22000

Rossiter, R.C. 1966. Ecology of the Mediterranean annual-type pasture, p 1-56. IN: A.G. Norman (ed.). Advances in agronomy. Academic Press, New York. 392 p.



Med. Climate Annual Range Ca, Australia Review

~~D. Dunmean~~ J. Clawson

# ECOLOGY OF THE MEDITERRANEAN ANNUAL-TYPE PASTURE

R. C. Rossiter

Commonwealth Scientific and Industrial Research Organization, Nedlands, West Australia



## I. Introduction

The "Mediterranean" climate is typified by mild wet winters and hot dry summers. In the Mediterranean Basin, where olive and the ever-green oak (*Quercus coccifera*) are generally accepted as the indicator plants of the true Mediterranean environment, the total annual rainfall varies from 200 mm. (8 inches) to 1000 mm. (40 inches) (Anonymous, 1951). However, the Mediterranean climate is also found in parts of California and Chile, the southwest of Cape Province in South Africa, and in parts of southwestern and southern Australia (Köppen, 1923; Whyte, 1949). Climatic data are given below (Table I) for two localities that can be regarded as having rather better than average Mediterranean conditions for plant growth.

Before the advent of clearing, fire, cropping, and grazing, trees and perennial shrubs together with perennial grasses were the dominant components of the vegetation in Mediterranean areas. Today, the pasture communities are characterized by either resistant shrubs (e.g., *Q. coccifera*) or numerous Mediterranean annual plants. These annuals thrive best on soils that are not too shallow (Litav *et al.*, 1963). They are almost invariably long-day plants (Aitken, 1955a,b; Ashby and Hellmers, 1959; J. P. Cooper, 1950; L. T. Evans, 1964; Knight and Hollowell, 1958; Lewis and Went, 1945; Silsbury, 1964). The number of genera among the dominant annuals is quite remarkably restricted—for the most part to *Bromus*, *Festuca*, *Hordeum*, *Trifolium*, *Medicago*, and *Erodium*. Pastures comprised essentially of these winter-growing annuals have been designated as "annual-type" by early Californian workers (Talbot *et al.*, 1939); and this term will be applied here also to define pastures consisting of winter-growing annuals, in which perennial species are either absent or else play a minor and insignificant role agronomically. Indeed, it may be argued that the occurrence and extent of the Mediterranean annual-type pasture may be taken to indicate the limits of the Mediterranean environment.

TABLE I

Climatic Data for Two Representative Mediterranean Localities[a,b]

| San Joaquin Experimental Range (Californian foothills) | | | Glen Lossie Field Station, Kojonup (southwestern W.A.) | | |
|---|---|---|---|---|---|
| Month | Total rainfall (inches) | Mean temperature (°F.) | Month | Total rainfall (inches) | Mean temperature (°F.) |
| July | 0.02 | 80.8 | Jan. | 0.48 | 70.4 |
| Aug. | 0.01 | 78.9 | Feb. | 0.54 | 70.1 |
| Sept. | 0.13 | 72.9 | Mar. | 0.93 | 60.9 |
| [Oct. | 1.23 | 61.2 | Apr. | 1.27 | 60.3 |
| Nov. | 1.47 | 49.3 | May | 2.78 | 54.7 |
| Dec. | 3.63 | 44.7 | June | 3.70 | 51.0 |
| Jan. | 3.35 | 43.0 | July | 3.59 | 49.2 |
| Feb. | 4.53 | 46.6 | Aug. | 3.04 | 50.3 |
| Mar. | 3.54 | 50.5 | Sept. | 2.25 | 52.6 |
| Apr.] | 1.92 | 56.7 | Oct. | 1.80 | 55.7] |
| May | 0.35 | 65.7 | Nov. | 0.88 | 61.3 |
| June | 0.02 | 73.7 | Dec. | 0.63 | 65.7 |
| Year | 20.2 | 60.3 | Year | 21.9 | 59.0 |

[a] Growing season period shown in brackets.

[b] The extremes of monthly rainfall and temperature are greater at the Californian site than the Western Australian one. Moreover, the mean monthly temperature ranges (maximum-minimum), which are not given in Table I, are again greater at the Californian site. Mean elevation above sea level is almost the same for both sites, i.e., slightly more than 1000 feet.



Apart from the Mediterranean Basin itself, the Mediterranean annual-type pasture occupies extensive areas. For example, California has more than $20 \times 10^6$ acres (Sampson *et al.*, 1951), while in southern Australia the area is more than $40 \times 10^6$ acres if the annual pastures of the wheat belts of New South Wales and Victoria are included. In the southwest of Western Australia alone, the present area of sown pasture, almost entirely of the annual type, exceeds $8 \times 10^6$ acres, and I estimate that the area will reach $16 \times 10^6$ acres by 1970. The importance of these pastures becomes evident when it is realized that, in southern Australia, they support approximately 1 sheep per acre under low rainfall conditions and are capable of maintaining more than 5 sheep per acre under good conditions, on a year-long basis.

The Mediterranean annual-type pasture has potential scope for marked and rapid seasonal changes in botanical composition and in chemical composition also. It is therefore not surprising that this pasture has attracted the research worker in pasture ecology and pasture physiology, and in pasture utilization. My main aim is to review ecological studies, together with those physiological investigations which may have relevance to the field situation; then to consider the question of animal performance in relation to species composition; and finally, to discuss pasture productivity in the ecosystem and to indicate possible directions for further research. Most of the literature available to the reviewer is of either Californian or Australian origin, and although most of the relevant research has been done in these regions, important references may well have been overlooked.

## II. Factors Affecting Botanical Composition on Different Sites

### A. Geographic

Many, if not most species of the annual-type pasture appear to have originated from the Mediterranean Basin. Moreover, some restricted communities of winter annuals found on shallow limestone soils in England are believed to represent a reduced outlier of Mediterranean origin (Ratcliffe, 1961). In several instances, e.g., *Medicago polymorpha*,[1] *Avena barbata*, *Hordeum leporinum*, *Bromus mollis*, the same species are found in Chile, South Africa, California, and southern Australia, as well as in the Mediterranean proper. There are, however, notable differences, e.g., the relative prominence of the legume *Adesmia* in Chile (Bailey, 1961), and its absence in California and southern Australia.

A comparison of the genera and species in California and southern

[1] *Medicago polymorpha* L. previously known as *M. denticulata* Willd (Simon and Simon, 1965).

Australia provides several points of interest. Most of the prominent "resident" annuals in the former were introduced prior to 1900 (Robbins, 1940), while in the latter, many "naturalized" species arrived at about the same period (Ewart, 1930). Some of the dominant species are identical, e.g., *Bromus rigidus*, *Hordeum leporinum*, and *Erodium botrys*. But, apart from the sown species *Trifolium subterraneum*, the genus Trifolium is represented mainly by *T. microcephalum*, *T. variegatum*, *T. tridentatum*, and *T. ciliolatum* in California, and *T. glomeratum*, *T. campestre*, *T. tomentosum*, and *T. dubium* in southern Australia. *Vulpia myuros* and *V. bromoides* are similar to *Festuca megalura* (*Vulpia megalura* ?) in growth habit and extreme earliness of flowering. *Bromus mollis* plays a much more prominent role in California than in southern Australia. However, the most striking difference between the pastures in these two regions is the presence, if not abundance, of the composite *Cryptostemma calendula* in southern Australia, and its absence in California. This species, known in Australia as capeweed, is of South African origin. The writer has observed it on a sandy soil in Portugal, but it is evidently of no significance in the Mediterranean Basin.

Morley (1961) in discussing subspeciation in *Trifolium subterraneum* has drawn attention to the fact that a far higher proportion of the Australian varieties belong to the Tallarook group[2] than is found in collections from any other locality in the Mediterranean Basin. This suggested that either the Tallarook group comprises very invasive strains, or else the Australian strains came from a relatively restricted area (probably not from the western Mediterranean). In addition, Morley (1961) considers that, in view of the extreme variation in the Tallarook group, it is unlikely that many Australian strains have arisen *de novo*. With subterranean clover, therefore, we have good evidence for botanical differences at the varietal level in distant geographic areas. However, the species, as such, is not nearly so prominent in California as in southern Australia, and while the reasons are not by any means apparent, strain differences in Rhizobium may be involved. The importance of interactions between bacterial strain, host variety, and root temperature has been established by Gibson (1962).

As a rule, Mediterranean annuals are principally self fertilized (Fryxell, 1957), *Lolium rigidum* being a notable exception. Stebbins (1957) in a discussion on reasons for the origin of self fertilization, remarked on the fertility insurance conferred on self-fertilized plants subjected to the periodic droughts and annual fluctuations in a Mediterranean-type climate. But particular attention was drawn to a notion (due originally to H. G. Baker) concerning long distance dispersal. As Stebbins has argued (1957, p. 344): "Accidental long distance dispersal of a single propagule can lead to establishment of a colony only in a species capable of self fertilization. If the type thus established is well adapted to its newly found ecological niche, it can spread throughout the area where these conditions are found, even though its capacity for genetic variation is much reduced."

[2] A more general account of subspeciation has recently appeared (Morley and Katznelson, 1966) in which the Tallarook group has been designated *T. subterraneum* ssp. *subterraneum*.



It seems clear that many species, and probably strains also, have migrated from the Mediterranean Basin to each of the other four main areas with Mediterranean climates. But no obvious migration patterns have emerged, perhaps because of effects of chance over the comparatively short period of migration. What is not clear is whether new species or varieties have arisen on any significant scale since migration, thus adding a further component to the broad differences in floristic patterns.

### B. Climatic

Relatively little has been published on variation in botanical composition due to general climatic conditions within any geographic region. The increasing abundance of perennials (mainly perennial grasses) as rainfall increases (Talbot *et al.*, 1939; Crocker and Tiver, 1948) is to be expected. It seems that, by and large, the most important annual species have wide climatic tolerances with respect to rainfall, if not temperature also. However, the relative importance of a species may well be dependent on general climate, or more particularly on length of growing season. In the southwestern part of Western Australia, for example, where light-textured slightly acid soils are widespread, capeweed (*C. calendula*) is usually a dominant species over a rainfall range of about 12 to 25 inches, but becomes less frequent as rainfall increases beyond 30 inches; this may hold for erodium (*E. botrys*) also. On the other hand, *Bromus rigidus* becomes less important as rainfall decreases, being replaced by *B. rubens* and *B. madritensis*.

