# ALPINE PHYTOMASS AND PRIMARY PRODUCTIVITY IN CENTRAL OTAGO, NEW ZEALAND

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SUMMARY: Phytomass was measured and net potential productivity estimated for normal climatic conditions on the Otago rainshadow mountains. Seven tall snow tussock grasslands were compared with lower-statured cushion, herbfield and short grassland communities. Total phytomass ranged from *c.* 5-9 Kg $m^{-2}$ (22 000-40000 Kcal $m^{-2}$) in tall tussock and *c.* 2-4 Kg $m^{-2}$ (8100-16500 Kcal $m^{-2}$) in cushion, herbfield or short grassland vegetation. Root: shoot ratios of less than unity, in all communities, probably reflect the oceanic nature of the climate.

Total annual potential net production ranges from c. 0.7-1.0 Kg $m^{-2}$ (3200-4600 Kcal $m^{-2}$) in tall tussock, and *c.* 0.4-0.7 Kg m-2 (1700-3400 Kcal m-2) in cushion or herbfield and is 1.0 Kg $m^{-2}$ (4200 Kcal $m^{-2}$) in an induced mid-altitude *Poa colensoi* turf grassland. Growing season efficiency ratings (0.5-1.2%) tend to increase with altitude, suggesting an adaptation to the short, climatically erratic summers. The *c.* 150-200 day growing seasons are nevertheless considerably longer than for continental tundras abroad. Turnover times are typically *c.* 11 years, but may be up to 20 years at high altitudes. Growth is suppressed, presumably by cool. short growing seasons at high altitudes and perhaps by soil moisture stress at the base of the alpine zone.

The Otago alpine cushion and herbfield communities achieve phytomass and productivity values within the range for world tundras. The larger values for tall tussock stands are, however, not unusual when compared with other natural large-statured herbaceous or shrub vegetation types.

## INTRODUCTION

Knowledge of energy flows and material cycles is fundamental to predictive ecosystem modelling-perhaps the ultimate ecological objective. With the logical succession from individualistic research in biology to the multi-disciplinary cooperative approach (Whittaker and Woodwell, 1969; Coupland *et al.,* 1974; Wielgolaski, 1975b; Numata, 1975; Bliss, 1977; and others involved in the International Biological Programme-IBP) systems ecology has become a reality. New Zealand ecologists have, however, been slow to embark on such integrated analyses (cf. Lieth and Whittaker, 1975; Reichle *et al.,* 1975) despite earlier hopes that this country would participate in the IBP (Egunjobi, 1969).

This paper sets out to stimulate interest in the development and application of techniques for modelling the dynamics of New Zealand's unique, and often threatened, ecosystems by debating some theoretical questions relating to critical productivity analysis, and by furnishing examples of basic ecosystem information from the Otago alpine zone. The inappropriateness of traditional harvest methods (Milner and Hughes, 1968) to measuring productivity in New Zealand's large-statured, evergreen, herbaceous communities, was a hindrance that at least prevented perpetuation of the serious errors inherent in the technique. Latterly, productivity of indigenous communities has been estimated by extrapolation from the measured growth of individual shoots or tillers (Wraight, 1965; Bliss and Mark, 1974; Evans *in* White, 1974; Williams, 1977; this study). Elsewhere, ingenious attempts have been made to rectify the under-estimates attributable to *in situ* death and degradation of plant parts that occur simultaneously with growth, and also to growth that continues after peak biomass has been attained. Wiegert and Evans (1964), Lomnicki *et al.* (1968) and Bradbury and Hofstra (1976) used paired plots to separate the growth and degradation processes; Coupland (1973) corrected productivity estimates by using increases of ash concentration in dead leaves as an inverse measure of carbohydrate losses; Williamson (1976) applied leaf turnover times in the correction of harvest data, and Wielgolaski (1975a, b) made adjustments appropriate to his interpretation of tundra flow diagrams, confirmed by direct photosynthetic assimilation measurements. In most of these examples corrected production was at least double that inferred from the raw harvest data.

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Theoretical considerations concerning some of these methods are discussed later.

My usage of terms and their definitions are detailed below. In general, they follow Macfadyen (1948), Westlake (1963), Newbould (1967), Egunjobi (1969) and Milner and Hughes (1968).

*Biomass:* total dry weight of organic matter (aerial and subterranean) per unit area of an ecosystem at a given time (usually mid-summer). Phytomass' is plant biomass and total phytomass comprises root and shoot values. No distinction is made here between biomass (as living matter) and standing crop (to include dead matter) due to the virtual impossibility of separating these components (e.g., xylem elements in wood and cell walls from protoplasts). Phytomass is divided into three broad categories: 'live' (used synonomously with 'green' foliage, although living leaf sheaths are not green); 'dead' (refers only to material organically attached to living plants); and 'litter' (detached material). Litter may be further divided into standing litter, if it is trapped in the tussock crown, and ground litter if it lies between the tussock bases. Unless otherwise stated, 'litter', in this paper, will refer to standing litter. Ground litter theoretically encompasses all soil humic matter, but this makes a significant contribution only in peaty soils.

*Bioenergy:* total energy content of the biomass, or (if phytoenergy) of plants.

*Gross Primary Production* (G *PP):* total, theoretical, dry weight equivalent of organic matter produced in a given time from the photosynthetic fixation of carbon, per unit area.

*Net Primary Production (NPP):* GPP minus respiratory losses of the producers, or the total amount of dry weight available to higher trophic levels (including decomposers) and to the processes of photo-oxidation and leaching. This definition is broader than existing concepts and warrants further debate. Total NPP comprises root plus shoot production. Potential production is point production at a vegetated spot, scaled up to a square metre. This assumes the same point productivity in discontinuous vegetation (e.g., a fellfield) and in its anticipated derivative climax cover (continuous sward). The assumption may not always be warranted, as in arid zones where the continuity of root systems will define the climax condition.

FIGURE 1. *Location map of the study area showing the positions of The Remarkables (R), the Old Man Range (0) and the Rock and Pillar Range (RP), in relation to the Otago/Southland rainshadow (unhatched area). Alpine regions, above the 1000 m contour, are stippled.*

Dead and litter production denote the transfer of tissues, energy and minerals from the 'live' compartment to dead attached and thence to the detached (litter) compartments respectively. Root and rhizome 'production' refers to the weight increments of these compartments as beneficiaries of primary production. This transfer sense of production has a precedent in the concept of secondary production.

*Yield:* NPP minus losses from photo-oxidation, leaching and other 'invisible' degradation processes. This is generally the harvestable production that is also theoretically available to herbivores. This is a very imprecise term.

*Productivity:* rate of production. Production has been used to connote both phytomass and phyto-energy increments, although Macfadyen (1948) proposed the term 'activity' to describe the overall power of an ecosystem to utilise the sun's energy. This 'activity' consisted of the sum of energy flows, in a given time, for all trophic levels. Here I shall use the terms:

*Gross Energy Fixation (GEF):* energy equivalent to GPP.

*Net Energy Fixation (NEF):* energy equivalent to NPP.

According to these definitions, yield rather than NPP has been the quantity measured in most production studies and consequently global estimates of production, collated from these sources, are likely to be somewhat low.

FIGURE 2. *Co-dominant* Chionochloa rigida *(background. taller) and* C. macra *(shorter) tussocks of the* 13: 0: MR *upper low-alpine. tall snow tussock grassland. In the middle-ground are recently burnt tussocks and locally dominant intertussock. short grassland/ herbfield* (/3: 0: PH, *Table* 6). *Date: May,* 1972.

