Seasonal growth of the overstorey and understorey in mediterranean-type shrublands and heathlands in the south eastern Cape, South Africa

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The phenological model of Specht et al. (1983) was tested by determining the seasonality of shoot growth and leaf loss of the overstorey and understorey components of vegetation on nutrient-poor, base-rich and calcium-rich soil suites in the mediterranean climate region of the south eastern Cape. Results were largely consistent with the predictions of the model although certain inconsistencies were noted. The model is discussed critically in terms of its assumptions and predictions.

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Deur die seisoenagtigheid van lootontwikkeling en blaarverlies van die komponente van die bogaal en onderlaag van plantegroei op voedselarme, basisryke en kalsiumryke grondreekse in die midellandseklimaatstreek van die suidoos Kaap te bepaal, is die fenologiese model van Specht et al. (1983) getoets. Die resultate het grotlik met die voorspellings van die model ooreenkom en sommige onreeksmaatigheid is opgemerk. Die model is in terme van die opname en voorspellings krities bespreek.

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Keywords: Heathlands, mediterranean-type vegetation, overstorey, shoot growth, understorey

Introduction

The current interest in the structure and functioning of mediterranean-type vegetation has led to the assertion that the global physiognomic similarity of these formations makes it probable that they have similar trends of phenophase sequences (Kummerow 1983). There is some evidence from northern hemisphere mediterranean vegetation to support this assertion (Kummerow 1983).

In mediterranean-type ecosystems a distinction is made between shrublands on relatively fertile soils (Specht 1979; Di Castri 1980; Specht & Moll 1983) and heathlands on infertile soils (Specht 1979). In the latter it is postulated that low levels of soil nutrients are of overriding importance in determining plant structure (Specht 1979; Cowling & Campbell 1980), leading to a global heathland concept associated with a particular soil suite rather than any single climatic regime. Whereas most species of mediterranean shrublands show growth flushes in spring (Kummerow 1983), dominant heathland shrubs in mediterranean climate regions of Australia and South Africa grow mainly in summer (Kruger 1981; Specht et al. 1981).

Recently Specht (Specht et al. 1981; Specht et al. 1983) developed a model to explain and predict the growth of overstorey and understorey species in mediterranean-type vegetation on base-rich, nutrient-poor and calcium-rich soil suites in southern Australia and South Africa. This model predicts that the overstorey and understorey species of shrublands on base-rich soils would show spring (Sep. – Nov.) and/or autumn (Mar. – May) growth while leaf fall would be delayed until the dry season of the year (in late spring or summer, Dec. – Feb.). Similar phenophases are predicted for understorey heathland species on nutrient-poor soils; overstorey species would grow in late spring or summer with leaf fall occurring at the same time. Specht et al. (1983) further predict that because of nutrient stresses induced by the high pH of calcium-rich soils, communities on this soil suite would show a similar seasonality to heathlands.

Specht et al. (1983) argue that the timing of shoot growth and leaf fall on the different soil suites confers ecophysiological advantages. On base-rich soils, where nutrients are assumed to be non-limiting, shoot growth precedes leaf fall and the additional new foliage would increase photosynthetic production during the favourable spring and autumn periods. In heathlands on nutrient-poor soils 'shoot growth in late spring and summer follows the release of nutrients from decomposing litter during spring' (Specht et al. 1983). In this way nutrient cycling is maximized both externally via decomposing leaf litter and internally from absconding leaves. Furthermore the
absence of winter growth in both heathlands and shrublands means that soil moisture is conserved during the wet period to be used later in the ‘more favourable warmer months’ (Specht et al. 1983).

In this paper we test the phenological predictions of Specht’s model (Specht et al. 1983) by measuring and observing shoot growth and leaf loss periodicity in overstorey and understorey species over a period of 14–16 months in communities on nutrient-poor, base-rich and calcium-rich soil suites in the mediterranean-type climate region of the south eastern Cape. We did not measure changes in soil moisture and aspects of nutrient cycling which would provide a true test of Specht’s model and explain the ‘ecophysiological advantages’ of the shoot growth and leaf loss periodicities predicted by the model.

A detailed account of the phenology of the communities together with information on the study sites and methods is presented in Pierce & Cowling (1984).