There is firm evidence for the influence of climate on distribution at the subspecific level for the sown legume subterranean clover (*T. subterraneum*) in southern Australia. Trumble (1937a) first drew attention to the importance of length of growing season or "influential rain period" for delimiting adaptation in South Australia. He considered that a maximum growing season of 6 months was required for the Dwalganup (early) strain, and 7.5 months for Mt. Barker (mid-season). Rainfall per se was not the key factor, since Trumble's "influential rain period" was based on monthly ratios of precipitation to evaporation. Donald (1960) has since reviewed the subject of subterranean clover distribution in relation to climatic factors, and presents evidence for two temperature boundaries, warm and cold, in addition to the now well known arid boundary. For Mediterranean conditions, however, the arid boundary is by far the most important. As Donald (1960) has pointed out, in the typical Mediterranean climate of southwestern Western Australia, a growing season of 7 months may suffice for the Mt. Barker strain and about 4 months for early strains. Indeed, recent studies by Millington (1960) and G. B. Taylor (unpublished) with early strains Geraldton and Northam A suggest that the arid boundary is less than 4 months. The arid boundary has gradually been extended into lower rainfall areas, at least in Western Australia, largely due to early flowering strains, and it is interesting to speculate whether the limit has yet been reached. The interesting very early strain Carnamah, described by Rossiter and Millington (1961) has not, to date, proved successful, so that the solution may well lie in directions other than extreme earliness of flowering.

Although maturity grading, a measure of earliness of flowering (Rossiter, 1959), is generally recognized as a principal factor governing distribution of clover strains in a Mediterranean environment, no close correlation has been found between maturity grading (M.G.) and length of growing season for Australian strains. Donald (1946) found $r = +0.55$ for 13 Australian strains, while the writer found $r = +0.56$ for 20 "local" strains in Western Australia. Furthermore, for any given site, a range of strains with divergent M.G.'s, may be found (Morley, 1961). In a recent paper (Rossiter, 1966) I have discussed the question of success and failure of subterranean clover strains in a Mediterranean environment. The general significance of M.G., or more particularly of seed producing capacity in pure swards, to success or failure is clear. But the patterns depend on the particular ecological situation. In any case, several strains may successfully cohabit, and factors which at present are unknown appear to determine success among high seed-yielding strains.

Evidence for the importance of strains among sown pasture species is also available for two other plants. The commercial strain of barrel medic (*Medicago tribuloides*) has proved very successful on moderately heavy-textured alkaline soils of the Australian wheat belt (Amor, 1965). For the drier parts of Western Australia, however, the earlier flowering Cyprus strain seems more successful (Argyle, 1962). Also in Western Australia, the early Merredin strain of Wimmera ryegrass (*Lolium rigidum*) is better adapted than the commercial strain to the drier wheat belt (Reeves and Fisher, 1960).

Reverting to the resident (or volunteer) annuals, it would be surprising, in view of the wide climatic tolerances for many species, if climatic ecotypes did not exist. This provides an interesting field which, to date, has received scant attention. According to Hiesey and Milner (1965), only a small fraction of the world's plant species has been examined for the presence of ecological races. Knowles (1943) in a study of populations of soft bromegrass (*Bromus mollis*) in California, separated two ecotypes—an early maturing interior ecotype, and a later coastal one—with additional strain variation in each. The two ecotypes differed mainly in time from sowing to heading (*c.* 180 days and 155 days for the coastal and inland ecotypes, respectively). This annual grass is much more important as a component of annual-type pastures in California than in southern Australia, for reasons that are not clear. In Western Australia, local strains are later flowering than the inland Californian ecotype. This may provide a partial explanation, but results from current field studies with early strains are not encouraging.

McKell *et al.* (1962b) examined populations of medusa head (*Taeniatherum asperum*), a fairly recently introduced annual grass in the western United States. They found a relation between rate of seed germination and mean annual rainfall, but argued that insufficient time (*c.* 60 to 70 years at most) had elapsed for much ecotype differentiation to occur, and that many strains may represent geographic races. This situation appears somewhat similar to that in *Bromus carinatus*, where a very large number of races (or strains) has been reported (Harlan, 1945).

### C. Edaphic

Perhaps the most striking illustration of the importance of the soil factor is shown by the legume component on light-textured acid soils as against heavier-textured alkaline soils; these soils often occur in close juxtaposition in the wheat belt areas of Western Australia. Trumble and Donald (1938a) first drew attention to this in South Australia in areas with a growing season of $< 7.5$ months. They observed that the "naturalized" bur medic (*Medicago polymorpha*) and especially barrel medic (*M. tribuloides*) were highly suited to the calcareous alkaline soils, on which subterranean clover was not successful; the Dwalganup strain of *T. subterraneum* was, however, suited to the nonalkaline soils. The agronomic advantages of barrel medic over common bur medic have been mentioned by numerous workers (e.g., Trumble, 1939; Carlin, 1958; Amor, 1965). There is some evidence that another species, harbinger medic (*M. littoralis*) is better suited than barrel medic to the light-textured "mallee" soils of South Australia (Crawford, 1962) and Victoria (Mann, 1959).

Reasons for the differential soil preferences of clovers and medics are as yet not completely understood: they appear to be complex. Jensen (1943) showed that the pH levels for satisfactory root nodule formation are higher in lucerne than in subterranean clover. The review of Millikan (1961) indicates that subterranean clover is appreciably more susceptible to zinc deficiency than is lucerne. The molybdenum requirements for N fixation may be higher in medics than in clover (Anderson and Thomas, 1946; Andrew and Milligan, 1954). And calcium, nitrogen, phosphate, and aluminum nutrition appear to be involved (Munns, 1965). On the other hand, Aitken and Davidson (1954) observed satisfactory growth of subterranean clovers and medics (bur and barrel) in pot culture over a pH range of 4.8 to 9.3 on four soils. Their evidence suggested that the natural occurrence of annual medics on alkaline mallee soils is largely due to higher seed production—relative to subterranean clovers—following dry conditions at flowering. Yet medics may not be outstanding for drought resistance. Argyle (personal communication) at Merredin in Western Australia found that seed yield in barrel medic was reduced from 422 pounds/acre to 152 pounds per acre as a result of moisture stress during reproductive development. The failure of barrel medic on moderately acid soils may sometimes be due to deleterious effects of pathogenic organisms on seedling emergence (Kleinig, 1965).

Comprehensive ecological studies on "naturalized" annual species of *Medicago* in the Macquarie region of New South Wales (Andrew and Hely, 1960; Hely, 1962; Hely and Brockwell, 1964) have shown the overriding importance of the edaphic factor in determining distribution. Medics are well adapted to this region where, although rainfall is distributed about evenly through the year (mean annual rainfall about 15 to 20 inches), effective rainfall is confined essentially to the winter months. The frequency of *Medicago* was low where surface soil pH was < 6.5, *M. minima* and *M. laciniata* being the commonest species, and *M. polymorpha* being rare. *Medicago polymorpha* showed the greatest tolerance to poor drainage conditions, while *M. tribuloides* was common only on the black earths. This tolerance of bur medic to wet situations may be due in part to resistance to pathogenic organisms causing "damping-off." In pot culture work, Andrew (1963) found that *M. minima* was much more susceptible than *M. polymorpha*. Bur medic also tolerates saline conditions better than *M. minima* (Greenway and Andrew, 1962). On acid soils of moderately high rainfall, the Yarloop strain of *Trifolium subterraneum* has long been recognized for high adaptation to waterlogged conditions (Quinlivan, 1962). Like many species suited to such habitats, it is extremely shallow-rooted (Humphries and Bailey, 1961; Ozanne *et al.*, 1965).

Pastures of the southeast of South Australia were surveyed in detail some years ago by Crocker and Tiver (1948) and Tiver and Crocker (1951), using the point quadrat method. The influence of soil type as a modifying factor in botanical composition emerges from their data, although such effects are frequently overriden by other factors, e.g., trace element deficiencies and sowing of subterranean clover. On the meadow podzolic soils, silvergrass (*Vulpia myuros*), bromegrass (mostly *B. rigidus*), and barley grasses (*H. leporinum* and *H. hystrix*) were the most important of the annual grasses. Of the herbs, volunteer clovers (mostly *T. dubium, T. campestre, T. cernuum, T. glomeratum*) and *Erodium* spp. were prominent in the absence of subterranean clover; and capeweed (*C. calendula*) was prominent in its presence. The deep phase terra rossa soils were generally similar to the meadow podzolics in botanical composition. But on the shallow phase terra rossas, subterranean clover was almost completely absent, being replaced by *T. scabrum* and other clovers, in addition to medics (*M. polymorpha* and *M. minima*); the grass *Lagurus ovatus* was also prominent. On the coastal calcareous dune sands, where absence of legumes was due essentially to trace element deficiencies, *Bromus madritensis* and *Largurus ovatus* were the dominant species.



Where comparisons are appropriate, the relations between edaphic conditions and floristic composition in Western Australia resemble those in South Australia. For regions where the growing season is too short for the Mt. Barker strain of subterranean clover, the relations are summarized very generally in the accompanying tabulation.

| Dominant species | Light to medium-textured acidic soils | Medium to heavy-textured alkaline soils |
|---|---|---|
| Legumes | *Trifolium subterraneum* (Dwalganup and Geraldton strains) | *Medicago tribuloides*<br>*M. minima*<br>*M. polymorpha* |
| Grasses | *Bromus rigidus*<br>*Vulpia myuros* | *Hordeum leporinum*<br>*Lolium rigidum* |
| Miscellaneous herbs | *Cryptostemma calendula*<br>*Erodium botrys* | *C. calendula* |

Deep sandy soils are common in Western Australia, and on these *T. subterraneum* is often difficult to maintain. Lupines (*Lupinus digitatus* and *L. angustifolius*) are a feature of such soils, provided suitable management practices are adopted (Gladstones, 1960). However, the possibilities of serradella (especially *Ornithopus compressus*) as a pasture legume are being currently explored (Gladstones and Barrett-Lennard, 1964). Both lupines and serradella are deep-rooted, as compared with subterranean clover and barrel medic (Ozanne *et al.*, 1965), and this may enable the former species to tap additional nutrients at depth (e.g., potassium) and also subsoil moisture. Root nodulation failure is also less common in lupines and serradella (Parker, 1962).

