Phytomass and major nutrient pools in an 11-year post-fire coastal fynbos community

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Aerial and root phytomass data are presented for an 11-year post-fire coastal fynbos community. The former comprised 14 580 kg ha\(^{-1}\), which compared generally with heathland stands elsewhere. Root phytomass (13 970 kg ha\(^{-1}\)) was similar to Calluna vegetation but much lower than Australian heaths.

Major nutrient pools were in the order of 89,3 (N), 8,0 (P), 194,6 (Ca), 12,5 (Mg) and 38,5 (K) kg ha\(^{-1}\) for above-ground and 81,1 (N), 10,5 (P), 121,7 (Ca), 12,4 (Mg) and 16,4 (K) kg ha\(^{-1}\) for below-ground. Although these amounts showed a general comparability with other heathlands, P and, in particular, Ca, showed a certain degree of variation.

Soil nutrient pools displayed amounts of 5841,0 (N), 248,7 (P), 1119,9 (Ca), 552,5 (Mg) and 989,1 (K) kg ha\(^{-1}\). Mediterranean shrubland soils were, on the whole, far richer in nutrients than coastal fynbos and other heathlands. However, overlaps in eg. N, P and Ca content may occur between these soils. The supposed nutrient-poor/nutrient-rich heathland/shrubland dichotomy based on soil nutrient status, may therefore only apply to certain elements.

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Bogrondse en wortelwitmassa word gegee vir 'n kusfynbos-gemeenskap elf jaar na 'n brand. Die eersgenoemde, wat 14 580 kg ha\(^{-1}\) bevat, het oor die algemeen met ander heidelande ooreengekom. Wortelwitmassa was gelyk aan Calluna plantegroei, maar veel laer as die van Australiese heide.

Hoof-voedingstoewesheid in die omgewing van: 89,3 (N), 8,0 (P), 194,6 (Ca), 12,5 (Mg) en 38,5 (K) kg ha\(^{-1}\), en ondergronds: 81,1 (N), 10,5 (P), 121,7 (Ca), 12,4 (Mg) en 16,4 (K) kg ha\(^{-1}\). Alhoewel hierdie hoeveleheid 'n algemene ooreenkoms met ander heidelande toon, is daar 'n verskil ten opsigte van P en veral Ca.

Grondvoedingstoewewe het hoeveelhede van 5841,0 (N), 248,7 (P), 1119,9 (Ca), 552,5 (Mg) en 989,1 (K) kg ha\(^{-1}\) getoon. Mediterrane struiklandgrond was oor die algemeen veel ryker in voedingstoewewe as die van kusfynbos en ander heidelande. Oorvleueling in bv. die N-, P- en Ca-konsentrasie mag nietemin tussen hierdie gronde voorkom. Die bewering dat die plante van heidelande voedingstofarm is, terwyl die plante van struiklande voedingstofryk is as gevolg van die grondvoedingstoewewe, is miskien gevolglik slegs op sekere elemente van toepassing.

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Introduction

Heathlands and their almost ubiquitous association with oligotrophic soils (Specht 1979), as well as their unique structure and often floristics, have to date enjoyed a fair measure of scientific interest. For example, quantification of their phytomass and nutrient pools, although more recent than many other ecological studies, is now well established for British Calluna heaths (Gimmingham 1972). Outside Europe, the Australian heaths are also fairly well documented; the Dark Island site (Specht et al. 1958) is a prime example.

South Africa, despite its possessing one of the world's major heathland ecosystems, lags far behind in related studies conducted on this vegetation. Isolated above-ground determinations of phytomass have been made on mountain fynbos (Kruger 1977; Rutherford 1978; van Wilgen 1980) while van Wilgen & le Maitre (1981) have also calculated some rough above-ground nutrient pools for this veld type.

Despite the ever increasing interest in studies of this nature on mountain fynbos, it very often exhibits a marked structural diversity over short distances owing to variation in the local soil depth and topography (van Wilgen 1980). Consistent phytomass and hence nutrient pool data may thus be difficult to produce for specific ages of mountain fynbos. In addition rockiness in parts makes root extraction virtually impossible.