## STUDY AREA

### *Vegetation and climatic zones*

This work was part of a phyto-ecological study carried out in the rainshadow tundra biome of Otago/Southland (Fig. I). The occurrence of slim snow grass *(Chionochloa macra* Zotov) in the high-alpine zone is a distinguishing feature of these rainshadow mountains. The low-alpine zone may be characterized by the actual or potential presence of the nanophanerophyte life form which, in this geo-climatic region, is mostly associated with, or replaced by, tussocks of narrow-leaved snow grass *(Chionochloa rigida)*. However, where the high-country has been burnt and / or heavily grazed the original cover may be drastically depleted.

FIGURE 3. *High-alpine* C. macra *tall snow tussock grassland (fore-ground) at 10:*R*:*M, *grading back into a mosaic of (possibly) induced tall tussock / short grassland / herbfield / cushion-fellfield. Site 20:*R:P *is* < *100 m above this point. where snow tussock is more sparse and bare rock predominant. Date: April,* 1972.

Sites were studied on the Rock and Pillar Range, Old Man Range and The Remarkables of Central Otago (Fig. I). Stands were chosen to reflect, as far as possible, 'natural' or potential tussock grassland phytomass and productivity patterns across the alpine spectrum: specifically, from the base of the low-alpine zone (9:O:*R,* 10:RP:*R)*,* from data supplied by A. F. Mark; the low-alpine/high-alpine transition (13:O:*MR,* 13:RP:*M,* 14:RP:*M);* and from the high-alpine zone (16:O:*M* , 19:R:*M).* In addition, seral or intrazonal† communities *(*12:RP*:H.* 12:RP:*C,* 14*:*RP*:H.* 14:RP:*C*), from Bliss and Mark (1974), and 20:R:*P,* together with a secondary successional short (turf) grassland

(13:O:*P)* were contrasted with the nearby zonal[†] tall tussock communities. Examples of these communities are illustrated in Figures 2, 3 and 4. Site 20:R:*P* is a less continuous stand than shown in Figure 4 and sites 13:RP:*M* and 14:RP:*M* are small relict patches of tussock in an expanse of herbfield. Site 9:O:*R* is illustrated in March (1965a, p. 75) and 10:RP:*R* in Mark and Rowley (1976, p.61).

FIGURE 4. *Upper low-alpine. induced short (turf) grassland of* Poa colensoi *with relict* C. rigida *tussocks* (13:*0* P). *Date: March,* 1973.

*The environment*

Climatic and physical characteristics of all sites are summarized in Table 1. All climatic parameters were standardized, where possible, to reflect 1941-70 Normals. Equilibrium (i.e., *c*. actual) evapotranspiration was calculated using the Priestly and Taylor (1972) combination model.

Although growing seasons are generally a month shorter than the quoted snow-free season, growth commences almost immediately the snow recedes. Extreme temperatures, >20°C either side of the annual means, may be expected occasionally.

All sites were on moderate (<20°) north-facing slopes, except 9:O:*R* and 16:O:*M*, with south-east and flat aspects, respectively. The soils are high country to alpine yellow-brown earths (Bliss and Mark, 1974; Molloy and Blakemore, 1974), tending to podzols in the west. Some cushion and herbfield sites have eroded or skeletal soils (Bliss and Mark, 1974).

## METHODS

### *General*

Tussock sites were chosen from closed stands of apparently uniform composition in order to permit measurement of potential productivity in near-climax vegetation, minimize heterogeneity of the data and reduce the amount of production attributable to inter-tussock species (estimated using herbfield data from other sites). The stands chosen had been free from fire for at least 20 years, but were subject to light grazing by sheep and hares up to the commencement of this investigation. Moderate grazing alone is not detrimental to snowgrass (Mark, 1965c) and stocking rates are now relatively low *(c*. 0.2 sheep ha$^{-1}$, Otago Catchment Board Records) over much of the range of the more vulnerable C. *macra*.

The *Poa colensoi* swards were selected from extensive, more or less pure, stands (discontinuous patches in the case of 20: R:*P)*.

Tussock tillers (intravaginally-branching leafy shoots) were used as the basic unit of standing crop and production, and the number of these per unit area was determined by random sampling for tussock density (using 4 m$^2$ quadrats) and tiller number per tussock. The variable sample sizes are indicated in the Tables.

At 9:O:*R* and 13:O:*MR* two tussock classes (mature and immature) were recognised on basal diameter criteria, the cut-off diameters being *c*. 20 cm for *C. macra* and *c*. 35 cm for *C. rigida*.

### *Phytomass and phytoenergy*

Random collections of tillers were made during mid to late summer. Three age-size classes-primary, secondary and small tillers (Table 2, Figure 5 and see Results) - were recognised, and each was divided into dead attached leaf, standing litter, 'green' or live leaf, stem and inflorescence. These components were oven-dried at *c*. 90°C and weighed. Triplicate samples were ground in a Casella mill (1 mm mesh), pelletised and their ash-inclusive caloric content measured in a Gallenkamp ballistic bomb calorimeter.

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[*] Site notations: Number indicates altitude (m x $10^2$), middle letter(s) is an abbreviation for the mountain range (O = Old Man, RP = Rock and Pillar, R = Remarkables) and the last letter combination designates the dominant species / growth form / community. (*M* = *C . macra* tall tussock grassland, *R* = *C. rigida* tall tussock grassland, MR = co-dominant, H = herbfjeld, C = cushion/fellfield, *P* = *Poa colensoi* short grassland). The 20:R:*P* population represents a distinct entity with rigid pungent leaves *(Poa* cf. *acicularifolia).*

[†] Zonality is used here in the soil classification sense where a zonal soil-vegetation system is the climax development on a mesic 'normally' drained and exposed site, whereas intrazonal systems may develop on poorly-drained or excessively-exposed sites e.g., 12: RP:*C*.

Root samples were washed from triplicate soil blocks (*c*. 0.1 m3) excavated from profiles under: a) tussock centres, b) overhanging canopies and c) open inter-tussock zones. The proportions of these three categories were determined from random point intercepts along transects. Inter-tussock shoot and litter material was also harvested from blocks (b) and (c).

FIGURE 5a. *Relationships of small (st) and secondary (s) tillers to primary (P) tillers of* C. rigida. *The three primary tillers shown, have, from left to right, progressively older (young) tillers in the axils of their mature (outside) leaves (M). The left hand primary tiller supports a 'small tiller' (see Figure 5b) and the centre and right hand primary tillers support younger and older 'secondary tillers' respectively, with increasingly separated flexible leaf blades. The height of the primary tillers is* c. *70 cm.*

Aerial phytomass (ash-inclusive) was calculated by multiplying the densities of the three tiller classes by their various component weight contributions, with the addition of an estimate of inter-tussock phytomass based on percent cover and harvest data. Root biomass (live plus dead, ash-inclusive) was calculated from the average amounts in each of the three vegetation/soil profile categories, weighted according to the cover contribution of each. Where sampling did not penetrate to the base of the soil profile, extrapolated values were determined from log-normal regressions. A similar procedure was used for *P. colensoi* turfs, except that tiller density was measured directly from counts within 5 x 5 cm quadrats. Only a single tiller class was recognised.

Phytoenergy is the sum of the products of the phytomass components and their respective energy contents.

FIGURE 5b. *Close-up view (of left hand example in Figure 5a) of an axillary 'small tiller' (st) showing its non-separated leaf blades and its characteristic basal sheathing leaves.* M = *split mature leaf of primary tiller.*

*Production*

Three replicate primary tillers from each of 10 tussocks were chosen at each site for measurement. Subsequent random sampling showed that only 13:RP:*M* and 14:RP:*M* experimental tillers departed in size significantly from the 'true' population means. Mature leaves of the 30 tillers from these two sites were respectively 32 % and 22 % shorter ($p < 0.01$) than the random samples. The establishment of inter-seasonal growth differences should not, however, be affected by the non-random sampling; this is an advantage of the non-destructive technique. In the case of the *P. colensoi* sites a total of 20 tillers was measured from several turfs.