In the annual-type pastures of California, bur medic (*M. polymorpha*) seems to be much more important, relative to southern Australia, on non-alkaline granitic soils. But this species, together with *Erodium cicutarium* and wild oats (*Avena fatua*) is more abundant on the heavier soils than on the light ones; and likewise *Trifolium* spp., *Erodium botrys*, soft brome (*B. mollis*) and *Festuca megalura* are more prominent on lighter soils (Bentley and Talbot, 1951). An interesting example of the importance of the edaphic factor is provided by a comparison of swales and slopes at the San Joaquin Experimental Range (Bentley and Talbot, 1951). Swale

TABLE II

Mean Botanical Composition for Swales and Slopes on San Joaquin Range[a]

| Plant | Per cent composition | |
|---|---|---|
| | Swales | Slopes |
| *Bromus mollis* | 3 | 28 |
| *Festuca megalura* | 20 | 10 |
| *Hordeum hystrix* | 42 | — |
| Total grasses | 67 | 46 |
| *Erodium botrys* | 11 | 39 |
| *Trifolium* spp. | 8 | 3 |
| Other legumes | 1 | 5 |
| Other forbs | 6 | 6 |
| Grasslike plants | 7 | — |

[a] From Bentley and Talbot (1951).

areas remain green for 2 to 3 weeks longer than slopes, and produce about twice as much herbage. Botanical composition data, calculated as 4-year means, are summarized in Table II.

The low percentage of legumes may perhaps be explained by the protection from grazing which the areas received before sampling (in May). There are two main points of interest: first, the much higher proportion of *Erodium botrys* on the slopes than in the swales; and second, the difference in the grass components. Under broadly comparable mean rainfall and temperature conditions at "Glen Lossie" Field Station, Kojonup, in Western Australia, lower lying areas (swales) are also dominated by *Hordeum hystrix*, but such areas are often slightly saline.

## III. Factors Affecting Yield and Botanical Composition on the Same Site

### A. Fertilizers

Some of the most spectacular effects on botanical composition, and on total yield, at least in pastures sown to subterranean clover, have resulted from the use of trace elements. One of the earliest of these effects was the molybdenum response in clover found by Anderson (1942) in



South Australia. Another was the zinc response in subterranean clover observed by Dunne and Elliott (1950) in Western Australia; in the absence of applied zinc, the 2 clovers *T. cernuum* and *T. dubium* and also Wimmera ryegrass made excellent growth. Many other examples are reported in the literature (e.g., Stephens and Donald, 1958).

Only the more important of the *major* nutrients will be considered here.

#### 1. *Potassium*

Responses in clover on K-deficient soils were reported more than 30 years ago (see Stephens and Donald, 1958) and are now well documented. An interesting example of differential species response on a deep sandy soil at Perth, Western Australia (Rossiter, 1947) is tabulated below.

| Species component | Dry matter yield (g./m.$^2$)[a] | |
|---|---|---|
| | − K | + K |
| *Trifolium subterraneum* | 187 | 316 |
| *Lupinus digitatus* | 1027 | 874 |
| *Lolium rigidum* | 16 | 25 |
| Other species | 30 | 14 |
| Total | 1260 | 1229 |

[a] 100 g./m.$^2$ = 892 pounds per acre.

Gladstones *et al.* (1964) have recently confirmed the observations that lupines are more tolerant of K deficiency than is subterranean clover. Asher and Ozanne (1961) considered that the superior capacity of lupines to grow on K-deficient soils may be related to lower root cation exchange capacity (C.E.C.), viz., 19 meq./100 g. dry weight compared with a value of 27 for subterranean clover. These workers also thought that the inability of this clover to compete with annual grasses on deficient soils, as found by Fitzpatrick and Dunne (1956) in Western Australia, might be explained in terms of root C.E.C. Further studies by Asher (unpublished thesis) showed large species differences in response to K concentration in nutrient solution. The species could be ranked as follows for K concentrations required for the plants to achieve 50% of maximum growth: lupines < silvergrass < Wimmera ryegrass < ripgut bromegrass = serradella < erodium < rose clover = subterranean clover < capeweed < barrel medic. Although there is some conformity to the root C.E.C. values given previously, Asher found no correlation over the 11 species for which values were available. In the field, rooting depth may also be important, as indicated earlier, and the deep-rooting nature of capeweed may well compensate for poor absorption at low solution

## 2. *Sulfur*

Except where ordinary superphosphate is regularly used, sulfur deficiency is not uncommon on annual-type pastures in southern Australia or in California. This deficiency has not been recognized until recent years (Stephens and Donald, 1958), and the first recorded response on a "natural" pasture in Australia was by Hilder and Spencer (1954) where *Medicago* spp. (*M. polymorpha* rather than *M. minima*) responded more than grasses. In California, following the early work of Conrad *et al.* (1947), sulfur responses were observed on the San Joaquin Experimental Range (Bentley and Green, 1954; Bentley *et al.*, 1958; Wagnon *et al.*, 1958). Total herbage production was increased by almost 60 per cent (5-year period). Initial responses were characterized by a stimulation to clover growth (mostly *T. microcephalum*) as shown by botanical composition data calculated from Table 1 of Bentley and Green's paper (see tabulation below).

| | Grasses | Clovers | Other legumes | Erodium | Misc. forbs |
|---|---|---|---|---|---|
| – S | 66% | 10% | 4% | 16% | 4% |
| + S | 62% | 24% | 1% | 8% | 4% |

Sulfur responses have since been reported elsewhere in California (W. A. Williams *et al.*, 1956; M. B. Jones, 1963a, 1964). Moreover, McKell and Wilson (1963) have suggested that rose clover may be better adapted than subterranean clover to low levels of soil sulfur. A feature of these field responses is the ultimate increase in annual grass production following the initial legume response. That the grass response is not entirely due to soil nitrogen build-up was shown by Walker and Williams (1963); soft brome, but not the forbs, responded to sulfur in the presence of applied nitrogen.

## 3. *Nitrogen*

The use of nitrogen fertilizers on Californian rangelands, at rates of up to almost 80 pounds N per acre has resulted in total yield increases of more than 3-fold (Hoglund *et al.*, 1952; M. B. Jones, 1960). Nitrogen fertilization can lead to earlier depletion of soil moisture in spring, and thus retard the growth of summer weeds (McKell *et al.*, 1959). This depletion is apparently not associated with deeper rooting (McKell *et al.*, 1962a). At high levels, nitrogen can stimulate the growth of sown perennial grass (Martin *et al.*, 1964). Invariably, N has decreased the proportion, and usually the yield, of clovers. An example of N effects on yield and composition is given in the tabulation below from M. B. Jones (1963b); the data are averaged from two fairly comparable sites sampled in April, 1957.



| Treatment | Dry matter yield (pounds/acre) Soft brome | Total grasses | *Erodium* | Clover | All species |
|---|---|---|---|---|---|
| No N | 310 | 670 | 910 | 280 | 2260 |
| 160 pounds N per acre | 670 | 1460 | 2430 | 40 | 4280 |

These figures may be compared with those (Rossiter and Pack, unpublished) from a 14-year-old Dwalganup clover pasture at Perth, Western Australia, which had been top-dressed regularly with superphosphate and received N for the first time in 1954. Plots were sampled in September of that year (see tabulation below).

| Treatment | Dry matter yield (pounds/acre) Ripgut brome | Total grasses | Capeweed | Clover | All species |
|---|---|---|---|---|---|
| No N | 740 | 835 | 690 | 1465 | 2990 |
| 150 pounds N per acre | 2350 | 2620 | 2130 | 100 | 4850 |

Here, the effect of N on the clover component was relatively greater. The prospect of losing subterranean clover has, no doubt, inhibited the use of nitrogen fertilizers on clover pastures in southern Australia.

The striking effects of N supply (with phosphate nonlimiting) on the associated growth of subterranean clover and Wimmera ryegrass, were demonstrated in the early pot-culture study of Trumble and Shapter (1937). At high N supply, the clover was suppressed, almost to extinction. Elegant studies conducted much later by Stern and Donald (1962a,b), again with these two species, were directed to the importance of light relationships in the mixed swards, at various levels of N supply. Yield of clover showed direct dependence on light energy supply at the clover leaf "surface"; and it was concluded that heavy shading by grass, resulting from high N supply, may lead ultimately *to elimination of the clover component from the sward.* There seems little, if any, doubt that the mechanism so clearly set out by Stern and Donald has been the reason for many failures of clover in the field where unduly low stocking rates have been used. Nevertheless, moderately low levels of N may be useful under some conditions for stimulating total pasture production while still retaining the clover, provided that stocking rates are high (E. A. N. Greenwood *et al.*, unpublished).

R. A. Evans (1960), in California, conducted a pot-culture study with *Erodium botrys*, *Bromus mollis*, and *Festuca megalura*, grown singly and in combination. He found that differential N uptake and also shading were responsible for the dominance of erodium and soft bromegrass when all three species were grown together. The ability of erodium, under such conditions, to assume an erect growth habit, an ability shared with capeweed, is of particular interest. Both erodium and capeweed become extremely prostrate under high grazing pressure in the field, and are thus very "plastic" species.

Little is known of interactions between N supply and other factors, e.g., temperature. These may be complex, as found by M. B. Jones *et al.* (1963) in *Bromus mollis*. The growth response to fertilizer N was greatest where soil temperatures averaged 8°C. to 13°C.; there was little response below 7°C.

### 4. *Phosphate*

The widespread use of subterranean clover in southern Australia has been dependent in large measure on the associated use of superphosphate, and the "sub and super" story has been frequently recounted (e.g., Underwood, 1951). But even on "natural" pastures, superphosphate has had profound effects not only on total yield and, of course, animal production, but also on botanical composition. The early work of Trumble and Frazer (1932) is of particular interest. On a pasture at the Waite Agricultural Research Institute, Adelaide, dominated initially by perennials (mostly *Danthonia* spp.) they found that superphosphate, applied at 185 pounds/acre/year gave mean increases of about 50 per cent in herbage production and sheep-carrying capacity over a 7-year period. Throughout this period, the control plots showed comparatively little variation in botanical composition, *Danthonia* constituting about 40 to 50 per cent of the total herbage. For the plots treated with superphosphate, the changes in dominant species are tabulated below.

| | |
|---|---|
| 1st year | *Trifolium* spp. (70 per cent) |
| 2nd year | *Vulpia* spp. + *Trifolium* |
| 3rd year | *Erodium botrys* |
| 4th year | *Erodium botrys* + *Trifolium* |
| 5th year | *Vulpia* spp. + *Erodium botrys* |
| 6th year | *Echium* (50 per cent) |
| 7th year | *Echium* (75 per cent) |

The clovers were mostly *T. arvense* and *T. glomeratum*, and the *Echium* sp. was *E. plantagineum* (Salvation Jane or Paterson's Curse). Some of the differences between years were due to seasonal conditions—a factor to be discussed later—but the time sequence generated by superphosphate, viz., *Danthonia* → clovers → nonclovers, is well established (Trumble, 1935; Donald and Williams, 1954; Moore and Biddiscombe, 1964). Results of other early studies at Kybybolite, South Australia (J. G. Davies *et al.*, 1934) even suggested an alternating cycle of grass and clover dominance, following the initial upset of equilibrium.



