Karoo vegetation occurs on the extensive flats and plains of the interior of the Cape Province. The vegetation of this hot, low-rainfall area is highly variable. Acocks (1975) distinguishes many Karoo "veld types" with those in the vicinity of fynbos including Karroid Broken Veld, Succulent Karoo, Spekboomveld and Western Mountain Karoo. In the south-western Cape, Karroid Broken Veld is the most extensive of these types and includes the most south-westerly situated karroid part, the Robertson Karoo. Here, the most extensive truly karroid plant community is the often succulent, mosaic of areas dominated by *Pteronia paniculata* and *Euphorbia mauritanica* (Olivier, 1966; Joubert, 1968). Soils in this area often occur on colluvium derived primarily from Bokkeveld shales. Soils are usually shallow sandy loam with clay content increasing with depth, and low pH, except in *Euphorbia mauritanica* clump formations (Joubert, 1968). Stability of this karroid vegetation is seldom affected by fire since it does not sustain fire. The vegetation is, however, commonly utilized often throughout the year mainly by sheep (Joubert, 1968). Highly selective grazing pressure helps to maintain an abundance of succulents and other unpalatable plant individuals. Excessive disturbance may result in increase of species such as *Galenia africana* (Joubert, 1968). After identifying the succulent nature of several pioneers in this type of vegetation in the Worcester Veld Reserve, Olivier (1966) concluded that succulence may be expected to result in a relatively stable community condition.

The transition vegetation typically encountered between karoo and fynbos is *Elytropappus rhinocerotis*-dominated communities or renosterveld (Levyns, 1956) more particularly so-called Mountain Renosterbosveld (Acocks, 1975). This zonation corresponds closely to, for example, the vegetation gradient in parts of California where vegetation of arid lower altitudes, sometimes containing a high proportion of succulents, gives way to sage communities which, in turn, are replaced by chaparral at higher elevations (Mooney, Gulman & Parsons, 1974). There is a close physiognomic similarity between the sage and Renosterbosveld transitions (R. H. Whittaker, personal communication). In a vegetational gradient in the mediterranean-climate area of Chile, Mooney *et al.* (1970) report a sage equivalent present alongside evergreen scrub, while in Israel Naveh (1967) refers to a sage equivalent in "the Batha on the ecotones of the Mediterranean and Irano-Turanian territories". A possible transitional analogue in southern Australia is the Mallee-Broombush vegetation, which is shown to extend between higher rainfall heath areas and a desert margin (Specht, 1966). Mountain Renosterbosveld areas receive higher rainfall than adjacent karoo areas as indicated, for example, in the Robertson Karoo (Joubert, 1968). The Renosterbosveld of the last-mentioned area occurs typically on Bokkeveld phyllite beds with a sometimes relatively deep loamy soil with arable potential, but often underlain by clay (Joubert, 1968). Mountain Renosterbosveld often occurs on south-facing slopes, but in the south-western Cape in areas of high rainfall, it also occurs on north-facing slopes. Thus, in the Robertson Karoo, it has no aspect preference at elevations above about 450 m (Joubert, 1968) and on hills along an increasing rainfall gradient towards the large mountain mass of the Swartberg near Ladismith in the Little Karoo, Renosterbosveld occurs on the south side of some more distant hills, but on the north-facing slope of a hill closer to the main mountain (Levyns, 1950).

Recognition of the natural position of renosterbos communities has been blurred by the apophytic spread of renosterbos (Levyns, 1929a), which has resulted in it becoming one of the most common plants in the Cape Province (Levyns, 1956). In the western Cape, despite the vegetative growth period of renosterbos occurring in late summer (Levyns, 1956), which is atypical relative to that of fynbos, it nevertheless appears certain that Renosterbosveld is a development of fynbos vegetation (Levyns, 1950) and that, particularly in the Mountain Renosterbosveld where renosterbos shows no sign of being an invader (Acocks, 1975), renosterbos may be considered to be naturally dominant. Although fire in Renosterbosveld has often been reported (Mitchell, 1921; Levyns, 1927; 1929a, b; Du Toit & Du Toit, 1938; Van Rensburg, 1962) most of these have been in Coastal Renosterbosveld. Despite the inflammability of renosterbos, in some more open parts of Mountain Renosterbosveld observation shows that burning is often incomplete. Dominance of renosterbos is not reduced by grazing, since the plant is highly unpalatable (Levyns, 1929a), probably because of its aromatic leaves (Marloth, 1908), which corresponds to aromatic plants in the sage of California and its equivalent in Israel (Naveh, 1967). One may conclude that, apart from arable pressures, the lack of many major disturbing effects in the Mountain Renosterbosveld results in various areas of relative stability.