Coastal fynbos on the other hand occupies sandy flatland with a general homogeneity in topography and often with little variation in the local soil type over large areas (soils tend to be deep and in most cases are podsolized to some extent). It is not uncommon to find stands of ericoid-leaved shrubs and Restionaceae occurring in large homogeneous patches. This veld type (43, Acocks 1975) is being intensively studied at the Fynbos Biome's research site at Pella (Mitchell 1980). Although investigations into the nutrient status of major communities here is a priority, no published data are available (G. Brown, pers. comm.). In fact, basic nutrient data from inter alia fynbos in the western Cape (Low 1980) are scant, to say the least.

Current data (Durand 1981; Low 1980; Low 1981) reveal that fynbos of this region is found on soils which have some of the lowest nutrient levels for world heathlands. However, despite the real need to establish what these nutrient levels are, several studies appear to be aimed primarily at specifics such as soil/plant phosphorus relationships (Brown et al. 1980).
1980; Jongens-Roberts et al. 1980) rather than at producing an inventory of soil and plant nutrient pools. The latter is seen as a fundamental prerequisite to more refined research on nutrient fluxes in fynbos.

The work reported here presents an account of the phytomass and major nutrient pools in a coastal fynbos community on the Cape Flats. It forms part of a larger study into four different ages of this veld type and is aimed at establishing preliminary phytomass and nutrient pool relationships within coastal fynbos and with heathlands elsewhere.

The community under investigation which was adjacent to the suburb of North Pine, Kraaifontein (Figure 1), was sampled during July 1979. It comprised fairly homogeneous 11-year post-fire coastal fynbos (age determined by counting stem growth flushes) dominated by *Phylica cephalantha*, an ericoid-leafed shrub of about 1,1 m tall. Soils were of an oligotrophic nature, acidic and extremely low in nutrients (Table 1).

### Methods

Three random representative plots, each 2 m × 2,5 m in size, were chosen in the 11-year-old coastal fynbos.

(a) Phytomass

(i) Above-ground

Live and dead-standing material was clipped at ground level, the former being sorted into species or family. Litter was collected separately.

(ii) Below-ground

From one of the plots roots were extracted from 150 mm horizons to a depth of 1,80 m. A 3-mm sieve was used for this purpose, three sub-samples of soil being retained from each horizon. Roots were divided into non-fibrous live (lignotuber, tap root, laterals), fibrous and dead fractions.

All plant material was transported to the laboratory, dried at 80 °C to constant mass, and weighed. Soil sub-samples were allowed to air dry.

(b) Analyses

(i) *pH* (Table 1 only) was determined on a combination of 10 g soil and 20 cm³ 1 mol dm⁻³ KCl.

(ii) *Organic matter* was determined from loss on ignition of soil for 8 h at 450 °C.

(iii) *Total nitrogen*. 4 g soil were digested with 7 cm³ conc. sulphuric acid (containing 34 g salicylic acid dm⁻³), 0,5 g sodium thiosulphate powder and selenium as catalyst. An aliquot of the completed digest was steam distilled into 5 cm³ 2% boric acid and back titrated with 0,01 mol dm⁻³ HCl, using Tshiroy's reagent as indicator.

(iv) *Total phosphorus and cations*. 5 g soil were digested with 5 cm³ 60% perchloric acid.

**Determination of elements**

Phosphorus was assayed using a slight modification of the molybdenum blue method described in Anon (1974). Cations were determined by atomic absorption spectrophotometry.

### Results

Phytomass and nutrient pool data appear in Table 2 (above-ground) and Table 3 (below-ground). Above and below-ground, and soil nutrient pool totals are displayed in Table 4. Figure 2 summarizes the nutrient data in histogram form.

Above-ground

Ericoid-leafed shrubs (particularly *Phylica cephalantha* (1317 g m⁻²)) dominated the live phytomass (1458 g m⁻² total) as well as having the highest amounts of nutrients. In the herbaceous fraction, the Restionaceae (*Staberoha* and *Thamnochortus*) were prominent. Nutrient pools were 7,67(N), 0,72(P), 17,47(Ca), 1,09(Mg) and 3,67(K) g m⁻² • Dead mass was 1607% and nutrients were between 507% (K) and 1407% (N) that of the live component. Both live and dead fractions showed similar sequences of nutrient pool sizes (live: Ca > N > K > Mg > P and dead: Ca > N > K > Mg > P).
Table 2 Above-ground phytomass and nutrient content\(^{a}\) in an 11-year post-fire coastal fynbos community