The South Australian workers (Trumble and Donald, 1938b) soon extended their studies to sown pastures. They made the important point, from regression analyses, that the N accumulated (from subterranean clover growth) in the previous year was highly significant in determining grass growth in the early part of the growing season, but that *later* in the season phosphate assumed a major role in grass growth. On many soils of low inherent fertility, especially in respect to N status, in the southwest of Western Australia, pastures sown to the Dwalganup and/or Yarloop strains of subterranean clover may remain very clover dominant (> 70 per cent clover) for 5 to 8 years, especially if stocking rates are high. Such pastures have frequently been associated with "clover disease," a breeding disorder in sheep induced by the intake of plant estrogens (Bennetts *et al.*, 1946).

The effects of phosphate supply per se on floristic changes are difficult to disentangle in the field, because of the concomitant changes in N supply associated with the legume. However, in a recent experiment (Rossiter, 1964), I assessed the long-term effects of varying phosphate supply on botanical composition of a sown pasture—after the changes elicited by *initial* phosphate application had abated. The ecological patterns proposed are tabulated.

| Phosphate supply | Dominants | Subdominants |
|---|---|---|
| Low (no applied phosphate) | *Erodium botrys*<br>*Hypochoeris glabra* | *Vulpia* spp.<br>*T. subterraneum* |
| Intermediate | *T. subterraneum*<br>*E. botrys* | *Vulpia* spp.<br>*Cryptostemma calendula* |
| High | *Bromus rigidus* (or *Hordeum leporinum*)<br>*C. calendula* | *E. botrys*<br>*T. subterraneum* |

Some further data of interest are provided by Crocker and Tiver (1948) on a 20-year-old natural *Danthonia* pasture at Kybybolite, South Australia. Table III has been derived from their table.

In the Kybybolite experiment, differences between the two rates of applied superphosphate were of minor importance compared with the dramatic change, due to phosphate, from *Danthonia* dominance to clover-erodium dominance. In the Kojonup experiment (Rossiter, 1964), native *Danthonia* spp. and *Stipa* spp. were rigorously excluded, but they invaded and eventually dominated adjacent areas which had become very deficient in phosphate. Again, in both experiments, ripgut bromegrass and capeweed were the dominant species under high phosphate supply where subterranean clover had been previously introduced.

TABLE III
The Effects of Superphosphate on Botanical Composition of a Pasture, Initially *Danthonia* Dominant, after 20 Years[a]

| Species component | Superphosphate (pounds/acre/year) Nil | 90 | 180 | 180[b] |
|---|---|---|---|---|
| *Danthonia* spp. | 59 | 5 | 1 | — |
| *Vulpia* spp. | 8 | 12 | 8 | 5 |
| *Hordeum* spp. | — | 7 | 3 | 8 |
| *Bromus rigidus* | — | — | — | 43 |
| Other grasses | 13 | 1 | 2 | 1 |
| *Trifolium* spp. (nat.) | 3 | 44 | 62 | — |
| *T. subterraneum* | — | — | — | 30 |
| *Erodium botrys* | 2 | 29 | 22 | 2 |
| *Cryptostemma calendula* | — | 1 | 1 | 10 |
| Miscellaneous herbs | 15 | 1 | 1 | 1 |

[a] From Crocker and Tiver (1948, p. 14).
[b] Subterranean clover was introduced accidentally.

A unique set of data is given by L. F. Myers and Moore (1952) on changes in a winter weed population of a citrus orchard, due to fertilizer treatment. A summary of their point quadrat results, obtained more than 20 years after treatments began, is tabulated below:

| | Number of hits/300 needles Control | N | P | N + P |
|---|---|---|---|---|
| Capeweed | 217 | 474 | 201 | 302 |
| Bur medic | 40 | 0 | 304 | 11 |
| Grasses[a] | 48 | 81 | 61 | 432 |

[a] Annuals, mainly *Hordeum leporinum*, *Bromus catharticus*, and *Poa annua*.

There was no winter irrigation, and no grazing. The continued dominance of bur medic on the P only plots suggested that fixed nitrogen was diverted to the citrus crop. The high capeweed dominance with N only may possibly indicate the superior competitive capacity of capeweed at low phosphate supply, rather than a low requirement for phosphate.

Results from culture solution experiments by Asher and Loneragan (1966) are relevant to the above field studies. The response of 8 winter annuals to phosphate concentration was measured after a growth period of 4 weeks. All species made appreciable growth at the low concentration of 0.2 $\mu M$ phosphate. However, maximum growth was reached at widely different phosphate levels: 1 $\mu M$ for silvergrass; 5 $\mu M$ for erodium, subterranean clover, lupines, ripgut bromegrass; slightly $> 5\ \mu M$ for capeweed; and at least 24 $\mu M$ for barrel medic and flatweed. As the authors point out, these species responses are in general agreement with the pattern of dominants observed in the field study by Rossiter (1964); they also support the results of Crocker and Tiver given earlier. However, there is an obvious discrepancy with flatweed (*Hypochoeris glabra*). The high P requirement indicated by the solution culture work suggests that this species may have an exceptional ability to absorb phosphate from difficultly available sources in the field. Unfortunately, no data comparable to those for other annuals for depth of rooting (Ozanne *et al.*, 1965) or for root C.E.C. (Asher and Ozanne, 1961) are available.



Millikan (1961) in Victoria has shown from solution culture studies that the naturalized cluster clover (*T. glomeratum*) may be more sensitive than subterranean clover to phosphate deficiency. This may perhaps be relevant to Crocker and Tiver's observation (see Table III) that the proportion of native *Trifolium* spp. remained very high, even with high phosphate supply.

## B. Seasonal Conditions

### 1. *Between-Year Variation*

It is common knowledge among graziers that total pasture production differs from year to year, particularly in low rainfall areas. For a "natural" pasture at Adelaide, South Australia, Trumble and Cornish (1936) showed that rain at critical periods, rather than total annual rainfall, determined total pasture yield. The correlation ($r = +0.95$) was strongest for the April–June period inclusive, coinciding with the early stages of pasture growth. In addition, November rainfall, which was negatively correlated with April–June rainfall, showed a high negative correlation with total yield. The possibility of using deep-rooted perennials to utilize late spring rains was suggested. Newman (1963) and J. N. Black (1964) have recently stressed the importance of early germination date for the production of winter annuals. At Kojonup, Western Australia, pasture production even in early August was related neither to autumn rainfall nor date of opening rains (Rossiter, 1964), a lack of correlation due possibly to periods of moisture stress not revealed by figures for monthly rainfall. Low winter temperatures may also limit total yield, as observed by Talbot and Biswell (1942) in California.

That the prominence of certain species in annual-type pastures was dependent on particular seasonal conditions, as between one year and another, was well recognized by Trumble and Frazer (1932) in South Australia and by Talbot *et al.* (1939) in California. The expressions "good clover year" and "poor clover year" have long been used in both countries. An early illustration of year to year variation is given (see tabulation), based on the Californian survey data of Talbot and Biswell (1942), as percentage herbage cover.

| Species | 1935 | 1936 | 1937 | 1938 | 1939 |
|---|---|---|---|---|---|
| *Erodium botrys* | 34 | 42 | 33 | 15 | 28 |
| *Bromus mollis* | 1 | 20 | 32 | 17 | 27 |
| *Festuca megalura* | 14 | 17 | 9 | 10 | 13 |
| *Trifolium* spp. | 6 | 1 | 1 | 11 | 4 |

An example of extreme fluctuations is reported by Talbot *et al.* (1939) for 1934 (very "poor" year) and 1935 (very "good" year) for the southern part of the San Joaquin Valley. It seems significant that only 3 species—*Erodium cicutarium*, *Lepidium nitidum*, and *Bromus rubens*—made up 97 per cent of the herbage area in the dry year, while 15 species were implicated for this percentage figure in 1935. Moreover, *Erodium cicutarium* declined from 70 per cent in 1934 to < 30 per cent in 1935. The importance, particularly in practice, of changes in total yield of forage from year to year has, of course, been emphasized by the above workers. Yet the significant role that drought-resistant species such as *E. cicutarium* may play in a dry year also requires emphasis.

Talbot and Biswell (1942) also recognized the importance of date of "opening" rains (i.e., commencement date for growing season) in relation to botanical composition. *B. mollis* and *E. botrys* were likely to be abundant with early effective rains, while late rains favored a greater range of species, including legumes.

More recent studies have been done by Heady (1958, 1961) at Hopland Field Station in Mendocino County, California. In the first paper, where three distinct sites were involved, he drew attention to year to year changes, mentioning especially the contrast between 1953 (a grass-dominant year) and 1955 (favorable to *Erodium botrys*). The importance of weather conditions during seedling establishment was again stressed, and the observation was made, in the early autumn of 1954, that seedlings of *E. botrys* and *B. mollis* survived drought conditions, whereas those of *Medicago polymorpha* did not. Further data, but from ungrazed plots, are given in Heady's 1961 paper, for an 8-year period. Over this span, the range in percentage composition at the end of the growing season was as follows: *Bromus mollis*, 5 to 21 per cent; other grasses, 18 to 66 per cent; legumes, 1 to 17 per cent; *Erodium botrys*, 6 to 45 per cent; and other broad-leaved plants, 6 to 32 per cent. The high rainfall (60 inches) of 1958 was associated with extreme grass dominance, but the much lower rainfall, and especially the extended dry periods, of 1960 led to *Erodium* dominance. The drought resistant properties of *Erodium* were known to the early South Australian workers: L. J. Cook (1942) at Kybybolite observed that both erodium and capeweed were favored by dry seasons, whereas "clover likes wet seasons."



Seasonal conditions were shown to be especially important during the years of directional change set in motion by the use of superphosphate. When the non-clover-dominant stage is reached, often after 3 to 5 years, the clover may virtually have been eliminated from the pasture. This is the "stalled" condition which was investigated in Western Australia by Meadly (1946). One of the main factors, perhaps the most important, was the periodicity of rains at the beginning of the growing season. An early "break" (opening) followed by a dry spell frequently resulted in loss of clover seedlings, and subsequent dominace by *Erodium*. Clearly, repetition of this pattern could lead to complete loss of the clover after hard seed reserves are exhausted.

