graduated plastic raingauge mounted 1.2 m above ground level at the sampling site. Such raingauges measure a lower rainfall

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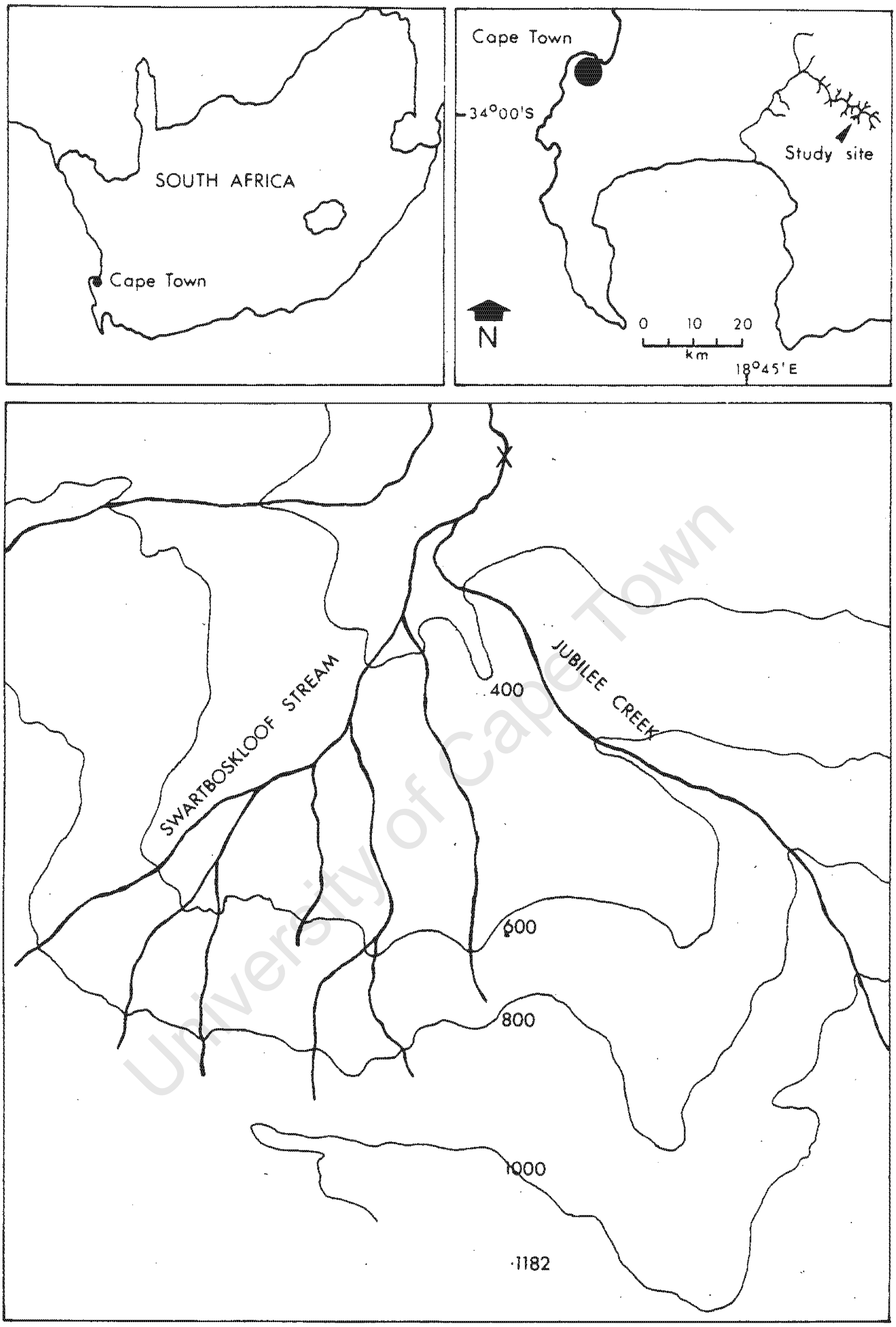

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Fig. 1: Outline map of the study area. Position of the sampling site indicated by a cross. Contoursin metres.

than standard gauges due to the shallowness of the receiving funnel and a tendency for the plastic material to retain water on its surface, thus a correction factor:

$$Rst = -0.17 + 1.09x \quad \text{(Bosman, 1981)}$$

was introduced to convert rainfall values (x) to standard rainfall (Rst).

Sampling of stream water over a 24 hour period was also carried out in February 1987 and February 1988 in order to characterize stream chemistry under baseflow conditions. Sampling was carried out manually at two-hour intervals at the bridge site.

Discharge was determined from depth and velocity measurements taken under the bridge at the time of sampling. Streamflow was measured using the velocity-area method described by Herschy (1985). Current velocity was measured with an Ott flow meter. pH was measured in the field with a Lilliput pH meter accurate to 0.1 pH units.

Samples of stream water and rainwater were filtered in the field through Whatman GF/F filters and collected in 250 ml bottles pre-cleaned in 5 % Extran solution (phosphate-free) and double-distilled water. Nutrient samples were frozen immediately on dry ice, and the remaining samples stored on ice until arrival at the laboratory (usually within 24 hrs of collection) where they were stored at -20 ^{o}C in darkness prior to analysis.

Nitrate, ammonium and soluble reactive phosphorus were measured by automated analysis (Technicon Auto-Analyser) following the methods described by Mostert (1983). Chloride determinations were made using the volumetric method described by Golterman *et al.* (1978). Total alkalinity was determined using the acidimetric method (Golterman *et al.*, 1978), with methyl-orange end-point indicator. Total dissolved solids in baseflow were

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measured by evaporating one litre of filtered sample to dryness in a pre-weighed glass beaker.

Regression analysis was used to determine relationships between discharge and ionic concentration. Because both independent and dependent variables are subject to errors of measurement, functional regression (Ricker, 1973) was used throughout.

RESULTS

Hydrology

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Basic hydrological information on each of the four storms is given in Table 1. The pre-burn winter storm (August 1986) was the largest during 1986 with respect to both rainfall and discharge, and the largest of the four storms sampled. The post-burn winter storm was the second largest of 1987. Both winter storms were associated with maritime fronts. The pre-burn summer storm (January 1987) occurred as a result of a high pressure cell over the Atlantic which caused an on-shore flow on the west coast and deflected the wind to the north-west, bringing rain to the Cape. Rainfall during this event was unseasonally heavy. The April storm, a maritime frontal event, represented a more typical summer storm, and was the smallest of the four events sampled. This storm occurred 26 days after the Swartboskloof catchment was burnt, and was the first post-burn rain event of significance, the 8.5 mm which fell intermittently over a 2-day period 7 days earlier having little effect on discharge.

Owing to logistical problems, no samples were collected between 30 - 48 hours after the start of the first winter storm (August 1986). Discharge during this period was estimated from measurements obtained from the gauging weir situated on the main Swartboskloof

Table 1 Basic hydrological information on each of the four storms.

	EVENT			
	Aug '86	Jan '87	Apr '87	Aug '87
Duration of event (hrs)	81	75	44	62
Rain during storm (mm)	201	94	48	152
Maximum intensity ($mm\ h^{-1}$)	6.3	7.1	2.9	7.6
Total runoff (m^3)	397,431	47,383	14,858	317,110
Runoff as a % of rainfall	53.0	13.5	8.3	55.9
Days without rain prior to event	8	15	6	4
Last rainfall (mm)	32	5.3	8.5	10
Rainfall in preceding 30 days (mm)	164.2	9.3	38.8	223.8
Mean max. air temp. in preceding 30 days (°C)	17.9	25.7	24.0	16.4

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stream, following intercalibration of the two sites. Because of the large variability in rainfall between sampling events, rainfall intensities given for each of the storms should be regarded as minimum values only.

Antecedent conditions in the catchment were similar for the two summer and two winter storms, with relatively low air temperatures and high rainfall during the 30 days preceding each of the winter storms and high air temperatures and low rainfall preceding the summer storms (Table 1). Response to rainfall was rapid in the winter storms, with periods of heavy rainfall coinciding with peaks in discharge (Fig. 2). The intermittent nature of the rainfall resulted in three discharge peaks during each of the winter storms. Rainfall during the summer storms was less protracted, with most of the rain falling within the first 30 hrs of each event.

Lags between rainfall and discharge peaks were apparent during each of the summer storms (Fig. 2). Lags were longest in the January storm, with approximately 21 hours elapsing between the first rainfall peak and the first discharge peak, and approximately 18 hours between the second rainfall and discharge peaks. During the April storm, lag periods of approximately 4 and 7 hours were recorded between the two rainfall and discharge peaks.

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Baseflow chemistry

Stream chemistry during the two 24-hour sampling events, and details of antecedent conditions, are given in Table 2. The January to March period of 1988 was the driest since 1950 (SAFRI, unpublished data), yet, despite differences in antecedent rainfall between the two years, differences in discharge and stream chemistry were small. Stream water at baseflow was poorly buffered and very low in dissolved substances. With the exception of

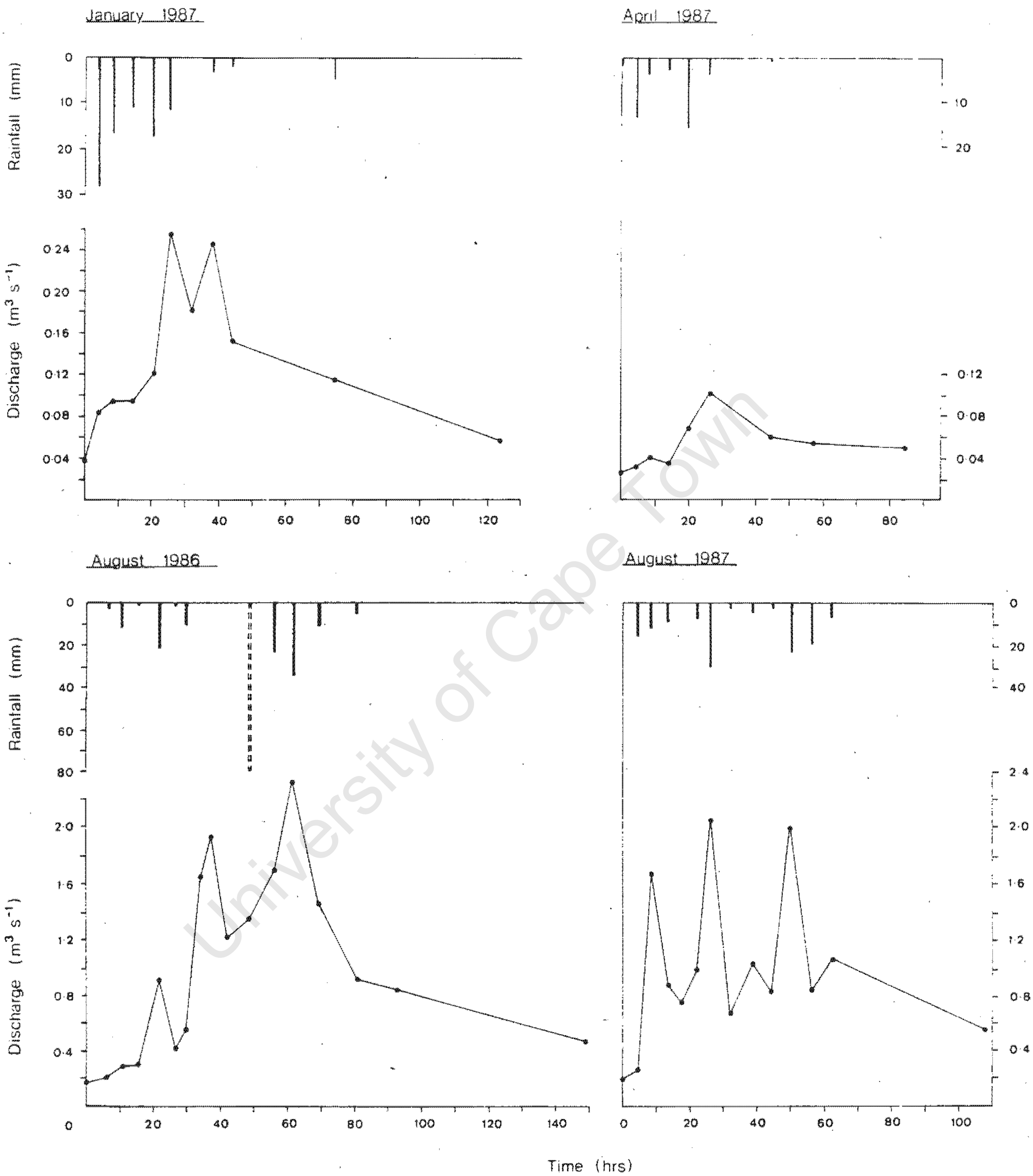

Fig. 2: Rainfall and discharge during each of the four storms. No samples were collected between 30 - 48 hours after the start of the pre-burn winter storm (August 1986); rainfall indicated by a broken line thus represents total rainfall during this period. Note differences in y axis scales between summer and winter storms.

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Table 2 Stream chemistry during, and climatic conditions prior to, the two 24 hr sampling events. Discharge in $m^3\ s^{-1}$; HCO_3^- and Cl^- in mmol l^{-1}; PO_4^{3-}-P, NH_4^+-N and NO_3^--N in μmol l^{-1}, total dissolved solids in mg l^{-1}.

Variable	Pre-burn		Post-burn	
	Feb 1987 (n=13)		Feb 1988 (n=13)	
	$\bar{x}$	sd	$\bar{x}$	sd
Discharge	0.035	0.003	0.037	0.005
pH	5.56	-	6.07	-
HCO_3^-	0.07	0.01	0.06	0.002
Cl^-	0.23	0.006	0.22	0.004
PO_4^{3-}-P	0.06	0.03	0.09	0.03
NH_4^+-N	4.10	2.10	2.65	1.14
NO_3^--N	0.44	0.17	0.93	0.26
TDS (n=2)	25.7	0.06	26.7	0.21
Mean max. air temp. preceding 30 days	24.4	3.93	27.4	4.26
Rainfall (mm) preceding 30 days	118.6	-	12.6	-
Days without rain (mm)	3	-	13	-
Last rainfall (mm)	11.2	-	1.2	-

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NH_4^+-N, variation in the concentration of individual ions during each sampling event was small.

Storm chemistry

Changes in ionic concentration with discharge during the winter and summer storms are shown in Figs. 3 and 4 respectively. Mean volume-weighted ionic concentrations in stream water (Table 3) were obtained by summing the products of flow volume and mean ionic concentration between each sampling event and dividing by total flow volume (calculated from the onset of rain to 24 hours after rain had stopped). Mean volume-weighted ionic concentrations in rainwater were obtained in a similar way, by summing the products of ionic concentration and volume of rain recorded for each sample and dividing by total volume.

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Mean volume-weighted pH values for stream water during all storm events were higher than rainwater values but lower than baseflow values. The difference in pH between rainwater and stream water values was greatest for the summer storms. In all four storms, H^+ ion concentration appeared positively related to discharge, although only in the pre-burn winter storm was this relationship significant ($y = -1.68 + 5.03x$, $r = 0.527$, $P < 0.05$), as lag periods of varying length were observed between discharge peaks and pH troughs. (Figs. 3 & 4). Lags were considerably shorter during the winter storms (maximum lag recorded was approximately 8 hours during the pre-burn winter storm). In the summer storms, the longest lag period was observed during the April event, when approximately 18 hours elapsed between the largest discharge peak and the lowest pH trough. During this storm, two of the three pH troughs coincided with periods of heavy rainfall.

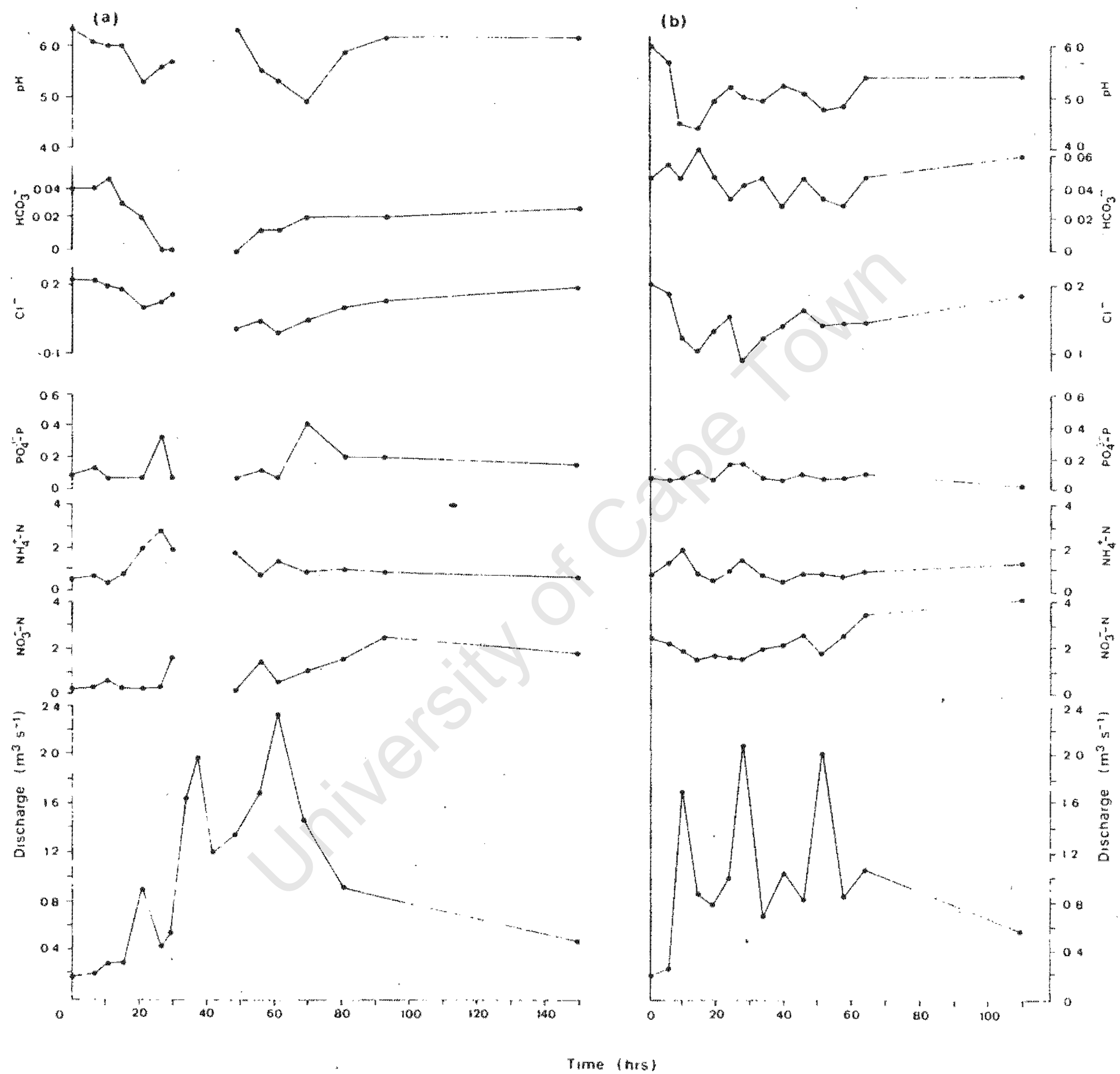

Fig. 3: pH, ionic concentration and discharge during the two winter storms; a = August 1986, b = August 1987. Chloride and HCO_3^- in mmol ℓ^{-1}; PO_4^{3-}-P, NH_4^+-N and NO_3^--N in µmol ℓ^{-1}.

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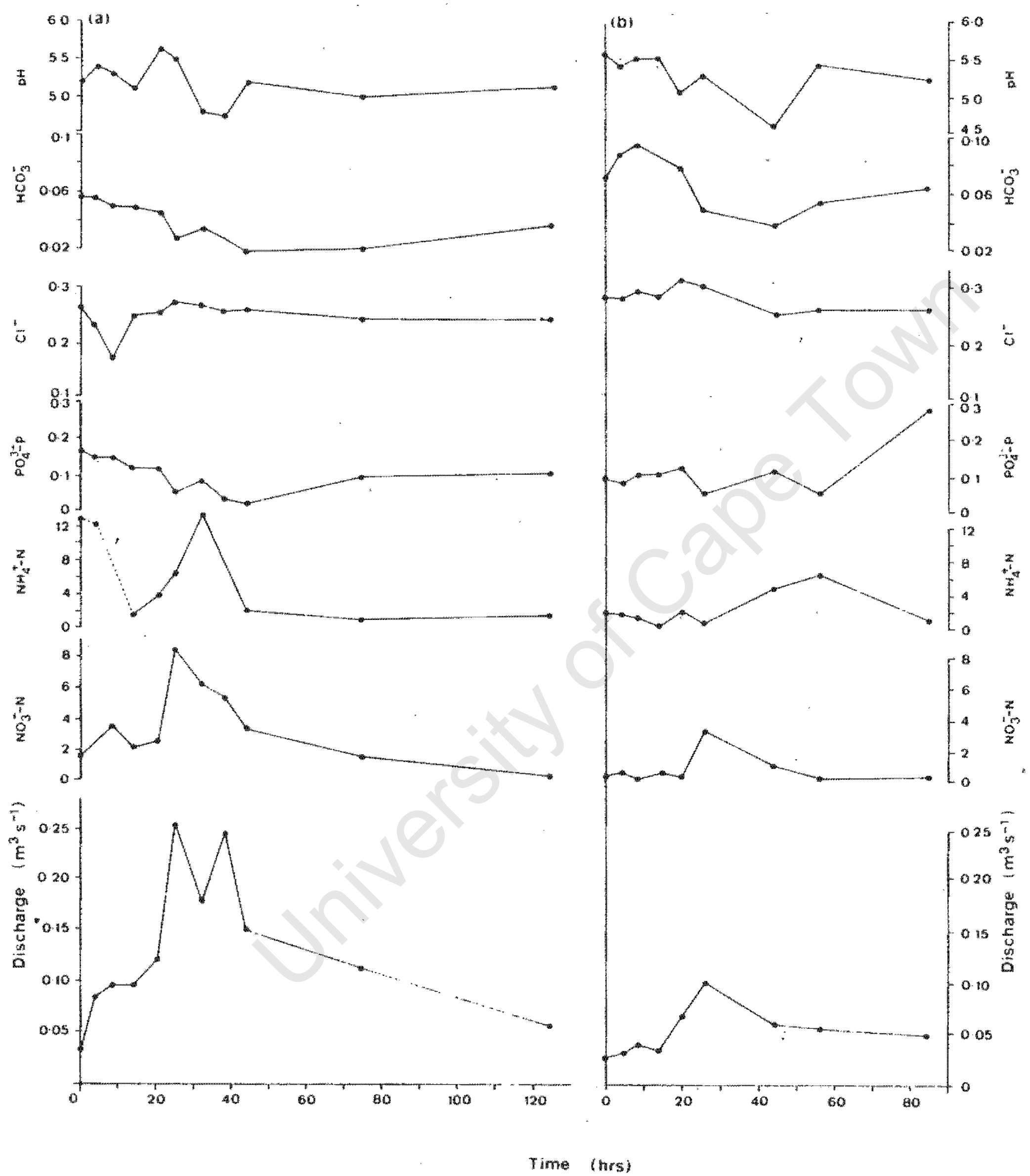

Fig. 4: pH, ionic concentration and discharge during the two summer storms; a = January 1987, b = April 1987. Chloride and HCO_3^- in mmol ℓ^{-1}; PO_4^{3-}-P, NH_4^+-N and NO_3^--N in µmol ℓ^{-1}. Contamination of the first two NH_4^+-N samples collected during the January storm is suspected.

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Bicarbonate concentrations were highest in baseflow, with the two post-burn storms approaching these concentrations and pre-burn concentrations considerably lower. Bicarbonate concentrations in rainwater were not measured, but are expected to be lower than in stream water. Initial rises in HCO_3^- concentration were observed in all but the January storm. After this, HCO_3^- concentration decreased with increasing discharge, and rose during the recession period of each storm. During the January storm, a significant inverse relationship existed between HCO_3^- concentration and discharge ($y = 0.063 - 0.189x$, $r = 0.61$, $P < 0.05$).

Chloride concentrations in stream water during the two winter storms were inversely related to discharge (pre-burn: $y = 0.21 - 0.04x$, $r = 0.93$, $P < 0.001$; post-burn: $y = 0.201 - 0.056x$, $r = 0.70$, $P < 0.05$). Peaks in discharge were generally accompanied by sharp drops in Cl^- concentration (Fig. 3). Mean volume-weighted stream water concentrations were similar in both winter storms, and were higher than rainwater concentrations (Table 3) but lower than baseflow concentrations (Table 2). Concentrations increased to pre-event levels as discharge fell during the recession period of each event.

The opposite pattern was observed during summer storms. Stream water concentrations were similar to baseflow concentrations and, during the April storm, peaks in discharge were accompanied by peaks in Cl^- concentration. A marked drop in Cl^- concentration was observed at the start of the January storm, after which concentrations peaked with the first peak in discharge. Chloride concentrations decreased during the recession stage of each event.

Although not significant, a positive relationship appeared to exist between PO_4^{3-}-P concentration and discharge during both winter storms, with lags between peaks in discharge and peaks in concentration (Fig. 3). During the pre-burn winter storm, two peaks in PO_4^{3-}-P concentration were recorded, the first approximately 5.5 hours after the first

Table 3 Mean volume-weighted ionic concentrations in rainwater and streamwater for each of the four storms. Bicarbonate and Cl^- in mmol l^{-1}, PO_4^{3-}-P, NH_4^+-N and NO_3^--N in µmol l^{-1}.

SPATE	pH		HCO_3^-		Cl^-	
	Rain	Stream	Rain	Stream	Rain	Stream
Aug 1986	5.11	5.47	-	0.013	0.095	0.158
Jan 1987	3.74	5.08	-	0.029	0.056	0.251
Apr 1987	3.74	5.03	-	0.057	0.045	0.282
Aug 1987	4.43	4.95	-	0.044	0.073	0.141

SPATE	PO_4^{3-}-P		NH_4^+-N		NO_3^--N	
	Rain	Stream	Rain	Stream	Rain	Stream
Aug 1986	0.13	0.16	5.45	1.30	0.74	1.03
Jan 1987	0.07	0.08	-	4.59	1.96	3.46
Apr 1987	0.12	0.10	2.17	3.25	1.49	1.26
Aug 1987	0.04	0.08	3.11	0.99	1.13	2.46

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discharge peak, the second approximately 8.5 hours after the third discharge peak. During the post-burn winter storm, the first peak in PO_4^{3-}-P concentration occurred approximately 4 hours after the first discharge peak, the second at the time of the second discharge peak, and smaller increases approximately 12 hours after the third discharge peak and approximately 6 hours after the small rise in discharge observed between the second and third discharge peaks. Decreases in concentration were observed for both events during the recession period.