The object of the present study was to investigate biomass differences between the highly distinct vegetational zones from low-lying Karoo through the intermediate renosterbos community to both main variations of fynbos. Information concerning biomass within such a gradient is needed as a first step toward evaluating, in terms such as those given for Arizona by Whittaker & Niering (1975), the functional differences associated with these elevational gradients. For proper comparison of data, relatively stable areas were considered.

STUDY AREA

A suitable area, with the vegetational gradient described above was located on the north-facing slopes of the Riviersonderend Mountains, south of the town of Worcester in the Robertson Karoo. Here the Worcester Fault has resulted in a roughly 1 200 m height difference from the base of the mountain to the summit of Jonaskop Peak, which is 1 646 m above sea level at co-ordinates 19° 30′ E, 33° 58′ S. The equatorial aspect results in a higher shortwave energy load than that of the polar aspect (Holland & Steyn, 1975), which is reflected in higher potential evapotranspiration and occurrence of generally more xeric plant communities on the north-facing slopes. In contrast to the steep south-facing slope, the north slope consists of a generally gradual rise with relatively few rock precipices. Sample sites on this slope all varied between 5° and 15° slope. Strong winds are not infrequent and rain falls in winter.

The site selected for sampling low fynbos was situated near the summit of the mountain at about 1 520 m above sea level and consisted of a mature restionaceous community with *Elegia* sp. cf. *E. grandis*, *Tetraria involucrata* and *Restio* spp. as dominants with occasional *Thamnochortus* sp. and *Metalasia muricata*. Community height was approximately 80 cm with about 30 % surface sandstone.

The site selected for tall fynbos was at about 910 m above sea level and was dominated by a fairly dense stand of *Protea laurifolia* individuals about 1,5–2,5 m high with a lower layer of *Chondropetalum*, *Restio*, *Thamnochortus* and *Erica* species with some *Elytropappus gnaphaloides* and *Phaenocoma prolifera*. The area had not been burned for several years as evidenced by presence of some moribund Restionaceae tufts and several *Protea* individuals at least 14 years old (estimated by node counts using method of Van der Merwe, 1969). However, a proportion of *Protea* individuals was much younger, possibly indicating that the community was not yet in a complete stable state. Ground cover included up to 50% surface pebbles and occasional rock outcrops.

The north-facing Renosterbos Community site was situated about 560 m above sea level with virtually no surface rock. Community height was between 70–80 cm and was dominated by mature *Elytropappus rhinocerotis* and *Relhania genistaefolia.* Other more important species were *Pteronia incana, Anthospermum tricostatum, Montinia caryophyllacea* and isolated *Dodonaea viscosa.* Herbaceous species included *Polygala affinis, Hyobanche sanguinea, Oxalis eckloniana* and *Ursinia anthemoides.*

The Succulent Karoo Community site was situated in a shallow valley in between the foothills of the mountain at about 390 m above sea level. There was no rock cover and, although some soil erosion was present in the vicinity, this was not so in the area sampled. The 30–40 m high community was dominated by *Pteronia paniculata, Delosperma* sp. and *Euphorbia mauritanica.* Also present were *Drosanthemum* spp., *Galenia africana, Cotula zeyheri, Crassula* sp. cf. *acutifolia, Pteronia incana* and *Senecio radicans.* A few rare but characteristic emergents that did not fall within the sample quadrats included *Cotyledon paniculata, Euclea undulata, Lycium oxycarpum, Eriocephalus ericoides* and *Aloe microstigma.* This community corresponds closest to the *Pteronia paniculata* Community of Joubert (1968) and Olivi r (1966) with some lesser affinities to their *Euphorbia mauritanica* Community.