Study area

The study area is located in the Humansdorp region of the south eastern Cape on a level coastal plain which cuts across two geological formations: sandstone of the Table Mountain Group (TMG) and shales of the Bokkeveld Group. Along the coast there are deposits of recent calcareous sands. It was therefore possible to study eight communities on different substrates or soil suites all of which experienced similar mesoclimatic conditions. Details on the floristics, structure, soils and land-use of the communities and an account of the climate of the region are given in Pierce & Cowling (1984).

Soil suites and shrubland types

Table 1 shows the correspondence of the communities we studied with Specht & Moll’s (1983) soil suites. Specht & Moll (1983) use the terms highly leached and moderately leached instead of nutrient-poor and base-rich, respectively. We prefer Specht’s (1979) earlier terms (latter above, Table 1) since in South Africa, many heathland (fynbos) soils which are infertile are not leached (Bond 1981; Campbell 1983; Cowling 1983) and do not have an eluvial horizon which characterizes the zone of maximum leaching (Brady 1974).

In a recent symposium (Day 1983), nutrient-poor soils were defined as having a pH of less than 6.0, a total nitrogen of less than 0.12% and a sum of exchangeable cations (S-value) of less than 7 me/100 g soil (see also Specht & Moll 1983).

Calcium-rich soils have a high pH (> 7) and large amounts of exchangeable calcium. According to Specht & Moll (1983), in the South African mediterranean-type region nutrient-poor soils support fynbos (a heathland) while base-rich soils support shrublands, including ‘Olea-Sideroxylon open scrub’ and disclimax ‘renosterveld’. An important feature of the shrublands is the presence of a ‘savanna understorey’ of seasonal grasses and forbs, in contrast to the evergreen sclerophyllous understorey of heathlands. Calcium-rich soils support ‘a stunted overstorey of evergreen sclerophyllous trees and shrubs over a ground stratum showing a gradation from seasonal grasses and herbs to evergreen hemicryptophytes’ (Specht & Moll 1983).

In our study area heathlands on nutrient-poor soils included communities 1 and 2 in Table 1. They differ from Specht’s (1979) heathland concept in that the understorey includes many seasonal grasses. In the mediterranean-type region of South Africa the most widespread shrubland on base-rich soils is renosterveld (Boucher & Moll 1980) which has an understorey of seasonal grasses and forbs and an overstorey of small leaved sclerophyllous and semi-succulent shrubs. Specht & Moll (1983) regard the ‘Olea-Sideroxylon’ open scrub (Kaffrarian thicket in Table 1) as the true South African mediterranean-type shrubland analogous to the maquis, matorral, chaparral and mallee of other mediterranean-type regions (Di Castri 1980). Cowling (1983) has argued that in the Cape region thicket is restricted to special edaphic sites and was certainly never widespread in the past. We sampled renosterveld (communities 3 and 4) and thicket (community 5) on base-rich soils. On calcium-rich soils we sampled a heathland (dune fynbos), a grassy heathland (dune grassland) and a shrubland (dune thicket) (communities 6–8 in Table 1).

Both Cowling (1983) and Campbell (1983) have criticized Specht’s shrubland concepts as applied to the South African mediterranean-type region. Many non-heathland types (e.g. renosterveld) occur on soils which are nutrient-poor. Moreover shrublands on true base-rich soils are not ‘open scrubs with a savanna understorey’ (Specht & Moll 1983) but rather closed shrublands with a sparse understorey of shade tolerant herbs.

Table 1: Communities on substrates corresponding to Specht & Moll’s (1983) soil suites. Details on floristics, structure and soils are given in Pierce & Cowling (1984)

| Order | Community | Substrate | Soil suite | Strata | Number of species monitored |
|-------|-----------|-----------|------------|--------|--------------------------|
| 1. Grassy Fynbos | Restioid grassland | T.M.G Sandstone | Nutrient-poor | Understorey | 31 |
| 2. Grassy Fynbos | Grassy fynbos | T.M.G Sandstone | Nutrient-poor | Understorey | 7 |
| 3. South Coast Renosterveld | Shale grassland | Bokkeveld shale | Base-rich | Understorey | 28 |
| 4. South Coast Renosterveld | Renosterveld | Bokkeveld shale | Base-rich | Understorey | 6 |
| 5. Kaffrarian Thicket | Kromme River thicket | Bokkeveld shale | Base-rich | Understorey | 17 |
| 6. South Coast Dune Fynbos | Dune grassland | Recent sand | Calcium-rich | Understorey | 28 |
| 7. South Coast Dune Fynbos | Dune fynbos | Recent sand | Calcium-rich | Understorey | 10 |
| 8. Kaffrarian Thicket | Dune thicket | Recent sand | Calcium-rich | Understorey | 13 |