A significant, inverse relationship existed between PO_4^{3-}-P concentration and discharge during the January storm ($y = 0.187 - 0.639x$, $r = 0.803$, $P \leq 0.05$). The relationship between PO_4^{3-}-P concentration and discharge was not significant during the April storm. Nevertheless, despite a slight rise in PO_4^{3-}-P concentration at the start of this event, the main discharge peak was accompanied by a sharp drop in concentration. Ionic concentration rose during the recession period of both summer storms.

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Concentrations of NO_3^--N in stream water were higher during stormflow than during baseflow, with highest concentrations recorded during the January event. Rainwater concentrations were generally intermediate between baseflow and stormflow concentrations. During the summer storms, a significant, positive relationship existed between NO_3^--N concentration and discharge (January: $y = -1.128 + 34.14x$, $r = 0.887$, $P < 0.001$; April: $y = 8.071 + 2.400\, ln x$, $r^2 = 0.432$, $P < 0.05$). During the pre-burn winter storm, NO_3^--N concentrations were low during periods of high discharge, but peaks in concentration were recorded prior to all three discharge peaks. Concentrations increased during the recession period. Nitrate concentration was inversely, although not significantly related to discharge during the post-burn winter storm, the first trough in concentration occurring approximately 5 hours after the first discharge peak and successive troughs coinciding with discharge peaks. A marked rise in concentration was recorded during the recession period of this storm, as for the pre-burn winter event.

Mean volume-weighted concentrations of NH_4^+-N in stormflow during the two summer events were approximately three times those of the winter storms, and were similar to baseflow concentrations. Although this would suggest an inverse relationship between concentration and discharge, peaks in NH_4^+-N concentration appeared to be associated with discharge peaks in all four storms. During the pre-burn winter storm, the first peak in NH_4^+-N concentration was recorded approximately 5.5 hours after the first discharge peak. A second, smaller peak coincided with the third discharge peak. Ammonium concentrations at the start of the January event were very high, and contamination of the first two samples is suspected. The main concentration peak recorded during this event occurred approximately 7 hours after the first discharge peak. During the April storm, concentration peaks were recorded approximately 11.5 and 30 hours after the first and second discharge peaks respectively. Lags were not observed during the post-burn winter event. Two peaks in NH_4^+-N concentration, the second smaller than the first, were seen to coincide with the first and second discharge peaks. No peak in concentration was observed at the third discharge peak. Mean volume-weighted concentrations of NH_4^+-N in stream water were lower than mean rainwater concentrations during the two winter storms and higher than rainwater concentrations in the January storm. Data for rainwater concentrations during the April storm are not available.

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DISCUSSION

Hydrology

Antecedent soil-moisture content has long been recognised as a major factor governing the infiltration rates of soils. Rainwater entering the soil during rain events percolates downwards until it reaches an impermeable layer or the top of the saturated layer. At this point, the water tends to pond up and flow laterally through the soil in the direction of greatest hydraulic conductivity. The lag time between the beginning of rainfall and the beginning of the hydrograph rise (and, similarly, between rainfall and discharge peaks) depends upon the percolation time, which is shorter when antecedent soil-moisture is high (Whipkey & Kirkby, 1978). In the present study, the rapid response of discharge to rainfall during both winter events, when soil-moisture levels were high, indicates that percolation time was short, and direct runoff - the sum of channel precipitation, surface runoff and rapid interflow (Ward, 1975) - the major component of streamflow. Surface runoff (overland flow) appears to be of minor importance in vegetated mountain catchments in the fynbos biome (Versfeld, 1981), and is probably confined to dynamic, expanding and contracting seep zones, which include saturated areas surrounding stream channels and areas of low hydraulic conductivity.

Antecedent conditions in the catchment prior to the two summer storms differed markedly from those prior to the two winter storms. Comparatively low soil-moisture levels as a result of low antecedent rainfall and, before the January storm, the increased effectiveness of evapotranspiration, permitted the percolation of rainwater to greater depths, resulting in marked lags between rainfall and discharge peaks. Stormflow during both summer events was thus dominated by delayed interflow, an unknown proportion of which may have been displaced pre-event water. Sklash and Farvolden (1979), for example, reported that pre-event water may comprise up to 80 % of storm runoff. Lag periods between rainfall peaks and discharge peaks were shorter during the April storm than during the January storm. This may have been due to higher antecedent rainfall prior to the April event which resulted in higher soil-moisture levels. Accruals to soil moisture after burning are favoured by factors such as reductions in interception and transpiration losses, although these gains may be compensated by increased soil evaporation (Bosch *et al.*, 1984). Alternatively, the fire may have had a direct influence on the rate at which water moved through the catchment during storms. Reduced infiltration in the upper soil layers of burnt catchments has been

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reported by many authors (eg. Lowdermilk, 1930; Friedrich, 1955; Debyle & Packer, 1972; Wright *et al.*, 1976; Wells, 1986), which leads to an increase in surface runoff. Versfeld (1981) reported no increase in overland flow from burnt plots in the study area, but cautioned against extrapolation of these findings to larger areas as they pertained only to small areas on highly permeable soil.

Storm chemistry

Analysis of chemical data revealed that even over relatively small changes in discharge, as observed during the April storm, there were concomitant changes in the concentration of each of the variables measured. pH values for rainwater, particularly that collected during the summer storms, were very low. These values are, however, typical for the south-western Cape (van Wyk, 1988), and not necessarily a sign of acid rain (Bohm, 1985). The pH of infiltrating rainwater tends to increase with its passage through the soil due to replacement of H^+ ions in solution by metallic cations in the soil-exchange complex (Feller, 1977). Differences between mean volume-weighted values for rainwater and stream water are thus indicative of soil contact times and contact surface areas for each storm. pH appeared to be inversely related to discharge in all four storms, although pH troughs usually occurred several hours after discharge peaks. Lynch *et al.* (1986) ascribe lags between peaks in discharge and H^+ ion concentration to shifts in the chemical equilibrium of the stream, with the buffering capacity of the stream becoming overwhelmed by excess H^+ ions shortly after peak discharge. Conversely, Jenkins (1989) considers these lags to be due to changes in the relative proportions of pre-event and event water contributing to stormflow, with event water, of low pH, dominating until just after peak discharge, and pre-event water increasing in dominance thereafter. The underlying cause of the lags observed between discharge peaks and pH troughs in the present study is not clear. The former explanation does not appear to apply, as periods of lowest HCO_3^- concentration coincided with lowest pH values in the April storm only. The small troughs in pH in the early part of the April storm during periods of heavy rainfall may have been due to the dissociation of organic acids, as polyphenol concentrations in stream water were relatively high at these times (Britton, unpublished data).

The initial rises in HCO_3^- concentration observed in all but the January storm were probably due to the flushing of accumulated products from the soil into the expanding stream channel following infiltration-induced interflow higher up the slope. Since the April storm was the first of significance to occur after the fire, the marked initial rise in concentration at the start of this event may represent the flushing not only of HCO_3^- derived from respiration (the main source of HCO_3^- in undisturbed catchments - Tiedemann *et al.* 1979) but also of HCO_3^- produced as a result of oxide conversion following fire. Mean volume-weighted concentrations of HCO_3^- in stream water were higher for the post-burn storms than for the pre-burn storms. These results agree with an earlier finding (Britton, in press) that HCO_3^- concentrations in the main Swartboskloof stream increased significantly during the post-burn year. Apart from the initial rises, HCO_3^- concentrations otherwise decreased with increasing discharge during the course of all four storms. Similar behaviour has been reported by Edwards (1973) for English rivers.

Changes in the concentrations of Cl^-, PO_4^{3-}-P and NO_3^--N in stream water in response to changes in discharge differed markedly between summer and winter storms. Mean volume-weighted concentrations of Cl^- in rainwater were similar for all storms, and were lower than baseflow concentrations. The inverse relationship between Cl^- concentration and discharge during the winter storms reflects the dominance of direct runoff during periods of high discharge. During the drier months, the longer residence times of water in the soil between rain events and longer percolation times during events allow a greater opportunity for solutional contact with the mineral constituents of the soil. Chloride concentrations in water moving through the catchment during summer storms thus tended to be relatively high, and

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a positive relationship appeared to exist between discharge and ionic concentration. The destruction of vegetation in the surrounding catchment appeared to have no effect on seasonal relationships between ionic concentration and discharge or on mean volume-weighted concentrations of Cl^- in stream water. This is undoubtedly because Cl^- is not a major plant nutrient and thus even in undisturbed catchments, concentrations in soil-water will be little affected by plant uptake.

Unlike the mobile Cl^- ion, the PO_4^{3-} ion reacts vigorously with various components of the soil (Bailey, 1968; Kurtz & Melsted, 1973), and sorption of PO_4^{3-}-P by the soil will take place as rainwater percolates down through soil horizons. This 'chemical sieving' action is recognized as playing a major role in maintaining low dissolved inorganic P concentrations in forest streams, and accounts in part for the conservative nature of forest catchments for P (Ryden *et al.*, 1973). Furthermore, P is a limiting plant nutrient in fynbos ecosystems (Rundel, 1983; Groves, 1983) and, where nutrient supply is a major determinant of plant growth and survival, there may be an increase in the efficiency of uptake of nutrients (Lamont, 1983). Soluble reactive phosphate entering the catchment in rainwater during summer storms, as well as PO_4^{3-}-P derived from leaching of the litter layer, may thus be subject to vigorous uptake by plants. The combined effect of uptake and sorption processes may explain the low PO_4^{3-}-P concentrations in stream water and the general inverse relationship between discharge and ionic concentration during summer storms.

Sorption of PO_4^{3-}-P by the soil matrix and the uptake of PO_4^{3-}-P by plants will also take place during the winter storms, but the influence of these processes on stream water concentrations is expected to be considerably smaller. The relatively large proportion of direct runoff contributing to streamflow during winter storms reduces the opportunity for contact of PO_4^{3-}-P with either root systems or with lower soil horizons. Singer & Rust (1975) did not measure P in subsurface flow, but reported large losses of soluble P in surface runoff from deciduous forests. Bath (1989) suggested that concentrations of dissolved inorganic P in subsurface flow during the winter are higher than in surface runoff due to dissolution and desorption processes, and ascribed lags between discharge peaks and concentration peaks to changes in the relative contributions of surface and subsurface flows to discharge. Lags observed in the present study during winter storms may similarly reflect shifts in the dominance of sources contributing to direct runoff.

There appeared to be little difference between pre- and post-burn relationships between ionic concentration and discharge, which suggests that geochemical processes operating within the catchment exert a stronger control on PO_4^{3-}-P concentrations in stream water than plant-uptake dynamics. Differences in volume-weighted concentrations of PO_4^{3-}-P in stream water between the winter storms appear to be due to differences in volume-weighted concentrations in rainwater.

Nitrogen is also a limiting element in fynbos ecosystems (Groves, 1983), but the results of the present study provide little evidence for the existence of strong retentive mechanisms operating within the catchment. Nitrate is one of the most mobile ions in soil-water systems and is concentrated by biological activity in the upper soil horizons. Concentrations of NO_3^--N in stream water during storms were higher than concentrations at baseflow, and higher than rainwater concentrations in all but the April storm. These results indicate that much of the NO_3^--N in stormflow is soil-derived.

Seasonal differences in the relationship between NO_3^--N concentration and discharge during storm events appear to be caused by differences in the rate at which water moves through the catchment. During winter storms, NO_3^--N concentrations in stream water were generally low during periods of high discharge, but increased markedly during the recession period. This behaviour has been reported by a number of authors (eg. Cornish, 1982; Muraoka & Hirata, 1988; Pionke *et al.*, 1988), and reflects the dominance of direct runoff, of low NO_3^--N concentration, during periods of high discharge and of delayed interflow, of

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higher NO_3^--N concentration, during the recession period. Small peaks in NO_3^--N concentration were observed prior to discharge peaks in the pre-burn winter storm. These may reflect changes in dominance from interflow to direct runoff, but are more likely to be due to the flushing of NO_3^--N from source areas in the near-stream zone as the discharge network expands. Such peaks were not observed during the post-burn winter storm, probably because much of the NO_3^--N in the near-stream zone had been flushed out several weeks earlier by the largest storm of the year. Water percolating through the catchment during the summer storms mobilized NO_3^--N throughout the soil profile resulting in transport to the stream in delayed interflow. Concentration peaks thus corresponded with discharge peaks. Decreases in NO_3^--N concentration during the recession period of each event may have been due to increases in the relative contribution of baseflow.

The prescribed burn appeared to have little impact on relationships between NO_3^--N concentration and discharge during summer and winter events. Nevertheless, concentrations of the ion were higher during the post-burn winter storm than during the pre-burn winter storm, even though the former event occurred well into the wet season and several weeks after the largest storm of the year. These results agree with an earlier finding (Britton, submitted) that NO_3^--N concentrations in Swartboskloof stream water increased significantly after the burn. Increases in NO_3^--N concentrations following burning may reflect enhanced nitrification and reduced demand for NO_3^--N by vegetation (Tiedemann *et al.*, 1978).

Peaks in NH_4^+-N concentration were associated with discharge peaks in all four storms, although major sources of the ion may have differed seasonally. During both winter storms, progressive decreases in concentration peaks indicate an 'exhaustion' effect, with much of the NH_4^+-N in the surface soil layers being flushed into the stream during the early stages of each storm. The higher concentrations of NH_4^+-N in stream water recorded during the summer storms probably reflect the mobilization of NH_4^+-N lower down in the

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profile. Highest concentrations of exchangeable NH_4^+-N in the surface to 20 cm layers of coastal fynbos soils were recorded in summer (Stock & Lewis, 1986) and ascribed to reduced uptake by plants and the reduced activity of nitrifiers. Ammonium moves less rapidly through the soil than NO_3^--N, as it undergoes substitution reactions with metal cations on the cation exchange complex, and this may account for the lags observed between peaks in discharge and ionic concentration observed in the April storm. The prescribed burn had little effect on the relationship between NH_4^+-N concentration and discharge, probably because uptake of NH_4^+-N in undisturbed fynbos catchments is low during summer due to low soil-moisture levels (W.D. Stock, U.C.T., *pers. comm.*) and, during winter, only a relatively small proportion of the NH_4^+-N in rapidly moving direct runoff will be taken up by plants.

In summary, the findings of this study suggest that certain ions eg. Cl^-, PO_4^{3-}, NO_3^-, exhibit variable response to changes in discharge according to seasonal variations in soil-moisture levels, whereas others eg. HCO_3^-, H^+, and NH_4^+, do not. Although only four storms were monitored, the general behaviour of ions in the former category appears to be predictable at either end of the soil-moisture continuum. If such relationships prove to be consistent, further research is warranted in order to determine, for example, at what point in the continuum the relationship between PO_4^{3-}-P concentration and discharge shifts from positive to negative, and whether these relationships apply to other catchments in regions of similar climate.

The prescribed burn appeared to result in an increase in the concentrations of NO_3^--N and HCO_3^- in stream water, although only in the case of NO_3^--N might this be attributable to reduced uptake by plants. The uptake of water-soluble elements by unburnt riparian strips has been reported to limit nutrient loss following fires (Richter *et al.*, 1982); and thus greater losses may have been expected had the riparian vegetation in the Swartboskloof catchment been destroyed. The destruction of fynbos vegetation by fire appeared to have

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little effect on relationships between ionic concentration and discharge. This may also be due to the riparian vegetation remaining intact, but a more likely explanation is that the movement of ions is affected more by geochemical processes operating within the soil and the chemical properties of the ions themselves than by plant-uptake dynamics.

Trajectories and rating curves

A number of authors (eg. Toler, 1965; Bond, 1979; Johnson & East, 1982; McDiffett *et al.*, 1988) have examined the relationship between ionic concentration and discharge by plotting ionic concentration against discharge and connecting the points in a time sequence. McDiffett *et al.* (1988) proposed that these trajectories may be used to identify the sources of many ions in stream water. Our results tend to support this idea. For Cl^-, PO_4^{3-}-P and NO_3^--N, which showed variable response to changes in discharge, clockwise trajectories were generally associated with summer storms and counterclockwise trajectories with winter storms (Fig. 5). The slopes of the trajectories for Cl^- and NO_3^--N were generally positive during summer and negative during winter, reflecting the generally positive association between ionic concentration and discharge during summer and negative association during winter. The reverse was observed for PO_4^{3-}-P. Ammonium exhibited clockwise trajectories in winter and counterclockwise trajectories in summer, which may reflect the flushing of NH_4^+-N from the surface layers of the soil in winter and mobilization of NH_4^+-N lower in the soil profile during summer. Species always associated with surface runoff in the Swartboskloof catchment (eg. polyphenols and ultrafine particulate matter - Britton, unpublished data) produced clockwise trajectories regardless of season. Nevertheless, inexplicable anomalies were found to exist. For example, NO_3^--N in stream water during the summer storms is most likely to originate from the same source (delayed interflow), and yet NO_3^--N trajectories cycled in a clockwise direction during the pre-burn storm and in a counterclockwise direction during the post-burn storm. Similarly, Cl^- and PO_4^{3-}-P

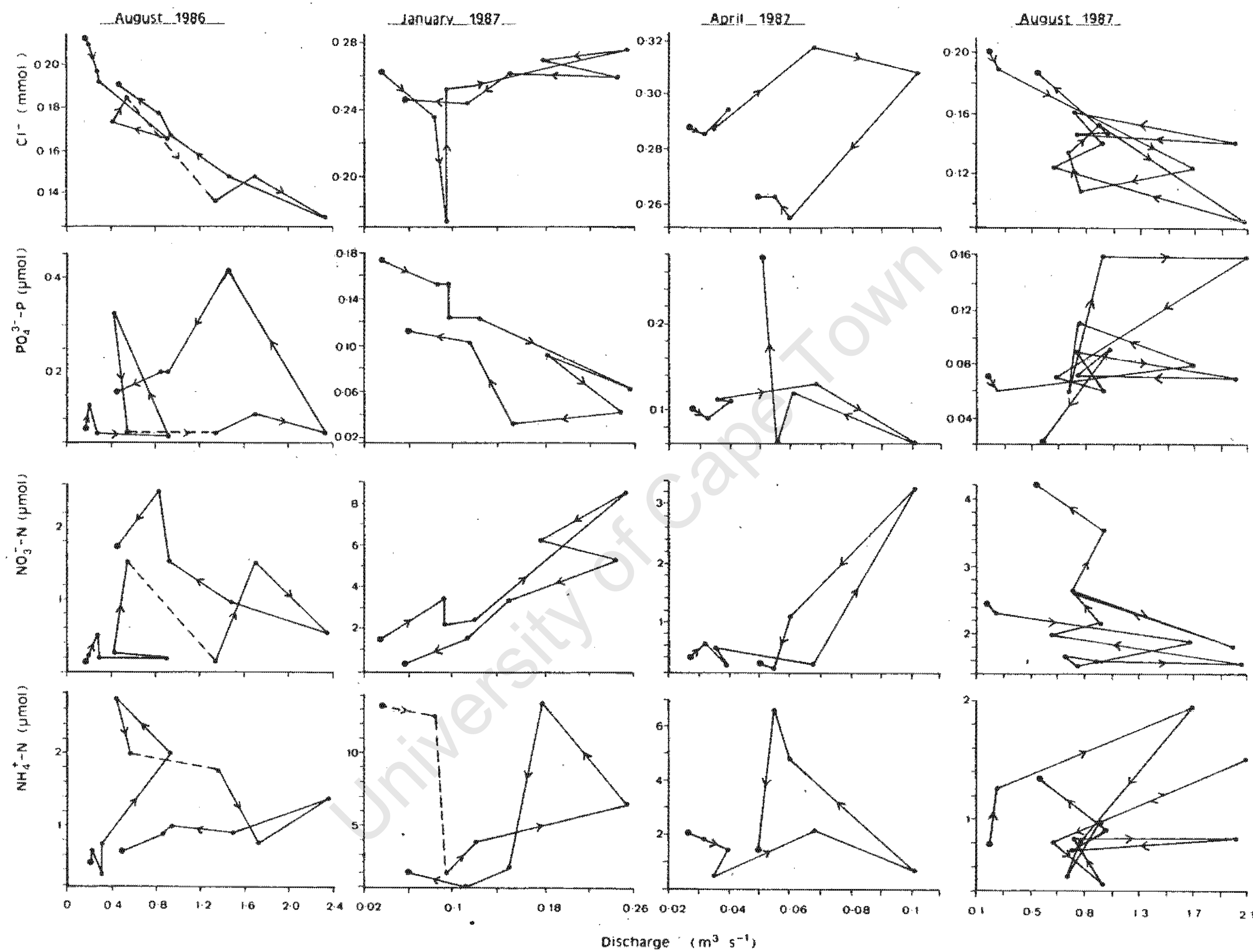

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Fig. 5: Trajectories for Cl^-, $PO4^{3-}$-P, $NO3^-$-N and $NH4^+$-N for each of the storms sampled. Contamination of the first two $NH4^+$-N samples collected during the January storm is suspected.

trajectories cycled in a counterclockwise direction during the pre-burn winter storm but in a generally clockwise direction during the post-burn winter storm. Further research into the processes underlying trajectories is clearly warranted before they can be used as diagnostic tools.

Rating curves for the estimation of solute concentration and load are constructed by plotting solute concentration against corresponding discharge for a wide range of discharges. Regression analysis is then used to estimate the parameters of the curve. Once a rating curve has been established for a particular stream, solute concentration (and hence solute load) at any discharge may then, theoretically, be estimated from the curve. The findings of the present study, however, raise doubts over both the construction of rating curves and their usefulness in the estimation of solute concentration and load. Sampling at regular intervals eg. daily or weekly, may fail to detect hysteretic relationships between solute concentration and discharge (where, for a given discharge, solute concentration is higher on the rising limb of the hydrograph than on the falling limb, or *vice versa*), and hence will provide a false representation of the relationship. Furthermore, the relationship between solute concentration and discharge may vary seasonally. For example, at a discharge of 0.25 $m^3 s^{-1}$, the concentration of NO_3^--N in Swartboskloof stream water during the pre-burn summer storm was approximately 8.3 μmol l^{-1}. At the same discharge for the pre-burn winter storm, NO_3^--N concentration was approximately 0.5 μmol l^{-1}. It may not even be possible to construct rating curves for some ions. In the present study, relatively few significant relationships existed between ionic concentration and discharge, and this is clearly due to the existence of lags between discharge peaks and ionic concentration peaks (or troughs) or to hysteretic relationships between ionic concentration and discharge. These findings clearly confirm the conclusions of Rieger *et al.* (1982), that variables are operating in a far more complex fashion than that assumed by the fixed coefficients of a regression equation.

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University of Cape Town

REFERENCES

BAILEY, G.W. 1968.
Role of soils and sediment in water pollution control. Part 1: Reactions of nitrogenous and phosphatic compounds with soils and geologic strata. U.S.D.I. Fed. Wat. Poll. Control Admin., Southeast Water Lab.

BATH, A.J. 1989.
Phosphorus transport in the Berg river, western Cape. PhD thesis, Univ. of Cape Town.

BOHM, M. 1985.
Rain acidity in Stellenbosch. S. Afr. J. Sci. **81**: 652-654.

BOND, H.W. 1979.
Nutrient concentration patterns in a stream draining a montane ecosystem in Utah. Ecology **60**: 1184-1196.

BOSCH, J.M., R.E. SHULZE, AND F.J. KRUGER. 1984.
The effect of fire on water yield, p. 328-348. *In*: P. de V. Booysen, and N.M. Tainton [eds.], Ecological effects of fire in South African ecosystems. Springer-Verlag.

BOSMAN, H.H. 1981.
Raingauges: Quality pays. Water S.A. **7**: 190-191.

BRITTON, D.L. (in press).
Fire and the chemistry of a South African mountain stream. Hydrobiol.

CORNISH, P.M. 1982.
The variation of dissolved ion concentration with discharge in some New South Wales streams, p. 67-71. Proc. First National Symp. on Forest Hydrology, Melbourne. Institution of Engs., Aust.

DEBYLE, N.V., AND P.E. PACKER. 1972.
Plant nutrient and soil losses in overland flow from burned forest clearcuts, p. 296-307. National Symp. on Watersheds in Transition, Logan, Utah.

University of Cape Town

EDWARDS, A.M.C. 1973.
The variation of dissolved constituents with discharge in some Norfolk rivers. J. Hydrol. **18**: 219-242.

FELLER, M.C. 1977.
Nutrient movement through Western Hemlock- Western Redcedar ecosystems in southwestern British Columbia. Ecology **58**: 1269-1283.

FRIEDRICH, C.A. 1955.
Fire on the Watersheds of the Nation, p. 185-191. U.S.D.A. Yearbook of Agriculture.

FRY, M. St. J. 1987.
A detailed characterization of soils under different fynbos-climate-geology conditions in the south-western Cape. M.Sc thesis, Univ. of Stellenbosch.

GLOVER, B.J., AND P. JOHNSON. 1974.
Variations in the natural chemical concentration of river water during flood flows, and the lag effect. J. Hydrol. **22**: 303-316.

GOLTERMAN, H.L., R.S. CLYMO, AND M.A.M. OHNSTAD. 1978.
Methods for physical and chemical analysis of fresh waters, 2nd.ed. Blackwell Scientific Publications.

GROVES, R.H., 1983.
Nutrient cycling in Australian heath and South African fynbos, p. 179-191. *In*: F.J. Kruger, D.T. Mitchell and J.U.M. Jarvis [eds.], Mediterranean-type ecosystems. The role of nutrients. Springer-Verlag.

HART, B.T., G. DAY, A. SHARP-PAUL AND T. BEER. 1988.
Water quality variations during a flood event in the Annan River, North Queensland. Aust. J. Mar. Freshwater Res. **39**: 225-243.