Elongation and die back of leaves in primary tillers, and in their associated secondary tillers, were measured for all leaves of a tiller, in the manner described by Mark (1965a). Length reductions in dead leaves were assigned to the litter category and dead tips of growing leaves that appeared ready to fall were measured, cut off and similarly assigned. Occasional unknown losses of leaf material from live shoots would result in small underestimates of both primary and litter production.

Emergence and elongation of small tillers and inflorescences were likewise recorded *(loc. cit.)*. Measurements were made three or more times through the growing season.

Length and number increments were converted to dry weight equivalents by the use of appropriate weight-to-length ratios determined from the random biomass samples (see next section and Tables 2, 3).

The aerial production equation for each primary tiller unit and its complement of secondary and small tillers, weighted in proportion to their respective field densities, is:

$$P_A = l_1.G_1.d_1 + l_2 G_2.d_2 + s.S.d_0 + f.F.d_4 + n.I.d_1$$

$P_A$ = aerial production in a given time; $l_1$ = sum of all leaf elongation in a primary tiller; $l_2$ = the same for a secondary tiller; s = small tiller elongation; f = inflorescence elongation; $G_1$, $G_2$, S and F = the corresponding live, dry, weight-to-length ratios; n = number of emergent new leaves; I = mean weight per stem internode; $d_1$-$d_4$ = corresponding organ densities (Tables 4,6).

*Theoretical basis for weight-to-length factor*

To allow for the foliage degradation that occurs simultaneously with growth, and for the weight increase that continues after leaf extension has ceased, elongation of leaves was multiplied by a theoretically derived, live weight-to-length ratio. Leaf tissue density declines after death for complex, and as yet unexplained, reasons (see Coupland, 1973), but translocation, leaching, photo-oxidation, biological decay and physical attrition may be involved. Furthermore, sheath weight increases after leaf elongation has ceased. Thus, it is not sufficient simply to multiply length increments and weight-to-length ratios separately for leaves of different ages. Without greater understanding of the processes involved, valid weight increases can only be incorporated in the formula by summing the increments of all leaves in a tiller and multiplying the sum by an average weight-to-length ratio of an entire reconstructed live leaf (Figure 6, Table 2). Here, weight losses are automatically compensated for by this live leaf ratio, undiminished by dieback and incorporating the

FIGURE 6. *Live leaf segments (hatched) taken from different-aged leaves in the reconstruction of a hypothetical whole leaf. Leaf widths of contiguous segments are matched in the construction. The discarded live parts are stippled and dead parts (used for the reconstruction of dead leaves) are shown plain.*

weight of mature sheath tissue in correct proportion. Essentially, the effect is the same as recording the number of new leaves that emerge in a given time and assuming that, on average, each represents the recruitment of biomass equivalent to the weight of an entire living leaf. Recording the weight increments as the leaves grow merely improves estimation of the seasonal apportionment of production, but because of the averaging effect of the composite ratio some precision is lost when considering short time periods.

The assumption here is that leaf death implies and follows disruption of phloem and xylem streams and that any free sugars trapped in the isolated dead part of the leaf at this instant are broken down *in situ* or leached out, together with some structural materials, resulting in a weight reduction (Figure 7). The cessation of photosynthesis would further reduce impetus for downward movement of photosynthate, but if it does move out of dead leaves to be recorded as part of the live leaf (or stem) weight, then weight-to-length ratios used here will be exaggerated by a corresponding amount (Figure 7). Chapman (1976) stated that 'as leaves senesce and die considerable amounts of material are translocated to other parts of the plant before they fall as litter'. However, although weight reduction of the order of 20% is commonly found in dead standing leaves *(loc. cit.)* there is no proof that the losses are due to translocation. In fact, Coupland (1973) reported that $C^{14}$ in green leaves of *Agropyron* spp. is almost entirely lost to the dead compartment in one season, whereas in *C. rigida* and *C. macra* it takes about 14 months (Payton, 1976). In view of the 2.6-3.2 years life of snow tussock leaves, these results suggest that little re-distribution of photosynthate occurs in leaves after initial assimilation and immediate transport. I have shown, by growing single tillers in pots at one field site (13:O:*MR),* that leaf dieback losses can account for only 20 % of stem plus root production.

FIGURE 7. *Status of a hypothetical live plant compartment (e.g., a leaf) at two harvest or measuring times. If weight loss, associated with die back, is transferred to production of new tissue, then a full 'translocation model' is appropriate, with no adjustment to harvestable production (i.e., yield) required. A full* 'in situ *degradation model' requires the type of analysis employed in this study. Reality may lie somewhere between these extremes.*

Furthermore, Zlotin (in Coupland, 1973) claimed that photochemical processes, in the absence of organisms, account for up to 75% of weight loss in the early stages of shoot degradation. Until further evidence comes to hand, persistence with the described method seems to be justified. However, the dieback losses are presented so that they may be subtracted from my production results if more caution is desired.

It is important to consider that if this working assumption is valid then non-destructive simulated harvests (i.e., periodic measurement of components and the subsequent budgeting of the changes and transferences of their weight equivalents-e.g., Wielgolaski, 1975b) may still slightly underestimate net production. Similarly, allowance for litter disappearance (Wiegert and Evans, 1964; Lomnicki *et al.,* 1968; or Milner and Hughes, 1968) may only provide part of the solution by not considering the changes that occur in standing leaves. Conversely, rejection of my hypothesis will require transformation of my results as suggested above.

*Dead material and litter*

Production of dead material is determined from the general formulae:

$$(1-g).\,D \text{ and } mf.\,DF$$

where g = increment of live or green leaf length; D = weight-to-length ratio of reconstructed whole dead leaf; mf = culm length at the end of summer; DF = weight-to-length ratio of dead inflorescence (Tables 2, 3).

When $g>1$ or $1<0$ then a (minimum) value can be ascribed to dead production (but only if $g \leq 0$) using the form: $g.\,D$.

Minimum litter production is calculated from positive solution of the functions: $(g-1).\,D$ and $-mf.Df$

*Roots*

Measurement of root production is still one of the most intractable problems in ecosystem dynamics. Four theoretical (Chapman, 1976) and two empirical approaches were considered:

(a) $$\text{root production} = \frac{\text{maximum root biomass}}{\text{turnover time}}$$

Turnover time is derived from the monomolecular decay curve using an instantaneous fractional loss rate based on decomposition studies.

(b) annual loss of roots $\simeq$ annual root production = $\frac{\text{root biomass}}{\text{life of roots}}$

Root life is here assumed to be *c*. 3 years, the same as for leaves.

(c) $\frac{\text{shoot production}}{\text{shoot biomass}} = K \times \frac{\text{root production}}{\text{root biomass}}$

'K' is taken to equal one, without contrary evidence available.

(d) $\frac{\text{shoot production}}{\text{living shoot biomass}} = K \times \frac{\text{root production}}{\text{living root biomass}}$

Live roots are assumed to make up 60 % of the total.

(e) $\frac{\text{root production}}{\text{root biomass}}$ = 17%. (Bliss and Mark, 1974).

(f) Isolated tillers were grown in flats and pots, set in the ground at some field sites, to gain an impression of the potential root growth of a primary shoot. At the main experimental site (13:O:*MR)* local field soil was used. Estimates were made of the relationship between root growth in isolated and tussock-bound tillers, based on the observation that root: shoot ratios increased to a plateau as equilibrium conditions were approached, and that this trend was an inverse reflection of relative root and shoot production.

The mean of the various estimates available for each site was taken to be root production for the purposes of this work. The coefficients of variation of the site means were *c*. 50%.