*Order concept according to Cowling (1983)
*Terms according to Specht (1979)
tion by Specht et al. (1983) of these strata in South African mediterranean-type vegetation is imprecise.

We classed phanerophytes as overstorey species and chamaephytes, hemicyrptophytes, geophytes, annuals and other forbs as understorey species. In heathlands Specht et al. (1983) recognize a midstratum of ericoid shrubs (Ericaceae) in addition to the overstorey (Proteaceae) and understorey (Restionaceae) strata. This heathland stratum is usually included with the understorey (Specht & Moll 1983). In our fynbos site, proteoids (Leucadendron salignum, Leucospermum cuneiforme) formed a single 1.0-1.2 m stratum with ericoids (Erica pectinifolia, E. diaphana). We included all these species in the overstorey. Similarly the small leaved shrubs in the dune fynbos (e.g. Agathosma apiculata, Passerina vulgaris) and the renosterveld (Metalasia auriculata, Elytropappus rhinocerotis) were classed as overstorey species. In the thicket types, overstorey shrubs included the broad leaf sclerophyll species Sideroxylon inerme, Pterocelastrus tricuspidatus, Euclea spp. and Olea spp.

Methods

Details on the sampling methods and the list of species are given in Pierce & Cowling (1984) where 173 species were studied. However, the occurrence of the same in more than one community meant that 185 species in all were observed. We monitored active growth of species in the eight communities (Table 1) and expressed the results in bar graphs depicting the percentage of total species of each stratum actively growing in each month for 12, and for some communities 16 months from January 1981 to March 1982. Leaf fall was measured for selected species (Pierce & Cowling 1984) and qualitative observations were made for the rest.

Results

The results showing percentage species in the overstorey and in the understorey actively growing each month for nutrient-poor, base-rich and calcium-rich soil suites, are shown in Figures 1, 2 & 3 respectively.

On nutrient-poor soils, most species of the restioid grassland (understorey only) grew in early spring with a lesser peak in autumn (Figure 1a). Leaf senescence of geophytes occurred in late spring after or immediately prior to flowering. Leaves of grasses senesced in late spring (Oct/Nov) but remain attached to the parent shoot. Growth periodicity was consistent with Specht's predictions but patterns of leaf loss appeared to be anomalous. Grassy fynbos had a distinctive summer growth peak (Figure 1b & c). In general litter fall was not entirely synchronous with shoot growth. Leaf loss in Leucadendron salignum was variable although there was evidence of a January peak, while Leucospermum cuneiforme shed most leaves in autumn (Pierce & Cowling 1984). This latter pattern could be consistent with Specht's wide prediction of 'late spring (or) . . . increase markedly towards the end of the dry period' for leaf loss of the overstorey on nutrient-poor soils (Specht et al. 1983).

Both ericoid overstorey species showed non-seasonal leaf loss (Pierce & Cowling 1984) although Erica pectinifolia did show a slight mid- to late summer as well as autumn peak. The overstorey shoot growth and, to a lesser extent, leaf loss conformed with Specht's predictions. However, the grassy fynbos understorey showed maximum growth in summer which is at variance with the model. Two understorey hemicyrptophytes (Restio triticeus, Tetraria involucrata) showed spring and/or autumn peaks but the C4 grass, Diheteropogon filifolius, grew in summer (Pierce & Cowling 1984). All chaemaephytes (e.g. Helichrysum spp., Selago glomerata) grew in summer. There were no geophytes present in the grassy fynbos site.