HERSCHY, W.R., 1985.
Streamflow measurement. Elsevier.

University of Cape Town

JENKINS, A. 1989.
Storm period hydrochemical response in an unforested Scottish catchment. Hydrol. Sci. Journal **34**: 393-404.

JOHNSON, F.A. AND J.W EAST.
Cyclical relationships between river discharge and chemical concentration during flood events. J. Hydrol. **57**: 93-106.

KURTZ, L.T. and S.W. MELSTED. 1973.
Movement of chemicals in soils by water. Soil Sci. **115**: 231-239.

LAMONT, B.B. 1983.
Strategies for maximizing nutrient uptake in two mediterranean ecosystems of low nutrient status, p. 246-274. *In*: F.J. Kruger, D.T. Mitchell and J.U.M. Jarvis [eds.], Mediterranean-type ecosystems. The role of nutrients. Springer-Verlag.

LEWIS, W.M. AND M.C. GRANT. 1979.
Relationships between stream discharge and yield of dissolved substances from a Colorado mountain watershed. Soil Sci. **128**: 353-363.

LOWDERMILK, W.C. 1930.
Influence of forest litter on run-off, percolation and erosion. J. Forestry **28**: 474-491.

LYNCH, J.A., AND C.M. HANNA. 1986.
Predicting pH, alkalinity and total acidity in stream water during episodic events. Wat. Resour. Res. **22**: 905-912.

McDIFFETT, W.F., A.W. BEIDLER, T.F. DOMINICK AND K.D. McCREA. 1989.
Nutrient concentration-stream discharge relationships during storm events in a first-order stream. Hydrobiol. **179**: 97-102.

MOSTERT, S.A. 1983.
Procedures used in South Africa for the automatic photometric determination of micronutrients in seawater. S. Afr. J. Mar. Sci. **1**: 189-198.

MURAOKA, K., AND T. HIRATA. 1988.
Streamwater chemistry during rainfall events in a forested basin. J. Hydrol. **102**: 235-253.

University of Cape Town

NAKAMURA, R. 1971.
Runoff analysis by electrical conductance of water. J. Hydrol. **14**: 197-212.

PINDER, G.F., AND J.F. JONES. 1969.
Determination of the groundwater component of peak discharge from the chemistry of total runoff. Wat. Resour. Res. **5**: 438-445.

PIONKE, H.B, J.R. HOOVER, R.R. SCHNABEL, W.J. GBUREK, J.B. URBAN, AND A.S. ROGOWSKI. 1988.
Chemical-hydrologic interactions in the near-stream zone. Wat. Resour. Res. **24**: 1101-1110.

RICHTER, D.D., C.W. RALSTON, AND W.R. HARMS. 1982.
Prescribed fire: Effects on water quality and forest nutrient cycling. Science **215**: 661-663.

RICKER, W.E. 1973.
Linear regressions in Fishery Research. J. Fish. Res. Board Can. **30**: 409-434.

RIEGER, W.A., L.J. OLIVE, AND J.S. BURGESS. 1982.
The behaviour of sediment concentrations and solute concentrations in small forested catchments, p. 79-83. Proc. First National Symp. on Forest Hydrology, Melbourne. Institution of Engs., Aust.

RUNDEL, P.W. 1983.
Impact of fire on nutrient cycles in mediterranean-type ecosystems with reference to chaparral, p. 192-207. *In*: F.J. Kruger, D.T. Mitchell and J.U.M. Jarvis [eds.], Mediterranean-type ecosystems. The role of nutrients. Springer-Verlag.

RYDEN, J.C., J.K. SYERS, AND R.F. HARRIS. 1973.
Phosphorus in runoff and streams. Advan. Agron. **25**: 1-45.

SINGER, M.J., AND R.H. RUST. 1975.
Phosphorus in surface runoff from a deciduous forest. J. Environ. Qual. **4**: 307-311.

SKLASH, M.G. AND R.N. FARVOLDEN. 1979.
The role of groundwater in storm runoff. J. Hydrol. **43**: 45-65.

University of Cape Town

STOCK, W.D., AND O.A.M. LEWIS. 1986.
Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. J. Ecol. **74**: 317-328.

TIEDEMANN, A.R., J.D. HELVEY, AND T.D. ANDERSON. 1978.
Stream chemistry and watershed nutrient economy following wildfire and fertilization in Eastern Washington. J. envir. Qual. **7**: 580-588.

TIEDEMANN, A.R., C.E. CONRAD, J.H. DIETERICH, J.W. HORNBECK, W.F. MEGAHAN, L.A. VIERECK, AND D.D. WADE. 1979.
Effects of fire on water. A state of knowledge review. U.S.D.A. For. Serv. Gen. Tech. Rep. WO-10.

TOLER, L.G. 1965.
Relation between chemical quality and water discharge in Spring Creek, southwestern Georgia, p. 209-213. U.S. Geol. Surv. Prof. Pap. 525-C.

TRUDGILL, S.T. 1977.
Soil and vegetation systems. Oxford University Press.

VAN LILL, W.S. 1976.
'n Klimaat beskrywing van die Jonkershoek Bosnavorsingstasie met die doel om klimaatverandering wat stroom afvoer kan beinvloed, opte spoor. M.Sc thesis, Univ. of Stellenbosch.

VAN WYK, D.B. 1988.
Water quality in mountain catchments in the fynbos biome. *In*: J.M. King, [ed.], Hydrology and hydrobiology in the fynbos biome. Foundation for Research Development, Occ. Rep. 26.

VERSFELD, D.B. 1981.
Overland flow on small plots at the Jonkershoek Forestry Research Station. S. Afr. For. J. **119**: 35-40.

WALLING, D.E., AND I.D.L. FOSTER. 1975.
Variations in the natural chemical concentration of river water during flood flows, and the lag effect: some further comments. J. Hydrol. **26**: 237-244.

University of Cape Town

WARD, R.C. 1975.
Principles of Hydrology. McGraw-Hill.

WELLS, W.G.(II). 1986.
The influence of fire on erosion rates in California chaparral, p. 57-62. *In*: J.J. DeVries [ed.], Proc. Chaparral Ecosystems Research Conf., Santa Barbara, California.

WHIPKEY, R.Z., AND M.J. KIRKBY. 1978.
Flow within the soil, p. 121-144. *In*: M.J. Kirkby [ed.], Hillslope hydrology. John Wiley & Sons.

WHITE, F. 1978.
The Afromontane region, p. 463-513. *In*: M.J.A. Werger, and J.C. van Bruggen [eds.], Biogeography and ecology of southern Africa. Monogr. Biol. **31**. W. Junk.

WRIGHT, H.A., F.M. CHURCHILL, AND W.C. STEVENS. 1976.
Effect of prescribed burning on sediment, water yield and water quality from dozed Juniper lands in Central Texas. J. Range Management **29**: 294-298.

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Fire and the dynamics of allochthonous detritus in a South African mountain stream

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SUMMARY. 1. Input of allochthonous material, standing stocks of benthic organic matter (BOM) and suspended particulate organic matter (POM) were measured in a south-western Cape mountain stream from March 1986 to February 1988. The surrounding fynbos-dominated catchment was subjected to a prescribed burn in March 1987.

2. Litter-fall in the pre-burn year exhibited a distinct seasonal pattern, with peak falls during the early summer. Although the riparian canopy was not directly affected by the fire, in that it did not burn, a heavy, aseasonal leaf-fall occurred shortly afterwards. The following summer, litter-fall was less than half that of the pre-burn summer.

3. Standing stocks of BOM were significantly higher in autumn than in winter in the pre-burn year and were inversely related to discharge. Despite the heavy post-burn leaf-fall and low litter-fall during the post-burn summer, there was no significant difference between pre- and post-burn BOM standing stocks.

4. Proportions and quantities of fine benthic organic matter (FBOM) in the soft BOM fraction were significantly higher in the post-burn spring, and monthly accumulation of ultra-fine benthic organic matter (UBOM) was also significantly higher in the post-burn spring and summer. These results may reflect accelerated decay rates of BOM in response to enhanced post-burn nitrate concentrations in stream water.

5. Export of CPOM was low in comparison to FPOM and particularly to UPOM, and the stream appears to be highly retentive of CPOM.

6. The natural resilience of the riparian vegetation minimizes the potentially disturbing effects of fire on the stream environment. As a result, the prescribed burn had a less than expected effect on both standing stocks of BOM and the stream environment in general.

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Introduction

Inputs of allochthonous material to low-order, shaded streams represent the major food source of benthic macroinvertebrates (e.g. Egglishaw, 1964; Minshall, 1967; Cummins *et al.*, 1973; Fisher & Likens, 1973) since primary production in such environments is normally low. Thus, disturbances that alter the quantity or quality of allochthonous material entering a stream, or

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the timing of input, may be predicted to affect benthic invertebrate populations by altering the quantity or quality of food available. Although much work has been directed at quantifying terrestrial inputs to streams (e.g. Fisher & Likens, 1973; Winterbourn, 1976; Conners & Naiman, 1984), standing stocks of benthic organic matter (e.g. Wakefield, Harrison & Kovalak, 1980; Naiman & Sedell, 1979a; Cowan & Oswood, 1983; King *et al.*, 1987) and in-stream transport of particulate organic matter (e.g. Bormann, Likens & Eaton, 1969; Bilby & Likens, 1979; Dance, Hynes & Kaushik, 1979; Naiman & Sedell, 1979b), little research has been carried out on the effects of disturbance within a catchment on these aspects of stream ecology. More specifically, the effects of fire on the dynamics of allochthonous detritus in mountain streams is an unstudied field, even though the effects of fire on hydrologic processes, erosion, sediment loads, turbidity and water chemistry have been well documented (see Tiedemann *et al.*, 1979, for a comprehensive review). The present study is therefore the first to address the subject in a mediterranean-type ecosystem.

Regions with mediterranean-type climates occur in five widely separated parts of the world, namely the south-western and western parts of south-eastern Australia, the southern Cape of South Africa, southern California, central Chile and the Mediterranean Basin (Dell, Hopkins & Lamont, 1986). With the exception of Chile, fire represents the major disturbance factor in all mediterranean ecosystems (Keeley, 1986), and the fire regime of all five regions has been manipulated by man to a greater or lesser extent in order to achieve various management objectives (Fox & Fox, 1986). In the south-western Cape of South Africa, prescribed (deliberate) burning is carried out in order to optimize yields of high-quality water, maintain diversity in the indigenous flora and reduce the risk of wildfire (Bands, 1977). This paper presents findings on the effects of a late-summer prescribed burn on the regime of allochthonous input to a second-order mountain stream in the south-western Cape, and the consequent effects on standing stocks of benthic organic matter. The study forms part of a wider research programme investigating the short-term effects of prescribed fire on the chemistry and ecology of the stream. The effects of fire on stream chemistry, and on the benthic invertebrate fauna, will be reported elsewhere.

The study area

The study area, Swartboskloof, is a 373 ha, fan-shaped catchment situated in the Jonkershoek Valley (34°00'S, 18°57'E) approximately 60 km east of Cape Town. The valley forms part of a State-owned Mountain Catchment Area, managed by the Forestry Branch of the Department of Environment Affairs, and is a source of potable and irrigation water. The climate of the region is mediterranean, with hot, dry summers and cool, wet winters. Rainfall is strongly seasonal, with approximately 60% of the annual total falling from June to September. Mean annual rainfall for the Swartboskloof catchment over the 1986–87 study period was 2764 mm (South African Forestry Research Institute – SAFRI, unpublished data).

The slopes of the Swartboskloof catchment are vegetated by sclerophyllous, fire-adapted mountain 'fynbos' shrubland, characterized by the presence of members of the plant families Proteaceae, Ericaceae and Restionaceae. Riparian vegetation consists of evergreen trees of Afromontane origin (White, 1978) which are restricted to sandstone boulder screes and boulder-lined watercourses. The riparian vegetation forms an almost closed canopy over the main Swartboskloof stream and its tributaries, and extends outwards from between 10 and 20 m on either stream bank.

The main Swartboskloof stream is 2.1 km long and 1–4 m wide. The stream bed consists of boulders, stones and gravel derived from granite and sandstone talus. The stream is perennial and seasonally fed by four tributaries. Streamflow varies from 340 to 15,900 m^3 day^{-1} (SAFRI, unpublished data). Water quality can be characterized as acid (pH 4.6–6.6) and very low in dissolved substances (total dissolved solids, 20.5–33.1 mg l^{-1}) (Britton, unpublished data). Water temperatures range from 10 to 20°C (SAFRI, unpublished data).

Prior to the most recent burn, the Swartboskloof catchment had been protected from fire since 1958. On 17 March 1987 the entire catchment was deliberately burnt in an operation lasting approximately 30 h. The fire was considered to be of low to moderate intensity (D. Versfeld, SAFRI, pers. comm.).

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Methods

The study site is situated immediately above a gauging weir on the main Swartboskloof stream at an altitude of 350 m. Sampling was carried out at monthly intervals from March 1986 to February 1988, providing one year each of pre- and post-burn data.

Litter input was measured by means of five litter traps suspended beneath riparian trees at the study site. The traps were of the type described by King *et al.* (1987) and Stewart & Davies (1990), each consisting of a tightly-woven, reinforced plastic mesh bag (1.2×0.8 m) held open by a wire ring, 1.8 m in circumference, giving a mouth area of 0.26 m^2. A small rock was placed inside each bag to reduce movement in high winds, and six small perforations were made at their bases to permit drainage of rainwater. Litter bags were emptied at monthly intervals and samples were pooled. In anticipation of the burn, the bags were removed at the end of February 1987, and consequently there are no values for litter-fall during March 1987. The bags were replaced at the end of March, after the burn, and monthly collections of litter resumed thereafter. Lateral transport of allochthonous material was not measured.

Wood, bark, flowers and unidentified fragments were separated, and leaves sorted to species. All material was oven-dried at 60°C for 48 h and weighed. As Stewart & Davies (1990) point out, values obtained do not take into account leaching losses that must have occurred prior to collection, primarily during periods of high rainfall in winter.

Benthic organic matter (BOM) was collected with a square-sided benthic sampler that sampled 0.1 m^2 of stream bed. The sampler was fitted with 80 μm mesh nylon netting. Sampling began in April 1986, and three samples were collected at random each month. Each sample was preserved in 70% alcohol (which may have resulted in some leaching of organics and hence weight loss). The BOM was sorted into wood, bark, leaves, flowers and other coarse organic fragments (coarse benthic organic matter, CBOM), and each fraction was then oven-dried at 60°C for 48 h and weighed. The remaining fine benthic organic matter (FBOM) fraction (80–950 μm) invariably contained substantial amounts of inorganic material (gravel, silt, etc.), which was difficult and time-consuming to separate by eye. All fractions were therefore burnt at 450°C for 5 h, and values for BOM are expressed as g ash-free dry weight (AFDW). The benthic fauna was retained and will be reported on elsewhere.

Ultra-fine benthic organic matter (UBOM <80 μm) was sampled with a cylindrical stainless steel corer, 285 mm in diameter, following the method described by King *et al.* (1987). Relative monthly accumulation of BOM was measured in the present study; the cylinder was placed in the same position each month to keep environmental variables as constant as possible. The sampler was pushed into the stream bed as deeply as possible, and all loose rocks and stones were removed from within. The substratum was then disturbed vigorously with a wooden rod and the upwelling benthic detritus was scooped out together with the water in the cylinder. With repeated agitation, it was possible to remove most of the fine benthic detritus as it became suspended. The process was continued until the water in the cylinder was clear. The volume of collected water was measured and passed through an 80 μm sieve.

In the laboratory, subsamples of UBOM were concentrated on pre-combusted and weighed glass fibre filters (Whatman GF/F, pore size 0.6 μm), dried, weighed and burned at 450°C for 2 h to determine organic content.

Particulate organic matter in the water column was sampled with a drift net (mesh size 80 μm) with a mouth area of 0.047 m^2. The net was held in the stream for a 10 min period (5 min or less during periods of high discharge) and the amount of water passing through the net determined by multiplying net mouth area by flow rate obtained from gauging weir measurements. Each sample was split into coarse particulate organic matter (CPOM >950 μm) and fine particulate organic matter (FPOM >80 μm, <950 μm) fractions. The FPOM fractions from the water column contained varying amounts of inorganic material (fine silt, etc.), and therefore both FPOM and CPOM fractions were burned at 450°C for 5 h to determine organic content. Values for particulate organic material are expressed as g ash-free dry weight (AFDW).

Ultra-fine particulate organic matter (UPOM <80 μm) in stream water was measured by passing up to 6 litres of water first through an 80 μm sieve and then through pre-combusted

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and weighed glass fibre filters (Whatman GF/F), as for UBOM, above. Sampling was carried out twice monthly in May and June of the post-burn year.

Measurements of stream discharge were obtained from a 90° V-notch weir constructed by SAFRI. Rainfall measurements for the Swartboskloof catchment were obtained from SAFRI.

Regression analysis was used to determine relationships between discharge and concentrations of particulate organic matter and benthic organic matter (Zar, 1984). The Kruskal-Wallis test (Zar, 1984) was used to test seasonal differences in BOM within the pre- and post-burn years. The Mann-Whitney test (Zar, 1984) was used to determine the significance of differences in seasonal values between the pre- and post-burn years. Autumn was defined as March–May, winter as June–August, spring as September–November, and summer as December–February. Seasonal values were calculated as the mean of monthly values.

Results

Litter-fall

1. *Pre-burn year.* Total litter-fall trapped during the pre-burn year (March 1986 to February 1987) amounted to 486 g m^{-2}, of which soft litter (leaves, flowers, seeds and fragments) comprised 91% (445 g m^{-2}). Wood and bark accounted for the rest. Leaves represented the major component of the soft litter fraction (327 g m^{-2}), with *Cunonia capensis* (L.) and *Ilex mitis* (L.) dominant (Table 1). Litter-fall from riparian trees showed a distinct seasonal pattern. Peak soft litter-fall occurred in early summer, with 53% of the annual total (234 g) falling during December and January (Fig. 1). 64% of the hard litter fell during September, October and November. Most was wood (97–99%) and the remainder bark.

2. *Post-burn year.* Although the prescribed fire burnt virtually all the vegetation on the slopes of the catchment, the riparian vegetation was burnt at the edges only, and the canopy appeared unaffected. One week after the prescribed burn, however, a heavy aseasonal leaf-fall commenced within the riparian zone. This period of heavy leaf-fall lasted approximately 2 months (Fig. 1), by which time the canopy had opened up considerably and appeared unusually sparse. Leaves from *Ilex mitis* dominated leaf-litter entering the traps in April (42% by weight), and *Cunonia capensis* leaves dominated in May (57%). Total soft litter-fall during these 2 months was 389 g m^{-2}, 1.7 times greater than that recorded during the 2 months of peak litter-fall in the pre-burn year. By June 1987, leaf-fall had returned to pre-burn levels.

The summer peak in litter-fall in the post-burn year took place in January and February 1988. Total soft litter-fall during these months, however, was only 194 g m^{-2}: less than half the amount recorded for the pre-burn summer peak. The spring peak of hard litter-fall witnessed in the pre-burn year was less well defined in the post-burn year.

Benthic organic matter

1. *Pre-burn year.* Mean monthly standing stocks of soft BOM (leaves, flowers, fragments and FBOM) and hard BOM (wood and bark) are shown in Fig. 2. Over the pre-burn sampling

TABLE 1. Mean proportions by weight of leaf litter contributed by riparian trees during the pre- and post-burn years. (*n* is number of monthly collections.)

	Pre-burn (n=12)		Post-burn (n=11)	
Species	Mean (%)	SE	Mean (%)	SE
Brabejum stellatifolium	4.93	1.14	7.89	3.12
Brachylaena neriifolia	8.17	1.08	2.11	0.60
Cunonia capensis	42.02	4.54	45.28	5.99
Ilex mitis	25.05	3.66	22.69	3.75
Metrosideros angustifolia	5.12	0.92	3.08	0.59
Podalyria calyptrata	10.66	2.24	4.09	1.24
Maytenus acuminata	2.92	1.24	11.65	3.45
Hartogia schinoides	0.62	0.59	3.09	2.86
Other	0.51	0.41	0.12	0.11

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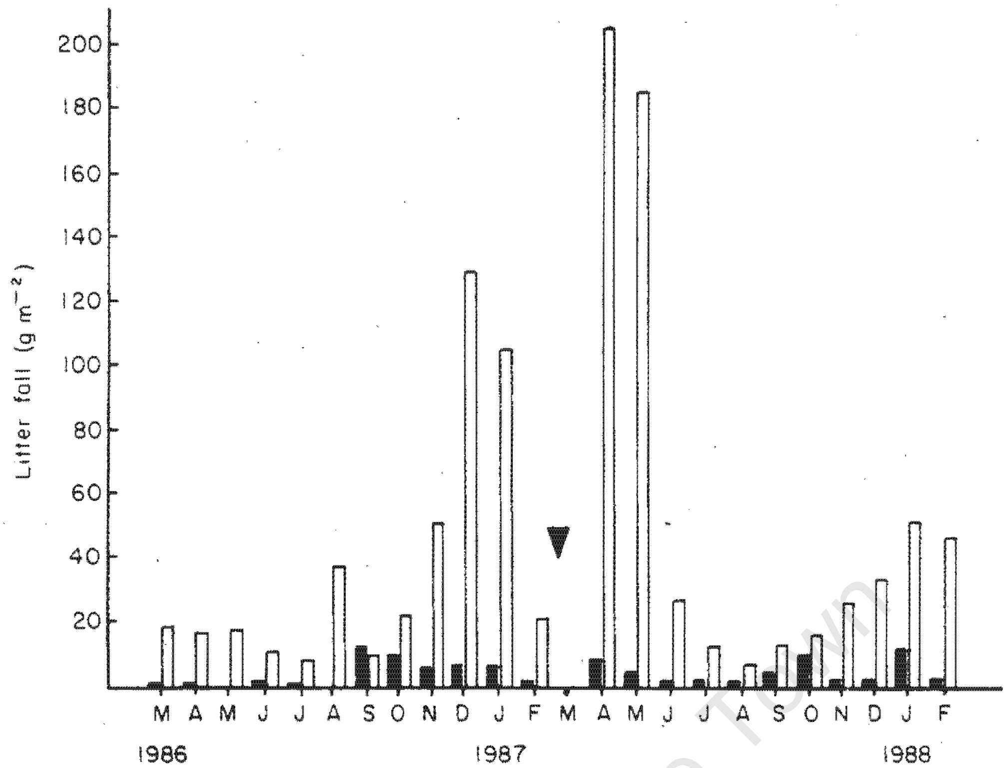

FIG. 1. Litter-fall from riparian trees in Swartboskloof from March 1986 to February 1988. Open bars represent soft litter (leaves, flowers, seeds, fragments), shaded bars represent hard litter (wood and bark). The arrow indicates the timing of the burn.

period (April 1986 to February 1987), monthly standing stocks of total BOM ranged from 10 g AFDW m^{-2} (July) to 173 g AFDW m^{-2} (February) of which 9 g (July) to 72 g (February) was soft litter and 1 g (July) to 101 g (February) was hard litter. FBOM ranged from 5.0 g AFDW m^{-2} (September) to 18.2 g AFDW m^{-2} (February) and constituted an annual mean of 42.6% (SE=3.48%) of the soft BOM fraction (Fig. 3). Mean monthly standing stocks of soft BOM varied inversely with total discharge during the week preceding each sampling date ($y=1000.6x^{-0.353}$, $r=0.617$, $P<0.05$). There was no significant relationship between standing stocks of hard BOM and discharge. Large standard errors were often associated with monthly means for the hard BOM fraction, and this was invariably due to the presence of a large stick in one of the three samples.

Seasonality in the quantities of BOM was evident, although significant differences (Kruskal-Wallis test, $P<0.05$) in seasonal values existed between autumn and winter only. High discharges during winter and early spring scoured out litter which had accumulated on the stream bed, and resulted in low standing stocks of BOM. Falling discharges during late spring coincided with an increase in leaf litter-fall, and leaves and debris started to accumulate on the stream bed. Peak litter-fall occurred in December, and falls remained high until the end of January. Peak soft BOM levels occurred during the summer, although the seasonal mean is deceptive as large standard errors were associated with the December and February monthly means. To a lesser extent, this was also true for the hard BOM fraction. A summer storm (101 mm rainfall in 3 days), which occurred in the week preceding the January sampling date, flushed away some of the accumulating litter and temporarily depressed hard and soft BOM levels.