### *Decomposition*

Individually-labelled replicates of fresh, mixed, dead leaf material were pinned to the ground surface and field samples of mixed roots were buried (10 cm) in 1 mm mesh nylon bags at three sites (14:RP:*M*, 10:RP*:R,* 14:O*:MR)* in order to measure decomposition rates over one year. The root and leaf materials for the experiment were collected from each of the *Chionochloa* species present at the three sites, weighed, and restored to their origins as described. The differences between species at 13 :O: *MR* and between decomposition rates at 13:O:*MR* and 14:RP:*M* were not significant so the results have been lumped. Estimates of decomposition were doubled, based on the observation (Biederbeck *et al.,* 1974) that weight of micro-organisms could result in this much error. Instantaneous fractional decay rates (k) were determined from the expression:

$$k = \log_e . (1-k')$$

where k' = annual fractional loss of weight.

### *Net energy fixation (NEF)*

NEF was calculated by summing the energy equivalents of the phytomass increments for each of the tiller components (foliage, using green leaf phytoenergy, stems, roots). Energy values for dead and litter 'production' were similarly estimated.

### *Error terms*

Because many of the results reported here comprise compound values derived from sums of components (e.g., number of primary tillers per square metre, summed from immature and mature tussocks), standard errors could only be estimated from the coefficients of variation of the largest contributing factor.

## RESULTS

### *Phytomass and phytoenergy*

'Mature' tussock densities in pure stands range from *c*. 0.7-1.67 m$^{-2}$ *(C. rigida)* to *c*. 2.-5.3 m$^{-2}$ *(C. macra)* resulting in primary tiller densities of *c*. 400-1400 m$^{-2}$ and inter-tussock plant cover of *c*. 20-80% (Table 4). The three classes of tillers ($1^0$ : $2^0$ : small) occurred in the proportions 61 : 29 : 10 *(C. macra)* and 73: 21: 7 *(C. rigida)*.

The dead plus litter compartments contributed *c*. 69% to the total tiller weights of both *C. macra* (2.0-4.6 g) and *C. rigida* (6.0-12.6 g). Standing litter accounted for about two-thirds of all dead foliar material within the tussock crown and the weight of live foliage was always less than half of this category (Table 5). Ash-inclusive phytoenergy of tissue ranged from 3.848 Kcal g$^{-1}$ dry weight for roots to 4.81 Kcal g$^{-1}$ for stems. Other values from Bliss and Mark (1974) were used for some inter-tussock species.

Total phytomass for the tussock grasslands ranged from *c*. 5-9 Kg m$^{-2}$ (22 000-40 000 Kcal m$^{-2}$) depending largely on the openness of the canopy (or burning/ grazing/recovery history). Root: shoot ratios, even when 'rhizomes' are included as 'roots', are considerably less than unity (Table 5).

Induced and natural cushion communities and herbfields are typified by their short stature, very high shoot densities, relatively small phytomass (2-4 Kg m$^{-2}$ or 8 000-17 000 Kcal m$^{-2}$) and slightly greater root: shoot ratios compared with tall tussock grassland (Table 6).

*Decomposition*

Instantaneous fractional decomposition rates (k) are given in Table 7. Root decomposition at 10:RP:*R* was significantly greater than that from sites 300m higher ($p < 0.01$) while leaf decomposition was slightly less (n.s.). Estimated times for 95% decay in tall tussock grassland are 7 to > 10 years for leaf litter and 4 to > 12 years for roots.

*Net primary production and fixation*

Primary axial stems probably exceed 5 years in age and generally reach 12-20 years before flowering occurs. Each tiller comprises 3.5-5.0 exposed, at least partially green, leaves which emerge at the rate of 1.2-1.8 per year giving an average life span of 2.6-3.2 years (Table 8). In a steady state grassland, the number of primary tillers 'consumed' in flowering, and dying from other causes, over a long period, will be compensated for by the initiation and development of primordial tillers in the axils of the older leaves of mature, and flowering, primary tillers.

Small tillers remain in that class for about one year (sometimes longer at high altitudes) before passing into the secondary tiller category. They are then distinguished by the separation of their individual flexible leaf blades and also by the loss of the special sheathing leaves which impart a bilateral symmetry to members of the small tiller class, in keeping with their lateral position (Figure 5).

Table 8 reveals that the ratio of new tiller production to tiller deaths, from all causes, greatly exceeds a steady state balance. Since this study was conducted during warmer than average (flower-inducing) seasons, a greater tiller mortality from flowering might have been expected (Mark, 1965b; Payton, 1976).

Table 9 includes information on the duration of the growing season, average and peak daily productivity, total annual production of foliage, stems plus inflorescences, roots (estimated), dead foliage and litter for the tall tussock stands. The table entry "NPP-foliage dieback" gives the more conservative estimate of primary production. The further subtraction of an undetermined fraction of the litter production (perhaps about 30 % which is decomposed in a year) would be equivalent to 'yield'.

Total NPP ranged from 960-1260 g m$^{-2}$ yr$^{-1}$ (4200-5730 Kcal m$^{-2}$ yr$^{-1}$) with the highest values at the mid-altitude sites. Root: shoot production ratios are closely related to those of biomass distribution.

Productivity of cushion and herbfield associations (Table 10) is not much less than that of snow tussock grasslands, especially when the values from Bliss and Mark (1974) are expressed on a 100% cover basis and an estimate of stem production is included. Annual 'potential' NPP of 430-1130 g m$^{-2}$ (2100-4700 Kcal m$^{-2}$), which such modification of Bliss and Mark's data provides, overlaps the snow tussock grassland values, although the low-alpine 13:O: *P* induced short grassland is probably out of place in this group.

Average daily production increased with altitude, in snow tussock grassland, from *c.* 4 to 7 g m$^{-2}$ day$^{-1}$ with peak values of 6-11 g m$^{-2}$ day$^{-1}$ being attained in late December (Table 9). The equivalent values for cushion and herbfields were 2.4-4.7 g m$^{-2}$ day$^{-1}$ (average) and up to 8.4 g m$^{-2}$ day$^{-1}$ (peak, Table 10).

An attempt was made to predict productivity levels at the study sites under a 'normal' climatic regime by relating the significantly different shoot production values from three seasons' observations ($p < 0.01$) to the degree-day and rainfall-evapotranspiration

TABLE 8. *Leaf balance in primary tillers; and tiller balance per unit area for* Chionochloa rigida *and* C. macra *at five tall snow tussock grassland sites.*

| SITES | 9:O:*R* | 13:O:*M* | *R* | 13:RP:*M* | 14:RP:*M* | 19:R:*M* |
|---|---|---|---|---|---|---|
| LEAF BALANCE (tiller$^{-1}$) | | | | | | |
| Number of green leaves | 4.05 | 4.23 | 4.93 | 3.55 | 4.32 | 4.17 |
| Number of new leaves yr$^{-1}$ | 1.60 | 1.62 | 1.81 | 1.18 | 1.60 | 1.30 |
| $\bar{x}$ LEAF LIFE SPAN (years) | 2.53 | 2.61 | 2.72 | 3.01 | 2.70 | 3.21 |
| TILLER BALANCE (No. m$^{-2}$) | | | | | | |
| Inflorescence production | - | - | 3.5 | 46.2 | 19.8 | 170.2 |
| Tiller deaths (all causes) | *c.* 37 | 60.5 | 6.2 | 80.8 | 39.7 | 212.7 |
| New tiller production | 81.6 | 219.2 | 35.2 | 473.1 | 317.4 | 382.9 |
| Ratio new: dying tillers | *c.*2.2 | 3.6 | 5.7 | 5.9 | 8.0 | 1.8 |

characteristics of those seasons, and finally extrapolating back to long-term normals. The expression which produced the best fit was:

$$P = 0.00175\ d\ (O\text{-}A) + 0.816\ (p < 0.05)$$

where P = net shoot production relative (geometrically) to that for 1971-72 (which was set at unity) and d(O-A) = cumulative degree-day departure from 1941-70 standard air temperature normals for the October to April growing season.