| Species/family                  | Phytomass (g m\(^{-2}\)) | N   | P   | Ca   | Mg   | K    |
|---------------------------------|---------------------------|-----|-----|------|------|------|
| *Phylica cephalantha*           | 1317                      | 6761,1 | 664,3 | 16368,4 | 980,9 | 3174,1 |
| *Leucospermum hypophyllocarpo- dendron* | 14                      | 61,5  | 6,8  | 148,1 | 22,9  | 4,9   |
| *Anthospermum aethiopicum*      | 22                        | 157,3 | 10,1 | 220,8 | 17,8  | 93,6  |
| *Serruruia furcellata*          | 4                         | 15,9  | 1,8  | 56,4  | 4,6   | 24,3  |
| *Erica sp.*                     | 4                         | 22,1  | 1,9  | 53,4  | 2,0   | 8,4   |
| Restionaceae                    | 96                        | 644,2 | 34,7 | 617,2 | 62,6  | 356,9 |
| Cyperaceae                      | 1                         | 9,4   | 0,7  | 10,2  | 1,2   | 5,9   |
| **Total live**                  | 1458 (244)                | 7,67 (1,94) | 0,72 (0,20) | 17,47 (2,73) | 1,09 (0,47) | 3,67 (0,90) |
| Dead standing                   |                           |       |      |       |       |      |
| Shrubs                          | 118                       | 284,7 | 18,7 | 719,9 | 73,7  | 30,1  |
| Restionaceae                    | 79                        | 407,8 | 27,4 | 495,6 | 43,6  | 87,5  |
| **Total dead**                  | 273 (1,08)                | 1,26 (0,35) | 0,08 (0,01) | 1,99 (0,36) | 0,16 (0,03) | 0,18 (0,02) |
| **Total above**                 | 1731 (336)                | 8,93 (1,75) | 0,80 (0,19) | 19,46 (2,42) | 1,25 (0,44) | 3,85 (0,88) |

\(^{a}\)Totals in g m\(^{-2}\) otherwise in mg m\(^{-2}\). Data represent means from phytomass and nutrient contents of material from three plots. Figures in parentheses represent standard deviations.

Below-ground

Amounts of 747 (non-fibrous live), 269 (fibrous) and 381 (dead) g m\(^{-2}\) were recorded for the below-ground phytomass. Total mass was 1397 g m\(^{-2}\) for a soil depth of 1,80 m. Nutrient pools in the different fractions were: 2,86(N), 0,77(P), 7,29(Ca), 0,78(Mg) and 0,91(K) g m\(^{-2}\) (non-fibrous live); 2,35(N), 0,12(P), 2,15(Ca), 0,24(Mg) and 0,48(K) g m\(^{-2}\) (fibrous); and 2,90(N), 0,16(P), 2,73(Ca), 0,22(Mg) and 0,25(K) g m\(^{-2}\) (dead). Nutrient pool sequences followed the pattern of Ca > N > K > Mg > P for both fibrous and dead. The total live fraction (non-fibrous and fibrous — fibrous material was extracted as a mat and not divided further into live or dead fractions although the former was thought to dominate. Dead fibrous roots occurred frequently in the dead root component) represented over two and a half times that of the dead, the latter, however, possessing a large potential nutrient reserve, as is evidenced by the figures in Table 3.

**Soil (0 – 1,80 m depth)**

Organic matter (< 3 mm fraction) content was 11078 g m\(^{-2}\). Nutrient pools were 584,10(N), 24,87(P),

Table 3 Phytomass and nutrient content\(^{a}\) of root fractions in an 11-year post-fire coastal fynbos community. All amounts in g m\(^{-2}\)

| Fraction          | Phytomass | N   | P   | Ca   | Mg   | K    |
|-------------------|-----------|-----|-----|------|------|------|
| Non-fibrous live  | 747       | 2,86| 0,77| 7,29 | 0,78 | 0,91 |
| Fibrous           | 269       | 2,35| 0,12| 2,15 | 0,24 | 0,48 |
| Dead              | 381       | 2,90| 0,16| 2,73 | 0,22 | 0,25 |
| **Total**         | 1397      | 8,11| 1,05| 12,17| 1,24 | 1,64 |

\(^{a}\)Nutrient data for respective fractions combined from 150 mm horizons to a depth of 1,80 m. Material collected from one profile only.
111,99(Ca), 55,25(Mg) and 98,91(K) g m$^{-2}$ (N > Ca > K > Mg > P). As with the plant material totals, P was the lowest while N was more than five times higher than those of Ca or K (Table 4).