Monthly values for UBOM that accumulated in the cleared core area ranged from 9 g AFDW m^{-2} (June) to 61 g AFDW m^{-2} (May) (Fig. 4). Mean monthly accumulation was 38 g AFDW m^{-2} (SE=4.8). Peak values in the autumn of the pre-burn year were followed by low winter values as discharge increased, after which values for monthly accumulation rose

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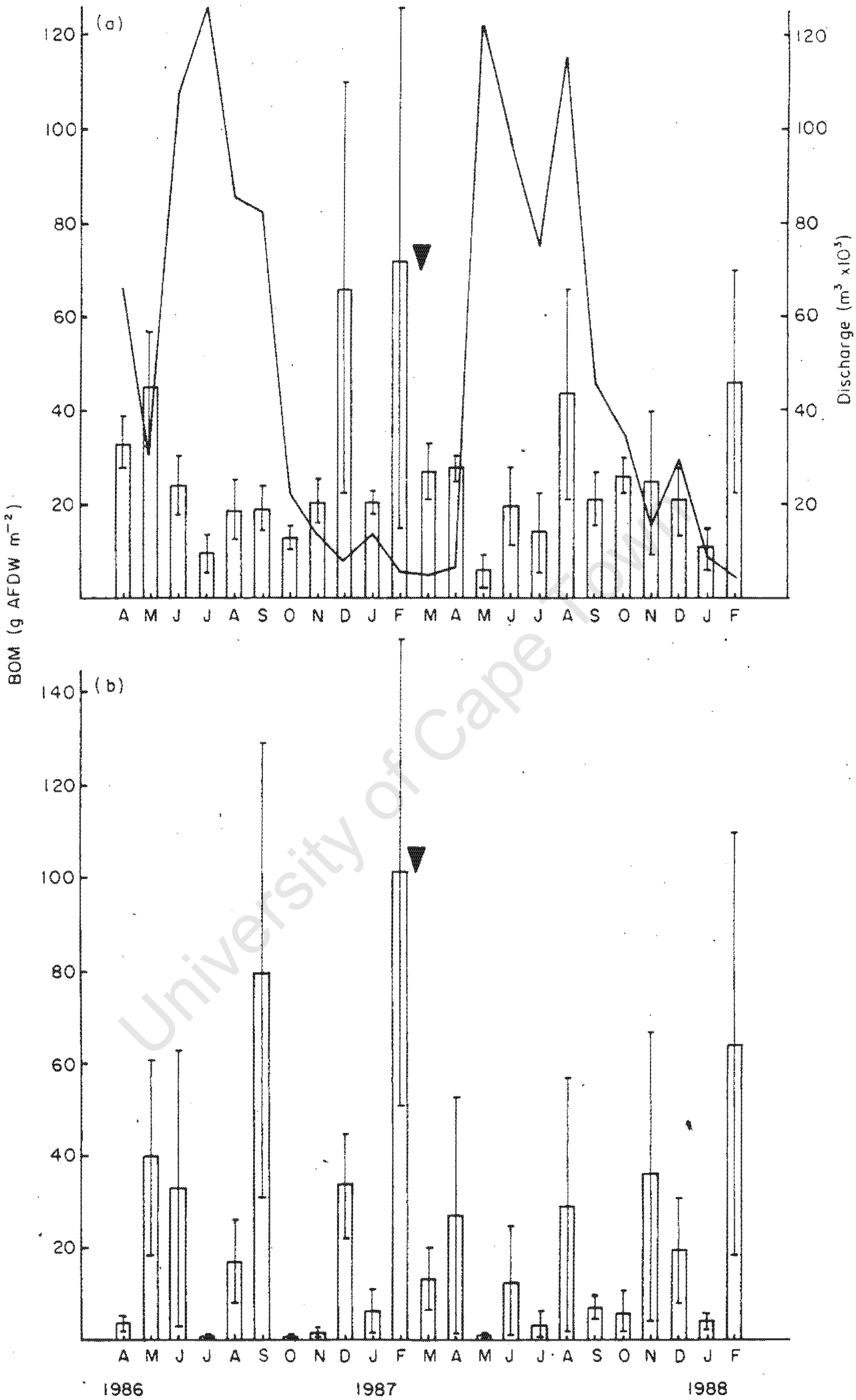

FIG. 2. Benthic organic matter in the Swartboskloof stream from April 1986 to February 1988: (a) soft BOM (leaves, flowers, fragments and fine benthic organic matter); (b) hard BOM (wood and bark). Values represent the mean of three samples except April 1986 which represents the mean of two samples. Bars indicate standard errors. Total discharge during the week prior to each sampling date superimposed on graph (a). Arrows indicate the timing of the burn.

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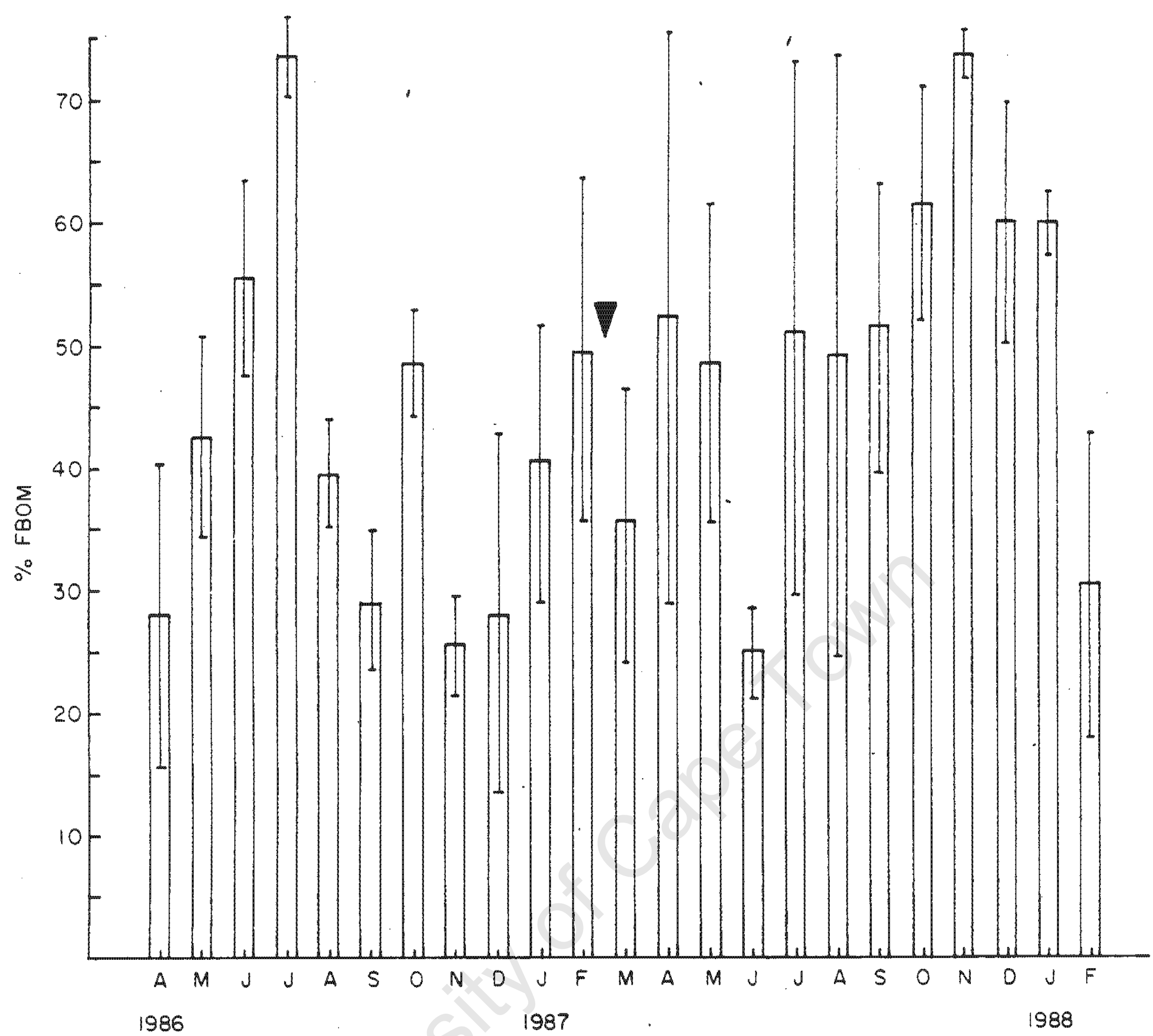

FIG. 3. FBOM as a percentage of the soft BOM (FBOM + CBOM) fraction from April 1986 to February 1988. Values represent the mean of three samples except for April 1986 which represents the mean of two samples. Bars indicate standard errors. The arrow indicates the timing of the burn.

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during the spring and summer. UBOM accumulation was significantly and negatively related to total discharge during the 3 days preceding each sampling date ($y=661.8x^{-0.320}$, $r=0.639$, $P<0.05$).

2. *Post-burn year*. Mean monthly standing stocks of BOM ranged from 7 g AFDW m^{-2} (May) to 111 g AFDW m^{-2} (February) of which 6 g (May) to 46 g (February) was soft litter and 1 g (May) to 64 g (February) was hard litter. FBOM ranged from 2.4 to 17.9 g AFDW m^{-2} and constituted an annual mean of 49.8% (SE=4.08%) of the soft BOM fraction. Seasonality in BOM standing stocks in the post-burn year was less distinct, with no significant differences between seasonal values and no significant relationship between discharge and standing stocks. Heavy leaf-fall in April, which occurred at a time of very low flow, was not accompanied by an increase in soft BOM (Fig. 2). Concentrations of total BOM were low from May to July, but increased in August despite high discharges on the day of sampling and during the preceding week. Peak annual litter-fall took place at the start of 1988 and, although low in January, BOM standing stocks reached peak post-burn levels by the end of February. Mean BOM standing stock during the summer of the post-burn year was only 55% of the pre-burn mean, but because of the large standard error associated with the pre-burn mean, differences between the years were not significant. Furthermore, no significant differences existed between pre- and post-burn autumn, winter or spring

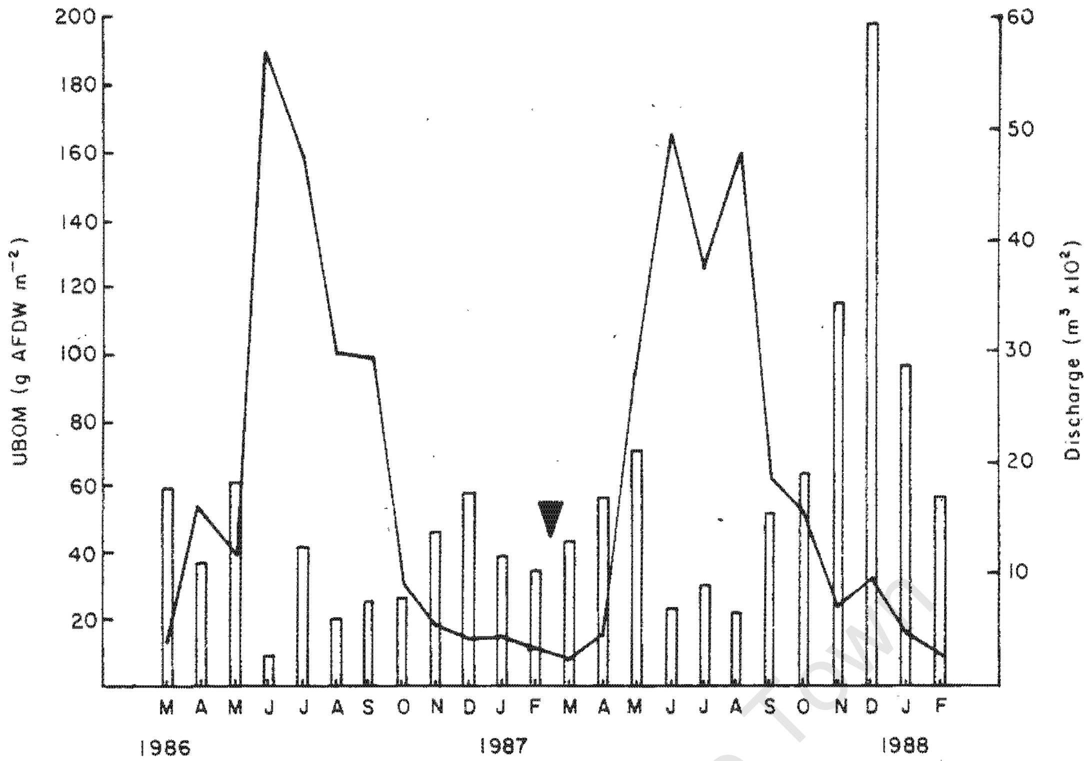

FIG. 4. Monthly UBOM accumulation in Swartboskloof from March 1986 to February 1988. Total discharge during the 3 days preceding each sampling date are superimposed. The arrow indicates the timing of the burn.

values for soft, hard or total BOM. Compared to the pre-burn year, proportions of FBOM in the soft BOM fraction were significantly higher during the spring of the post-burn year ($P<0.05$) (Fig. 3), and quantities of FBOM were also significantly higher ($P<0.05$) during that period.

Monthly accumulations of UBOM in the post-burn year ranged from 22 g AFDW m^{-2} (August) to 199 g AFDW m^{-2} (December) with a mean monthly accumulation of 69 g m^{-2} (SE=14.3). An inverse relationship generally existed between UBOM concentration and total discharge during the 3 days preceding each sampling date, although this relationship was not significant. Seasonal values for accumulated UBOM were comparable with pre-burn values in the autumn and winter, but were significantly higher ($P<0.05$) during the spring and summer, when post-burn values were 2.3 and 2.7 times pre-burn values, respectively.

Suspended particulates

1. *Pre-burn*. CPOM concentrations in the pre-burn year ranged from 0.002 g AFDW m^{-3} (February) to 0.5 g AFDW m^{-3} (March). Concentrations were highest in autumn, as increasing discharges dislodged BOM and leaf packs in the stream and suspended litter which had accumulated on the dry stream bed during periods of low flow and peak litter-fall. Sampling during winter generally took place after rain events which may explain why concentrations of CPOM measured during this season were low, as suspended material tends to settle out rapidly as flow subsides. Peak litter-fall in early summer did not result in a large increase in CPOM concentration (Fig. 5). As discharge fell, retention of organic matter increased, and leaves and wood falling into the stream accumulated on the stream bed and formed leaf packs behind boulders and other obstructions.

FPOM in drift samples ranged from 0.06 g AFDW m^{-3} (February) to 0.53 g AFDW m^{-3} (March). FPOM concentrations were also influenced by the flushing effect of increasing stream discharge during autumn, and highest levels of FPOM were measured during this season. High discharges during winter continued to scour out FBOM retained by the stream bed, and concentrations decreased progressively

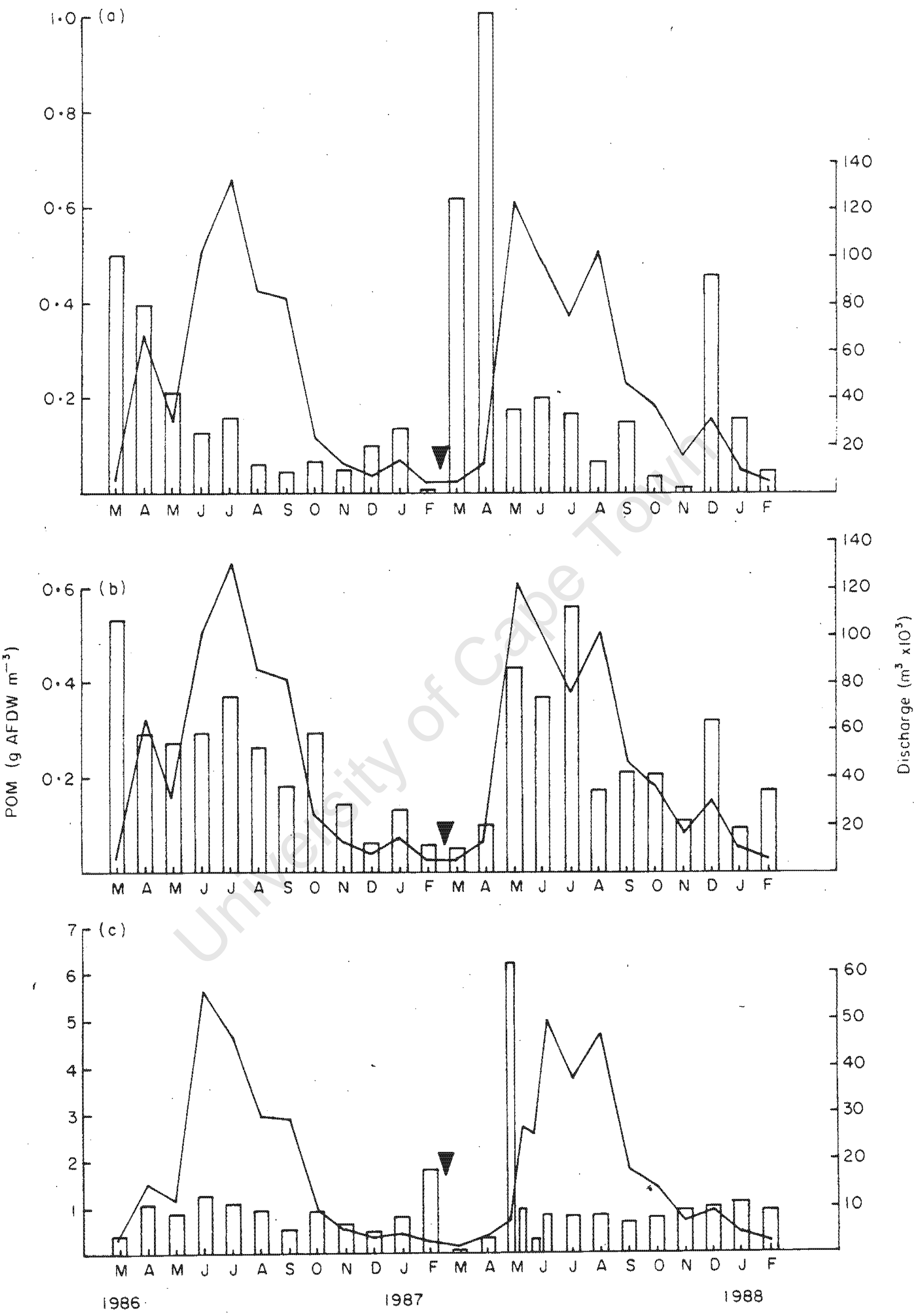

FIG. 5. Suspended particulate organic matter (POM) in Swartboskloof stream water from March 1986 to February 1988: (a) CPOM, (b) FPOM, and (c) UPOM. Total discharge during the week preceding each sampling date superimposed on (a) and (b) and total discharge in the preceding 3 days superimposed on (c). Note the different scales on the *y* axis. Arrows indicate the timing of the burn.

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during spring with decreasing discharge, reaching lowest levels in summer. The summer storm (101 mm) referred to earlier, which took place in the week preceding the January sampling date, resulted in increased discharge and increased concentrations of FPOM and to a lesser extent CPOM in drift samples.

The largest proportion (by weight) of total POM in stream water was contributed by the UPOM fraction. Over the pre-burn sampling period, the UPOM fraction constituted a mean of 69.6% (SE=4.7%) of total POM, whereas FPOM represented 18.7% (SE=2.5%) and CPOM 11.7% (SE=2.8%) of the total. UPOM concentrations ranged from 0.37 g AFDW m^{-3} (March) to 1.83 g AFDW m^{-3} (February), and were positively associated with total discharge during the 3 days preceding each sampling date. Seasonality in UPOM concentrations differed from that of the larger fractions. Concentrations were highest during winter, dropped to a spring minimum and then increased during summer.

Despite the fact that discharge has an obvious influence on concentrations of suspended particulate organic matter, no significant relationships were detected between discharge and concentrations of the three POM fractions. Variation in stream discharge alone therefore does not account for most of the variation in POM concentration.

2. *Post-burn*. Concentrations of CPOM in the first 2 months after the fire were very high despite low discharges (Fig. 5), and occurred as a result of heavy post-burn leaf-fall in the riparian zone. By the end of May, after substantial flushing flows, CPOM concentration in drift samples had dropped markedly. As in the pre-burn year, CPOM concentrations were lowest during spring.

FPOM concentrations were comparatively low in March and April, but rose dramatically in May as discharge increased. Highest concentrations of FPOM in drift samples were recorded in July, after which concentrations fell, despite high discharges in August. Following 7 days of light rainfall (60 mm total), increased discharges in the week preceding the December sampling date resulted in increases in both FPOM and CPOM in drift samples (Fig. 5).

Post-burn UPOM concentrations were very low in March and April when discharge was low. Discharge increased slightly at the beginning of May, and this increase was accompanied by a dramatic, short-lived increase in UPOM concentration (Fig. 5). During winter and early spring, there was little variation in UPOM concentration, although a small but progressive increase was recorded from October to January. Excluding values for March and April (when CPOM concentrations were exceptionally high), mean proportions of the different fractions of POM were very similar to values obtained for the pre-burn year. CPOM constituted 10.3% (SE=2.3%) of total POM, FPOM 20.0% (SE=2.8%) and UPOM 69.7% (SE=4.0%).

As in the pre-burn year, although POM concentrations were clearly affected by discharge, no significant relationships existed between the variables.

Discussion

Litter-fall

Results obtained for pre-burn riparian litter-fall were similar to measurements obtained for other small catchments in the Jonkershoek Valley. Pre-burn litter-fall of 486 g m^{-2} a^{-1} in Swartboskloof fell within the 434–500 g m^{-2} a^{-1} range reported for Langrivier (King *et al*., 1987), and the 284–614 g m^{-2} a^{-1} range recorded for four different sites in the Valley over 4 years (D. Versfeld, SAFRI, unpublished data). Litter-fall was also similar to the 426 g m^{-2} a^{-1} reported by Stewart & Davies (1990) at a another fynbos site. Litter from riparian trees fell throughout the year, but exhibited a distinct seasonal pattern, with peak fall of soft litter in summer and a less distinct spring peak of hard litter. As reported for Langrivier, leaves represented the dominant fraction in litter (67% in the pre-burn year and 62% in the post-burn year).

Although evergreen Afromontane forests do not burn readily (Everard, 1986), raising the temperature of leaves above 55°C for short periods usually causes premature abscission (Luke & MacArthur, 1978, cited in Granger, 1984). This must account for the heavy, aseasonal leaf-fall observed shortly after the Swartboskloof catchment was burnt. Post-burn soft litter-fall probably amounted to more than the 389 g m^{-2} recorded for April and May, as the litter-traps were only replaced 1 week after the fire. Peak summer litter-fall in the post-burn year occurred in January and February, and was less than half that measured during the pre-

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burn summer peak in December and January. It is not known to what extent this can be attributed to the leaf-fall which took place immediately after the fire, but it seems reasonable to assume that such a heavy and aseasonal loss could influence litter-fall the following year. Despite low leaf-fall in the post-burn summer, total litter-fall in the post-burn year was 1.4 times higher than in the pre-burn year, and fell outside the ranges recorded by King *et al.* (1987) and Versfeld (unpublished data). Abnormally high leaf-fall must represent enhanced nutrient loss from the catchment, in terms of both the quantity of leaves falling into the stream after the fire and the quality of these leaves. Mattson (1980), for example, reported that the nitrogen content of growing leaves was considerably higher than in leaves prior to abscission.

Benthic organic matter

Standing stocks of BOM during the pre-burn year were strongly influenced by discharge, and seasonality was evident although significant differences existed between autumn and winter values only. Monthly and seasonal values were within the ranges reported by King *et al.* (1987) for a site in the Langrivier catchment at an altitude of 366 m, although seasonality in the Swartboskloof catchment was less pronounced than in Langrivier. The lowest recorded levels of BOM (excluding UBOM) in Swartboskloof in the pre- and post-burn years were similar at 9.9 and 6.5 g m^{-2} respectively, and these values may approximate the baseline storage capacity of the system.

Despite the heavy, aseasonal leaf-fall that followed the burn, there was no evidence of a corresponding increase in soft BOM levels. Leaves falling into the stream at this time floated on the surface of the water, collecting in large numbers in pools and backwaters. This may be explained by the fact that the leaves killed by the heat of the fire were predominantly in the active growing state, as opposed to the pre-abscission state, and their waxy cuticles were thus still largely intact. Insufficient time elapsed for waterlogging and settling on to the streambed to occur before the onset of the winter rains, when the leaves were carried away by a rise in discharge. Relatively low litter inputs in the summer of the post-burn year were reflected by lower standing stocks of BOM compared with the previous summer, yet no significant differences in seasonal standing stocks of BOM existed between years. A prescribed burn of low to moderate intensity, in which the riparian vegetation is not killed, thus appears to have little effect on the quantity of food available to benthic invertebrates, at least in the short term.

During the pre-burn year, proportions of CBOM and FBOM in the soft BOM fraction showed no significant seasonal pattern, although proportions of FBOM appeared to be lower during spring and early summer than during winter (Fig. 3). Except in June and July, CBOM constituted the dominant fraction. In spring of the post-burn year, however, the proportions and quantities of FBOM were significantly higher than in the pre-burn year, and FBOM was more abundant than CBOM from September to January. In addition, monthly UBOM accumulation during spring and summer of the post-burn year was significantly higher than in the preceding year. These increases in the finer fractions of BOM may have been caused by changes in stream chemistry. A significant increase in nitrate concentration was recorded in Swartboskloof stream water after the burn, persisting from May to August (Britton, unpublished data). Mean nitrate concentration during this period (30.9 μg NO_3-N l^{-1}) was 1.9 times higher than in the preceding pre-burn winter. It is possible that microbial activity (and hence decay rates of BOM in the Swartboskloof stream) may have been accelerated by enhanced nitrate concentrations resulting in the observed increase in proportions and quantities of FBOM and UBOM. Meyer & Johnson (1983) reported enhanced decomposition rates of two species of leaves in a North Carolina stream where anthropogenic disturbance in the surrounding catchment had brought about elevated nitrate concentrations. They ascribed more rapid decay rates to accelerated microbial processing in response to nitrate enrichment. Triska & Sedell (1976) failed to demonstrate a stimulatory effect of nitrate enrichment on leaf decay, but as Meyer & Johnson (1983) pointed out, inconsistencies in findings may be due to the leaf species involved, or to the fact that streams differ in ways other than just nitrate concentration. Measurements of microbial activity or rates of leaf decay were not undertaken during the present study, so a stimulatory effect of increased nitrate concentrations in Swartboskloof stream

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water cannot be confirmed. Nevertheless, if activity did increase, the fire may have indirectly affected the quality of food available to benthic invertebrates and hence the processing dynamics of riparian detritus. Irons, Oswood & Bryant (1988) reported that nitrogen concentrations in leaf litter appeared to influence food choice by caddisfly larvae, and proposed that increased soil nutrient availability – through fertilization or nutrient release following forest fires – should increase the nutrient content of plant detritus and hence substantially influence the palatability of benthic leaf detritus to stream detritivores. Such changes in nutrient content may also influence the processing dynamics of allochthonous material as well as the abundance, composition and growth of stream consumers. Sampling in the present study did not continue long enough for this hypothesis to be tested, but since recurrent fires are a general feature of fynbos ecosystems, the subject warrants further attention.

Suspended particulates

The amount of CPOM exported in Swartboskloof stream water was small in relation to FPOM and particularly to UPOM (except for March and April in the post-burn year, when leaf-fall was very heavy), which indicates that the system is highly retentive of CPOM. The activities of microbes and macroinvertebrates help to reduce the CBOM to smaller size categories of detrital organic matter, and since small particles are easily moved by water and difficult to trap (Malmqvist, Nilsson & Svensson, 1978; Bilby & Likens, 1979; Naiman & Sedell, 1979b), they dominate the organic matter exported by streams. Naiman & Sedell (1979b) reported that for all four of the streams they studied in Oregon's Cascade Mountains, more than 70% of organic particulate drift consisted of very fine particulate organic matter (VPOM 0.45–53 μm).