Examples of extreme changes in botanical composition are given by Tiver and Crocker (1951) for the southeast of South Australia. One of these (as percentage cover from their Fig. 9) is tabulated below.

| | 1945 | 1946 | 1947 | 1948 | 1949 |
|---|---|---|---|---|---|
| Annual grasses[a] | 25 | 3 | 9 | 21 | 54 |
| Sub. clover | 12 | 90 | 48 | 72 | 33 |
| Capeweed | 58 | 6 | 43 | 7 | 13 |
| Other spp. | 5 | 1 | 1 | 1 | — |

[a] Mostly *Bromus rigidus*.

At this locality (Kybybolite), opening rains usually begin in March or April. In 1946, however, the season opened in mid-January, with good subsequent rains. Subterranean clover germinated profusely, much more so than other species, and dominated (90 per cent) the pasture. In 1945 and 1947, although unusually early germinating rains occurred, subsequent drought periods led to heavy seedling mortality in grasses, and especially in the clover, whereas capeweed largely survived. Thus capeweed, as well as *Erodium*, seems highly resistant to moisture stress during early vegetative growth.

Further evidence on seedling persistence during temporary drought comes from studies by Biddiscombe *et al.* (1954) at Trangie, N.S.W. The two species, *Erodium cygnorum* and *Hordeum leporinum* (barleygrass), survived better than *Medicago* spp.

A long-term study (1953–1962) on seasonal changes was conducted on three sites, set-stocked at 2 sheep per acre, at "Glen Lossie" Field Station, Kojonup, Western Australia (Rossiter and Pack, unpublished). The fluctuations in content of subterranean clover from year to year are shown in Fig. 1. The high 1953 figure for site B—it was high also in 1952—was probably due to the area having been recently cropped to a cereal. (The other two sites had not been cropped for several years.) Fluctuations in clover content, though strong, were not violent: the peaks in 1957 and 1960 were associated with good April and March openings, respectively. Moreover, the fluctuations were greater on site A than on site B, and least on site C. Results from pasture sampling and from observation indicated that the reduced fluctuations were closely related to increased mean grazing pressure.

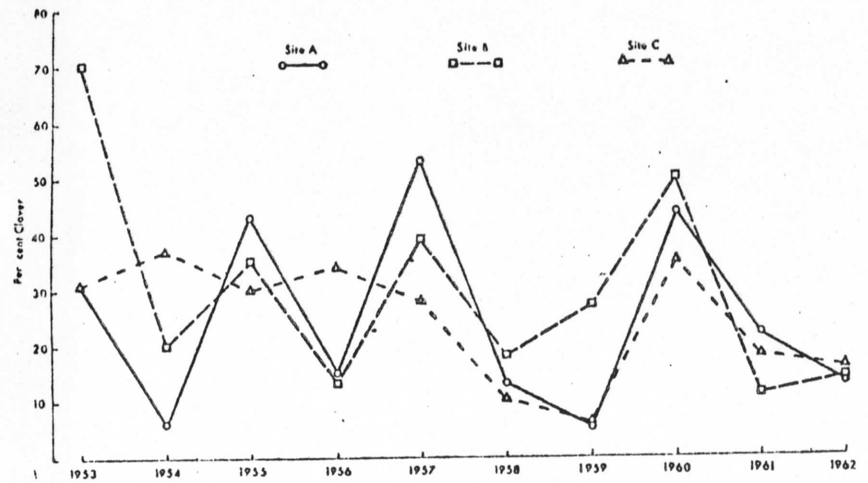


FIG. 1. Fluctuations in percentage of subterranean clover from year to year on three sites at Kojonup, Western Australia. Each percentage value represents a mean of three within-year estimates, based on dry weight. All sites set-stocked at 2 wether sheep per acre.

In 1955 and 1956, heavy early rains in February and March were followed by prolonged dry spells. The relative numbers of seedlings which survived from the early rains were as follows:

| Year | *T. subterraneum* | *C. calendula* | *E. botrys* | *B. rigidus* | *V. myuros* |
|---|---|---|---|---|---|
| 1955 | 9% | 28% | 53% | 45% | 10% |
| 1956 | 12% | 85% | 62% | 41% | 5% |

Again the superior drought resistance of capeweed and erodium seedlings is revealed, but ripgut bromegrass also performed well. The three pastures showed year-to-year changes in all species components, but over the 10-year period, sites A and B remained ripgut brome–clover dominant, and site C, capeweed–erodium–silvergrass–clover dominant.

The tendency for subterranean clover to dominate swards in years in which the season opens early, and continues without drought periods, has been repeatedly emphasized by Australian workers (Meadly, 1946; Tiver and Crocker, 1951; Tiver, 1954; Willoughby, 1954). Although the



reasons for this phenomenon will be discussed below, experimental evidence has not always supported the field observations. Results of an experiment at Perth (Rossiter and Pack, unpublished) on an old clover pasture, in which date of seasonal opening was controlled by irrigation and by covering of plots, are summarized in Table IV. The effects of opening date on early growth rate of the pasture were striking, and were presumably related to temperature. Although the late March opening was associated with early clover dominance, the February opening, in which seedling emergence and establishment were lower, resulted in capeweed dominance. This was due primarily to the unusually high growth rate of

TABLE IV
Effect of Time of Commencement of Growing Season on Early Pasture Performance: Perth (1955)

| Opening date | Estab. counts (no./dm.²): Sub. clover | Estab. counts: Capeweed | Estab. counts: Grasses | First 5-weeks growth period: Mean temp. (°F.) | Yield (g./m.²) | Sub. clover (%) | Capeweed (%) | Grasses (%) |
|---|---|---|---|---|---|---|---|---|
| February 21 | 8.8 | 6.8 | 0.7 | 77 | 60.8 | 25 | 73 | 22 |
| March 28 | 14.0 | 10.5 | 2.0 | 65 | 49.7 | 53 | 40 | 7 |
| May 2 | 4.2 | 12.0 | 4.0 | 59 | 9.1 | 21 | 68 | 11 |
| June 6 | 4.0 | 8.1 | 3.8 | 53 | 0.9 | 12 | 57 | 31 |

the capeweed seedlings for the 5-week period. Capeweed dominance with early "breaks" may thus not always be due to superior drought resistance. The low establishment counts for annual grasses with early "breaks" support Willoughby's (1954) observations at Canberra. Also of interest are the low counts for the clover in the May and June "breaks." Lowered temperatures may be implicated (see below).

A detailed competition study with subterranean clover and barley grass was conducted by D. F. Smith (1965) in "micro-swards." Treatments included two densities, two levels of N, presence and absence of early moisture stress, and two planting dates (early, April 13; and late, May 11). As might be anticipated, the clover suffered a more severe check to growth than the grass, as a result of moisture stress: dry conditions after the "break" usually favored the grass. Also, because of the more rapid decline in growth rate of the clover following the later "break" (presumably due to lower temperatures), the later "break" usually favored the grass. However, complex interactions occurred due in part to a marked stimulation to clover growth from N in the absence of moisture stress after the early "break."

Although evidence for year-to-year variation in botanical composition is overwhelming, the explanation of these changes is far from satisfactory.

Heady (1958) made the cogent comment that, for any single growing season, the relative proportions of plant species, on a number basis, were established before December of each year. For southern Australia, we need only read "June" for "December." This contention, if sound—and I think it is—leads to a consideration of factors influencing germination, seedling emergence, and early seedling growth rates of individual species and strains.

Mature nondormant seeds of winter annuals have temperature optima usually within the range 15°C. to 20°C. for maximum speed of germination, but, as a rule, are capable of germination over a wide temperature range, from slightly above 0°C. to >30°C. (Trumble, 1937b; Toole and Hollowell, 1939). Ashby and Hellmers (1955) conducted germination tests at day/night temperatures of 30/17°C., 23/10°C., and 17/4°C. and observed no appreciable treatment differences for soft bromegrass, *ripgut* bromegrass, and rose clover; they concluded that such species were likely to germinate uniformly at all seasons of the year in southern California. *Bromus rubens*, however, germinated best at 17/4°C., i.e., at "winter" temperatures. Field germination in relation to soil temperatures has been discussed by Trumble (1937b), but whether soil temperatures per se after summer rains are sufficiently high to restrict germination is unclear.

During the summer months, germination of seeds or dispersal units may be partly blocked by various dormancy mechanisms. The importance of hard-seededness in subterranean clover strains for long-term survival and seed conservation has been stressed by Morley (1961), Ballard (1961), and Quinlivan and Millington (1962). Hard-seededness is likewise important in other small-seeded winter clovers and medics (Trumble, 1937b; Toole and Hollowell, 1939; Meadly, 1947), including rose clover (W. A. Williams and Elliott, 1960); and also in *Ornithopus compressus* (Barrett-Lennard and Gladstones, 1964) and some lupines, especially *L. digitatus* (Gladstones, 1958). The proportion of hard seeds (from those set in the previous season) falls progressively over the summer months in the field (Quinlivan and Millington, 1962; G. B. Taylor and Rossiter, unpublished), and restrictions to germination of clover seed with summer rains are correspondingly eased. However, my colleagues and I have presumptive evidence that dormancy,[3] other than that due to hard-seededness, may place a further restriction on some early strains of subterranean clover (e.g., Geraldton and Northam A) compared with others (e.g., Dwalganup and Carnamah). Dormancy has been demonstrated for a number of small-seeded legumes (Grant Lipp and Ballard, 1959).

[3] The term "dormancy" is used in different ways (Evenari, 1965), often to include hard-seededness. For convenience, I shall hereafter follow Ballard (1958) and distinguish hard-seededness from other types of dormancy.



Why, then, are very early seasonal "breaks" so often associated with relatively high numbers of subterranean clover plants, and clover dominance? The reasons are by no means clear, but dormancy in the nonlegume pasture components may be involved. Although Trumble (1937b) was unable to find evidence of dormancy in annual grasses at Adelaide, South Australia, other workers have reported marked dormancy in nonclover species, e.g., Meadly (1936) for Wimmera ryegrass, Laude (1956) for 12 annual grasses, and especially for *Erodium botrys*, and Rossiter (unpublished) for several annual grasses, erodium, and also capeweed. Some of my own data for seeds collected in 1954–1955 at Perth are given below. Germination tests, commenced 1 month after seed ripeness, were done in sand, in the open, with 200 seeds per sample. Percentage germination after 21 days was as tabulated below.

| Test begun (date) | Dec. 10 | Jan. 20 | Mar. 15 | Apr. 30 |
|---|---|---|---|---|
| Mean ambient temperature (day/night) for 21 days (°C.) | 25/19 | 28/22 | 27/21 | 18/14 |
| *Bromus rigidus* (%) | 16 | 79 | 95 | 93 |
| *Bromus arenarius* (%) | 1 | 3 | 73 | 91 |
| *Hordeum leporinum* (%) | 1 | 46 | 88 | 96 |
| *Vulpia myuros* (%) | 1 | 16 | 68 | 70 |

Unfortunately, subterranean clover was not included in these tests, so that direct comparisons are not possible. But it is known that many strains, including Dwalganup and Mt. Barker, have low dormancy (Morley, 1958a).