Results from this regression were averaged with those for the equally significant function for the December to February 'd':

$$P = 0.00174d\ (D\text{-}F) + 0.957$$

Thus, at the d origin, P = 0.887 of 1971-72 net shoot production. Different ratios were estimated for 9:O:*R* and for Bliss and Mark's (1974) data based on the temperature characteristics recorded during the relevant growing seasons (see Table 1).

There was a suggestion of a relationship between December rainfall departures from normal and

TABLE 9. *Primary production in five tall snow tussock grasslands. Included are: details of growing season; net primary production (NPP) on daily and annual bases; annual dead leaf and litter production in mass (g* $m^{-2}$ $yr^{-1}$*) and energy (Kcal* $m^{-2}$ $yr^{-1}$*) units; production ratios of root: shoot, dead: NPP (foliage), and litter: dead (foliage); and annual net energy fixation (NEF). Annual NPP and NEF are separated into three components (foliage, stem + inflorescence and root). Season duration and dates, and peak daily production values are based on quadratic regressions fitted to shoot productivity-time data. "NPP minus foliage die back losses" provide a more conservative alternative estimate of production (see text). N.R. these data relate to the warmer than average summers reported in Table I.*

| SITES | 9:O:*R* | 13:O:*MR* | 13:RP:*M* | 14:RP:*M* | 19:R:*M* |
|---|---|---|---|---|---|
| Growing season (days) | 267 | 219 | 226 | 228 | 148 |
| Beginning -- end | 24VIII-18V | 4IX-IIIV | IX-15V | 3X-19V | 16X-13IV |
| **X Daily prod. (g $m^{-2}$)** | **3.58** | **5.53** | **5.59** | **5.47** | **7.10** |
| Date of peak prod. | 8 XII | 22 XII | 19 XII | 18 XII | 30 XII |
| Peak prod. (g $m^{-2}d^{-1}$) | 5.74 | 7.91 | 10.64 | 9.87 | 9.36 |
| NET ANNUAL PRODUCTION (g $m^{-2}$ $yr^{-1}$) | | | | | |
| Foliage | 521.4 | 796.9 | 719.4 | 793.9 | 592.2 |
| Stem + inflorescence | 28.2 | 45.7 | 40.3 | 40.8 | 35.9 |
| Total shoot | 549.6 | 842.6 | 759.7 | 834.7 | 628.1 |
| Total root | 406 | 368 | 504 | 413 | 422 |
| **Total NPP** | **956** | **1211** | **1263** | **1248** | **1050** |
| Total NPP minus foliage dieback losses | 909 | 1054 | 1109 | 1077 | 960 |
| DEAD LEAF PROD. (g) | *c*.486 | 580.5 | 472.9 | 525.8 | 312.3 |
| LEAF LITTER PROD. (g) | c.260 | 325.4 | 209.5 | 262.6 | 188.1 |
| PRODUCTION RATIOS | | | | | |
| Root: shoot | 0.74 | 0.44 | 0.66 | 0.50 | 0.67 |
| Dead leaf: leaf NPP | *c*.0.93 | 0.73 | 0.66 | 0.66 | 0.53 |
| Litter: dead leaf | *c*. 0.53 | 0.56 | 0.44 | 0.50 | 0.60 |
| NET ENERGY FIXATION (Kcal $m^{-2}$ $yr^{-1}$) | | | | | |
| Foliage | 2419 | 3747 | 3476 | 3808 | 2826 |
| Stem + inflorescence | 134 | 217 | 196 | 197 | 173 |
| Total shoot | 2552 | 3964 | 3673 | 4005 | 2999 |
| Total root | 1657 | 1502 | 2057 | 1686 | 1723 |
| Total NEF | 4209 | 5466 | 5730 | 5691 | 4722 |
| DEAD LEAF PROD. (Kcal.) | *c*. 2255 | 2730 | 2285 | 2522 | 1491 |
| LEAF LITTER PROD. (Kcal.) | *c*. 1206 | 1530 | 1012 | 1260 | 898 |

productivity, but this could be verified only with further data from the drier low-altitude sites. Tables 11 and 12 summarise the estimates of 'normalised' total net production, fixation and efficiency for all sites (% efficiency = total net energy fixation x 100/ photosynthetically-active radiation incident during the growing season). The estimated coefficient of variation for all of the tussock grassland productivity data is *c*. 48% which dictates a S.E. of *c*. 100 g.

A multiple regression between net fixation (NEF), seasonal accumulated degree-days (D) and "annual estimated evapotranspiration/mean annual precipitation" (E) suggested that a curvilinear relationship exists between net annual tussock production and correlates of altitude in Central Otago. The regressions are:

$$\mathrm{NEF} = 0.639 + 1.221\mathrm{D} - 0.00053\mathrm{D}^2 + 1699.7\mathrm{E} - 1467.5\mathrm{E}^2 \ (p = 0.03)$$

$$\mathrm{NEF} = 0.1936 + 1.587\mathrm{D} - 0.00073\mathrm{D}^2 + 787.3\mathrm{E} \ (p=0.002)$$

Both regressions account for 99% of the variation.

The dominant effect of increasing accumulated temperature and the correlated evapotranspiration ratio is for NEF to increase. However, above a certain point (1.15) the E ratio becomes critical and thereafter increasing water stress (and the concomitant temperature) has a depressing effect on growth. It must be admitted that the 9:O:*R* values (not originally collected for production estimation) upon which this hypothesis depends are suspect, and verification, preferably with a more completely closed tussock stand.

## DISCUSSION

The magnitude of these phytomass and productivity results at first appears to be unusually high. However, in line with the most recent evidence, I shall suggest that it is our earlier precepts that may require critical re-examination.

### *Structural aspects of tundra*

A comparable study to the present one has been recently completed by Williams (1977) in two mid~Canterbury montane to low-alpine tall tussock communities, also dominated by *C. rigida* and *C. macra*. Although Williams' stands were similarly mature and closed, his tussock parameters of

TABLE 11. *Estimated 'Normal' Total NPP, NEF efficiency (per snow-free season, photosynthetically-active radiation basis) and NPP per degree-day (of snow-free season) for five tall snow tussock grassland sites. The non-normalised values for* 9:O*:R are included as the upper limit of an estimated range, since accuracy of the transformation (lower estimate) is suspect.*

| SITES | 9:O:*R* | 13:O:*MR* | 13:RP:*M* | 14:RP:*M* | 19:R:*M* |
|---|---|---|---|---|---|
| NPP (g $m^{-2}$ $yr^{-1}$) | 73-956 | 1037 | 1006 | 994 | 899 |
| NEF (Kcal $m^{-2}$ $yr^{-1}$) | 3238-4209 | 4352 | 4562 | 4531 | 4042 |
| EFFICIENCY % | 0.60-0.77 | 1.09 | 1.15 | 1.18 | 1.22 |
| NPP DEGREE-DAY$^{-1}$ | 0.36-0.46 | 0.77 | 0.78 | 0.88 | 1.61 |

TABLE 12. *Estimated 'Normal' Total NPP, NEF, efficiency (per snow-free season, photosynthetically-actil'e radiation basis) and NPP per degree-day (of snow-free season) for six cushion, herbfield and short grassland sites. * = from Bliss and Mark* (1974). *All values are expressed on a 100% cover (stems included or estimated) basis.*

| SITES | 12:RP:*H** | 12:RP:*C** | 13:0:*P* | 14:RP:*H** | 14:RP:*C** | 20:R:*P* |
|---|---|---|---|---|---|---|
| NPP (g $m^{-2}$ $yr^{-1}$) | 697 | 529 | 998 | 449 | 470 | 405 |
| NEF (Kcal $m^{-2}$ $yr^{-1}$) | 3387 | 2677 | 4179 | 2207 | 2309 | 1694 |
| EFFICIENCY % | 0.79 | 0.46 | 1.03 | 0.50 | 0.50 | 0.53 |
| NPP DEGREE-DAY$^{-1}$ | 0.50 | 0.38 | 0.70 | 0.35 | 0.37 | 0.78 |

phytomass and productivity tend to be lower than those reported here, mainly because of his smaller values for tiller density. My primary tiller densities of 370-1400 m$^{-2}$ and green foliage weights per primary tiller of 0.6-3.0 g compare with his respective values of 250-450 m$^{-2}$ and 0.7-3.0 g *(loc. cit.)*. Nevertheless, five of my seven tall tussock sites support total phytomasses (5127-6637 g m$^{-2}$) within the range reported by Williams (3 800-6 800 g m$^{-2}$), and the other two (c. 8750 g m$^{-2}$) are more like the 5900 g m$^{-2}$ (above-ground phytomass only) of Wraight's (1965) much lower-statured alpine carpet grass *(Chionochloa australis)* association.