**Table 4** Total above and below-ground, and soil phytomass (organic matter) and major nutrient pools for an 11-year post-fire coastal fynbos community. Amounts in g m$^{-2}$. Percentages appear in parentheses

| Phyтомass | N   | P   | Ca  | Mg  | K   |
|-----------|-----|-----|-----|-----|-----|
| Above-ground | 1731 | 8,93 | 0,80 | 19,46 | 1,25 | 3,85 |
| Below-ground | 1397 | 8,11 | 1,05 | 12,17 | 1,24 | 1,64 |
| Soil (0-1,80 m) | 11078$^a$ | 584,10 | 24,87 | 111,99 | 55,25 | 98,91 |
| (97,2) | (93,1) | (78,0) | (95,7) | (94,7) |

$^a$Organic matter content (<3 mm)

**Discussion**

Above-ground phytomass data on the coastal fynbos studied here are comparable with those of similar aged stands of heath found elsewhere (Table 5). A marked exception was found in a 12-year-old stand of mountain fynbos (5583 and 4188 kg ha$^{-1}$) (van Wilgen & le Maitre 1981); lower values here were due to a predominance of herbaceous rather than woody (shrub) species. The other sites, particularly those reported in this paper and the *Calluna* heaths, have ericoid-leaved shrubs as the dominant growth form. It is also noteworthy that all sites possessed (sandy) oligotrophic soils.

However, litter amounts showed a large between-site variation, being by far the greatest in *Calluna* heath (Table 5). This is not unexpected as the latter tends to occur on wet, cold sites where organic matter decomposition would be low.

No breakdown of heath roots into non-fibrous and fibrous has to date been presented and a comparison is therefore not possible at this stage. Total quantities given by Forrest (1971) for an 11,5-year-old *Calluna* stand (11410 kg ha$^{-1}$) are similar to the combined non-fibrous and fibrous (live) component in this study (10160 kg ha$^{-1}$). However, for a sand heath, Groves & Specht (1965) obtained a figure of about 24 000 kg ha$^{-1}$, more than double these levels. Dead material was also far higher in the latter.

Topsoil nutrient pools showed general agreement between different heathland sites (Table 6). This agreement is important as heathland soils are supposedly linked *inter alia* by their low nutrient or oligotrophic characteristics (Specht 1979) and it is of significance that phosphorus is considered to be a major limiting factor in the development of sclerophyll vegetation (Beadle 1954; Beadle 1962). Amounts of P are the lowest in the five major nutrients recorded in Table 6 (16,2 – 37,5 kg ha$^{-1}$). The Blanchland Moor soil was an exception, possessing high topsoil levels of 334 kg ha$^{-1}$ yet displaying only 5 kg ha$^{-1}$ in the aerial mass. Levels of soil P in heathland are, on the whole, some 10 or more times lower when compared with Mediterranean shrublands in California and France (Table 6). Notwithstanding this, the Blanchland Moor soil has a P value which is more typical of these nutrient-rich shrublands, although it supports *Calluna* heath. This apparent anomaly indicates that at least some heaths may be found on soils which have high total amounts of nutrients, yet have low nutrient availabilities. The latter situation can arise through, for example, (irreversible) fixation of a particular element. Low (unpub.) has in addition found P amounts in a coastal fynbos topsoil of some 390 kg ha$^{-1}$.

Levels of N, Mg and K in calcareous chaparral soils were also often comparable with and sometimes lower than those of certain heathlands. Caution should thus be exercised when interpreting the nutrient status of a particular soil based on absolute concentrations or pool sizes.