Concentrations of POM in drift samples were influenced by discharge, although no significant relationships between discharge and any of the size fractions were detected in either the pre- or the post-burn year. In explanation of a similarly non-significant relationship between discharge and FPOM concentrations, Fisher & Likens (1973) reported that FPOM concentration was higher for a given discharge on the rising limb of a hydrograph than it was for the corresponding discharge on the falling limb which indicates that the actual time of sampling is important. Furthermore, Bilby & Likens (1979) concluded that fine particulate organic carbon (FPOC) concentration in stream water is dependent not only on discharge but also on the amount of FPOC on the stream bed (and possibly in the canopy) and the duration of dry weather before rain events.

Despite the increase in FBOM in the post-burn spring, there was no obvious increase in levels of FPOM in drift samples during this period. Concentrations of UPOM however rose slightly from October to January in spite of a general decrease in discharge. The very high concentration of UPOM recorded in early May probably occurred as the result of a heavy storm (71.4 mm) that commenced 4 days prior to the sampling date and lasted 3 days. This storm was the largest of the first four storms to occur after the fire, and in the absence of a full, protective riparian canopy, heavy rain may have washed particulate material from the stream bank into the stream channel, resulting in the high concentrations observed in stream water. Because of the high soil-moisture deficit of the catchment, discharge did not increase markedly during this event. The pre-burn peak in UPOM concentration, which took place in February, is also thought to be attributable to light rainfall (9.6 mm) which commenced 3 days prior to the sampling date and lasted 2 days.

Fire as a disturbance factor

The responses of stream communities to disturbance have received considerable attention (see review by Resh *et al.*, 1988), particularly the effects of flow-related disturbances such as spates. The effects of spates are predominantly abiotic, and often result in dramatic reductions in numbers or biomass of invertebrate taxa (Resh *et al.*, 1988). Recovery to pre-impact conditions may take from 1 month to several years, depending on the timing and severity of the disturbance and the availability of nearby colonizers (Fisher, 1983). Natural major biotic disturbances are uncommon, but fire in mountain catchments may be considered one of these as it has the capacity to grossly alter the input of allochthonous organic material upon which stream communities are dependent for food.

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Studies in southern Appalachian streams have shown that differences in benthic insect communities are associated with differences in the quantity and quality of allochthonous detrital inputs and primary production (Woodall & Wallace, 1972), and that change in riparian vegetation is a major factor influencing long-term changes in aquatic insect populations (Haefner & Wallace, 1981). Furthermore, Gurtz, Webster & Wallace (1980) concluded that the recovery of allochthonous inputs to pre-disturbance levels depends upon the resilience of the forest ecosystem, not of the stream. It can be hypothesized, therefore, that the effects of fire on stream communities should be long-lasting if the riparian vegetation is destroyed, with recovery directly related to the recovery of the riparian community. Abiotic effects associated with the destruction of the riparian vegetation may also include increased light penetration to streams, increases in stream temperature, increased runoff, increased silt loads and increased nutrient supply, which may alter the stream environment and reduce the quality of stream water. The importance of riparian vegetation in maintaining the integrity of the stream environment is widely recognized, and buffer strips (zones of vegetation left along stream banks) are increasingly advocated in order to protect streams from the impacts of logging (Newbold, Erman & Roby, 1980). Studies in northern California streams suggest that most or all of the effects of logging can be prevented by buffer strips (Newbold *et al.*, 1980).

In the Swartboskloof catchment, the natural resilience of the riparian vegetation greatly reduced the potential impacts of fire on the stream environment. Fynbos vegetation forms a vertically continuous 'fuel bed', 1–2 m deep, whereas in the forest, tree canopies are approximately 5 m above the litter layer and are 5–7 m deep. The arrangement of fuel in forests is considered to be less conducive to fire spread, and appears to be the reason why fires do not penetrate forest patches (Van Wilgen, Higgins & Bellstedt, 1990). In addition, live foliage in forest has a considerably higher moisture content than does fynbos vegetation and a lower crude fat and energy content (Van Wilgen *et al.*, 1990). Although leaf-fall from riparian trees was very heavy in the first 2 months after the burn, the canopy did not remain sparse for long, and had fully recovered within 6 months. The prescribed burn had little effect on BOM levels and is thought to have had little impact on the stream environment in general. Thus, although fire represents a major disturbance in the surrounding catchment, its effects on the stream environment are apparently minor, provided that riparian vegetation remains intact. Analysis of pre- and post-burn benthic invertebrate fauna, necessary in order to confirm this hypothesis, is presently underway and will be reported elsewhere.

Acknowledgments

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References

Bands D.P. (1977) Prescribed burning in Cape fynbos catchments. In: Mooney, H.A. & Conrad, C.E. (technical coordinators) Proceedings of the symposium on the environmental consequences of fire and fuel management in mediterranean ecosystems, Palo Alto, California. *U.S. Department of Agriculture, Forestry Service, General Technical Report*, **WO-3**, 245–256.

Bilby R.E. & Likens G.E. (1979) Effect of hydrological fluctuations on the transport of fine particulate organic carbon in a small stream. *Limnology and Oceanography*, **24**, 69–75.

Bormann F.H., Likens G.E. & Eaton J.S. (1969) Biotic regulation of particulate and solution losses from a forest ecosystem. *Bioscience*, **19**, 600–610.

Conners M.E. & Naiman R.J. (1984) Particulate allochthonous inputs: relationships with stream size in an undisturbed watershed. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 1473–1484.

Cowan C.A. & Oswood M.W. (1983) Input and storage of benthic detritus in an Alaskan Subarctic stream. *Polar Biology*, **2**, 35–40.

Cummins K.W., Petersen R.C., Howard F.O., Wuycheck J.C. & Holt V.I. (1973) The utilization of leaf litter by stream detritivores. *Ecology*, **54**, 336–345.

University of Cape Town

Dance K.W., Hynes H.B.N. & Kaushik N.K. (1979) Seasonal drift of solid organic matter in two adjacent streams. *Archiv für Hydrobiologie*, **87**, 139–151.

Dell B., Hopkins A.J.M. & Lamont B.B. (Eds) (1986) *Resilience in Mediterranean-type Ecosystems*, pp. 1–4. W. Junk, The Hague.

Egglishaw H.J. (1964) The distributional relationship between the bottom fauna and plant detritus in streams. *Journal of Animal Ecology*, **33**, 463–476.

Everard D.A. (1986) The effects of fire on the *Podocarpus latifolius* forests of the Royal Natal National Park, Natal Drakensberg. *South African Journal of Botany*, **52**, 60–66.

Fisher S.G. (1983) Succession in streams. *Stream Ecology: Application and Testing of General Ecological Theory* (Eds J. R. James and G. W. Minshall), pp. 7–27. Plenum Press, New York.

Fisher S.G. & Likens G.E. (1973) Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs*, **43**, 421–439.

Fox B.J. & Fox M.D. (1986) Resilience of animal and plant communities to human disturbance. *Resilience in Mediterranean-type Ecosystems* (Eds B. Dell, A. J. M. Hopkins and B. B. Lamont), pp. 39–64. W. Junk, The Hague.

Granger J.E. (1984) Fire in forest. *Ecological Effects of Fire in South African Ecosystems* (Eds P. de V. Booysen and N. M. Tainton), pp. 177–197. Springer-Verlag, Ecological Studies Series, 48.

Gurtz M.E., Webster J.R. & Wallace J.B. (1980) Seston dynamics in southern Appalachian streams: effects of clear-cutting. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 624–631.

Haefner J.D. & Wallace J.B. (1981) Shifts in aquatic insect populations in a first-order southern Appalachian stream following a decade of old field succession. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 353–359.

Irons J.G., Oswood M.W. & Bryant J.P. (1988) Consumption of leaf detritus by a stream shredder: Influence of tree species and nutrient status. *Hydrobiologia*, **160**, 53–61.

Keeley J.E. (1986) Resilience of mediterranean shrub communities to fires. *Resilience in Mediterranean-type Ecosystems* (Eds B. Dell, A. J. M. Hopkins and B. B. Lamont), pp. 95–112. W. Junk, The Hague.

King J.M., Day J.A., Davies B.R. & Henshall-Howard M.-P. (1987) Particulate organic matter in a mountain stream in the south-western Cape, South Africa. *Hydrobiologia*, **154**, 165–187.

Luke R.H. & MacArthur A.G. (1978) *Bushfires in Australia*. Australian Government Publishing Service, Canberra. (Cited in Granger, 1984.)

Malmqvist B., Nilsson L.M. & Svensson B.S. (1978) Dynamics of detritus in a small stream in southern Sweden and its influence on the distribution of the bottom animal communities. *Oikos*, **31**, 3–16.

Mattson W.J. (1980) Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, **11**, 119–161.

Meyer J.L. & Johnson C. (1983) The influence of elevated nitrate concentration on rate of leaf decomposition in a stream. *Freshwater Biology*, **13**, 177–183.

Minshall G.W. (1967) Role of allochthonous detritus in the trophic structure of a woodland springbrook community. *Ecology*, **48**, 139–149.

Naiman R.J. & Sedell J.R. (1979a) Benthic organic matter as a function of stream order in Oregon. *Archiv für Hydrobiologie*, **87**, 404–422.

Naiman R.J. & Sedell J.R. (1979b) Characterization of particulate organic matter transported by some Cascade Mountain streams. *Journal of the Fisheries Research Board of Canada*, **36**, 17–31.

Newbold J.D., Erman D.C. & Roby K.B. (1980) Effects of logging on macroinvertebrates in streams with and without buffer strips. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 1076–1085.

Resh V.H., Brown A.V., Covich A.P., Gurtz M.E., Li H.W., Minshall G.W., Reice S.R., Sheldon A.L., Wallace J.B. & Wissmar R.C. (1988) The role of disturbance in stream ecology. *Journal of the North American Benthological Society*, **7**, 433–455.

Stewart B.A. & Davies B.R. (1990) Allochthonous input and retention in a small mountain stream, South Africa. *Hydrobiologia* (in press).

Tiedemann A.R., Conrad C.E., Dieterich J.H., Hornbeck J.W., Megahan W.F., Viereck L.A. & Wade D.D. (1979) Effects of fire on water – a state-of-knowledge review. *U.S. Department of Agriculture, Forestry Services, General Technical Report*, **WO-10**.

Triska F.J. & Sedell J.R. (1976) Decomposition of four species of leaf litter in response to nitrate manipulation. *Ecology*, **57**, 783–792.

Van Wilgen B.W., Higgins K.B. & Bellstedt D.U. (1990) The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* (in press).

Wakefield R.H., Harrison A.D. & Kovalak W.P. (1980) Seasonal changes in the quantity and nitrogen content of coarse detritus in a southern Ontario stream. *Internationale Revue der Gesamten Hydrobiologie*, **65**, 883–888.

White F. (1978) The Afromontane Region. *Biogeography and Ecology of Southern Africa* (Eds M. J. A. Werger and J. C. van Bruggen), pp. 463–513. *Monographiae Biologicae* **31**. W. Junk, The Hague.

Winterbourn M.J. (1976) Fluxes of litter falling into a small beech forest stream. *New Zealand Journal of Marine and Freshwater Research*, **15**, 321–328.

Woodall W.R. & Wallace J.B. (1972) The benthic fauna in four small southern Appalachian streams. *The American Midland Naturalist*, **88**, 393–407.

Zar J.H. (1984) *Biostatistical Analysis*, 2nd edn. Prentice-Hall, Englewood Cliffs, New Jersey.

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THE BENTHIC MACROINVERTEBRATE FAUNA OF A SOUTH AFRICAN MOUNTAIN STREAM AND ITS RESPONSE TO FIRE

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SUMMARY

1. The effects of a late-summer prescribed burn on the temperature and benthic macroinvertebrate fauna of a south-western Cape mountain stream were investigated over a period of 12 months.

2. The temperature regime, like the discharge regime, is well-defined and relatively predictable from year to year. As in other mediterranean-type ecosystems, seasonal changes in the structure of the invertebrate community and the relative abundance of different feeding groups appear to be associated primarily with changes in the physical environment.

3. Although the riparian vegetation was only slightly damaged by fire, a heavy, aseasonal leaf fall occurred shortly afterwards. The canopy remained sparse for approximately four months, however, stream temperature in the post-burn year was not demonstrably affected, probably because the canopy remained open during the winter months.

4. The fire appeared to have had little effect on the invertebrate fauna. It is concluded that the riparian vegetation is of major importance in maintaining the integrity of the stream environment.

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INTRODUCTION

It is widely recognized that streams are an expression of the land they drain. The slope of the valley, the depth and permeability of the soil and patterns of precipitation greatly affect the pattern of flow and the dissolved organic matter content of the stream water (Hynes, 1975). Terrestrial vegetation plays an important role in regulating the thermal conditions of small streams (Brown & Krygier, 1970; Meehan *et al.* 1977), and litter-fall from overhanging trees often represents the major food source of benthic invertebrates (eg. Egglishaw, 1964; Cummins *et al.*, 1973) since primary production in shaded streams is usually low. Removal of riparian vegetation by logging results in marked increases in stream temperature (Brown & Krygier, 1967, 1970; Graynoth, 1979; Webster *et al.*, 1983), which may have serious consequences for aquatic insects (Ward, 1984). Furthermore, modification of allochthonous inputs to southern Appalachian streams following clearcutting has been shown to result in significant changes in species composition and abundance of benthic invertebrates (Haefner & Wallace, 1981; Webster *et al.*, 1983). Similar findings have been reported for northern Californian streams following logging (Newbold *et al.*, 1980).

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In the south-western Cape of South Africa, as in other mediterranean-type ecosystems, recurrent fires are recognised as a natural feature of the environment (Keeley, 1986). The indigenous vegetation of the area, 'fynbos', is fire-adapted, and periodic fires are necessary in order to maintain the complete range of terrestrial plant species (Bands, 1977). Prescribed (deliberate) burning of mountain catchments is presently carried out at 12-15 year intervals in order to maximize yields of high-quality water, maintain diversity in the fynbos and reduce the risk of wildfire (Bands, 1977).

Although the effects of fire on hydrologic processes and stream chemistry have been well documented (see review by Tiedemann *et al.*, 1979), there is little published information on its effects on benthic macroinvertebrate communities. Minshall *et al.* (1989) speculated that increased flows, streambed erosion and high suspended sediment concentrations in the aftermath of fires in the Greater Yellowstone Area may bring about massive invertebrate drift from streams draining the burned areas. Effects on benthic invertebrate feeding groups were also forecast, with shredder populations expected to be almost absent during recovery from a fire, due to the destruction of leaf-litter sources.

Both the effects of logging and the speculated effects of fire on stream communities pertain to the removal or destruction of the riparian vegetation. In the south-western Cape of South Africa, the natural riparian vegetation of fynbos-dominated mountain catchments is resistant to fire, burning only under extreme fire conditions (van Wilgen, 1987). Nevertheless, heavy leaf falls may occur shortly afterwards leaving the canopy temporarily open. Although such falls may have no significant effect on standing stocks of benthic organic matter (Britton, 1990), the opening of the canopy may result in a temporary increase in stream temperature, with consequences for the benthic invertebrate community.

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The aim of the present study was to investigate the effects of fire in a small, fynbos-dominated catchment on stream temperature and on the species composition and abundance of benthic macroinvertebrates. A further aim of the study was to investigate the factors which influence the structure and functional organization of benthic macroinvertebrate communities in mountain streams of the south-western Cape.

STUDY AREA

The study area, Swartboskloof, has been described in detail by Britton (in press). Briefly, Swartboskloof is a fan-shaped catchment, 373 ha in area, situated in the Jonkershoek Valley (34°00'S, 18°57'E) approximately 60 km east of Cape Town. The catchment ranges from

320 to 1200 m in altitude and has a north-easterly aspect. The climate of the region is mediterranean, with cool, wet winters and warm, dry summers. Rainfall is strongly seasonal, with around 60 % of the annual total falling in the four winter months of June to September. Rainfall during 1986 and 1987 in the Swartboskloof catchment, based on the average of five raingauges, amounted to 2599 and 2844 mm respectively (South African Forestry Research Institute - SAFRI - unpublished data).

The Swartboskloof stream is perennial and seasonally fed by four smaller streams. The main stream is 2.1 km long and 1-4 m wide, and streamflow varies from 340 to 15,900 $m^3 d^{-1}$ (SAFRI, unpublished data). The stream consists of riffles, runs and small waterfalls, with pools comprising less than 20% of stream area. The streambed is made up of bedrock, boulders and large stones. Finer materials (gravel, sand etc.) comprise less than 15% of the stream bed. Water quality has been described in detail by Britton (in press) and is characterized as acid (pH 4.6 - 6.6) and very low in dissolved substances (total dissolved solids, 20.5 - 33.1 mg l^{-1}).

The slopes of the Swartboskloof catchment are vegetated by sclerophyllous, fire-adapted mountain 'fynbos' shrubland, characterized by the presence of members of the plant families Proteaceae, Ericaceae and Restionaceae. Evergreen trees of Afromontane origin (White, 1978) are restricted to sandstone boulder screes and boulder-lined watercourses and form an almost closed canopy over the main stream and its tributaries. Litter-fall from riparian trees occurs throughout the year, although heavy leaf-falls take place during the early summer months (December and January) when more than 50% of the annual total falls (Britton, 1990). Soft litter collected in traps at the study site was dominated by leaves of <u>Cunonia capensis</u> (L.) and <u>Ilex mitis</u> (L.) (Britton, 1990).

Swartboskloof was deliberately burned on 17 March 1987, as part of the normal management of the area. The fire was considered to be of low to moderate intensity (D.

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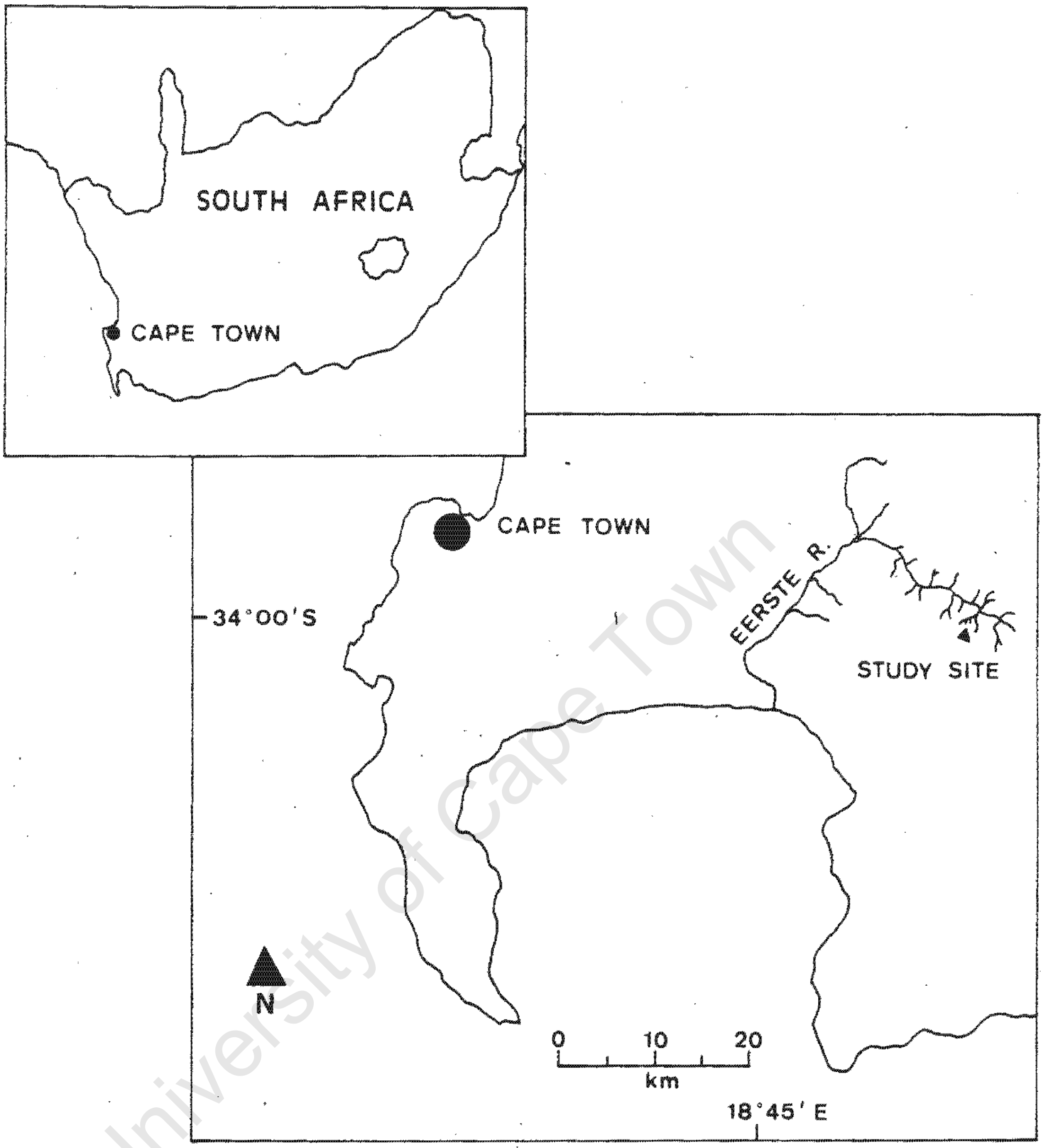

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Fig. 1: Outline map of the study area

Versfeld, SAFRI, *pers. comm.*). Although the fire consumed all the vegetation on the slopes of the catchment, the riparian vegetation burned only at the edges. Exposure of the canopy to high temperatures during the course of the burn, however, resulted in heavy leaf-fall, which lasted approximately two months and caused the canopy to open (Britton, 1990). By late September, six months after the burn, the canopy appeared to have fully recovered.

Despite the heavy post-burn leaf-fall, and low litter-fall during the following summer (the period of peak litter-fall from riparian trees), there was no significant difference between pre- and post-burn standing stocks of benthic organic matter (Britton, 1990). Burning had no demonstrable effect on stream flow after the burn (Britton, in press), and suspended sediment concentrations were not significantly higher in the post-burn year (Britton, unpublished data). Enhanced concentrations of NO_3^--N, HCO_3^-, Cl^-, K^+ and polyphenols were recorded in stream water after the fire (Britton, in press). Apart from NO_3^--N, however, the magnitude of these increases was small and, whilst indicative of disturbance in the surrounding catchment (Britton, in press), do not appear to constitute a major alteration in stream chemistry. Burning thus appeared to have little effect on the stream environment, although the effects of the temporary loss of the riparian canopy on stream temperature remain to be determined.

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METHODS

The study site is situated immediately above a gauging weir on the main Swartboskloof stream at an altitude of 350 m. At this low point in the catchment, the effects of the fire on stream temperature and on the benthic macroinvertebrate fauna are expected to be most pronounced. Sampling was carried out at monthly intervals from April 1986 to March 1988. Benthic invertebrates were sampled with a square-sided sampler (mesh size 80 μm) that sampled 0.1 m^2 of stream bed. Three samples were collected each month at random from riffle areas. The samples were preserved in the field in 70% alcohol. The patchy distribution of stream animals results in high variation around estimated abundances of benthic invertebrates, and reliability of sample data will obviously be increased with increasing sample size. Nevertheless, as Chutter & Noble (1966) and Canton & Chadwick (1988) have pointed out, reliable estimates of abundance in one habitat type, with reasonable coefficients of variation, may be obtained by taking three samples of 0.1 m^2.

Sorting of benthic samples was facilitated by splitting each sample into six size fractions (>4 mm, 2-4 mm, 950 μm - 2 mm, 500-950 μm, 250-500 μm and 80-250 μm) using sieves. The three lower size fractions were subsampled when necessary using a plankton splitter, and animals sorted using a dissecting microscope. Benthic organic matter associated with each sample was dried, weighed, ashed and re-weighed, and has been reported in a previous paper (Britton, 1990). Animals were identified to the lowest possible taxon. Since many species of aquatic invertebrates have not been described in South Africa (King *et al.*, 1988), identification beyond generic level was rarely possible. Dipterans and coleopterans were identified using Pennak (1978), ephemeropterans using Barnard (1932), plecopterans using Barnard (1934), and trichopterans using Scholtz & Holm (1985).

Measurements of streamflow were obtained from a 90° V-notch weir and data logger constructed and installed by SAFRI. Stream temperature was measured continuously by means of a temperature sensor and data logger installed by SAFRI at the study site.

Regression analysis (Zar, 1984) was used to determine relationships between air and stream temperature in the pre- and post-burn years. Comparisons of slopes and elevations of regression lines were made using Student's t tests (Zar, 1984). Regression analysis was also used to determine relationships between animal densities and stream temperature and discharge. Seasonal differences in animal numbers during the pre- and post-burn years were tested with the Kruskal-Wallis test (Zar, 1984). Where significant differences could

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be demonstrated, a non-parametric Tukey-type multiple comparison test (Zar, 1984) was used to determine between which of the samples significant differences occurred. In all cases, significance was accepted at the 5% level ($P<0.05$). Autumn was defined as March to May, winter as June to August, spring as September to November and summer as December to February. The March 1988 samples were excluded from seasonal analyses.

Two-way indicator species analysis (TWINSPAN) (Hill, 1979), a Fortran programme recommended for hierarchical classification because of its effectiveness and robustness (Gauch, 1982), was used to group all the benthic samples on the basis of species abundance. The programme also identifies a small number of indicator species which exhibit a strong differentiation into particular groups at each successive division.