The only similar tundras, in form and stature, to New Zealand's evergreen tall tussock grasslands, are those of the Subantarctic Islands, where total phytomasses of 5000-8000 g m$^{-2}$ (Jenkin, 1975; Hnatiuk, 1975) and 17785 g m$^{-2}$ (Smith and Walton, 1975) are recorded. The equatorial, alpine, tall bunch-grass associations (3500-4000 g m$^{-2}$) of Mt. Wilhelm, New Guinea, differ in that only 10% of their phytomass occurs below-ground (Hnatiuk, 1975).

Other natural herbaceous biomes of the world are associated with arctic-alpine, semi-arid temperate and tropical climates, and wetlands. *Eriophorum* sedge tundras may have total standing crops of 7600 g m$^{-2}$, but only a meagre 8 % of this occurs above ground (Wein and Bliss, 1974), whereas low-alpine/arctic shrub tundras and heaths can have above-ground standing crops exceeding 1000 g m$^{-2}$ with totals up to 9000 g m$^{-2}$ (Webber and May, 1977). For most continental tundras, values are generally less than 500 g m$^{-2}$ above-ground, but root biomass is usually several (2-16) times this (Scott and Billings, 1964; Bliss, 1966, 1970, 1977; Lieth and Whittaker, 1975; Webber, 1977). The cushion herb-field and short grassland communities of Central Otago's exposed alpine habitats, and an induced short grassland (13:O:*P)** have total phytomasses (2000-4000 g m$^{-2}$) which are in keeping with world tundra values, although distribution of mass can be quite different.

Root: shoot ratios, for all communities studied here, are less than unity (0.42-0.79 in low-statured vegetation; 0.4-0.75 in tall tussock; Tables 5 and 6). The exception (13:O:*PH)* is actually part of the 13:O: *MR* inter-tussock zone and, as such, has exaggerated root mass that is presumably influenced by the surrounding tussocks. These ratios are low by world standards, which suggests a relatively mild aerial environment here. Nevertheless, contrary to expectation, Bliss (1977) has shown that root: shoot ratios are not greatest at the most exposed fellfield sites, at least not in the high-Arctic (0.4-0.6 for cushion live ratios). It is the more continuous graminoid associations which have the largest values there (9-13; *loco cit.)*.

Temperate grasslands generally have peak aerial phytomasses approaching 1000 g m$^{-2}$ (Williamson, 1976), but high root: shoot ratios again, more especially in continental regions, ensure totals in the range 1200-5000 g m$^{-2}$ (Kuramoto and Bliss 1970; Coupland, 1973; Lieth and Whittaker, 1975; Numata, 1975). Tropical savannas may develop phytomasses of 2000-7000 g m$^{-2}$, while the only other natural herbaceous communities of similar stature are semi-aquatic rush and sedge stands (3000-15000 g m$^{-2}$ in Lieth and Whittaker, 1975). Thus, even though the tall snow tussock grasslands are physiognomically atypical of many tundras described in the literature, standing crops of these New Zealand grasslands *(c.* 4000-9000 g m$^{-2}$) are, in fact, quite similar to those of other regions where tree growth is restricted for any of a variety of reasons.

The preponderance of below-ground phytomass is the main feature which distinguishes continental cold and dry grasslands from oceanic tundras (notwithstanding the cushion values). In this respect, the New Zealand examples are decidedly oceanic. Moreover, Conrad's (1946) continentality index ** calculated for Central Otago (New Zealand's most continental area) is only about 10-15.

*Functional aspects of tundra*

Because refinements of theory and appropriate methodology for measuring NPP, in contrast to 'yield', have been comparatively recent, few of the many published productivity data can be directly compared with the results reported here. Wraight (1965), O'Connor (1967) and McLeod (1974) have all recorded foliage or shoot productivities of less than 500 g m$^{-2}$ yr$^{-1}$ for New Zealand mountain tussock grasslands, but, as previously suggested, these may be up to 100% too low, even for shoots. Typical aerial yields *(sic)* of North American tundra communities (100-400 g m$^{-2}$yr$^{-1}$) (e.g., Bliss, 1966, 1970) are greatly enhanced if root production estimates (100-800 g m-2, Shaver and Billings, 1975; Bliss, 1977; Dennis, 1977; Webber and May, 1977; Chapin III *et al*., 1978) are considered.

Harvest data corrected for 'invisible' losses have generally raised the known upper limits of

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* The induced condition of this turf grassland was confined by the isolation of old *Chionochloa* stems from the soil.

** Index values of 0-100 span extreme oceanic to extreme continental conditions, 30-40 being considered typically continental.

tundra annual production *(c.* 100-1000 g $m^{-2}$ for low-alpine / arctic tundra; Wielgolaski *et al.,* 1978; 17-280 g $m^{-2}$ in the high-Arctic; Bliss, 1977). These values cover the range estimated for Central Otago's cushion and herbfield communities (400-700 g $m^{-2}yr^{-1}$ or 1700.3400 Kcal $m^{-2}$ $yr^{-1}$) from the base of the high-alpine zone (normalised, 100% cover basis; cf. Table 12). Actual cover values were 44-65% for the cushion communities and *c*. 80 % for herbfields* (Bliss and Mark, 1974).

Normalised total NPP of tall snow tussock grassland, in the low- and high-alpine zones *(c.* 750-1040 g $m^{-2}$ $yr^{-1}$ or *c*. 3250-4560 Kcal $m^{-2}$ $yr^{-1}$), and of a low-alpine induced turf grassland (1000 g $m^{-2}$ $yr^{-1}$ or 4180 Kcal $m^{-2}$ $yr^{-1}$) reported here, conform to Williams' (1977) determinations (726 and 1083 g $m^{-2}$ $yr^{-1}$) at his similar, but lower altitude, tall tussock sites in Canterbury. Annual NPP values approaching 1000 g $m^{-2}$ can no longer be considered atypical (cf. Lieth and Whittaker, 1975) for tall-statured tundra near tree line, in the light of recent work demonstrating production near to, and in excess of, this figure (cf. Webber, 1977; Wielgolaski, 1975; Wielgolaski *et al.,* 1978). The almost year-long growing season of *Poa foliosa* tussock on subantarctic Macquarie Island (Jenkin, 1975) results in a NPP of 1000-5580 g $m^{-2}$ $yr^{-1}$. This is exceeded by the even more stupendous value of 6025 g $m^{-2}$ $yr^{-1}$ in South Georgia's *Poa {labellata* wet grassland (Smith and Walton, 1975). However, the tropical Mt. Wilhelm bunch grass association of similar habit, and also with a perpetual growing season, produces only about 300 g $m^{-2}$ $yr^{-1}$ aerially (Hnatiuk, 1975).