The two nutrients displaying the greatest range between soils were N and Ca. Amounts of the former are to all intents and purposes independent of geochemical cycling and

**Table 5** Above-ground phytomass data (kg ha$^{-1}$) from selected heathland sites of similar age. Ages of vegetation in parentheses

| South Africa | Britain | Australia |
|--------------|---------|-----------|
| Mountain fynbos from different sites in the | *Calluna* heath | |
| western Cape | | |
| Coastal fynbos, | NE Scotland | SE England |
| this paper | (Miller in | (Chapman in |
| | Gimmingham | Gimmingham |
| | 1972) | 1972; |
| | (Robertson & | Chapman | |
| | Davies 1965) | 1967) | |
| Above, live | 14580(11) | 14500(12) | 13220(11) |
| | 18430(10) | 19206(>10) | 11050(11)$^a$ |
| | 13078(10) | 9820(10) | |
| | 4188(12) | 11152(11) | |
| Litter | 2730(11) | 1815(12) | 14280(12) |
| | | 554(12) | |
| | | | |
| | | 6065(>10) | |
| | | | |
| | | | |
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| | | | |
| | | | |
| | | | |
are subject to input from rainfall or nitrogen-fixation. Variation in the activity of organisms affecting the latter will have a direct bearing on the accumulation of N in the system. This may be the reason for marked discrepancies between, for example, the N content of certain Calluna heath soils (e.g. at Poole Basin — 2210 kg ha⁻¹ (Chapman 1967)) as opposed to that of an Australian heath (750 kg ha⁻¹ (Specht 1969)), despite similar levels in P.

Variation in calcium is generally accounted for by the degree of the calcareous nature of the parent material in question. The heathland soils in Table 6 are all non-calcareous in origin but different levels of this element may depend largely on the extent of leaching of the soil profile. Mg and K levels also show some variability but they are generally lower than those of Ca. Direct comparison of cation pools is also complicated by the fact that some data represent total and others exchangeable amounts of Ca, Mg and K. This reflects a certain weakness or inconsistency in the approaches of many authors in studies of this nature, where data for total N and P but exchangeable Ca, Mg and K are presented. Low (1981, and Table 6) showed exchangeable cation levels to be consistently lower than their total counterparts; at times by a factor of three or more.

Table 6  Topsoil nutrient pools in some heathland and Mediterranean shrubland sites

| Heathland                          | Total (kg ha⁻¹) | N   | P   | Ca  | Mg  | K   |
|------------------------------------|-----------------|-----|-----|-----|-----|-----|
| Soil depth (mm)                    |                 |     |     |     |     |     |
| South-western Cape, South Africa   |                 |     |     |     |     |     |
| 11-year-old coastal fynbos, North Pine (this paper) | 0—150           | 968,2 | 24,6 | 251,8 | 113,9 | 104,8 |
| >10-year-old mountain fynbos,       |                 |     |     |     |     |     |
| Winterhoek Mountains (Low 1981)    | 0—150           | 321 | 20  | 273  | 108  | 60  |
| >20-year-old mountain fynbos,       |                 |     |     |     |     |     |
| Kogelberg, (Durand 1981)           | 0—120           | 720,0 | 16,2 | 10,8 | 36,0 | 25,2 |
| South-west Australia               |                 |     |     |     |     |     |
| 15-year-old heath, Dark Island (Specht et al. 1958) | 0—150 | 499,2 | 13,7 | 475,6 | 87,6 | 26,8 |
| General analysis for heath, Keith (Specht 1969) | 0—250 | 750,0 | 37,5 | 592,0 | 108,0 | 30,0 |
| Britain                            |                 |     |     |     |     |     |
| >10-year-old Calluna heath, Blanchland Moor (Robertson & Davies 1965) | 0—150 | 1991 | 334 | 66 | 19 | 127 |
| 12-year-old Calluna heath, Poole Basin (Chapman 1967) | 0—200 | 2210 | 37 | 229 | 236 | 288 |
| Shrubland                          |                 |     |     |     |     |     |
| California                        |                 |     |     |     |     |     |
| 25-year-old chaparral, Los Padres National Forest De Bano & Conrad 1978) | 0—100 | 1124,7 | 530,5 | 3323,2 | 190,4 | 113,2 |
| 16-year-old chaparral, Sequoia National Park (Rundel & Parsons 1980) | 0—100 | 2220 | 888 | 2699 | 466 | 122 |
| 9-year-old chaparral, San Dimas (Specht 1969) | 0—75 | 2136,6 | 547,5 | 2119,0 | 812,9 | 25,3 |
| France                            |                 |     |     |     |     |     |
| 11-year-old garrigue, Montpellier (Specht 1969) | 0—75 | 4407 | 342 | 3905 | 435 | 236 |

*Exchangeable cations
|1.5 g cm⁻³ | bulk density used in computing data
|1.2 g cm⁻³ | bulk density used in computing data
|Available form