Subsequent work confirmed the relatively low dormancy of ripgut bromegrass, and revealed large and unexplained between-site differences. In New Zealand, Harris (1961) found extremely low dormancy in *Hordeum murinum* and *Bromus mollis*. Some of the within-species differences may be due to environmental factors, e.g., differences in temperature during seed development (Grant Lipp and Ballard, 1962). In the field, dormancy of annual grass seeds may be greater than already indicated, especially if the seeds lie exposed to summer daylight. Hulbert (1955) with *Bromus tectorum*, and Cumming and Hay (1958) with *Avena fatua*, found that darkness promoted germination of dormant seed. Simulated heavy rainfall was found to promote germination in desert annuals by Went (1949) and Juhren *et al.* (1956). Leachable germination inhibitors have been detected in *Avena fatua* (M. Black, 1959), and *Hordeum leporinum* (Waisel and Adler, 1959), and prolonged leaching was found to overcome dormancy in *Bromus mollis* (Walker, unpublished data) at Perth.

D. F. Smith (personal communication) has stressed the importance of "resistance to high day temperature germination" which appears to vary considerably among annuals. In crimson clover, Hoveland and Elkins (1965) made the interesting discovery that, under an alternating temperature regime, the *initial* temperature was of key importance to germination. Clearly, further studies on temperature, and especially diurnal changes in temperature, are called for.

The rapid appearance of subterranean clover after late summer rains (Willoughby, 1954) may thus be connected with relatively low dormancy. It may also be related to speed of germination and of seedling emergence, as suggested by Willoughby (1954), a point on which critical evidence is lacking. But apart from these factors, it is commonly contended that the potential early growth rate of subterranean clover is superior to annual grass during the warmer autumn, and inferior during the colder winter (Willoughby, 1954; D. F. Smith, personal communication). Evidence on this point derived from the data of Table IV is tabulated below, as mean dry weight increase per plant during the first 5-week growth period.

| Opening date | Subterranean clover (mg.) | Capeweed (mg.) | Annual grasses (mg.) |
|---|---|---|---|
| February 21 | 17 | 64 | 20 |
| March 28 | 19 | 18 | 17 |
| May 2 | 4.6 | 5.1 | 2.4 |
| June 6 | 0.2 | 0.7 | 0.8 |

There is little support for the contention mentioned above, except that with the very late break (June 6) the growth rate of clover was lower than for other species. Further evidence on early growth rates is clearly needed.

Attention has already been drawn to the differences between species in seedling resistance to moisture stress following early "false breaks" to the growing season. It seems likely that these species differences may be accounted for largely in terms of root development. Ozanne *et al.* (1965) have shown that subterranean clover and silver grass (*Vulpia myuros*) which are susceptible to drought in the seedling stage (see p. 20) are shallow-rooted. However, moisture relations, especially in connection with liquid-seed contact, seem to be important during the germination process itself (Collis-George and Sands, 1959, 1961; Sedgley, 1963; Harper *et al.*, 1965). The subtle effects of microtopography of the soil surface on germination of *Bromus madritensis* and *B. rigidus* have been explained in terms of soil surface–awn contact, by Harper *et al.* (1965). A similar explanation may account for the superiority of *Hordeum leporinum* over *Lolium rigidum* for percentage establishment following surface-seeding (D. F. Smith, personal communication).



Apart from tolerance to moisture stress during seedling development, tolerance to heat may be important (Laude and Chaugule, 1953). With three species of *Bromus*, greatest heat tolerance occurred at day 7–8, i.e., immediately after emergence. Rapid losses occurred at about day 14, *B. catharticus* being less susceptible than either *B. marginatus* or *B. stamineus*.

Some indications of the manner in which environmental factors may influence the early growth stages of individual species have been outlined. These seem to account for some of the year-to-year variation observed in the field; but I doubt whether the field situation itself has been adequately described, let alone understood.

### 2. *Within-Year Variation*

Most investigations on seasonal changes have been concerned with year-to-year variation. However, Heady (1958) examined within-year changes on three annual-type pastures at Hopland Field Station, California, based on plant numbers per unit area. All species showed mortality as the season progressed, but larger ones (*Bromus rigidus*, *B. mollis*, and *Erodium botrys*) survived better than smaller ones. At maturity, plant densities were still high, mean total numbers for three sites ranging from 70 plants/dm.$^2$ to 200 plants/dm.$^2$ (1 dm.$^2$ = *c.* 0.1 ft.$^2$). Even higher values (180 to 790 plants/dm.$^2$) were reported by Biswell and Graham (1956), while Talbot *et al.* (1939) observed a maximum seedling density of >2000 plants/dm.$^2$ for *Festuca*.

In a study somewhat comparable to Heady's (1958), Rossiter and Pack (unpublished) in Western Australia also observed a decrease in plant density throughout the growing season. However, densities were much lower than in California; total seedling densities, for three sites over 10 years, varied mostly within 25 to 150 plants/dm.$^2$. On the other hand, the estimated densities of viable seeds, from soil samples at the end of summer, averaged about 250 seeds/dm.$^2$, a value close to that of Sumner and Love (1961) for three sites in California.

Of more interest is the within-year variation in botanical composition on a dry weight basis. Data for a well established pasture at Perth are given in Fig. 2; they are considered representative for this locality, at a year-long moderately high stocking rate (2.7 sheep per acre).

Throughout the major part of the growing season, the proportions of the pasture components—Dwalganup subterranean clover, capeweed, and annual grasses—showed relatively little change. The high percentage of clover at the first sampling (May 7) was not observed in other years, but the increase in grasses at the end of the growing season is a consistent feature each year. Winter temperatures at "Glen Lossie" Field Station, Kojonup, Western Australia (see Table I) are 3 or 4°C. lower than at Perth, but here also within-year changes in botanical composition on a subterranean clover-soft bromegrass pasture, stocked at 5 sheep per acre, were remarkably small (E. A. N. Greenwood *et al.*, unpublished data). At Canberra, however, where winter temperatures are lower than

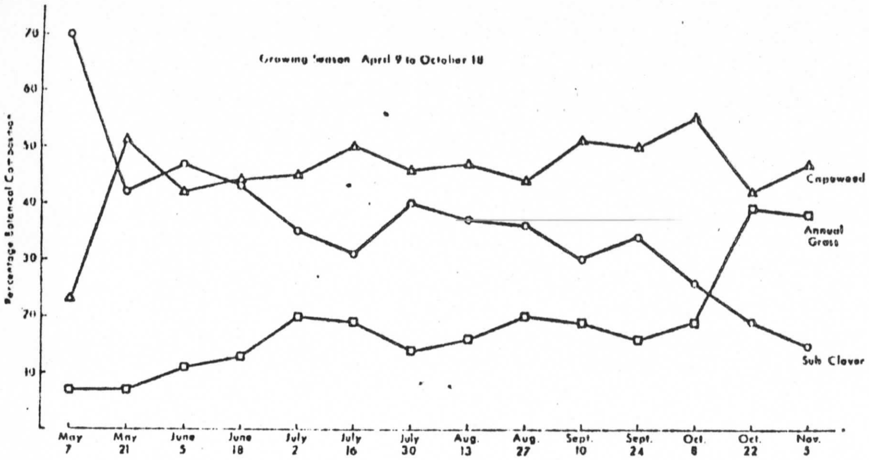


FIG. 2. Changes in the proportions (based on dry weight) of the components of an annual-type pasture during the growing season. Perth, Western Australia, 1951. Experimental area set-stocked at 2.7 wether sheep per acre.

at Kojonup, Willoughby (1954) considers that Wimmera ryegrass dominates the clover during winter, but not in autumn or early spring, provided that nutritional deficiencies are corrected.

The Western Australian data suggest that differences in growth rates between species components are small, or else that such differences, if real, are compensated by differential species consumption rate by the grazing animal. From a consideration of the growth studies conducted under controlled environment conditions (Mitchell, 1956a; Hellmers and Ashby, 1958; Mitchell and Lucanus, 1960; Rossiter, unpublished data), there is little to indicate marked species–temperature interactions for relative growth rates among Mediterranean annuals. Morley (1958b) found clear strain–temperature interactions during vegetative growth in subterranean clover. There may, moreover, be interactions during early seedling growth (see p. 24). The field situation is further complicated by defoliation, and it is possible that complex interactions occur between



species, temperature, and defoliation. Mitchell (1956b) has shown that short-term dry weight increments (at full light) following defoliation of white clover and subterranean clover were slightly higher at a mean temperature of 12°C. than at 22°C. Whether Wimmera ryegrass, or indeed other Mediterranean annuals, exhibit this behavior is not known.

Tiver (1954) has drawn attention to the importance of frost incidence in relation to botanical composition. Barleygrass, bromegrasses, and capeweed were observed to be more affected by frost than subterranean clover; hence the occurrence of several severe frosts tends to favor the clover by suppressing grasses and capeweed. Barley grass is evidently more susceptible to frost damage than Wimmera ryegrass, especially when not defoliated (D. F. Smith, personal communication). However, the damage in barley grass was negatively correlated with soil N status. Among the brome-grasses, *B. rigidus* and *B. rubens* are more susceptible to winter injury than *B. mollis*, *B. japonicus*, and *B. tectorum* (Hulbert, 1955). The latter species has extreme winter hardiness.

### C. Grazing and Defoliation

In California, complete exclusion of grazing animals from an annual-type pasture leads quickly to grass dominance, especially *Bromus rigidus* dominance, with associated loss of clovers, bur medic and *Erodium* spp. (Talbot *et al.*, 1939; Talbot and Biswell, 1942; M. B. Jones and Evans, 1960). These effects of continued protection probably apply, in general, in southern Australia also. Rossiter and Pack (1956) observed over a 7-year period that a capeweed–subterranean clover pasture was dominated by ripgut bromegrass after protection for 3 to 4 years; but eventually this grass was largely replaced by annual veldgrass (*Ehrharta longiflora*). Biswell (1956) has stated that the time trend for dominants in Californian pastures, following protection, is as follows: forbs → soft bromegrass → slender oats → ripgut brome. However, this eventual dominance by *B. rigidus* is in part a consequence of litter accumulation (see Section III, E, 2). Although interesting, complete exclosure leads to results that have doubtful—if not frankly misleading—agronomic significance.