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RESULTS

Stream temperature

Stream temperature ranged between 10.4 °C (October) and 20.0 °C (January) in the pre-burn year, and between 10.3 °C (July) and 21.8 °C (February) in the post-burn year. Mean maximum monthly temperatures from January 1986 to March 1988 are illustrated in Fig. 2. To determine whether the prescribed burn had any effect on stream temperature, ten-day means of maximum water temperature were plotted against ten-day means of air temperature (Fig. 3). For each year, a strong positive relationship was found to exist between the two variables. The slopes and intercepts of the two lines were calculated but were found not to differ significantly. Seasonal changes in discharge confound the relationship between air and water temperature, however, in that low flows amplify stream temperature response and *vice versa.* In order to minimize seasonal influences, the procedure was therefore repeated using daily measurements of maximum air and water

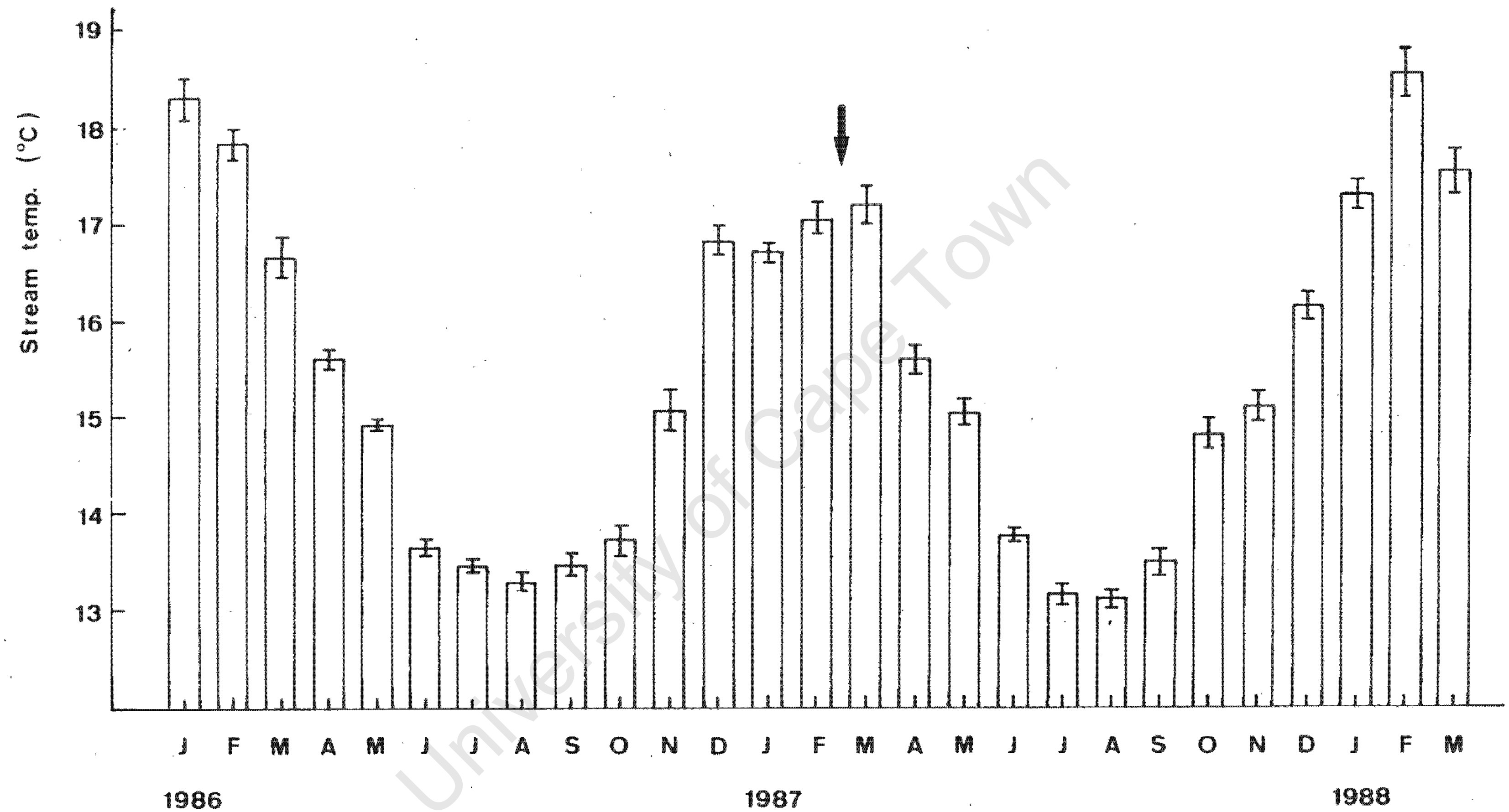

Fig. 2: Mean monthly maximum stream temperatures (± 1 SE) from January 1986 to March 1988. The arrow indicates the timing of the prescribed burn.

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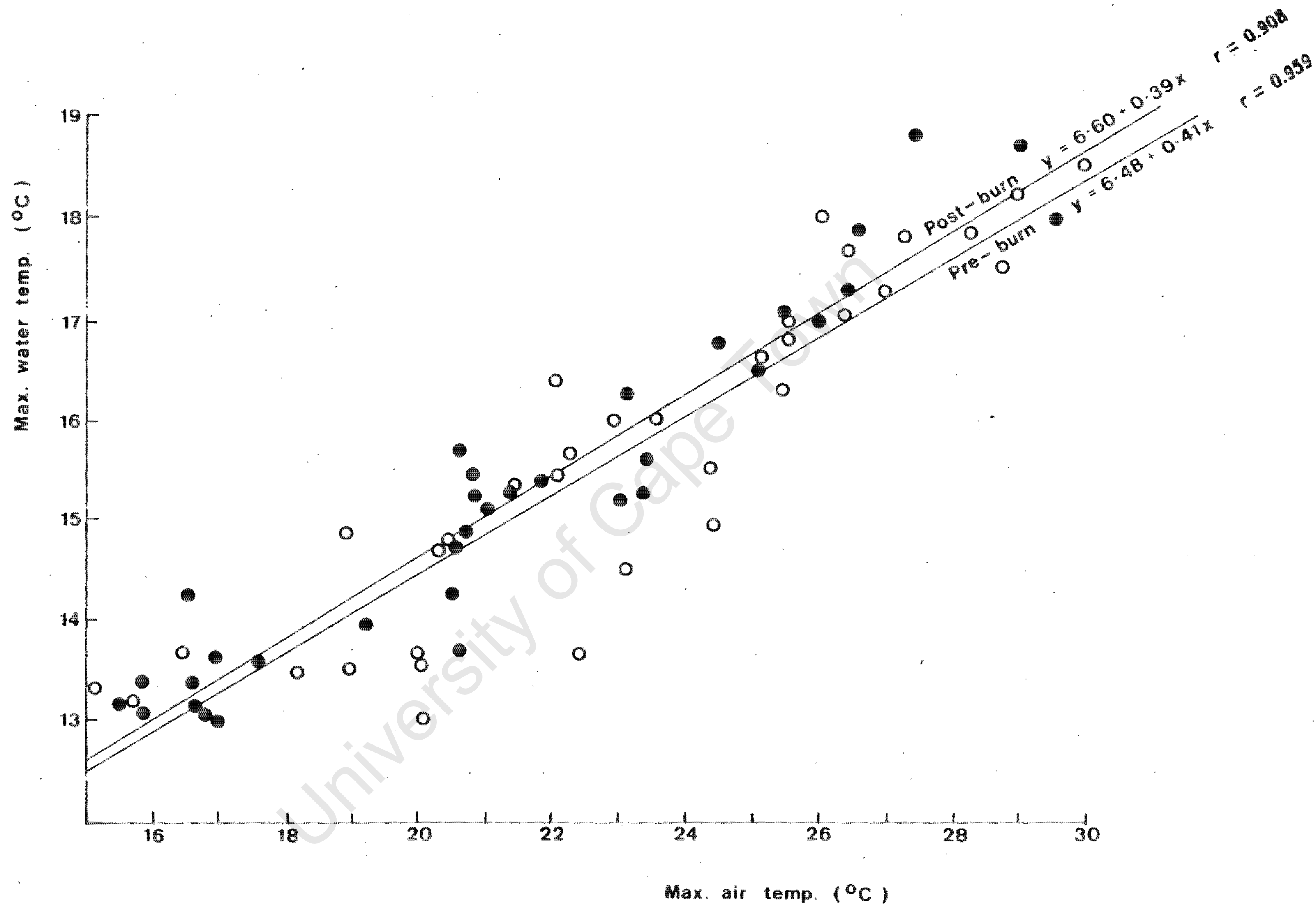

Fig. 3: Ten-day means of maximum stream temperature plotted against ten-day means of maximum air temperature for the pre- and post-burn study periods. Open circles represent pre-burn values, solid circles represent post-burn values.

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temperature for the months of February (1987 and 1988) when discharge was very low, air temperatures generally high and cloud cover low, and August (1986 and 1987) when discharge was generally high, air temperature low and skies overcast. Strong positive relationships were found between the variables in both months but there were no significant differences between slopes and intercepts of regression lines for the pre- and post-burn years. The procedure was also repeated for the month of June when, in the post-burn year, the canopy appeared most sparse after heavy leaf-falls in April and May (Britton, 1990). Again, however, there were no significant differences between either the slopes or intercepts of regression lines for the pre- and post-burn years.

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Macroinvertebrates

Forty-eight taxa of benthic macroinvertebrates were identified at the study site over the two year study period (Fig. 4). Insects accounted for over 92 % of all individuals collected. The fauna was dominated by dipteran larvae (53 % of all individuals collected), with Simuliidae representing between 7 and 62 % of total monthly numbers, and Chironomidae between 9 and 46 %. Coleoptera and Ephemeroptera were the next most abundant groups (both 15 % of all animals collected), followed by Plecoptera (7 %), Trichoptera (1 %), Odonata and Megaloptera (both <1 %). Non-insects included Oligochaeta (3 %), Nematoda (2 %), Hydracarina (2 %), Amphipoda (1 %), Decapoda and Planariidae (all <1 %). Copepoda, Ostracoda and Chydoridae were also recorded in benthic samples, the latter in large numbers during late summer and autumn. These three crustacean groups have been omitted from data analyses, however, as they were not consistently part of the benthic infauna.

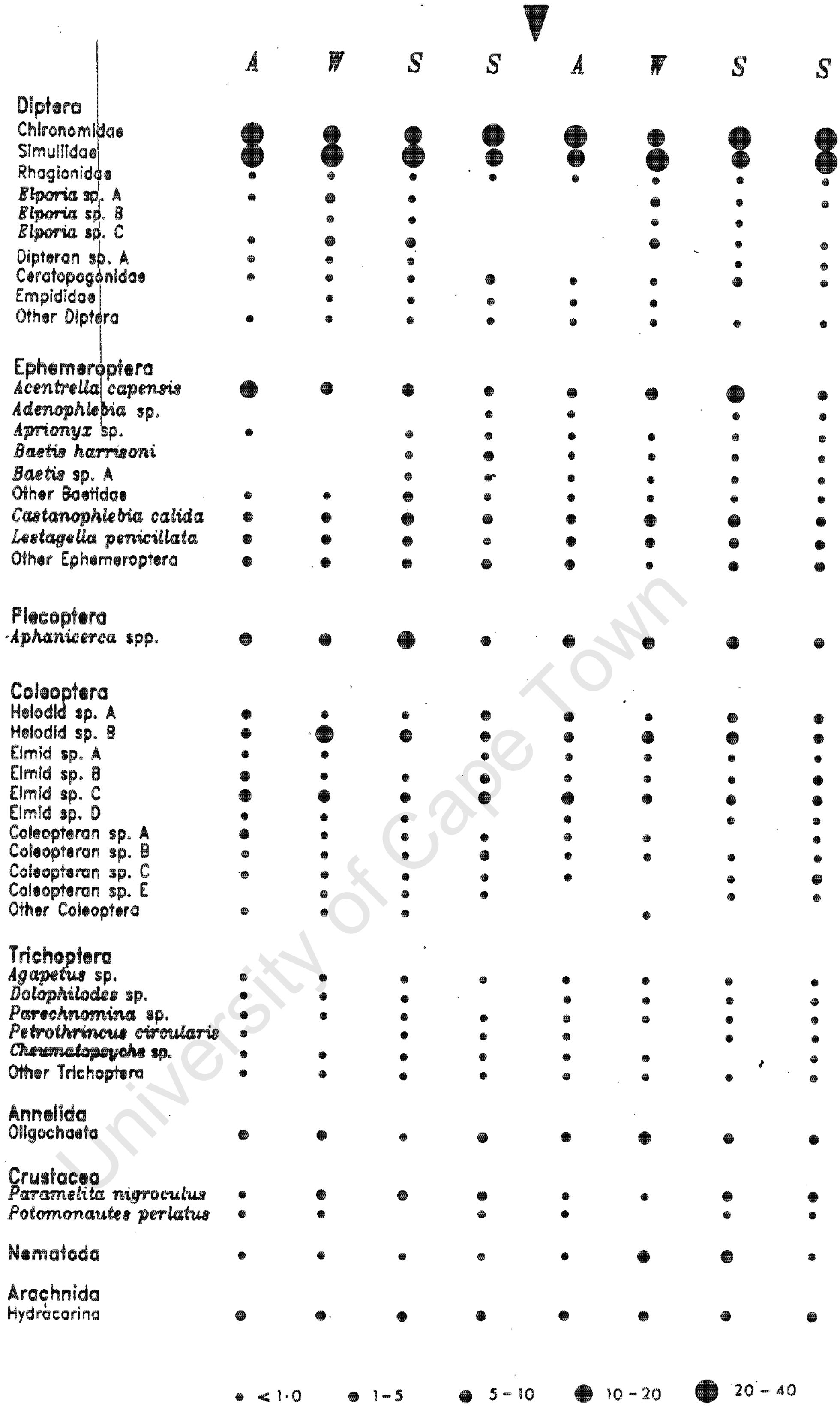

Fig. 4: Seasonal composition (%) of the invertebrate fauna. The arrow indicates the timing of the burn. Taxa representing <1% of the population in fewer than four of the eight seasons samples are not tabulated, but include an unidentified dipteran, two coleopterans, the trichopterans Chimarra sp., Petrothrincus triangularis and Rhyacophila sp; an anisopteran, a zygopteran, the megalopteran Taeniochauliodes sp. and the hemipteran Mesovelia sp.

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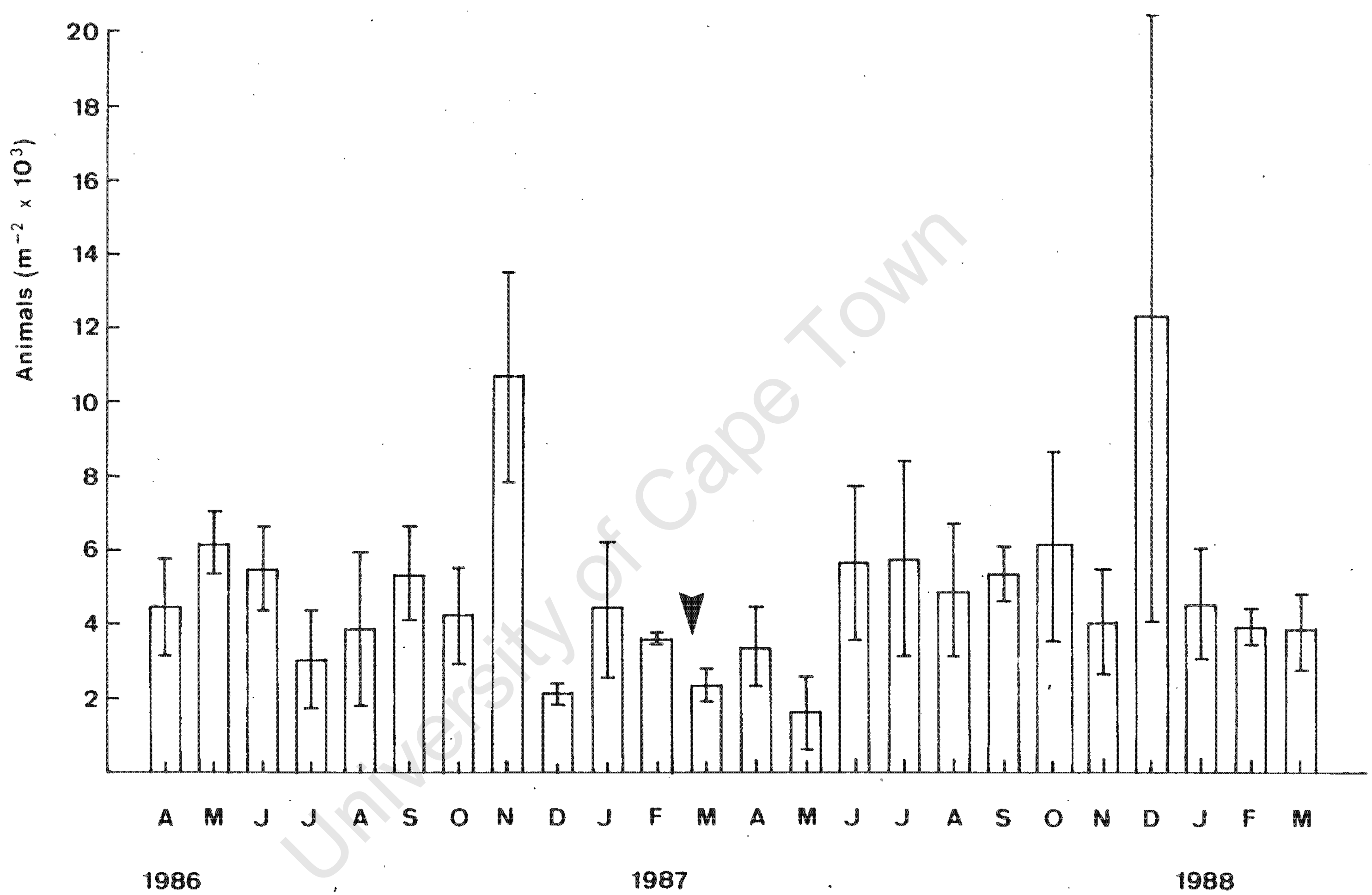

Fig. 5: Densities of benthic invertebrates ($\bar{x} \pm 1$ SE, n=3) over the two-year study period. The arrow indicates the timing of the burn.

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During the pre-burn year, animal numbers ranged from 2,100 (December) to 10,630 (November) m^{-2} (Fig. 5), with a monthly mean of 4,843 (SE = 539) m^{-2}. A mean of 67 % (SE = 2.1 %) of all invertebrates collected in the pre-burn year were sorted from the 500 μm - 2 mm fractions. Apart from November, when simuliids were very abundant and constituted 62 % of total animal numbers, monthly totals were similar, and there were no significant seasonal differences in animal numbers.

Monthly abundances of the two dominant taxa, simuliids and chironomids, appeared to be related to stream temperature and discharge (Fig. 6), although these relationships were not statistically significant. Simuliid numbers appeared to be negatively associated with stream temperature and positively associated with discharge, whereas chironomid numbers appeared positively associated with stream temperature and negatively associated with discharge. Thus, simuliids made up 31 % of the invertebrate population during the pre-burn winter and 10 % in summer, and chironomids represented 15 % of the population during winter and 42 % in summer.

The abundance of other taxa, occurring in lower densities, also appeared to be related to changes in stream temperature and discharge (Fig. 6), although again, these relationships were not statistically significant. Sixty percent of the taxa that varied in abundance with temperature and discharge showed lowest abundances during the austral summer (December - February), when discharge was low and stream temperature high. Of the remaining 40 %, which showed highest abundances during the summer, only one taxon (Helodid sp. A) represented more than 2 % of the population. In the pre-burn year, numbers of Acentrella, Castanophlebia, Lestagella, Plecoptera and Simuliidae were all significantly ($P<0.05$) higher in spring than summer. Numbers of the amphipod Paramelita were significantly ($P<0.05$) higher in spring than autumn. Helodid sp. B was generally (although not significantly) more abundant in spring than autumn, whereas Helodid sp. A was significantly ($P<0.05$) more abundant in summer than winter. Oligochaetes were

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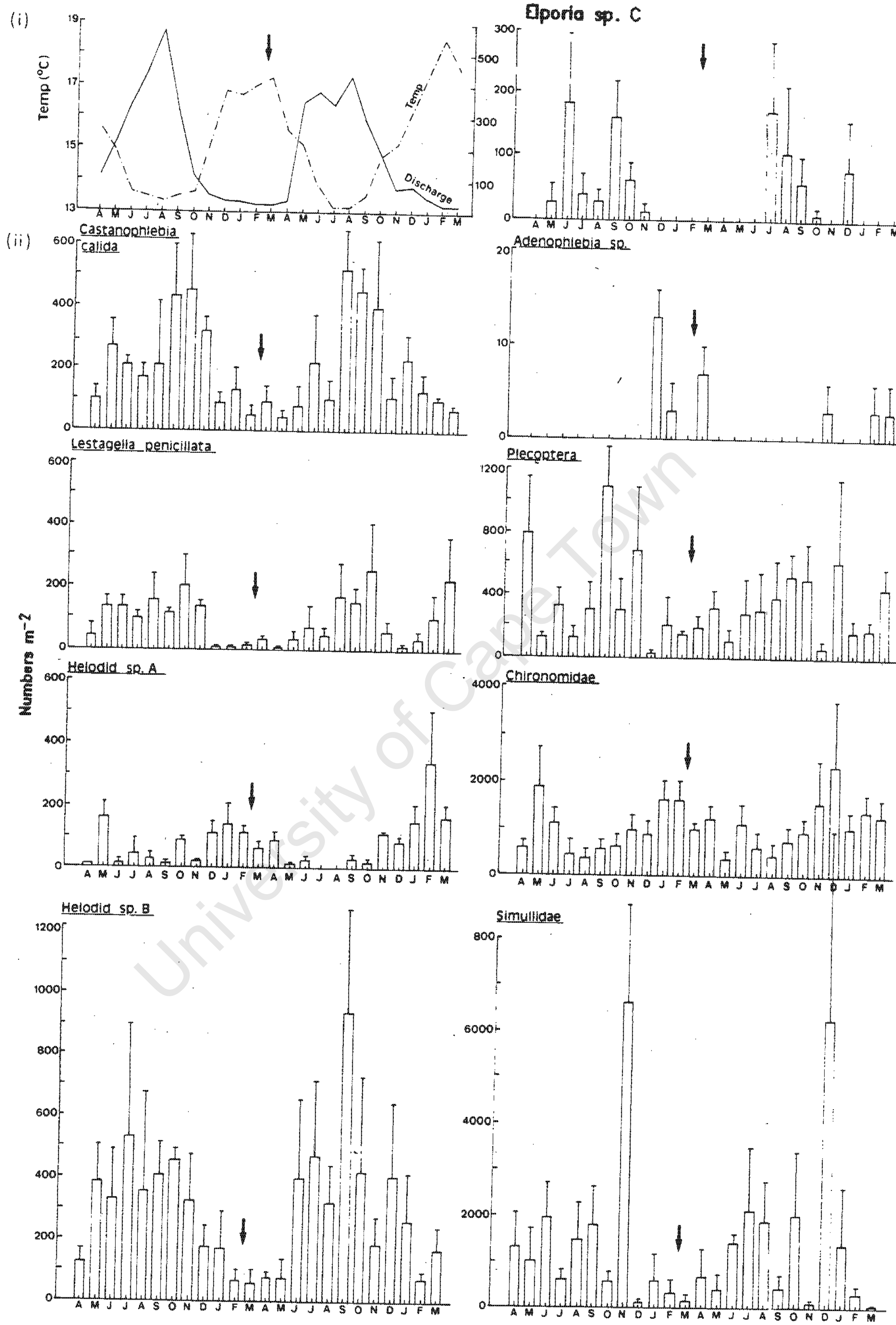

Fig. 6: (i) Mean maximum monthly stream temperature (°C) and monthly discharge ($m^3 \times 10^3$)

(ii) Densities of various taxa ($\overline{x}$ + 1 SE, n=3) during the pre- and post-burn years. The arrow indicates the timing of the burn. Note the different scales on the y axes of right-hand graphs.

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more abundant in summer than spring. Elporia species A, B and C were recorded in samples collected in winter and spring, but apart from eight individuals of species C collected in May, were absent during the summer and autumn. Conversely, Adenophlebia was recorded in summer and autumn but not in winter and spring. All other taxa exhibited non-significant seasonal differences in abundance.

During the post-burn year, animal numbers ranged from 1,580 (May) to 12,230 (December) m^{-2}, with a monthly mean of 4,853 (SE = 745) m^{-2}. As in the pre-burn year, there were no significant seasonal differences in total animal numbers. Many of the taxa appeared to exhibit temperature and discharge-related abundances, but fewer significant seasonal differences existed. Simuliids made up 34 % of the population in winter and 26 % in summer; conversely, chironomids represented 13 % of the population in winter and 26 % in summer. There were significantly ($P < 0.05$) more Castanophlebia and Helodid sp. B in spring than autumn and more simuliids in winter than autumn. Helodid sp. A was significantly ($P < 0.05$) more abundant in summer than winter. Elporia species A, B and C and Adenophlebia showed similar seasonal patterns of abundance to the pre-burn year. Apart from Chimarra sp., Petrothrincus triangularis, Rhyacophila sp., Taeniochauliodes sp. and Mesovelia sp. (all of which were rare in the benthic fauna), all taxa recorded in the pre-burn year were present in the post-burn year.