METHOD

Biomass was determined in late August using a harvest method with randomly placed square quadrats. Sampling intensity is given in Table 1 for each of the four communities. Clipping level was as close to the ground as possible. Live and dead individuals were clipped separately and live individuals were sorted into: (i) the single dominant species (if present); (ii) all other shrubs; (iii) graminoids* (hemicryptophytes), that is all Restionaceae, Cyperaceae and Gramineae and (iv) other herbaceous species. Besides weighing each clipping to the nearest 0,05 kg, subsamples from well mixed clippings of each category from each quadrat were weighed in the field to nearest 0,01 g, and later oven dried at 85°C to constant mass to convert all wet mass data to dry mass. A pocket calculator was employed during clipping to determine at what stage the 95% confidence limits fell below ±20% of the mean wet mass for each community. However, when later recalculated on a dry-mass basis, in three of the four communities, this percentage rose above ±20% of the mean (see Table 1). In the *Protea laurifolia* Community the mass (kg) of the *Protea* individuals was obtained using a sample area greater than the 52 m^2 used for the rest of the community. Measurement of stem diameter (cm) and individual height (cm) were made in a block with area of 750 m^2 and the allometric relationship given below Table 1 was applied. Assessment of comparative results of biomass obtained from quadrat clipping and from allometric relation in this community is not further considered here.

* Graminoids here include both Kruger's (1977) graminoid and restioid categories.

TABLE 1.—Above-ground plant biomass, mass and other statistics for each community

Community	Restionaceous	*Protea laurifolia*	*Elytropappus rhinocerotis*	Succulent Karoo
Elevation ... m	1520	910	560	390
Approx. mean annual rainfall ... mm	1200	800	500	300
Total sample size ... m^2	81	52	36	48
Quadrat size ... m^2	9	4	4	4
Total biomass ... kg ha^{-1}	14311	11064	11253	7564
Standard deviation ...	3006	2077†	3093	2780
Standard error ...	1002	576†	1030	803
95% confidence limits (±) ... kg ha^{-1}	2311	1255†	2375	1766
Percentage 95% confidence limits (±) ...	16,1	27,7†	21,1	23,4
Biomass of single dominant species ... kg ha^{-1}	—	6544*	5900	—
Biomass shrubs (remainder) ... kg ha^{-1}	347	1050	5275	7560
Biomass Graminoid ... kg ha^{-1}	13949	3470	47	0
Biomass herbaceous (remainder) ... kg ha^{-1}	14	5	22	4
Mass dead individuals ... kg ha^{-1}	199	358	2760	4063
Total mass ... kg ha^{-1}	14510	11422	14015	11627

†=for non-*Protea* biomass.
*=from larger sample, using ln (dry mass) = $-2{,}47+0{,}93$ [ln (diameter)^2 (height)]

RESULTS

Results are summarized in Table 1. In the Restionaceous Community, the graminoid group made up 97,5% of the total biomass of 14311 kg ha^{-1}, while dead individuals constituted only 1,4% of total plant mass. In the *Protea laurifolia* Community, *P. laurifolia* constituted 59,1% of the total biomass of 11064 kg ha^{-1}, while the graminoid group was 35,0% of this amount. Dead individuals made up 3,5% of total plant mass. In the Renosterbos Community, *Elytropappus rhinocerotis* constituted 52,5%, other shrubs 46,9% and graminoids 0,4% of the total biomass of 11253 kg ha^{-1}. Dead individuals made up 19,7% of total plant mass. In the Succulent Karoo Community, the graminoid group was, to the nearest first decimal place, 0,0% of the total biomass of 7560 kg ha^{-1}. Dead individuals made up 35,0% of total plant mass. Total biomass of the Succulent Karoo Community was significantly lower (P=0,001) than that of the Restionaceous Community and significantly lower (P=0,1) than that of the Renostersbos Community. There was a progressive decrease in percentage biomass of graminoids with decreasing elevation (Fig. 1) and a progressive increase in percentage dead material mass with decreasing elevation (Fig. 2).

DISCUSSION AND CONCLUSIONS

Results suggest that there is a tendency for biomass to decrease from summit fynbos to basal Karoo vegetation and, assuming some generally positive relation between biomass and production in these specific communities, this decrease probably holds for overall production. Although microtopographic effects often result in decreased production with increasing elevation (Rickard, 1975), more pronounced elevational differences (below alpine limits) usually produce the reverse. Thus, Whittaker & Niering (1975) found that aboveground biomass and production rates both increased with increasing elevation from desert to summit of an Arizonan mountain. The major orographic effect of a mountain mass in increasing precipitation with altitude is probably the main variable affecting biomass and production along an elevational gradient although Whittaker & Niering (1975) caution that elevation is only a crude expression of probable moisture relationships. Nevertheless, work on moisture relations as a function of elevation includes, for example, findings that the severity of water stress induced by low soil temperatures is inversely related to elevation of some plant species habitats (Anderson & McNaughton, 1973).