Specht's model predicts spring or autumn growth and post-growth leaf loss for overstorey species on base-rich soils. The Kromme River thicket did show maximum shoot growth in spring (Figure 2a) and maximum leaf loss in midsummer (Pierce & Cowling 1984). Most shale grassland species (understorey only) grew in late winter/early spring as well as late summer/autumn (Figure 2b). Specht's predictions for growth periodicity of this stratum on base-rich soils are vague and therefore difficult to test. Specht et al. (1983) do suggest that on base-rich soils seasonal grasses and herbs complete their annual cycle by the end of spring; our data for the shale

![Figure 1](image1.png)

**Figure 1** Shoot growth of overstorey and understorey species in nutrient-poor soils. n = number of species observed; ▲ indicates start and ★ indicates end of study when initiated or terminated at different times for the separate communities.

![Figure 2](image2.png)

**Figure 2** Shoot growth of overstorey and understorey species in base-rich soils. n = number of species observed; ▲ indicates start of study of one community.
grassland shows a marked drop in growth in late spring/early summer (Figure 2b). Late summer growth could be the result of the anomalously high January and February rainfall during the sampling period (Pierce & Cowling 1984). The renosterveld overstorey showed clear spring and late summer/early autumn growth peaks (Figure 2c). Again, heavy late summer rainfall may explain the early onset of autumn growth. The renosterveld understorey showed late winter/early spring growth (Figure 2c). Overall shoot growth and leaf loss periodicity on base-rich soils was consistent with Specht's predictions.

On the calcium-rich soils, dune grassland (understorey only) (Figure 3a) and the dune fynbos understorey (Figure 3d) showed spring growth peaks. Specht's predictions for this stratum on calcium-rich soils are vague although it is suggested that phenophases should be similar to those on nutrient-poor soils (spring and autumn peaks) (Specht et al. 1983). Our data are consistent with this prediction. Overstorey growth and leaf loss periodicity on calcium-rich soils should be similar to the phenophases on nutrient-poor soils (Specht et al. 1983). Most dune fynbos overstorey species, however, grow in late spring and late summer/autumn (Figure 3c). Moreover maximum leaf loss in the two dominant overstorey species, Passerina vulgaris and Agathosma apiculata, does not coincide with their growth peaks (Pierce & Cowling 1984). Most dune thicket overstorey species grew in spring and late summer/autumn (Figure 3b) and showed maximum leaf fall in midsummer (Pierce & Cowling 1984). The results are not consistent with Specht's predictions. Both thicket communities showed similar phenophases and had similar compositions of subtropical trees and shrubs.

**Discussion**

We found evidence which both confutes and supports Specht's predictions for shoot growth and leaf loss phenophases in vegetation on different soil suites in a South African mediterranean-type region. Much of the confusion in testing Specht's model results from inexact assumptions and vague predictions.

There are problems with the overstorey/understorey characterization. No explicit definition of the strata in terms of readily observable growth form or life form attributes is given. In heathlands, nanophanerophytes could either be overstorey or understorey elements depending on the stratification of the community. The assertion that understorey species are short-lived and overstorey species long-lived (Specht et al. 1983) certainly does not apply to fynbos where understorey Restionaceae may persist long after seed regenerating overstorey Proteaceae have senesced and died. (cf. van Wilgen 1982). Specht et al. (1983) give Euclea, Rhus, Olea, Pterocelastrus and Sideroxylon, all subtropical genera with few or no species endemic to the South African mediterranean-type region, as typical of the overstorey component on base-rich soils. No mention is made of the renosterveld overstorey comprising small leaved endemic shrub genera (Elytropappus, Relhania, Aspalathus, Euryops). Certainly renosterveld is the most widespread shrubland on base-rich soils and although some renosterveld has been derived in historical times from a grassland (Cowling 1983) it cannot be ignored in the guise of a 'disclimax' community (Specht & Moll 1983; cf. Cowling 1983).

Overstorey shoot growth on base-rich soils 'normally occurs in spring, sometimes in autumn, while leaf fall follows shoot growth as soil drought increases in late spring and summer' (Specht et al. 1983). If shoot growth occurs in autumn, when will leaf fall occur? The base-rich understorey is predicted to grow any time between autumn and spring. This component is assumed to be entirely 'seasonal' and to die back during the unfavourable midsummer season. Not all of our understorey species showed this seasonality. Predictions for vegetation on calcium-rich soils are especially vague and we doubt whether high pH limits nutrient uptake in organically enriched dune thicket soils.