The TWINSPAN programme was run using percentage abundance and total abundance data for individual and pooled monthly samples collected over the entire sampling period. The classification using transformed data did not produce interpretable groupings, whereas classification using untransformed data both for individual samples and for pooled monthly samples produced similar results, the samples grouping primarily by season. A summary of the results using pooled samples is shown in Fig. 7. The main division separated samples collected in winter (June, July and August) from those collected in the remaining three seasons. Indicator species for the winter group were Elporia species A and B. One sample

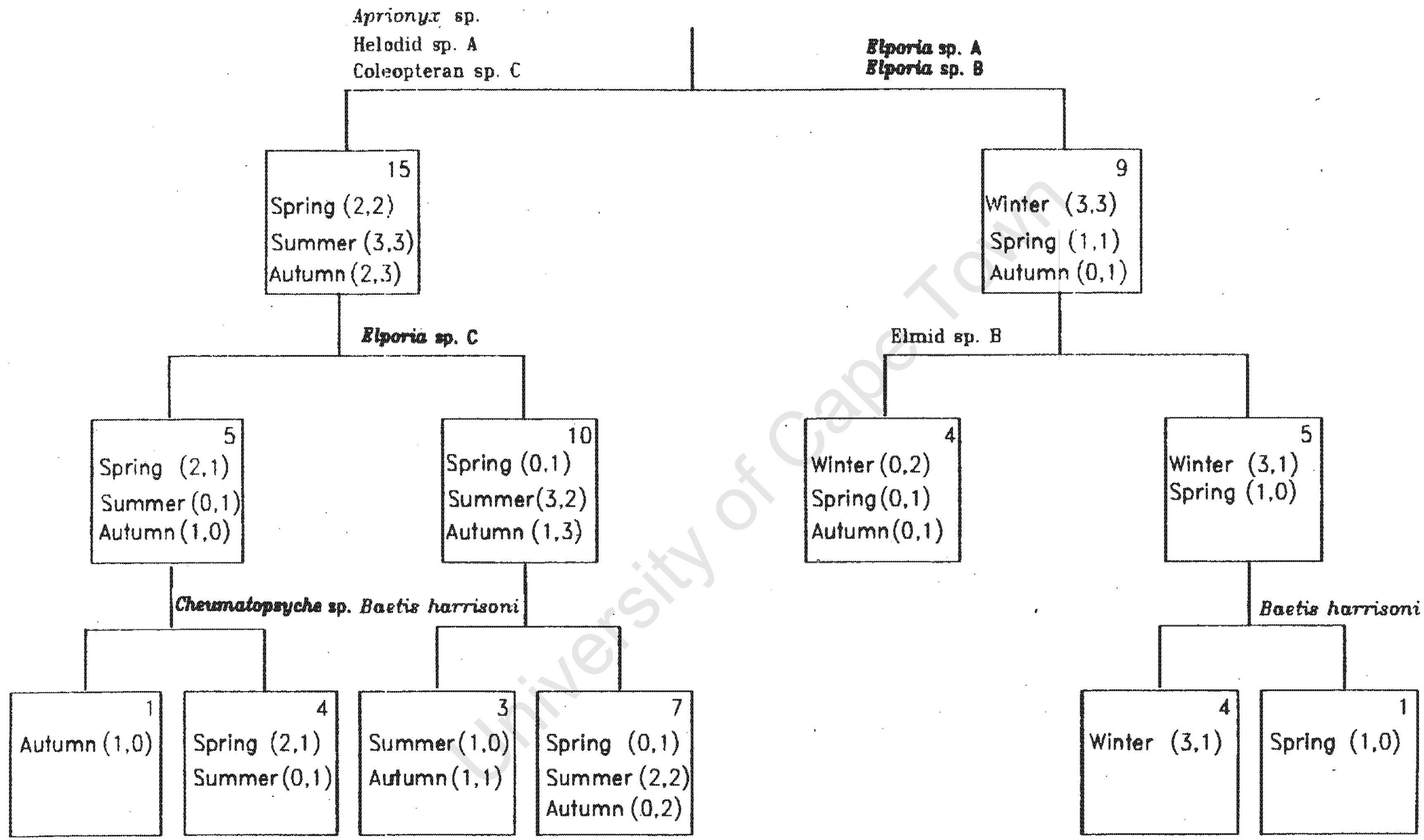

Fig. 7: Classification of invertebrate samples (pooled into seasons) by TWINSPAN. Major indicator species for each division are indicated and the number of samples in each group are given in the top right-hand corner. The first figure in parentheses indicates the number of pre-burn samples, the second indicates the number of post-burn samples.

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from May 1987 and two from September (1986 and 1987) were also included in this group. In the first division of the winter group, separation took place into predominantly pre- and post-burn samples, regardless of season. The second and final division led to the isolation of one of the September samples. Indicator species for the other major grouping, consisting of spring, summer and autumn samples, were Aprionyx, Helodid sp. A and Coleopteran sp. C. This group underwent a further two divisions, the first of which separated most of the spring samples from summer and autumn samples. The indicator species at this division for the summer and autumn group was Elporia sp. C. Division of the predominantly spring samples separated off a late autumn sample. The remaining group, which consisted mainly of summer and autumn samples, underwent one further division which was not based on season. Unlike the winter group, there was no evidence for subdivision of the spring, summer and autumn group into pre- and post-burn samples.

Although not illustrated here, it is of interest to note that when data for the 71 individual benthic samples were run through the programme, the samples within each month tended to cluster together throughout the division process, indicating that variability within months was lower than variability between months.

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DISCUSSION

Effects of the fire on stream temperature

Reduced shading of the stream following the heavy, post-burn litter-fall, was expected to result in an increase in stream temperature as a result of increased exposure to solar radiation. This did not occur. The range of stream temperature measured in the post-burn year was similar to that of the pre-burn year, and there were no significant differences between the slopes and intercepts of regression lines for maximum stream temperature plotted against maximum air temperature in the pre- and post-burn years. It was thus concluded that the prescribed burn had no demonstrable effect on stream temperature. This unexpected finding may be attributed to the timing of the burn, in that canopy cover was reduced during the winter months when rainfall was high, cloud cover often dense and air temperatures low. An equivalent fire in spring, rather than in autumn, could result in the stream being exposed to solar radiation during the hottest, clearest months of the year. Under such circumstances, stream temperature might be more markedly affected.

<u>Effects of the fire on the benthic fauna</u>

Densities of benthic macroinvertebrates during the pre-burn year were similar to those reported for Langrivier, another fynbos stream in the Jonkershoek Valley (King *et al.*, 1988), although winter densities were generally higher in Swartboskloof. In both streams, the fauna was dominated throughout the year by insects, with dipteran larvae most abundant. As in Langrivier, invertebrate numbers increased dramatically in late spring in the Swartboskloof stream, but because numbers were not consistently high throughout spring, there were no significant seasonal differences in total invertebrate numbers during the pre- burn year.

Apart from five rare elements of the biota, all species recorded in the pre-burn year were present in the post-burn year and in similar densities. The results of TWINSPAN analyses indicate that the fire had only a limited effect on the benthic community. Analysis of data collected over the two-year period resulted in the grouping of invertebrate samples primarily according to season, indicating that seasonal differences in the faunal community were greater than any differences caused by the fire. Only in the winter group was there a distinction between pre- and post-burn samples.

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On the basis of these findings, it is concluded that the prescribed fire had little short-term effect on the aquatic invertebrate community. Riparian vegetation in fynbos-dominated mountain catchments, by virtue of its resistance to fire, appears to provide a natural buffer for the streams against the potentially disturbing effects of fire. Thus, whereas fire represents a major disturbance in the terrestrial environment, it cannot be considered one in the aquatic environment, at least given the intensity and timing of this fire in this system.

Temporal changes in macroinvertebrate community structure

Although the data record for stream temperature in the present study covers only a relatively short time span, the thermal regime of the Swartboskloof stream, like the regimes of rainfall and discharge, appears to be well-defined and predictable from year to year. Temporal changes in the structure of the invertebrate community appear to be associated with seasonal changes in the physical environment, evidenced by the apparent variation in abundance of many taxa with stream temperature and discharge. Most of these taxa were least abundant in summer, which may be a stressful period for aquatic invertebrates, because of relatively high stream temperatures. The two dominant taxa in Swartboskloof, simuliids and chironomids, exhibited opposite seasonal patterns of abundance over the study period. Thus, although there were no seasonal differences in total animal numbers, there was a temporal shift in the relative abundance of taxa throughout the year, with summer communities dominated by chironomids and winter communities dominated by simuliids. The results of TWINSPAN analyses, which separated invertebrate samples into two major seasonal groupings according to species composition and abundance, illustrate this finding. Streams in other mediterranean ecosystems, eg. southern California (Cooper *et al.*, 1986) and western Australia (Bunn *et al.*, 1986) also exhibit distinctive winter and summer invertebrate faunas, with the transition between the two communities closely associated with the hydrological cycle of the streams.

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Based on very slender evidence (Sedell *et al.*, 1975; Anderson 1976; Grafius, 1977), Anderson & Sedell (1979) have stated that "the life cycles of shredders are keyed to the predictable timing of seasonal inputs". Anderson & Cummins (1979) have generalized from these statements to say that "the life cycles of many shredders ...... are keyed to the autumnal pulse of leaf-fall, with the major growth period occurring in the late autumn and winter". Streams of the south-western Cape, like those of the jarrah forests of western Australia (Bunn, 1986), receive their major annual inputs of allochthonous material during summer. If the life cycles of southern-hemisphere shredders are synchronized with the annual pulse of leaf-fall, then greatest densities of shredders would be expected to occur during summer and autumn, in order to maximize consumption of energy. The amphipod Paramelita nigroculus is possibly the only true shredder present in the Swartboskloof stream (J.M. King, *pers. comm.)*, although the plecopterans also appear to be capable of exploiting coarse leaf particles (King *et al.*, 1988). In the pre-burn year, both Paramelita nigroculus and plecopterans were most abundant in spring, after which their numbers dropped markedly in summer despite litter-fall from riparian trees being heaviest at this time. A similar pattern was evident in the post-burn year. It would appear, therefore, that synchronization of shredder life cycles to take advantage of summer leaf-fall does not take place in either the northern jarrah forest streams (Bunn, 1986) or the Swartboskloof stream. Bunn (1986) explained the apparent failure of shredders to take advantage of summer leaf-fall on the poor food quality of senescent leaves, and high water temperatures at the time of peak litter-fall. Furthermore, the release of large quantities of phenols from summer litter fall, during periods of very low flow, may result in high concentrations of polyphenols in stream water which may be unfavourable to stream biota and inhibit microbial colonization of litter (Bunn, 1988). All three of these factors may be applicable to the Swartboskloof system. The food quality of Cunonia capensis (L.) and Ilex mitis (L.) leaves, the dominant riparian species at the study site, is low; C:N ratios have been reported to be 46-100 for C. capensis and 27-48 for I. mitis (King *et al.*, 1987). Polyphenol concentrations in

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Swartboskloof stream water appear to be closely associated with leaf-fall from riparian trees (Britton, in press), with highest concentrations recorded in early summer. Microbial processing of leaf-litter entering the Swartboskloof stream in summer probably takes place during autumn and winter, aided by physical abrasion at high discharges. By spring, well-conditioned CBOM may thus become available to shredding detritivores. Relatively high densities of both Paramelita nigroculus and plecopterans were recorded in spring of both the pre- and post-burn years, suggesting that the life-histories of both these taxa may be synchronized to exploit this food resource once it becomes nutritionally acceptable.

The invertebrate fauna of the Swartboskloof stream, like that of Langrivier (King *et al.*, 1988) is dominated by animals that feed on small particles of detrital organic matter. Although the stream is highly retentive of coarse particulate organic matter (CPOM) (Britton, 1990), these smaller particles dominate the organic matter exported by the stream because they are easily moved by water and difficult to trap (Bilby & Likens, 1979; Naiman & Sedell, 1979). The present study provides some evidence for a functional organization of the fauna that allows exploitation of the seasonal availability of this food resource. High discharges from late autumn to early spring result in the suspension of fine benthic organic matter and generally higher concentrations of fine and ultra-fine particulate organic matter (FPOM and UPOM) in the water column (Britton, 1990). During winter and spring of the pre-burn year and winter of the post-burn year, the fauna was dominated by simuliid larvae, which feed by filtering FPOM and UPOM from the water column (de Moor, 1982). Conversely, during late spring and summer, low flows facilitated the settling of FPOM and UPOM onto the stream bed (Britton, 1990), where it may be exploited by large summer populations of deposit-feeding chironomids, tolerant of relatively high stream temperatures. Similar temporal changes in the relative abundance of different feeding groups have also been recorded in streams of the northern jarrah forests of western Australia (Bunn, 1986).

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It is obvious that the hypothesis of Anderson & Cummins (1979) concerning the synchronization of shredder life cycles requires clearer definition, and that considerably more work and data collection in both northern and southern hemisphere systems is required in order to test the hypothesis. Nevertheless, in the present study, and in Bunn's (1986) study, the data for collectors support the more general concept of a functional organization of the fauna which allows exploitation of the seasonal availability of food.

In conclusion, it would appear that whereas fire has undoubtedly played a major role in the evolution of plant and animal life-histories in the terrestrial environment, the greatest influence on the life histories of the aquatic macroinvertebrates of the region have been the well-defined and predictable regimes of temperature and discharge. It is clear, however, that considerably more research is needed into the way that various environmental factors influence the life-history patterns of aquatic invertebrates before we can fully understand their vulnerability to fire and other catchment disturbances.

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University of Cape Town

REFERENCES

Anderson, N.H. (1976).
The distribution and biology of the Oregon Trichoptera. *Oregon Agricultural Experimental Station Technical Bulletin*, **134**.

Anderson, N.H. & Cummins, K.W. (1979).
Influences of diet on the life histories of aquatic insects. *Journal of the Fisheries Research Board of Canada*, 36, 335-342.

Anderson, N.H. & Sedell, J.R. (1979).
Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology*, **24**, 351-377.

Bands, D.P. (1977).
Prescribed burning in Cape Fynbos catchments. Proceedings of the symposium on the environmental consequences of fire and fuel management in mediterranean ecosystems (Technical Coordinators H.A. Mooney & C.E. Conrad), pp. 245-256. *U.S. Department of Agriculture, Forestry Service, General Technical Report* WO-3.

Barnard, K.H. (1932).
South African mayflies (Ephemeroptera). *Transactions of the Royal Society of South Africa*, XX (3), 201-260.

Barnard, K.H. (1934)
South African stoneflies (Perlaria) with descriptions of new species. *Annals of the South African Museum*, 30, 511-548.

Bilby, R.E. & Likens, G.E. (1979).
Effect of hydrological fluctuations on the transport of fine particulate organic carbon in a small stream. *Limnology and Oceanography*, 24, 69-75.

Britton, D.L. (1990).
Fire and the dynamics of allochthonous detritus in a South African mountain stream. *Freshwater Biology*, **24**, 347-360.

Britton, D.L. (in press).
Fire and the chemistry of a South African mountain stream. *Hydrobiologia*.

University of Cape Town

Brown, G.W. & Krygier, J.T. (1967).
Changing water temperatures in small mountain streams. *Journal of Soil and Water Conservation*, 22, 242-244.

Brown, G.W. & Krygier, J.T. (1970).
Effects of clear-cutting on stream temperature. *Water Resources Research*, 6, 1133-1139.

Bunn, S.E. (1986).
Spatial and temporal variation in the macroinvertebrate fauna of streams of the northern jarrah forest, Western Australia: functional organization. *Freshwater Biology*, 16, 621-632.

Bunn, S.E. (1988).
Processing of leaf litter in a northern jarrah forest stream, Western Australia: I. Seasonal differences. *Freshwater Biology*, 162, 201-210.

Bunn, S.E., Edward, D.H. & Loneragan, N.R. (1986).
Spatial and temporal variation in the macroinvertebrate fauna of streams of the northern jarrah forest, Western Australia: community structure. *Freshwater Biology*, 16, 67-91.

Canton, S.P. & Chadwick, J.W. (1988).
Variability in benthic invertebrate density estimates from stream samples. *Journal of Freshwater Ecology*, 4, 291-297.

Chutter, F.M. & Noble, R.G. (1966).
The reliability of a method of sampling stream invertebrates. *Archiv fur Hydrobiologie*, 62, 95-103.

Cooper, S.D., Dudley, T.L. & Hemphill, N. (1986).
The biology of chaparral streams in southern California. Proceedings of the Chapparal Ecosystems Research Conference (Ed. J.J. DeVries), pp. 139-151. *California Water Resources Center, Report* 62.

Cummins, K.W., Petersen, R.C., Howard, F.O., Wuycheck, J.C. & Holt, V.I. (1973).
The utilization of leaf litter by stream detritivores. *Ecology*, 54, 336-345.

University of Cape Town

de Moor, F.C. (1982).
A community of *Simulium* species in the Vaal River near Warrenton. *Unpublished PhD thesis, University of the Witwatersrand, South Africa.*

Egglishaw, H.J. (1964).
The distributional relationship between the bottom fauna and plant detritus in streams. *Journal of Animal Ecology*, 33, 463-476.

Gauch, H.G. (1982).
Multivariate analysis in community ecology. Cambridge University Press.

Grafius, E.J. (1977).
Bioenergetics and strategies of some Trichoptera in processing and utilizing allochthonous materials. PhD. thesis, Oregon State University, Corvallis.

Graynoth, E. (1979).
Effects of logging on stream environments and faunas in Nelson. *New Zealand Journal of Marine and Freshwater Research*, 13, 79-109.

Haefner, J.D. & Wallace, J.B. (1981).
Shifts in aquatic insect populations in a first-order southern Appalachian stream following a decade of old field succession. *Canadian Journal of Fisheries and Aquatic Sciences*, 38, 353-359.

Hill, M.O. (1979).
TWINSPAN - A FORTRAN Program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, New York 14850.

Hynes, H.B.N. (1975).
The stream and its valley. *Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie* 19, 1-15.

Keeley, J.E. (1986).
Resilience of mediterranean shrub communities to fires. Resilience in mediterranean-type ecosystems (Eds. B. Dell, A.J.M. Hopkins, & B.B. Lamont), pp. 95-112. W. Junk, The Hague.

University of Cape Town

King, J.M., Day, J.A., Davies, B.R. & Henshall-Howard, M-P. (1987).
Particulate organic matter in a mountain stream in the south-western Cape, South Africa. *Hydrobiologia*, 154, 165-187.

King, J.M., Day, J.A., Hurley, P.R., Henshall-Howard, M-P. & Davies, B.R. (1988).
Macroinvertebrate communities and environment in a southern African mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences*, 45, 2168-2181.

Meehan, W.R., Swanson, F.J. & Sedell, J.R. (1977).
Influences of riparian vegetation on aquatic ecosystems with particular reference to salmonid fishes and their food supply. Symposium on the importance, preservation and management of riparian habitat (Tech. Coordinators R.R. Johnson & D.A. Jones), pp. 137-145. *U.S. Department of Agriculture Forest Service, General Technical Report* RM-43.

Minshall, G.W., Brock, J.T. & Varley, J.D. (1989).
Wildfires and Yellowstone's stream ecosystems. *BioScience*, 39, 707-715.

Naiman, R.J. & Sedell, J.R. (1979).
Characterization of particulate organic matter transported by some Cascade Mountain streams. *Journal of the Fisheries Research Board of Canada*, 36, 17-31.

Newbold, J.D., Erman, D.C. & Roby, K.B. (1980).
Effects of logging on macroinvertebrates in streams with and without buffer strips. *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 1076-1085.

Pennak, R.W. (1978).
Freshwater invertebrates of the United States. 2nd ed. Wiley-Interscience.

Scholtz, C.H. & Holm, E. (1985).
Insects of Southern Africa. Butterworths, Durban.

Sedell, J.R., Triska, F.J. & Triska, N.S. (1975).
The processing of conifer and hardwood leaves in two coniferous forest streams I: Weight loss and associated invertebrates. *Verhandlungen der Internationale Vereinigung fur Theoretische und Angewandte Limnologie*, **19**, 1617-1627.

University of Cape Town

Tiedemann, A.R., Conrad, C.E., Dieterich, J.H., Hornbeck, J.W., Megahan, W.F., Viereck, L.A. & Wade, D.D. (1979).
Effects of fire on water - a state-of-knowledge review. *U.S. Department of Agriculture, Forestry Services, General Technical Report* WO-10.

van Wilgen, B.W. (1987).
Fire regimes in the fynbos biome. Disturbance and the dynamics of fynbos communities (Eds. R.M. Cowling, D.C. le Maitre, B. McKenzie & B.W. van Wilgen), pp. 6-14. *South African National Scientific Programmes Report* 135. CSIR, Pretoria.

Ward, J.V. (1984).
Ecological perspectives in the management of aquatic insect habitat. The ecology of aquatic insects (Eds. V.H. Resh & D.M. Rosenberg), pp. 558-577. Praeger Publishers, New York.

Webster, J.R., Gurtz, M.E., Hains, J.J., Meyer, J.L., Swank, W.T., Waide, J.B. & Wallace, J.B. (1983).
Stability of stream ecosystems. Stream ecology: application and testing of general ecological theory (Eds. J.R. Barnes & G.W. Minshall), pp.355-395. Plenum Press, New York.

White, F. (1978).
The Afromontane Region. Biogeography and ecology of southern Africa. (Eds. M.J.A. Werger & J.C. Van Bruggen), pp. 463-513. *Monographiae Biologicae* 31, W. Junk, The Hague.

Zar, J.H. (1984).
Biostatistical Analysis. 2nd. ed. Prentice-Hall, Englewood Cliffs, New Jersey.

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GENERAL DISCUSSION

Fire as a disturbance factor

In recognition of the strong linkages between terrestrial and aquatic ecosystems, it was hypothesized at the outset of this study that a major disturbance in the surrounding catchment would result in a major disturbance in the stream environment, manifested by changes in the quality and quantity of stream water and alterations in the regime of allochthonous inputs. The findings of this study, however, must lead to the rejection of this hypothesis. Water yield and stream temperature were not demonstrably affected by the fire and, although allochthonous inputs to the system were altered in the first post-burn year, this had no significant effect on standing stocks of benthic organic matter. Destruction of the fynbos vegetation did result in changes in stream chemistry, in that enhanced concentrations of some chemical species (NO_3^--N, HCO_3^-, Cl^-, K^+ and polyphenols) were recorded at one or more sites during the post-burn year. Apart from NO_3^--N, however, the magnitude of these increases was small and, whilst maybe indicative of disturbance in the surrounding catchment, do not appear to constitute a major alteration in stream chemistry. Although the results presented here are largely inconclusive (due to the short pre-burn data set and the lack of a control catchment for comparison), it appears that whereas fire represents a major disturbance in terrestrial ecosystems, it cannot be considered one in the aquatic ecosystem, provided the riparian vegetation remains intact.

Biotic and abiotic influences on stream chemistry

Although the fire will have disrupted the tight nutrient cycles associated with mature terrestrial vegetation, the expected overall increase in nutrient concentrations in stream water did not occur. Whilst NO_3^--N and, to a lesser extent, K^+ concentrations in stream water were elevated after the fire, NH_4^+-N, Ca^{2+}, Mg^{2+} and PO_4^{3-}-P concentrations were not significantly affected. Sodium concentrations were actually lower during the post-burn year. In explanation, the findings presented in Papers I and II suggest that whilst the concentrations of all dissolved species in stream water are the result of a large number of physical, chemical and biological processes, concentrations of major cations, PO_4^{3-}-P and NH_4^+-N in stream water are considerably less influenced by biological processes than are NO_3^--N concentrations.

The influence of biotic uptake on NO_3^--N concentrations was most apparent in the winter months, a finding which supports the hypothesis that uptake of nutrients by fynbos vegetation occurs mainly during winter, with water stress limiting uptake in summer (W.D. Stock, UCT, *pers. comm.*). Although few studies have investigated the seasonal uptake of nutrients by fynbos vegetation, Stock *et al.* (1987) have clearly demonstrated that uptake of N by *Thamnochortus punctatus*, a member of the structurally-dominant Restionaceae, occurs primarily in winter. Furthermore, Mooney and Rundel (1979) have shown that *Adenostoma fasiculatum*, a dominant member of chaparral vegetation in California, takes up N and P during the winter rainy season prior to any above-ground growth. Asynchronous growth patterns (ie. asynchrony between nutrient uptake and growth) in mediterranean-type vegetation appear to be an adaptation to the edaphic constraints imposed by the mediterranean climate (Stock *et al.*, 1987). By contrast, the greatest uptake of nutrients by plants in the Hubbard Brook Experimental Forest in North America occurs during summer, which accounts for the low concentrations of NO_3^--N in stream water during this season (Johnson *et al.* 1969). Low NO_3^--N concentrations in Swartboskloof stream water were also recorded in summer (Paper I), but during dry periods only. During summer and autumn storms, NO_3^--N was found to percolate readily to the stream, where relatively high concentrations were recorded. High NO_3^--N concentrations in stream water during summer and autumn storms may reflect enhanced activity of nitrifiers in the soil during spring and autumn, when environmental conditions are considered optimal for nitrification (Schaefer,

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1973; Stock & Lewis, 1986). It is speculated that the particularly high concentrations recorded during the January storm may reflect both low rainfall and lowered uptake of NO_3^--N by plants in the preceding three months, conditions which permitted the accumulation of NO_3^--N in the soil.

Although no data are available for soil-N concentrations in the Swartboskloof catchment, fire in a coastal fynbos system caused a significant, nine month increase in soil NO_3^--N due to the nitrification of NH_4^+-N deposited at the soil surface after the fire (Stock & Lewis, 1986). Because of the similarities that exist between the coastal fynbos and Swartboskloof soils, it is probable that the fire in Swartboskloof had a similar, effect on soil NO_3^--N concentrations (M. Loos, University of Stellenbosch, *pers. comm.*). Thus, as pointed out in Papers I and II, increased NO_3^--N concentrations in stream water after the fire may have been due not only to reduced uptake by plants but also to enhanced nitrification. The relative importance of each process, however, cannot be assessed.

Principle controls on the output of major cations, NH_4^+-N and PO_4^{3-}-P, appear to be geochemical processes operating within the catchment. The soil is the zone where active chemical weathering takes place, and where extensive ion exchange and storage are possible between soil solutions and the solid components of the soil (Johnson *et al.*, 1969). In a system where soluble ions and water are in constant flux, extremes of chemical change may be moderated by reversible ion exchange reactions and the formation or dissolution of various metastable compounds (Johnson *et al.*, 1969). In the present study, it is speculated that dissolved cations and PO_4^{3-}-P deposited in ash after the fire were adsorbed onto the soil-exchange complex rather than being washed directly into the streams. This would account for the general lack of significant increases in the concentration of these ions in stream water after the fire. Uptake of dissolved nutrients from ash by the unburned riparian vegetation and by post-fire vegetation may also, to a lesser extent, have limited nutrient loss from the catchment after the fire. It is likely that NH_4^+-N deposited at the soil surface after the fire disappeared rapidly due to nitrification (see Stock & Lewis, 1986).

It should be remembered that the findings of this study pertain to the effects of a late-summer burn on stream chemistry. The investigation into hydrochemical responses in the Swartboskloof catchment during storm events (Paper II) revealed that direct runoff may comprise a relatively large proportion of stream flow during winter events, when soil-moisture levels are high. Thus, if a prescribed burn is carried out in spring, when soil-moisture levels are still high after the winter rains, rainwater entering the catchment in subsequent storms will move rapidly through the soil to the streams, limiting the opportunity for adsorption of dissolved cations onto the soil-exchange complex. Under these conditions, it is likely that significant increases in cation concentrations in stream water will be detected.