From approximate relations between fynbos biomass and age since the last fire (Kruger, 1977), it appears that the Restionaceous Community with biomass of about 14000 kg ha^{-1} should be at least 10–15 years old and that the *Protea laurifolia* Community with biomass of about 11000 kg ha^{-1} should be at least 10 years old, which confirms the earlier estimate. The biomass of the Restionaceous Community falls within the biomass range given for a 16-year old fynbos heath community at Jakkalsrivier near Grabouw (Kruger, 1977), but that of the *Protea laurifolia* Community falls below the range for 10– and 17– year old north-facing mesophyllous evergreen sclerophyll scrub at Jonkershoek near Stellenbosch (Kruger, 1977). This lower biomass may relate to the greater aridity of the *Protea laurifolia* site relative to the Jonkershoek area. The biomass value of the *Protea laurifolia* Community is, notwithstanding, roughly of the same order as the 9000 kg ha^{-1} for 9-year old chamise chaparral in California (Specht, 1969), the approximately 9000 kg ha^{-1} for mediterranean garrigue (Long, quoted Specht, 1969), and the

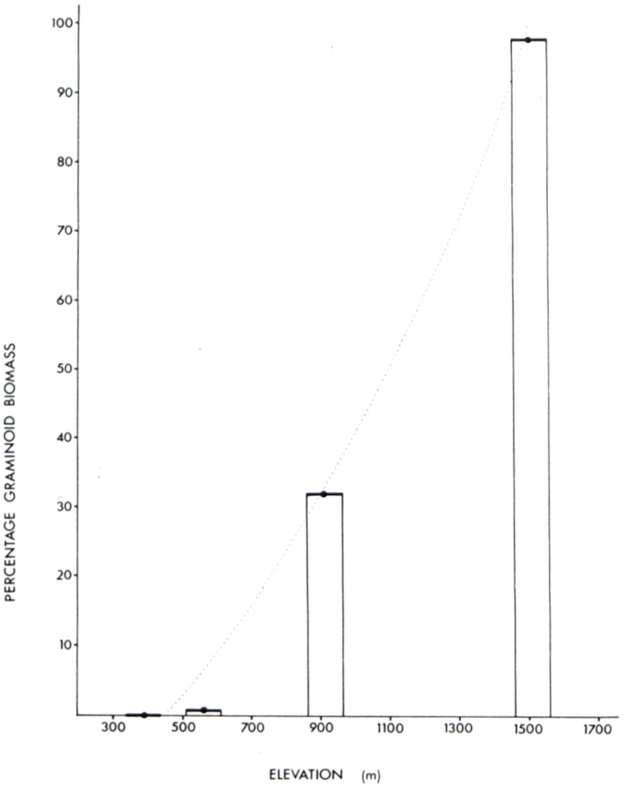

FIG. 1.—Relationship between elevation and percentage graminoid biomass with $y = -17,16 + 0,022x + 0,000036x^2$

between 11000 and 12000 kg ha^{-1} for roughly 10-year old mediterranean-type communities in Victoria, Australia (Jones, Groves & Specht, 1969). The Renosterbos Community biomass of 11000 kg ha^{-1} corresponds to the 9000 to 10000 kg ha^{-1} for 12-year old Australian Mallee-Broombush Community (Specht, 1966). Despite the much lower community height of renosterbosveld, its biomass is as great as that of the tall fynbos *Protea laurifolia* Community.

One of the important and characteristic components of fynbos vegetation is the graminoid component dominated by members of the Restionaceae and Cyperaceae (Werger, Kruger & Taylor, 1972). Kruger (1977) has referred to the reduced presence of this component in northern hemisphere mediteranean vegetation areas, with Australian sclerophyll vegetation having more in common with fynbos in this respect.

The percentage graminoid mass in both low and tall fynbos communities fell outside the 37–82% range for the fynbos communities described by Kruger (1977). The findings from the summit Restionaceous Community did not conform to the expectation that in suitable areas (Kruger, 1977) after four years of growth, the percentage of graminoid mass should drop progressively below the 60–75% level, since summit conditions do not appear to permit significant development of woody elements. Thus, the 97% of graminoid mass determined in the summit Restionaceous Community compares, for example, to an average of only 55% in microphyllous evergreen dwarf shrub with similar total biomass near Grabouw. The much lower 35% of graminoid mass in the *Protea laurifolia* Community conforms to the above-mentioned expectation, although lower than percentages obtained in any of the Grabouw-Stellenbosch fynbos communities sampled (Kruger, 1977), but is relatively close to the 32–28% of Restionaceae and Cypera-