Our findings may be explained by temperature and soil moisture, the factors suggested by Kummerow (1983) as determinants of phenophases. Shoot growth and flowering are temperature dependent while root growth and litter fall are soil moisture dependent (Kummerow 1983). He attributes the time difference between spring growers and late growing species to the availability of soil moisture to the former shallow rooted species, while the latter are deep rooted and able to tap deeper underground water sources. However, Kummerow (1983) considers soil moisture thresholds and the accumulation of warming hours of prime importance but feels his own model is not yet satisfactory.

The model of Specht et al. (1983) assumes that ecophysiological factors (e.g. water and nutrient availability) are of overriding importance in determining phenophases. Although the seasonal regime of the habitat will impose major constraints on plant growth, biological constraints are also important. For example, in many species of Restionaceae shoot growth must precede flowering since inflorescences are terminal. Flowering time, in turn may be affected by interrelations with disperser seasonality (cf. Bond & Slingsby 1983; Thompson 1981).

Biogeographical and historical factors can impose further constraints on the model. The South African mediterranean-type region is not isolated from the subtropical summer rainfall region but grades into it along the south and south east Cape coastal forelands. The area is thus exposed to migration of a subtropical flora. Many of the subtropical species are C₄ grasses which have high temperature optima for growth (e.g. **Figure 3** Shoot growth of understorey and overstorey species in calcium-rich soils. n = number of species observed; ▼ indicates end of study of one community.
Diheteropogon filifolius in the grassy fynbos understorey).

Referring to our data, it is not always possible to give ad hoc explanations for the deviations from Specht's predictions. Specht et al. (1983) explain their phenophase predictions in terms of seasonality in the availability to plants of water and nutrients. Implicit in the model is the assumption that nutrient uptake occurs concurrently with shoot growth. However, shoot and leaf growth may be the result of relocation of stored metabolites (Groves 1965). We lack these data and therefore could not provide a real test of the model. We question whether the implied seasonality of nutrient availability can be tested, given the difficulties of measuring plant-available soil nutrients (W. Stock, pers. comm.).

Specht is to be commended for developing so bold a phenological model. Our data were consistent with many of his predictions. However, on the basis of the inconsistencies, the model should be re-evaluated. Perhaps the notion of polarizing mediterranean-type shrublands and heathlands into overstorey and understorey components should be questioned. Is it not a continuum between the rhythms predicted for overstorey and understorey strata?

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Ordination of the herbaceous stratum of savanna in the
Nylsvley Nature Reserve, South Africa

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The purpose of the study was to determine the ecological status of representative herbaceous species with respect to environmental factors and subhabitats of which the spatial and temporal pattern could be elucidated.

The basal cover of the herbaceous vegetation was determined by means of the wheel-point method. Frequency data in each of 200 1 m² contiguous quadrats were ordered by means of detrended correspondence analysis (DECORANA).

The distribution of the species along the first axis is a function of conditions representing an open habitat with full sunlight and somewhat drier conditions to the left and a denser and/or shrub habitat with more shade and wetter, more favourable conditions to the right. The gradient along the second axis is that of disturbed conditions with more perennials at the lower end to disturbed conditions with more annuals at the upper end. From the scatter diagrams it can be concluded that the herbaceous layer is functionally homogeneous, that it represents a seral stage and that Eragrostis palens and Digitaria eriantha, both with the highest basal cover in the study area, are representative of a seral stage rather than of the climax. The lack of pattern in the herbaceous layer can be attributed mainly to the large number of annual and perennial pioneer and disturbance-indicating species. In a similar study Whittaker et al. (in press) concluded that the woody vegetation dominates the pattern.