New Zealand's tall tussock grasslands are even less peculiar when viewed in terms of other temperate, natural (dry) and disclimactic (humid) grasslands where total potential productivities range from *c.* 1000-1500 g $m^{-2}$ $yr^{-1}$ (Kuramoto and Bliss, 1970; Coupland, 1973: Lieth and Whittaker, 1975; Numata, 1975; cf. Williamson, 1976). However, in New Zealand's oceanic climate the bulk of estimated NPP occurs above ground (56% in cushion and herbfield, 63 % in tall tussock, but *c*. 48 % according to Williams, 1977) whereas in dry grassland biomes greater than 60% of net production is below ground (Coupland, 1973; Numata, 1975).

Because of the long growing season of 125-270 days (520-2060 degree-days) in parts of New Zealand's alpine zone (Tables I, 9, 10), compared with the usual 50-150 days (200-1100 degree-days) of continental tundra climates (Wielgolaski *et al.,* 1978), production rates are relatively low here, as a consequence of the similar annual productivities. Typical daily aerial net productivities up to 4.6 g $m^{-2}$ for tundra (Bliss, 1966) are effectively greater than the total values of 3.6-7.1 (tall tussock and induced short grassland) and 2.4-3.7 g $m^{-2}$ $day^{-1}$ (cushion and herbfield and short grassland) here. Average total values in subantarctic tussock grassland may be greater than 15 g $m^{-2}$ $day^{-1}$ (Jenkin, 1975) which compare with 8.3 (Wielgolaski, 1975b), 11 (Hadley and Bliss, 1964) and 2.2-10 g $m^{-2}$ $day^{-1}$ (Wielgolaski *et al.,* 1978) reported for northern tundra. High-Arctic productivity is less than 1 g $m^{-2}$ $day^{-1}$ *(Ioc. cit.).* In Central Otago, peak total production rates of 5.7-10.6 g $m^{-2}$ $day^{-1}$ (snow tussock) and 3.5-8.4 g $m^{-2}$ $day^{-1}$ (cushion and herbfield) cluster around the latter half of December. This suggests that light or some intrinsic growth rhythm overrides the temperature cycle, which normally peaks in January. Such a rhythm may be a manifestation of spring mobilisation of the previous summer's stored production (cf. Williams *et al.,* 1977), but Hadley and Rosen (1974) and Payton (1976, 1978) have discounted the importance of reserve storage in two of New Zealand's major alpine genera.

Efficiency ratings in tall tussock grasslands increase from 0.6-1.2 % over the altitudinal range studied (Table 11). The average for tall tussock fixation is 1.1 %, for an induced short grassland it is 1.0 % and for cushion, herbfield and natural short grassland it is 0.56 % (0.46-0.79 %) on 100 % cover basis (Table 12). These values compare with 0.7-2.1 % in alpine Fennoscandia and 0.8-1.5 % in arctic tundra (Wielgolaski *et al.,* 1978). Net production per degree-day similarly attains highest values at the highest altitude, both in snow tussock (0.4-1.61 g $dd^{-1}$; x = 0.89) and in cushion, herbfield and short grassland (0.35-0.78 g $dd^{-1}$; x = 0.51). Thus, daily rates of net production, production per degree-day of the growing season, and efficiency all tend to increase with shorter growing seasons-no doubt an important alpine adaptation.

Turnover times are generally assumed to be reflected by the value: "Biomass/Annual NPP" (Odum, 1971), but this is not strictly true. Rather, the expression: "(Biomass plus degradation losses incurred during turnover time)/ Annual NPP" should be used. Thus, turnover times here, corrected for these losses, for all vegetation types, have a mean of 10.9 years (S.E. = 2.4) with a maximum of 21.8 years for 20: R: *P*. This compares with a 6.9 year mean

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* It is conceded that the scaling of point-productivity up to a square metre basis for comparing site potentials may be spurious if fell-fields are not tending towards complete cover of the substrate. A cyclic regeneration-degeneration model (Watt, 1947) may be more appropriate in some circumstances.

(S.E. = 1.2) based on the first of the two formulae above.

The time for 95 % of roots to decompose is 4-18 years (x = 11.1) and for shoots 7.5-21 years (x = 12.7). Maximum values occur at high altitudes and have been estimated from a regression on data from Table 7. Thus a turnover time of about 11 years seems to be typical for reasonably moist and sheltered alpine conditions in Otago. These values compare with a $t_{95\%}$ (for leaf blades on the ground) of 10 years for *C. rigida* and *c.* 20 years for *C. macra* (higher altitude) at the mid-Canterbury sites of Williams *et al.* (1977). The lower decomposition rate of leaf litter at the lower altitude, that I have reported, suggests the effect of dry surface conditions overriding higher temperatures. In contrast, the faster root decomposition at the lower altitude indicates that moisture is not limiting in that soil. These data pinpoint the difference in moisture regime between Williams' low-altitude site and my *C. rigida* stands. The more typical steady lapse of decompos:tion rates with altitude has also been reported by Molloy *et al.* (1978) for two sites on the south Old Man Range and one (the lowest) on the main divide, all of which share a humid climate. They measured 19% annual dry weight depletion of leaf litter at *c.* 1000 m, *c.* 17.5% at 1340 m (at my 13:O*:MR* site) and 15% at 1525m (near the 16:O:*M* site). These data conform well with my non~transformed leaf decomposition values (i.e., half of those given in Table 7).

On humid South Georgia (Subantarctic), Smith and Walton (1975) have reported 12-90% first year dry-weight losses in litter which is similar to the 36-90% on Macquarie Island (Jenkin, 1975). The 20% decomposition measured by Widden (1977), in the Canadian high-Arctic is, like the New Zealand data, indicative of a more restricted summer season.

For tall tussock grasslands the equivalent of about 70± 7% of foliage NPP is diverted to the dead leaf compartment and of this *c.* 53 ± 7 % falls as leaf litter annually (see production ratios in Table 9). Subsequently, somewhere between 15-25% of the ground litter is decomposed. For *Poa colensoi* dead production is *c.* 75% of foliage NPP and litter production is equivalent to *c.* 90 % of that entering the dead compartments.

Grazing pressure on these grasslands amounts to, at most, 10 g $m^{-2}$ $yr^{-1}$ consumption by stock *(c.* 0.5 ewe equivalents $ha^{-1}$ [Otago Catchment Board Records] x 600 Kg $ewe^{-1}$ $yr^{-1}$ [K. F. O'Connor; *pers. comm.]* x 1/3 of year grazed) and *c.* 5 g $m^{-2}$ $yr^{-1}$ by grasshoppers (White, 1978). These results are typical for poor grazing ranges. Rawes and Welch (1969) have demonstrated consumption of *c.* 6 g $m^{-2}$ $yr^{-1}$ by sheep on an upland English moor and, in a high-arctic tundra, total herbivore consumption accounts for less than 2 g $m^{-2}$ $yr^{-1}$, on average (Bliss, 1975), although this may be locally boosted up to 20% of available forage (Bliss, 1977).

### *Environment and tundra status*

Scott and Billings (1964) showed that community productivity and phytomass was an aggregate response of many species reacting, more or less independently to many environmental factors. The most important were altitude, winter snow cover, moisture regime, soil movement, percent clay, extractable K and available subsoil water. Wielgolaski *et al.* (1978) have demonstrated that annual NPP is often correlated with live phytomass (of which NPP is *c.* 50-70%), community structure (chlorophyll content and leaf-area index) and cover, global radiation and length of growing season. Some of these correlations, and that with the degree-day (> 0°C) environment, were improved when two other factors of inferred importance (soil moisture and fertility) were held constant *(loc. cit.).* Bliss (1966) has suggested a better relationship with soil temperature than with air degree-days, and elsewhere Lieth (1975) has correlated evapotranspiration and precipitation with NPP. These conditional correlations partially explain why variation in plant production at differing microsites within a study area is often greater than that between study areas, as Wielgolaski *et al.* (1978) stress. This is borne out by the IBP productivity, efficiency and phytomass results reported by them, which contain both highly discrepant and very similar values, compared with those reported from this work; discrepant when, say, zonal* vegetation is compared with intrazonal vegetation, but similar when, say, low-alpine zonal vegetation is compared with low-arctic zonal vegetation (cf. Tedrow and Harries, 1960).