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Table 7  Major nutrient pools in some selected heathland communities of similar ages

| Component | Phyтомass | N | P | Ca | Mg | K |
|-----------|-----------|---|---|----|----|---|
| Above     | 14580     | 76.7 | 7.2 | 174.7 | 10.9 | 36.7 |
| Litter    | 2730      | 12.6 | 0.8 | 19.9  | 2.5  | 1.8 |
| Roots     | 13970     | 81.1 | 10.5 | 121.7 | 12.4 | 16.4 |
| Soil      | 110780b   | 5841.0 | 248.7 | 1119.9 | 552.5 | 989.1 |
| (<1,80 m) |           |     |    |     |     |   |
| Above     | 5583      | 24.40 | 0.79 | 11.01 | 4.42 | 20.33 |
| Litter    | 1815      | 8.71  | 0.27 | 4.99  | 1.00 | 1.00 |
| Roots     | -c        | -    | -   | -    | -    | -   |
| Soil      | -         | -    | -   | -    | -    | -   |
| (<0.76 m) |           |     |    |     |     |   |
| Above     | 4188      | 17.72 | 0.51 | 6.37  | 2.94 | 14.84 |
| Litter    | 554       | 2.66  | 0.08 | 1.22  | 0.30 | 0.30 |
| Roots     | -         | -    | -   | -    | -    | -   |
| Soil      | -         | -    | -   | -    | -    | -   |
| (>0.15 m) |           |     |    |     |     |   |
| Above     | 11115     | 104.8 | 2.7 | 91.4  | 34.6 | 45.7 |
| Litter    | 3088      | 40.8 | 0.9 | 32.1  | 18.5 | 4.9 |
| Roots     | 62796     | 305.7 | 4.4 | 229.5 | 136.8 | 69.2 |
| Soil      | 26365b    | 554.1 | 54.8 | 1025.2e | 258.9 | 98.1 |
| (>0.2 m)  |           |     |    |     |     |   |

a Including dead-standing component
b Soil organic matter
c Not determined or data not available
d Phyтомass and nutrient data interpolated from graphs
e Exchangeable cations

nutrients (with the exception of P) were by far higher in the Australian heath. By contrast the P content was more than double in coastal fynbos.

Recycling of nutrients
Internal recycling or redirection of nutrients from dying tissue is in all likelihood an important if not obligatory means of nutrient conservation in heath vegetation. Differences in major elemental concentrations between live and dead tissue (Table 8) generally show a decrease in the latter, with the exception of Mg (above-ground) and N (below-ground). Large decreases in P as well as in K concentration were found which may be due to recycling of these elements prior to and during the onset of tissue death. The increased Mg concentration is difficult to account for although it may be held the longest in dead tissue; that of N may be due to active free-living nitrogen-fixation in the soil, in the presence of abundant energy sources.

Table 8  Concentrations of major nutrients in live and dead fractions of 11-year post-fire coastal fynbos

|            | N          | P          | Ca          | Mg          | K          |
|------------|------------|------------|-------------|-------------|------------|
| Above      |            |            |             |             |            |
| live       | 5261       | 494        | 11982       | 748         | 2517       |
| dead       | 4615       | 293        | 7289        | 916         | 659        |
| % change   | -12.3      | -40.7      | -39.2       | +22.5       | -73.8      |
| Below      |            |            |             |             |            |
| live       | 5128       | 876        | 9291        | 1003        | 1368       |
| dead       | 7612       | 420        | 7165        | 577         | 656        |
| % change   | +48.4      | -52.1      | -22.8       | -42.5       | -52.0      |
Conclusions
This paper presents the first account of phytomass and major nutrient pools in a coastal fynbos community. Broad similarities with other heathlands were exhibited although certain disparities did exist. In certain cases soil elemental pools, notably N and K ‘overlapped’ with those from the higher nutrient shrublands. Nevertheless, the widely held nutrient-poor (heathland)/nutrient-rich (shrubland) dichotomy was clearly evidenced by the levels of Ca, P and Mg for the two Mediterranean-type soil systems.

A review of the literature showed British Calluna heath to be fairly well documented, while its Australian counterpart relies almost solely on Specht’s earlier Dark Island work Groves 1979). Data on a South African heathland now make intercontinental comparisons of this vegetation type possible on a much broader scale.

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