Die verspreiding van die spesies langs die eerste as van ordening verteenwoordig 'n droër oop habitat in volle sonlig links en 'n vogtiger, digter en struikhidat met meer skaduwee regs. Die gradënt langs die tweede as van ordening verteenwoordig minder versturing met meer eenjarige plantsoorte onder en meer versturing met meer eenjarige soorte bo. Daar kan uit die verstoringdiagrame afgelei word dat die kruisdiameter redelik homogene is, en 'n serale stadium van plantsoeksessie verteenwoordig en nie 'n klimaks nie. Eragrostis palens en Digitaria eriantha het die hoogste basale bedekking in die studie-area gehad. Die gebrek aan patroon ken aan die groot getal eenjarige en meerjarige pionier-en versturingspesies toegeskryf word. In 'n soortgelike studie het Whittaker et al. (in pers) gevind dat die houtagtige plantsoorte die patroon domineer.

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Die doel van die studie was om die ekologiese posisie van verteenwoordigende houtagtige spesies ten opsigte van omgewingsfaktore en subhabitats te bepaal waardeur die ruimtelike en tydelike patroon dan verklaar kan word.

Die basale bedekking van kruidagtige spesies is deur middel van die wielpuntmetode bepaal. Frekwensiedata is verkry uit 200 1 m² aaneengeskakelde kwadrate wat deur middel van DECORANA geordend is.

Die verspreiding van die spesies langs die eerste as van ordening verteenwoordig 'n droër oop habitat in volle sonlig links en 'n vogtiger, digter en struikhidat met meer skaduwee regs. Die gradënt langs die tweede as van ordening verteenwoordig minder versturing met meer eenjarige plantsoorte onder en meer versturing met meer eenjarige soorte bo. Daar kan uit die verstoringdiagrame afgelei word dat die kruisdiameter redelik homogene is, en 'n serale stadium van plantsoeksessie verteenwoordig en nie 'n klimaks nie. Eragrostis palens en Digitaria eriantha het die hoogste basale bedekking in die studie-area gehad. Die gebrek aan patroon ken aan die groot getal eenjarige en meerjarige pionier-en versturingspesies toegeskryf word. In 'n soortgelike studie het Whittaker et al. (in pers) gevind dat die houtagtige plantsoorte die patroon domineer.

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Keywords: DECORANA, ecological position, herbaceous stratum, ordination, pattern

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Introduction

A cooperative savanna ecosystem project was initiated in 1974 on part of the Nylsvley Nature Reserve by the Terrestrial Biology Section of the South African National Programme for Environmental Sciences. As part of phase I of this project (description and quantification of structural features of the ecosystem), the research reported here was undertaken. It was broadly directed towards the study of pattern within the herbaceous component of the vegetation. Briefly, the purpose of the quantitative study was to determine the ecological status of representative herbaceous species with respect to environmental factors and subhabitats by means of which the spatial and temporal pattern could be elucidated. The response of herbaceous species to the two main subhabitats, namely, under-tree and open treeless areas, was of particular concern. In a parallel study Lubke et al. (1976) investigated the woody component.

R.H. Whittaker has successfully applied ordination techniques to strip transect data to study pattern (Whittaker et al., 1979, in press). In vegetation rich in species and with a marked two-phase character, ordination appears to be especially useful for the identification and quantification of overall species compositional pattern i.e. community, rather than the species-by-species relationships studied by Kershaw (1957) and Greig-Smith (1964). The savanna vegetation at Nylsvley is rich in species and its under-tree and open subhabitats are comparable with the discontinuous phase (shrub clumps) and open continuous phase (grassy matrix) described by Whittaker et al. (in press) in mesquite grassland in Texas. After inspection, however, the two-phase pattern is not as distinct within South African savanna as that described in Texas (Whittaker et al. 1979).

Study area

The Nylsvley Nature Reserve, 3 129 ha in extent, comprises the farm Nylsvley 560 KR, situated between 24°36' and 24°42'S latitude and 28°40' and 28°44'E longitude, 16 km south of Naboomspruit in the Northern Transvaal, South Africa. Most of the ecosystem research has been concentrated in a 745 ha study area within the reserve.

The reserve is situated in an extensive undulating to flat terrain between 1 080 m and 1 140 m altitude. The Nyl river runs across the reserve from south-west to north-east in a strip of flat, low lying land that divides the reserve into a number of gently sloping elevations. The study area itself lies on the south-eastern elevation on the southern side of the Nyl river and is situated on sandstone, grits and conglomerate bands of the