It is important to bear in mind that the most common vegetation/soil type does not necessarily correspond to either a climax condition or, in the sense used here, to a zonal status (ct. Tedrow and Harries, 1960; and Ivanova's interpretation, summarised in Sokolov, 1976). Thus, the potential development for a particular macroclimatic energy regime may be limited to small areas if the landscape

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* To clarify: a zonal vegetation/soil state may be understood as an energetically defined climax condition that exists when no other factor (especially moisture) is limiting. Intrazonal systems are climax states controlled by factors other than the energy (light/heat) regime. Azonality refers to the early pioneer stage of a primary sere.

is dominated by either very exposed environments that have retarded attainment of climax status, or habitats with highly enleached or saturated soils of a post-steady-state nature.

The standing crop and NPP values presented here for tall tussock grasslands are considered to be representative of near-climax or potential/zonal status, for the prevailing macroclimate of the Central Otago mountains. Soil moisture, fertility and plant cover were each held more or less constant at non-limiting levels. Exposure and history (e.g., the effects of burning and grazing on induction of disclimax short grasslands and herbfields) are likely to be the most important uncontrolled variables, or remaining influences, on standing crop, since altitude appears to have only a slight effect in terms of depressing stature (Table 5). Choice of uniform tall tussock stands was, however, intended to diminish the historical influence. In line with the above interpretation, the shorter vegetation types discussed here may be regarded as either seral (of primary or secondary successions) or potential, intrazonal climax association (defined by exposure/desiccation levels). Annual production, in contrast to community structure, is clearly affected by elevation (degree-days) as well as by exposure and historical considerations. There is also a strong suggestion that the less favourable water balance at low altitudes in Central Otago may inhibit growth.

Unfortunately, Williams' (1977) montane site is nearly flat and retains very high (slightly negative) water potentials throughout the summer. It is therefore unsuitable for testing the postulated influence (implied by my results), on natural productivity, of the droughty, eastern South Island zonal soils that extend up to the base of the alpine zone.

Annual production in tall tussock grasslands here is about 35-50% of live phytomass. This lower proportion, than for all except the shrubby northern hemisphere tundras (Wielgolaski *et al.,* 1978), is probably indicative of the unusually large evergreen habit of New Zealand (and subantarctic) zonal tundra communities. Alternatively, this might be cited as corroborative evidence for the posited, restricted nature of zonal communities in the Arctic. Contrast this with the widespread zonal conditions that pertain in the Central Otago rainshadow mountains. Here an oceanic regime has enhanced vegetation/soil succession while post-glacial time and only moderate rainfall have been insufficient for soil deterioration to have advanced beyond incipient podzol formation.

Williams *et al.* (1977) have claimed that *C.* ma*cra* is slowly invading *C. rigida* tussock grassland as soils deteriorate--a feature of post-steady-state decline. However, there is evidence to support a contrary view, namely that *C. rigida* is extending its range upslope in response to a 'post-Little Ice Age' warming climate (Salinger and Gunn, 1975). The higher emergence: death ratio of tillers reported here (Table 8) for *C. rigida*. when codominant with C. *macra,* warrants further investigation in this regard. The greater numbers of new tillers produced compared with those dying, in both species, indicates the generally seral nature of these stands (13:O:*MR* is comparatively open and 13:RP:*M* and 14:RP:*M* are relict tussock patches), or an enhanced recovery (tillering) phase following a flowering season prior to this study.

## CONCLUSIONS

Some limitations in experimental design have been admitted, although most of the subjective element was inherent in the intention of measuring maximum, or potential, phytomass and NPP. Productivity has been expressed on a full cover basis for the sake of comparing potential growth, supportable by the (energy) environment, at the various sites (i.e., as a habitat index). But near the limits of growth (e.g., 20:R:*P),* actual current productivity could be from 0-70% of the point values reported here, depending on the predominance of bare rock.

Maximum phytomass of 8.8 Kg $m^{-2}$ is recorded in low-alpine, zonal, tall snow tussock grassland and declines gradually with increasing altitude. Exposed summit-ridge environments support intrazonal or seral communities of low stature (2-4 Kg $m^{-2}$), physiognomically similar to an induced short (turf) grassland. Their dynamics are, however, quite different.

In Central Otago, tall tussock productivity, on an annual basis (*c.* 1 Kg $m^{-2}$), appears to peak at mid-altitudes, although, on an average daily basis, it is greatest at the higher sites. This suggests, firstly, that the opposing influences of temperature/exposure and water balance (Table 1) are optimal for plant growth at mid-altitudes, and secondly that a genetic adaptation, for rapid growth in a short growing season, exists in high-altitude populations.

Grazing removes less than 2 % of total current shoot production in the alpine zone, although perhaps up to 5% of shoot yield. However, even when stocking rates are low, burning the tussock and rendering it more palatable (Williams and Meurk, 1977) can result in local concentrations of both stock and browsing insects. This may impair the grasslands' productive capacity, and thereby its ability to recover from fire (Mark, 1965c; Payton and Mark, ]978; Meurk, in prep.). The resultant patchwork of induced turf/herbfields and relict snow tussocks may be detrimental to the valuable hydrologic potential that the natural tussock confers on the high-country, at least where climates are characterised by high fog incidence (Mark and Rowley, 1976).

The productivity of the 'natural' cushion, herbfield and short grassland communities ($< 700$ g $m^{-2}$ $yr^{-1}$) relates more closely to world tundra, but it is suggested that many of the lower world values will be found to require substantial upward adjustment, to allow for various degradation processes that are difficult to monitor and consequently often neglected. If this prediction is realised, then NPP values of $\leq 1$ Kg $m^{-2}$ $yr^{-1}$ may prove to be the rule for low-alpine / arctic (and $\leq 0.5$ Kg $m^{-2}$ $yr^{-1}$ for high-alpine / arctic) zonal plant associations (i.e., mesic, well-drained, tall shrub / graminoid tundra). Such zonal situations may, however, be of limited extent in continental tundra regions. In terms of growing season, their moisture and energy regimes, phytomass and productivity, New Zealand alpine tundras appear to be physically and dynamically intermediate between those of subantarctic and typically continental provenances.

Questions raised explicitly, or implicitly, in this paper concern: (a) the definition of NPP; (b) the processes involved in leaf dieback; (c) the true nature of turnover-time; (d) the measurement of root production; (e) the relationship of productivity to energy and water balance; and (f) the applicability of the terms alpine, zonal, climax, steady-state or post-steady-state decline to the New Zealand vegetation/soil types discussed. Resolutions to these questions will remain speculative until: it is decided whether, or not, photo-oxidants, leachates and other 'invisible' causes of degradation, constitute 'litter', and hence a derivative, and accountable, part of NPP (a); tracer studies have been carried out, to determine the role of translocation in salvaging materials from dying tissue (b); decomposition rates have been more accurately assessed and movement of photosynthate between roots and shoots monitored (d); and further long-term studies of potential productivity have been carried out, especially in the drought-prone, subalpine zone of eastern South Island (e and f).

Some .of the information and conclusions presented here must remain tentative pending further study. It is felt that critical testing of assumptions which underpin the methods used in this study, and those in current use elsewhere, should precede further devotion of effort to productivity measurement, if future results are to extend usefully our existing knowledge of the broad production patterns of the biosphere. The associated interdisciplinary problems demand a second generation of the co-operative style, pioneered by the IBP.

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