A great deal of emphasis has been placed on grazing management, quite apart from stocking rate per se, by Californian workers. The loss of resident perennial grasses under a system of close continuous grazing (B. J. Jones and Love, 1945; D. W. Cooper, 1960) has led to an emphasis on deferred-rotation systems which will promote "desirable" species and inhibit "undesirable" ones. But such control may meet with indifferent success (Miller *et al.*, 1957) at least with sown perennial grasses—an experience shared in southern Australia (e.g., Rossiter, 1952, with the perennial grass *Ehrharta calycina*).

closures, or at low stocking rates, is presumably due (in the main) to dominance of the light environment, as shown by Stern and Donald (1962a). Changes among tall-growing species, such as the change from *Bromus rigidus* to *Ehrharta longiflora* (see p. 27) may be connected with tillering response to light intensity (L. A. Davis and Laude, 1964), differences in root development (Hironaka, 1961), or interactions of environmental factors (Donald, 1958).

Pasture swards subjected to controlled defoliation, with the object of maintaining optimum leaf area index (L.A.I.) usually give greater production per unit area than undefoliated swards, as exemplified by Davidson and Donald (1958) for subterranean clover. However, frequent and complete leaf removal must inevitably lead to greatly lowered production and eventually death. Field situations lie within these extremes. But little is known, on a comparative basis, of the way in which species respond morphologically or physiologically to defoliation or grazing, especially at high plant densities. Laude (1957) has studied the response of *Bromus mollis* to herbage removal. Growth cessation of a shoot resulted from removal of the entire terminal bud (immature inflorescence). Also, leaf regrowth occurred only if the leaf was not fully expanded when the upper part of the leaf tissue was removed; there was no leaf regrowth after full leaf expansion. Comparable studies with other annuals do not appear to be available. However, Marshall and Sagar (1965) have recently studied the influence of defoliation on the distribution of assimilates in Italian ryegrass (*Lolium multiflorum*) using $^{14}CO_2$. When a single undefoliated tiller remained, it initially supplied the defoliated tillers with $^{14}C$-products, thus reintegrating a system of apparently independent tillers. When all tillers were partially defoliated, labeled compounds were no longer translocated to the root system. A further experiment suggested that root reserves were not mobilized for regrowth following defoliation, thus supporting the main findings of May and Davidson (1958) in subterranean clover.

Further studies on herbage removal during reproductive development were done by Laude *et al.* (1957). In a greenhouse pot experiment, with repeated clippings made at 1½ inch height, soft bromegrass was found to continue tillering and heading for much longer than foxtail fescue (*F. megalura*). It was suggested that the latter species could be depressed relative to the former by continuing grazing through to termination of its growth. But whether control of the relative amounts of these two grasses could be satisfactorily effected in this way needs substantiation. In Western Australia, silvergrass (*Vulpia myuros*), the counterpart of foxtail fescue, is extremely resistant to heavy continuous grazing, more so, in fact, than is soft bromegrass. In a field study, Laude *et al.* (1957) found that *B. mollis* and *B. rubens* responded differently to single clippings early in the reproductive growth phase: increased heading and seed production, compared with uncut controls, was observed for soft brome, but not for red brome. Yet the relevance of such differences to the field situation is obscured, as the authors point out, by the fact that the inflorescences of red bromegrass are much less preferred by the grazing animal. Moreover, under most conditions, grazing pressure is seldom heavy during spring, when most plants are in an advanced stage of reproductive development. Further work by Laude and his colleagues (Stechman and Laude, 1962) has raised similar problems. Experiments with four grasses (soft bromegrass, ripgut bromegrass, Mediterranean barleygrass, and wild oats) indicate *similar reactions* to clipping treatments. And to quote the author's own words—are these "characteristics of value in estimating vigour in annual grasses?" Such characteristics can at best have only doubtful significance.



Subterranean clover is uniquely adapted to conditions of grazing or defoliation in respect of inflorescence position relative to leaf canopy, and also of seed burial. Continued defoliation *sensu stricto* will certainly reduce seed yields, but defoliation prior to flowering can *increase* seed yields compared with undefoliated swards (Rossiter, 1961). One of the factors involved is increased inflorescence production, arising from the promotion of branching. In crimson clover (*T. incarnatum*), Knight and Hollowell (1962) found that seed yields were little affected by defoliation up to April 1 (presumably, commencement of flowering stage). However, treatments in which clipping was done when the swards were 4 inches high rather than 8 inches—entailing more frequent clipping—always produced the higher seed yields. This interesting result suggests marked changes in plant morphology and perhaps other characteristics, and is worthy of further study, both in crimson clover and other annual legumes of similar general growth habit.

A major factor responsible for the persistence of such species as clovers (especially *T. subterraneum*), capeweed, and erodium under heavy grazing is the capacity of such plants to assume a prostrate growth habit, and thus sustain significant areas of photosynthetic leaf tissue. But other important factors may well be involved, in which species respond in different ways: e.g., pattern of tillering or branching, rate of leaf appearance, rate of individual leaf growth, ultimate leaf size, length of effective life of individual leaves, and (especially) root growth. However, during reproductive development, when grazing pressure is usually lowered—at least under set-stocking systems—differential selectivity of inflorescences by the grazing animal may be important. Adequate seed production must obviously be assured for species persistence in Mediter-

Despite past emphasis on the desirability of rotation systems in California, a recent experiment at Hopland Field Station, comparing set-stocking and deferred-rotational grazing, has shown no clear treatment differences in species composition (Heady, 1961). Indeed, Heady states: "Year-long grazing at reasonable stocking rates, is the best way to manage the California annual type." The present writer, and probably most agronomists in southern Australia, hold similar views on annual-type pastures.

Mowing for pasture hay, which is commonly practiced in southern Australia, often increases the proportion of clover, and reduces that of grasses, in undergrazed pastures. An increase in capeweed content may result from mowing in successive years (Crocker and Tiver, 1948).

There is remarkably little information, however, on the effects of stocking rate. In the San Joaquin experiment, where grazing was restricted each year to a grazing season of about 6 months (end of January to beginning of August), Bentley and Talbot (1951) commented on the "lack of pronounced changes" in botanical composition resulting from close through to light grazing—a range of about 2-fold in stocking rate. Consistent changes in the minor constituent, *Hypochoeris glabra*, were evident on both slopes and swales: this species was encouraged by close grazing. Again, on the swales, close grazing gave a higher percentage of *Festuca megalura* and a reduced content of *Hordeum hystrix*.

One of the features, if not the most important one, of sheep pastures in southern Australia over the last few years has been a trend to higher stocking rates. It now seems clear that many clover pastures hitherto were grossly understocked. Much of the impetus to this trend originated from studies at "Glen Lossie" Field Station, Kojonup, Western Australia, by Davies and his colleagues. H. L. Davies and Humphries (1965) found that mean wool yields (5-year period) increased from 12 to 48 pounds per acre as stocking rate increased from 1 to 5 sheep per acre. Changes in pasture composition due to stocking rates are illustrated by the data in Table V, from a stocking rate–lambing time experiment (H. L. Davies, 1966).

Similar species trends were shown toward the end of the growing season (October), when the general level of clover was much lower (c. 8 per cent), and of grasses, much higher. Further support for these composition changes is available from other studies on two sites at Kojonup (Rossiter and Pack, unpublished). Here also an increased stocking rate, from 2 sheep per acre to 4 sheep per acre, increased the proportions of capeweed and erodium, while the clover remained unaffected. However, partitioning of the annual grasses showed that while *Bromus rigidus* was markedly reduced at the higher stocking rate, silvergrass (*Vulpia myuros*) clearly increased. Somewhat similar effects of increased stocking rates were observed recently in a grazing experiment at Werribee, Victoria (Sharkey, personal communication). In terms of plant density, clovers declined slightly, barleygrass and Wimmera ryegrass showed a marked decline, while silvergrass was unaffected. This capacity of *Vulpia* to persist at high stocking rates is also evident from field observations and is in agreement with the performance of the related species *Festuca megalura* on swale areas in California mentioned earlier. The general decrease in proportion of annual grasses and the increase in capeweed, as stocking rates are raised, have been further supported by work in East Gippsland, Victoria (N. M. Elliott and B. C. Curnow, unpublished data). At the lowest stocking rate, subterranean clover was observed to decrease in percentage ground cover.

TABLE V

Mean Effect of Stocking Rate on Botanical Composition of a Sown Pasture at Kojonup, W. A.: July (1959-1961)

| Stocking rate (ewes/acre) | Per cent (dry weight basis) | | | | |
|---|---|---|---|---|---|
| | Sub. clover | Capeweed | *Erodium* | Misc. forbs | Grasses |
| 1.5 | 24 | 8 | 7 | 2 | 59 |
| 3.0 | 26 | 25 | 7 | 1 | 41 |
| 5.0 | 22 | 43 | 16 | 2 | 17 |

The above picture is somewhat at variance with the commonly held opinion, in southern Australia, that high stocking rates lead to clover dominance. There is indeed some field evidence in Western Australia to support this opinion, especially on relatively young pastures. Three pertinent situations can be envisaged: (1) available soil N supply may be inadequate to support vigorous nonlegumes; (2) adequate seed supplies of miscellaneous forbs such as capeweed and erodium, and of grasses such as barleygrass and (possibly) silvergrass, may not have reached the particular site; and (3) nonlegumes though present may be poorly adapted to the site, even when soil N supply is increased. The third situation is, I think, the most interesting, particularly because it concerns older pastures. Such situations are probably rare.

In broad terms, two main points can be made about the effects of grazing on annual-type pastures in southern Australia: (1) gross understocking usually leads to ripgut bromegrass dominance, and, more importantly to loss of clover; (2) high stocking rates result in a general loss of grasses, with pastures dominated by herbaceous plants—capeweed, erodium, and clovers.

The tendency for tall-growing species to dominate the pasture in exranean annuals; and if escape from the grazing animal is not possibly by seed burial, then some degree of unpalatability in the developing inflorescence and also the mature dispersal units seems to be a useful alternative mechanism.

### D. New Species and Strains

New plants are usually introduced into existing ecosystems because they are expected to give increased total productivity, or because they are considered "more desirable" species.

A number of perennial grasses have been recommended and tried for improving Californian rangelands (e.g., B. J. Jones and Love, 1945; Miller *et al.*, 1957) and also annual-type pastures in southern Australia (e.g., Trumble, 1949; Neal Smith, 1942). By and large, these attempts seem to have met with indifferent success, especially at moderate to high stocking rates. Where the rainfall is high (and the growing season fairly long), perennial grasses fare better (Carter, 1958) and give some stability to pasture composition (Tiver, 1954). The annual, Wimmera ryegrass (*Lolium rigidum*) is in wide commercial use in southern Australia, and although it commonly persists in pasture, it seldom dominates the grass component except on some heavy soils under low rainfall.