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It is speculated that spring burning may be detrimental not only to site productivity but also to aquatic invertebrate communities. In Paper IV it was concluded that a heavy leaf-fall following a spring burn would result in streams being exposed to solar radiation during the hottest, clearest months of the year, which could cause significant increases in stream temperature. Even if temperatures did not increase to lethal levels, alterations in the temperature regime may have profound effects on invertebrate growth rates, rates of food assimilation and emergence (see Ward & Stanford, 1979).

Biotic and abiotic influences on the benthic invertebrate fauna

Although the terrestrial flora and fauna of fynbos-dominated catchments in the south-western Cape exhibit marked adaptations to fire, it would appear that the aquatic communities of the area have evolved in the absence of an equivalent disturbance in the stream environment, perhaps due to the buffering effect of the riparian vegetation. The findings presented in Paper IV indicate that as in other mediterranean ecosystems, the greatest influence on benthic macro-invertebrate community structure has been that of the physical environment, with seasonal changes in invertebrate numbers associated primarily with the well-defined and relatively predictable regimes of temperature and discharge.

In both pre- and post-burn years, the main peak in numbers of shredders occurred around one month before the peak summer leaf-fall from riparian trees. This appears to conflict with the hypothesis developed in North America that shredders synchronize their life cycles to benefit from peak (autumnal) inputs of leaf litter (Anderson & Cummins, 1979). As described earlier (Paper IV), peak numbers of filter-feeding simuliids in the Swartboskloof stream coincided with periods of high flow and relatively high concentrations of suspended particulate organic matter, while peak numbers of the largely deposit-feeding chironomids coincided with periods of low flow and high concentrations of benthic particulate organic matter. Thus in this study, although the data for shredders negate Anderson & Cummin's (1979) hypothesis, the data for both shredders and collectors support a more generalized hypothesis. When not limited by factors other than food (eg., temperature or discharge), numbers of stream invertebrates of specific feeding groups may correlate with periods of maximum food availability, rather than periods of maximum litter input to the system.

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<u>The role of the riparian vegetation</u>

To a large extent, the less-than-expected effect of the fire on the stream environment and on the benthic macroinvertebrate community may be explained by the 'buffering' action of the riparian vegetation. Riparian vegetation is widely recognized as playing a direct, key role in the functioning of stream and river systems (Rogers & van der Zel, 1989). The specialized communities which comprise riparian zones perform a variety of functions including the control of water velocity by slowing and spreading flood waters, nutrient retention, thermoregulation by shading of shallow streams, and the enhancement of habitat heterogeneity, both aquatic and terrestrial (Rogers & van der Zel, 1989). Riparian vegetation also stabilizes stream banks, thereby decreasing erosion (Meehan *et al.*, 1977). Suspended sediment concentrations in Swartboskloof stream water measured at monthly intervals were slightly, but not significantly, higher in the post-burn year (Mann-Whitney, $P > 0.05$ - Appendix I), and although relatively high concentrations of suspended sediments were recorded during the post-burn winter storm sampled in August 1987 (Appendix II), the overall effect of the prescribed burn on sediment loads in Swartboskloof stream water appears to have been small. The riparian vegetation probably reduced sediment loss after the fire, and the rapid regeneration of graminoid and herbaceous components of the fynbos may also have contributed to the stabilization of surface soil layers throughout the catchment.

The comparatively minor effect of fire on sediment loads in the Swartboskloof stream contrasts markedly with findings for parts of the USA (see review by Tiedemann *et al.*, 1979). In chaparral systems, for example, surface erosion rates may accelerate by several orders of magnitude immediately after a fire, causing stream channels to become filled with large amounts of sediment and debris (Wells, 1986). Post-fire erosion appears to be a particularly common feature of chaparral ecosystems, as much of California chaparral occupies an extremely erosional environment, consisting of steep, highly dissected mountain slopes with deeply weathered rocks (Wells, 1986). Erosion in these environments following fire may be further exacerbated by the development of hydrophobic layers in the soil. These layers are formed when vapour and gases containing hydrophobic substances move downwards from the surface organic layer into the surface soil, where they condense on soil particles and inhibit infiltration. Water entering the catchment during post-fire storms is unable to infiltrate this layer, and the resulting increase in overland flow mobilizes the soil above the repellant layer, causing debris flows (Wells, 1986). The findings for the

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Swartboskloof catchment are somewhat ambiguous, in that hydrophobic soil was detected both before and after the prescribed burn. The overall conclusion, however, is that repellancy did not increase markedly as a result of the prescribed burn (D. Scott, University of Natal, *pers comm.*).

The one disadvantage often attributed by managers to riparian vegetation is that it utilizes water which would otherwise flow downstream (Bosch & Versfeld, 1982). In the present study, the lack of any major increase in stream flow after the fire is attributed primarily to the riparian vegetation remaining intact. It would appear, therefore, that management of mountain catchments for the maintenance of water quality (ie. retention of riparian vegetation) is not compatible with management for the maximization of water yield (ie. removal of riparian vegetation). Nevertheless, since destruction of such vegetation may create serious water quality problems, such as increased silt loads, increased temperatures and increased nutrient concentrations, it is clear that the advantages of keeping the riparian vegetation intact greatly exceed the disadvantages, if the water is intended for domestic use.

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Management of fynbos-dominated mountain catchments

The management of mountain catchment areas in South Africa is aimed at yielding the maximum quantity of water of the highest possible quality, whilst retaining optimum plant cover and variety of species (Department of Water Affairs, 1986). If we assume that the riparian vegetation plays a key role in maintaining the high quality of the water draining fynbos catchments, a primary management objective should be to ensure the continued integrity of this zone. In the present study, the low to moderate intensity of the prescribed burn had little effect on the riparian vegetation other than to induce a heavy leaf-fall shortly afterwards. Intense fires, however, may be considerably more destructive (Everard, 1986), with such vegetation burning under extreme conditions (van Wilgen, 1987). A strong case exists, therefore, for the use of prescribed fire in regulating the build-up of fuel in fynbos-dominated mountain catchments, since fire intensity generally decreases with decreasing fuel load (van Wilgen, 1987). Should wildfires occur between prescribed burns, their intensity will be moderated by fuel load, and thus the potentially extreme effects of wildfire on the riparian vegetation (and hence on the quality of water draining the catchment) will be avoided. Recognition of the role of hydrophobic layers in the acceleration of erosion provides further support for the use of prescribed burning in the regulation of fuel load, as the depth and thickness of the water-repellant layer is reported to be dependent on the intensity of the fire and the amount of vegetation and litter consumed (Debano & Rice, 1973).

Whilst prescribed burning to reduce fuel loads could, theoretically, take place every four years (the time needed for sufficient combustible material to accumulate - Kruger, 1977), burning at such short intervals will prevent the achievement of the major secondary management goal - that of nature conservation - since rotational burning at short intervals will be detrimental to the maintenance of plant species diversity. Van Wilgen (1981), for example, reports that continual short-rotation burning (ie. at 6-8 year intervals) results in the elimination of large seed-producing shrubs from fynbos vegetation. Furthermore, because fires may bring about substantial losses of nutrients (especially nitrogenous compounds) by volatilization, frequent burning may also be detrimental to site productivity. Thus, as pointed out in Paper I, although enhanced losses of N from the Swartboskloof catchment in surface runoff after the burn appear to be compensated by inputs of N in rain, volatilization of N and other nutrients, which was not quantified, may constitute a considerable loss from the system, requiring many years to recoup. The current state of knowledge of the volatilization of P compounds during fires is very poor, and data in the literature are conflicting (Rundel *et al.*, 1983). Cations are generally considered to be only slightly volatile during fire, but again, available data are highly variable (Rundel *et al.*,

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1983). This clearly requires further research, since fynbos systems are so oligotrophic that nutrient levels may be primary determinants of plant community structure and productivity.

The present 12-15 year burning policy is seen as a compromise, whereby the high diversity and vigorous growth of fynbos vegetation and a certain measure of control over fuel build-up may be attained. The mountain fynbos ecosystem is, however, highly complex and it is unlikely that any rigid or simple approach will achieve all the aims of management throughout the fynbos zone. Although the multidisciplinary Swartboskloof Programme provided answers to many questions posed at the outset of the study, our knowledge of this ecosystem and its requirements for effective conservation is still incomplete, and management should therefore be as flexible as practical considerations will permit. Gaps exist primarily in our understanding of nutrient cycling processes, and how these are affected by fire. The findings of this study have highlighted the need for research into the extent of volatilization of nutrients during fire; the effects of fire on microbial processes (eg. nitrogen fixation and nitrification); the effects of fire on the physical properties of the soils, especially soil-moisture and infiltration; and on groundwater flow paths and rates. Monitoring during the post-impact period should continue for a number of years, rather than within the confines of short research programmes designed to investigate the immediate effects of disturbance. Even more important is the need for long-term, pre-impact monitoring to establish the degree of natural temporal variation within the ecosystem. Seasonal and year-to-year variations in the fluxes of nutrients and water through a system, and associated biologic responses, often require long-term analysis before reliable generalizations can be drawn (Likens *et al.*, 1977). Without such records, it is impossible to determine with certainty when variations begin to exceed the normal range, thereby indicating that the system is disturbed or stressed.

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The influence of the sampling regime

The findings of this study show that whilst sampling at monthly intervals provides an overall characterization of stream chemistry and the stream biota, a realistic measure of the ranges of ionic concentration as well as an understanding of the processes influencing stream chemistry cannot be achieved unless supplemented by additional data collected on a different temporal scale and at extremes of discharge. In Paper II it was shown that at baseflow, during dry periods, the concentration of most of the ions measured in stream water varied little (Table II, Paper II). Variation in ionic concentration between years also appeared to be low. Conversely, during the wet season, discharge varied enormously in response to rainfall, and marked changes in stream chemistry accompanied these changes in discharge. On the basis of these findings, greater effort should be put into sampling during these latter, wet periods, particularly if quantification of ionic and particulate export is required. Individual storms should ideally be sampled as frequently as possible, at 4-6 hour intervals or less. Experience has shown that this is not practical when sampling is carried out manually, but may be feasible if some automated method of collection were available. Obviously, a certain amount of flexibility should be incorporated into sampling programmes. Sampling at 4-6 hour intervals during storms may be suitable for the Swartboskloof system, but may be unnecessary for large river systems, where hydrochemical responses may be considerably less rapid.

The influence of sampling frequency on estimates of ionic export during storm events can be demonstrated using data collected during the course of this study. In Paper I, estimates of ionic export from the gauged part of the catchment were obtained by multiplying mean ionic concentration for the pre- and post-burn years by total discharge during those years. This method has been repeated here for each of the four monitored storms and the results compared with those obtained using data collected at frequent intervals during the course of

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Table 1 Estimates of ionic export during storm events using two different methods. (a) = estimates based on frequent sampling of stream chemistry during the course of each event, (b) = estimates based on the mean of monthly values. Percentage by which (b) differs from (a) given.

	August 1986			January 1987			April 1987			August 1987		
	a	b	%	a	b	%	a	b	%	a	b	%
Cl^-	2,235	3,009	+35	423	359	-15	149	117	-21	1,592	2,499	+57
NO_3^--N	5.75	5.25	- 9	2.29	0.63	-72	0.26	0.29	+12	10.91	6.18	-43
PO_4^{3-}-P	1.94	1.15	-41	0.12	0.14	+17	0.04	0.04	0	0.85	0.86	+ 1
NH_4^+-N	7.23	6.52	-10	3.05	0.78	-74	0.68	0.32	-53	4.38	6.85	+56

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each storm, where the products of mean ionic concentration and discharge between each sampling event have been summed (Table 1).

Assuming that estimates obtained by the second method most accurately reflect export, it is apparent that use of the first method generally underestimates export. Furthermore, in the case of Cl^-, the differences between export estimates clearly reflect the failure of the first method to take into account seasonal differences in the relationship between concentration and discharge (Paper II). Estimates of ionic export during winter spates are thus overestimates, as the inverse relationship between ionic concentration and discharge is not taken into account, whereas estimates for summer spates are underestimates, as the method overlooks the positive relationship between ionic concentration and discharge. Export of NH_4^+-N during both summer storms and of NO_3^--N during the January storm are greatly underestimated by use of the first method, as relatively high soil-N concentrations during this season (see Stock & Lewis, 1986) are not taken into account.

Similar errors can be expected in the estimation of particulate export during storm events. Cuffney & Wallace (1988), working in headwater streams of the southern Appalachian mountains, reported that discrete sampling of particulate organic matter underestimated annual export by 29-71 %, when compared to estimates obtained through continuous sampling.

As pointed out in Paper I, because many concentration-discharge relationships are strongly influenced by short-term processes in the surrounding catchment, relationships between solute concentration and discharge for all but the most mobile of ions may go undetected when samples are collected at monthly intervals. The findings of the storm study have, in addition, shown that even for highly mobile ions such as NO_3^--N, a monthly sampling interval may provide a false impression of the relationship between ionic concentration and discharge. For example, when water samples were collected at monthly intervals (Paper I)

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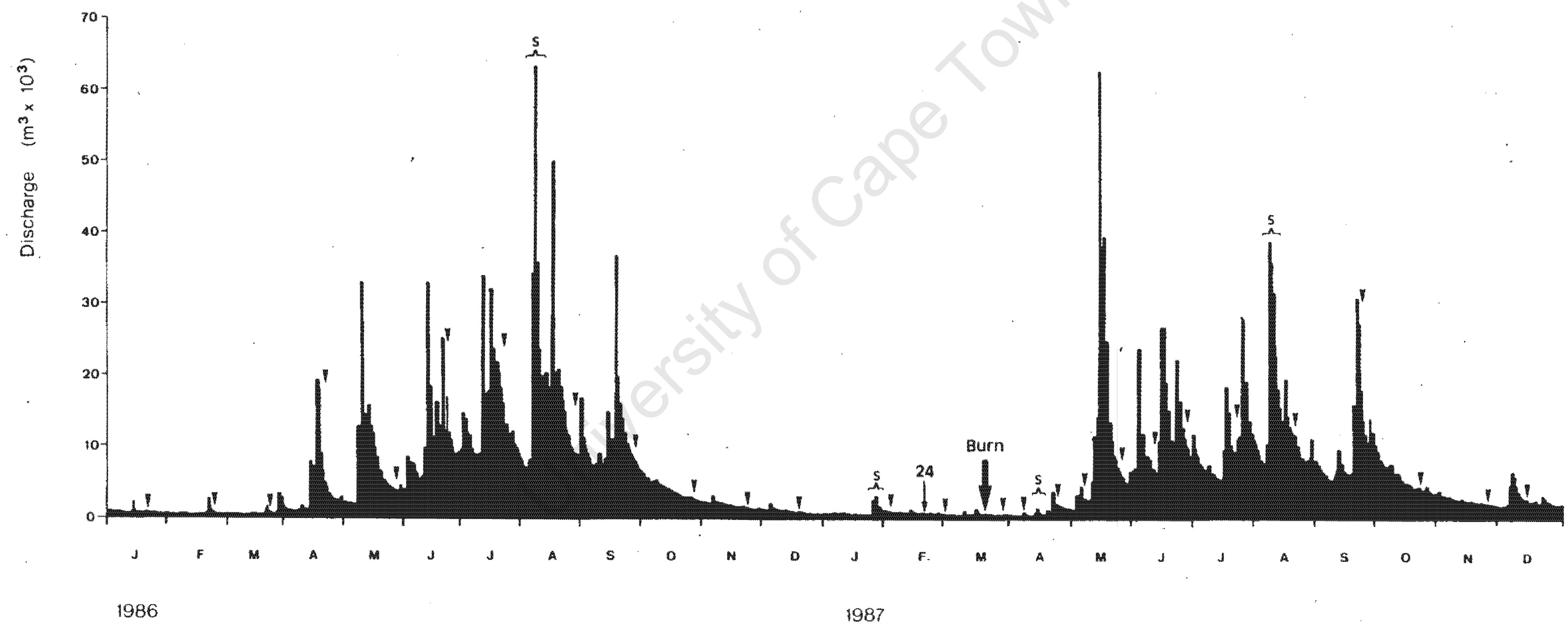

Fig. 1: Daily discharge from the gauged part of the Swartboskloof catchment during 1986 and 1987. Arrows indicate monthly sampling events, S indicates periods of intensive sampling during storm events, 24 indicates intensive 24-hour sampling event. Timing of the prescribed burn shown.

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it appeared that NO_3^--N concentration in stream water was positively associated with discharge, yet sampling during storm events revealed that this relationship existed for summer storms only. During winter storms, NO_3^--N concentrations appeared to be inversely related to discharge. The discrepancy may be explained by the fact that monthly samples were almost always collected on the falling limb of the hydrograph (Fig 1), a period during which NO_3^--N concentration falls during summer and rises during winter (Paper II).

CONCLUDING REMARKS

The findings of this study suggest that large changes in the surrounding catchment had little effect on the stream environment, and that the potential impact of the fire on the stream ecosystem was ameliorated by the riparian vegetation. It is clear, however, that more research is needed before we can fully understand the extent to which riparian vegetation in fynbos ecosystems acts as a 'buffer' against fire, research which will require the experimental manipulation of streamside vegetation.

Because of the short pre-burn data set and the lack of a control catchment for comparison, the results presented in this study on the effects of fire on stream chemistry and macroinvertebrates cannot be regarded as conclusive. The key to understanding many of these results lies in a thorough knowledge of the magnitude of natural year-to-year variation in these components of the stream ecosystem. Without such knowledge, it is not possible to determine with certainty when variations begin to exceed the normal range, thereby indicating that the system is disturbed.

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REFERENCES

Anderson, N.H. & K.W. Cummins (1979).
Influences of diet on the life histories of aquatic insects. J. Fish. Res. Board Can. 36: 335-342.

Bosch, J.M & D.B. Versfeld (1982).
Forestry and the management of riparian zones. Unpublished. Jonkershoek Forestry Research Centre. Department of Environment Affairs. 20 pp.

Cuffney, T.F. & J.B. Wallace (1988).
Particulate organic matter export from three headwater streams: discrete versus continuous measurements. Can. J. Fish. Aquat. Sci. 45: 2010-2016.

Debano, L.F.& R.M. Rice (1973).
Water repellant soils: their implication in forestry. J. For. 71: 220-223.

Department of Water Affairs (1986).
Management of the water resources of the Republic of South Africa. Department of Water Affairs, Pretoria.

Everard, D.A. (1986).
The effects of fire on the *Podocarpus latifolius* forests of the Royal Natal National Park, Natal Drakensberg. S. Afr. J. Bot. 52: 60-66.

Johnson, N.M., G.E. Likens, F.H. Bormann, D.W. Fisher & R.S. Pierce, (1969).
A working model for the variation in stream water chemistry at the Hubbard Brook Experimental Forest, New Hampshire. Wat. Resour. Res. 5: 1353-1363.

Kruger, F.J. (1977).
A preliminary account of aerial plant biomass in fynbos communities of the mediterranean-type climate zone of the Cape Province. Bothalia 12: 310-307.

Likens, G.E., F.H. Bormann, R.S. Pierce, J.S. Eaton & N.M. Johnson (1977).
Biogeochemistry of a forested ecosystem. Springer-Verlag, New York.

University of Cape Town

Meehan, W.R., F.J. Swanson & J.R. Sedell (1977).
Influences of riparian vegetation on aquatic ecosystems with particular reference to salmonid fishes and their food supply. In: R.R. Johnson & D.A. Jones (Tech. Coordinators), Importance, preservation and management of riparian habitat - a symposium, pp. 137-145. USDA For. Serv. Gen. Tech. Rep. RM-43.

Mooney, H.A. & P.W. Rundel, (1979).
Nutrient relations of the evergreen shrub, *Adenostoma fasiculatum* in the California chaparral. Bot. Gaz. 140: 109-113.

Rogers, K.H. & D.W. van der Zel, (1989).
Water quantity requirements of riparian vegetation and floodplains. In: A.A. Ferrar (Ed.), Ecological flow requirements for South African rivers, pp. 94-109. S. Afr. Nat. Sci. Prog. Report 162. CSIR, Pretoria.

Rundel, P.W., G.C. Bate, A.B. Low, P.C. Miller, P. Miller & D.T. Mitchell (1983).
Nutrient cycling processes. In: J.A. Day (Ed.), Mineral nutrients in mediterranean ecosystems, pp. 19-32. S. Afr. Nat. Sci. Prog. Report 71. CSIR, Pretoria.

Schaefer, R. (1973).
Microbial activity under seasonal conditions of drought in mediterranean climates. In: F. DiCastri & H.A. Mooney (Eds.), Mediterranean-type ecosystems: origin and structure, pp. 191-198. Springer, Berlin.

Stock, W.D. & O.A.M. Lewis (1986).
Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. J. Ecol. 74: 317-328.

Stock, W.D., J.E.M. Somerville & O.A.M. Lewis (1987).
Seasonal allocation of dry mass and nitrogen in a fynbos endemic Restionaceae species *Thamnochortus punctatus* Pill. Oecologia 72: 315-320.

Tiedemann, A.R., C.E. Conrad, J.H. Dieterich, J.W. Hornbeck, W.F. Megahan, L.A. Viereck & D.D. Wade (1979).
Effects of fire on water - A state of knowledge review. U.S.D.A. For. Serv. Gen. Tech. Rep. WO-10.

University of Cape Town

van Wilgen, B.W. (1981).
Some effects of fire frequency on fynbos plant community composition and structure at Jonkershoek, Stellenbosch. S. Afr. For. J. 118: 42-54.

van Wilgen, B.W. (1987).
Fire regimes in the fynbos biome. In: R.M. Cowling, D.C. le Maitre, B. McKenzie, R.P. Jones & B.W. van Wilgen (Eds.), Disturbance and the dynamics of fynbos biome communities, pp. 6-14. S. Afr. Nat. Sci. Prog. Report 135. CSIR, Pretoria.

Ward, J.V. & J.A. Stanford (1979).
Ecological factors controlling stream zoobenthos with emphasis on thermal modifications of regulated streams. In: J.V. Ward & J.A. Stanford (Eds.). The ecology of regulated streams, pp. 35-55. Plenum Press, New York.

Wells, W.G.(II) (1986).
The influence of fire on erosion rates in California chaparral. In: J.J. DeVries (Ed.), Proceedings of the chaparral ecosystems research conference, Santa Barbara, California 1985, pp. 57-62.

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APPENDIX I

Fine particulate inorganic matter (FPIM - >80 <950 um) and ultra-fine particulate inorganic matter (UPIM - >0.65 <80 um) in Swartboskloof stream water at site 1 during the pre- and post-burn years.

		FPIM (g m^{-3})	UPIM (g m^{-3})	Total (g m^{-3})
Pre-burn year (Mar 1986 - Feb 1987)				
March		0.85	0.89	1.74
April		0.56	0.91	1.47
May		0.51	0.24	0.75
June		0.85	0.26	1.11
July		0.89	0.00	0.89
August		0.46	0.35	0.81
September		0.32	0.20	0.52
October		0.49	0.22	0.71
November		0.27	0.82	1.09
December		0.10	0.52	0.62
January		0.28	0.25	0.33
February		0.09	1.77	1.86
	$\bar{x}$	0.47	0.54	0.99
	sd	0.28	0.49	0.48
Post-burn year (Mar 1987 - Feb 1988)				
March		0.09	0.26	0.35
April		0.14	0.10	0.24
May		-	6.90	-
May		0.82	0.90	1.72
June		-	0.60	-
June		0.74	0.72	1.46
July		0.87	0.42	1.29
August		0.32	0.92	1.24
September		0.34	1.15	1.49
October		0.32	0.85	1.17
November		0.16	0.88	0.98
December		0.54	0.88	1.42
January		0.15	1.02	1.17
February		1.78	1.11	2.89
	$\bar{x}$	0.52	1.19	1.29
	sd	0.48	1.67	0.67

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APPENDIX II

Fine particulate inorganic matter (FPIM - >80 <950 um) and ultra-fine particulate inorganic matter (UPIM - >0.65 <80 um) in Swartboskloof stream water at site 2 (Fig. 1, Paper 1) during each of the four storms sampled.

PRE-BURN August 1986				POST-BURN August 1987			
Time (hrs)	Discharge (m^3 s^{-1})	FPIM (g m^{-3})	UPIM (g m^{-3})	Time (hrs)	Discharge (m^3 s^{-1})	FPIM (g m^{-3})	UPIM (g m^{-3})
0	0.183	0.02	0.20	0	0.198	0.14	0.30
6.75	0.203	0.01	0.10	4.50	0.258	1.13	0.33
10.75	0.287	0.03	1.40	8.50	1.700	1.53	1.66
15.25	0.295	0.06	0.95	13.25	0.870	1.59	2.46
21.25	0.913	0.40	1.90	17.50	0.777	0.72	0.84
26.75	0.425	0.01	1.40	22.00	1.008	0.57	0.26
29.75	0.552	0.33	1.05	26.00	2.085	3.60	1.50
48.75	1.347	1.34	1.75	32.00	0.674	2.18	11.50
55.75	1.704	0.17	2.45	38.50	1.041	0.47	0.85
61.25	2.346	2.62	6.60	44.25	0.827	0.79	0.74
69.75	1.466	0.31	1.21	50.00	2.013	1.72	0.42
80.50	0.919	0.13	0.60	56.00	0.839	0.62	3.20
92.25	0.847	0.04	0.15	62.00	1.069	0.24	0.51
149.25	0.475	0.03	0.13	108.00	0.562	0.26	0.42

January 1987				April 1987			
Time (hrs)	Discharge (m^3 s^{-1})	FPIM (g m^{-3})	UPIM (g m^{-3})	Time (hrs)	Discharge (m^3 s^{-1})	FPIM (g m^{-3})	UPIM (g m^{-3})
0	0.035	0.35	0.50	0	0.027	0.02	0.43
4.00	0.085	0.44	2.40	4.50	0.032	0.05	0.15
8.50	0.095	0.35	2.00	8.25	0.040	0.05	0.31
14.25	0.095	0.25	0.94	14.00	0.035	0.03	0.20
20.50	0.121	1.09	1.20	19.75	0.068	0.68	0.91
25.25	0.255	0.79	1.30	26.00	0.102	0.44	0.63
32.00	0.179	0.37	0.50	44.25	0.060	-	0.16
38.00	0.247	0.19	0.45	56.25	0.055	0.02	0.22
44.00	0.151	0.19	0.55	84.00	0.050	0.02	0.26
74.75	0.114	0.05	0.30				
123.50	0.058	0.05	0.15				

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