Subterranean clover is a classic case of successful legume introduction. Its role has been discussed recently by Morley (1961), and its influence on botanical composition is shown in Table III. Pastures sown to specified strains of subterranean clover, at least in Western Australia, frequently contain "contaminant" strains which become evident after several years. In some instances mixtures of strains are deliberately sown. The outcome of competition, and the relative success of strains of *T. subterraneum* therefore, become a matter of some importance. J. N. Black (1960, 1963) has emphasized the importance of petiole length (which differs among strains), even under defoliation, but my own long-term field studies (Rossiter, 1966) do not support this contention. Apart from seed-producing capacity under pure sward conditions, the factors remain, for the most part, obscure. Selective grazing cannot be ignored, since variability between strains in acceptability to sheep has been frequently observed.

The Californian practice of sowing a mixture of three *Trifolium* spp.—rose clover, subterranean clover, and crimson clover—led to a study by W. A. Williams (1963) which was aimed at the elucidation of some of the factors responsible for the observed fluctuations in relative amounts of these species in the field. Williams emphasized competition for light, and found a pattern of changing relationships; subterranean clover, with the least photosynthetic capacity in the seedling stage, became dominant as it reached full canopy development. Any early advantage of cotyledon size or petiole length was not sustained. These data suggest that in the absence of grazing, subterranean clover is likely to dominate a mixture of this species and rose clover. Some recent observations in Western Australia suggest the opposite; and also that, under grazing, rose clover is suppressed well in advance of the flowering stage. The selective grazing component, however, is unknown. McKell *et al.* (1962c) found that the growth rate of rose clover was more adversely affected by low winter temperatures than that of subterranean and crimson clovers. This may be relevant to the competitive relations discussed above.



Crimson clover was previously sown into subterranean clover pastures, largely to provide a hay crop, in parts of Western Australia. Its failure to persist was due in part to lack of hard seed (Adams, 1931), although selection for hard-seededness has since been effective (Bennett, 1959). Crimson clover also appears to have low embryo dormancy (Toole and Hollowell, 1939), and this characteristic, together with low hard-seededness, may be the outcome of long selection under cultivation (Morley, private communication). There seem to be good reasons for investigating further the competitive relations of clovers, particularly because species mixtures may help to maintain *total* pasture production throughout year-to-year fluctuations in the climatic environment. Such mixtures may also allow greater latitude of adjustment of livestock use (W. A. Williams *et al.*, 1956).

On a fertile black soil in northern New South Wales, Andrew (1962) introduced 11 medics into a pasture community dominated by *M. minima*. During 3 years of natural regeneration, only *M. confinis*, *M. scutellata*, *M. tribuloides*, and *M. turbinata* were successful. It was claimed that successful competitors possessed the seedling drought-resistant properties of *M. minima*, and also high seed yields in this environment. Andrew (1962) also made the important point, and this holds for subterranean clover strains (Rossiter, 1959), that the impressive appearance of certain medics grown in rows may be no guide to field performance.

The position of the seed relative to the soil surface is an important factor in seedling establishment, especially in the year of sowing. Some information for subterranean clover illustrates the main principles. On a sandy loam soil, Dunne (1936) found no establishment with surface seeding (due to lack of root penetration), and poor establishment at sowing depths > $1\frac{1}{2}$ to 2 inches. Toms (1958) obtained best establishment at a sowing depth of 1 to $1\frac{1}{2}$ inches on a sandy-surfaced soil. However, seed size is an important consideration also, as shown by J. N. Black (1956). Some of his results for the Bacchus Marsh strain, sown at 21°C., are tabulated on the next page.

| | | | |
|---|---|---|---|
| Seed size (mg.) | < 3.0 | 5.0 | 8.0 |
| Emergence | | | |
| ½-inch depth | day 4 | day 4 | day 4 |
| 1¼-inch depth | day 6 | day 5 | day 5 |
| 2-inch depth | — | day 6 | day 6 |
| Maximum hypocotyl extension (cm.) | 3.7 | 5.2 | 6.7 |

Black also found that, while cotyledon weight at emergence was reduced following deeper sowing, area per cotyledon was scarcely affected, and it was the latter, not the former, which determined seedling growth rate. Seed size, among different small-seeded legumes, is related to emergence force (W. A. Williams, 1956), and this factor may be significant in some field situations.

### E. Other Factors

#### 1. *Insect Pests and Wildlife*

The red-legged earth mite (*Halotydeus destructor*) and lucerne flea (*Smynthurus viridus*) have contributed to "stalling" of clover pastures in southern Australia (Meadly, 1946; Tiver, 1954; Gross, 1963; Hagerstrom, 1964). Subterranean clover is especially vulnerable to both insects, and O'Neil (1958) observed that control by DDT + malathion not only increased winter growth of pasture but increased the relative amount of clover in spring from 15 per cent to 60 per cent. The extensive studies by Wallace and Mahon (1963) in Western Australia showed that control of red-legged earth mite by DDT was associated with increased total yield of pasture and changes in botanical composition (increases in percentages of clover and grasses, and decreases in capeweed). Heavy infestations of webworm (*Talis* sp.) larvae may reduce total pasture production by 50 percent, and yield of the grass component by 90 per cent (Wallace and Mahon, 1952). In natural environments, infestation of seeds by chalcid wasps may limit seed production, especially in *Medicago* spp. (Morley, private communication).

The effects of wild life, and especially rodents, on rangelands in California have been reported by Horn and Fitch (1942). High selectivity of pasture species was emphasized; e.g., *Erodium botrys* is particularly sought after by pocket gophers during the growing season. Howard (1950) has emphasized the depredations on broadcast seedings due to wild life, and suggested the use of dyed seeds and rodenticide treatment of seeds to reduce losses. Of interest was the finding that seeds of ryegrass (*Lolium* sp.) were not taken if other foods were available. In New South Wales, a detailed study on the effects of rabbit grazing on sown



pastures was done by K. Myers and Poole (1963). Pasture yields were decreased by about 25 per cent at a density of 10 to 20 rabbits per acre. Marked floristic changes were found: the proportion of Wimmera ryegrass was greatly reduced, and, compared with sheep grazing, clovers were much reduced and *Echium plantagineum* was increased.

#### 2. *Natural Mulch*

An experiment by Heady (1956a) in California, with manipulation of mulch (dry pasture residues) over a 4-year period indicated that both total amount and position of mulch may have large effects on subsequent botanical composition and plant growth rate. *Bromus mollis* and the composite *Baeria chrysostoma* were particularly sensitive to increasing amounts of mulch present at the beginning of the growing season, the soft brome increasing in percentage composition, and the composite decreasing. *Erodium botrys* was not much affected. There was little *Bromus rigidus* on the site when the experiment began, yet it seems surprising, in view of its capacity to dominate vegetation on protected sites (see Section III, C above), that this species did not increase during the 4-year period—even allowing for the overriding influence of annual weather conditions (Heady, 1961).

A significant linear relationship ($r = +0.73$) was found between amount of mulch and subsequent spring production; and this held for mulch levels as high as 2400 pounds per acre (Heady, 1956a). No clear explanation for such effects has been put forward, and the possibility that mulch influences mineral nutrient availability should be recognized. However, the finding warrants closer investigation, in southern Australia at least, where current emphasis is on high stocking rates. At Kojonup, Western Australia, E. A. N. Greenwood (unpublished data) observed that high amounts of *B. mollis* mulch led to poor early season growth, and that with very high amounts (>3000 pounds per acre) germination of soft brome seed was almost completely inhibited. Further work by Greenwood suggested the presence of a water-soluble germination-inhibitor in dry stems of *B. mollis*. Guenzi and McCalla (1962) reported the presence of water-soluble germination inhibitors in dry crop residues of several species.

#### 3. *Fire*

Hervey (1949) working near Berkeley, California, found that burning of mature forage was followed by an increase in *Erodium* spp. and bur medic and a decrease in grasses. The responses both in total yield and composition change were less where preceded by heavy grazing. In the southwest of Western Australia, Wallace (private communication) noted changes in spring herbage after burning during the preceding summer (see tabulation).

| Conditions | Grasses (%) | Sub. clover (%) |
|---|---|---|
| Control (no burning) | 77 | 12 |
| Moderate burn | 65 | 20 |
| Severe burn | 12 | 66 |

The main effect of burning, though probably not the only one, is removal of mulch, and the outcome is broadly similar to mechanical removal of mulch. There seems little justification for the use of fire, however, in connection with the management of annual-type pastures.

### 4. *Cultivation*

Simple cultivation has often proved successful in maintaining Wimmera ryegrass (*L. rigidum*) on heavy-textured soils (Shier, 1952) in Western Australia. On lighter soils, however, the grass frequently fails for other reasons, and cultivation has seldom been efficacious (Rossiter, unpublished data). Repeated cultivation, e.g., on fire breaks, often promotes capeweed—at times to the exclusion of other species—for reasons that are by no means clear.

Perhaps the most interesting observation associated with cultivation is the maintenance of almost pure stands of barrel medic (*M. trib[illegible]oides*) during the pasture phase of cereal–pasture rotations on mallee soils in South Australia (Winn, 1965). Amor (1965) states that barrel medic pastures generally deteriorate with age, and that cropping results in vigorous medic growth in cereal stubbles for reasons which are apparently not known.

### 5. *Herbicides*

Chemicals such as 2,4-D and 2,4,5-T and their derivatives have been extensively used in California for "brush" control (Berry, 1958). Herbaceous weeds, such as thistles and tarweeds can also be controlled by 2,4-D, but as Berry (1958) points out, adequate control of range weeds by herbicides is "far too expensive." Subterranean clover is susceptible to chlorinated phenoxyacetic derivatives, although seed production is much less affected by M.C.P.A. than 2,4-D ester or 2,4-D amine (Meadly and Pearce, 1955, 1957). However, rose clover and crimson clover are less tolerant of 2,4-D than subterranean clover (Ormrod and Williams, 1960). It is thus not surprising that control of undesirable plants in annual-type pastures has been sought by agronomic manipulation.

Recently, diquat has been used successfully for control of thistles and capeweed, and paraquat for grassy pasture weeds (Ross, 1963). Diquat



(Squires, 1963) and paraquat (Cuthbertson, 1965) have been used to control *Hordeum leporinum* in clover pastures. In South Australia, Cocks (1965) reported that diquat gave good control of capeweed, and permitted the establishment of perennial grasses by sod-seeding. This technique for establishing perennial grasses in areas now dominated by winter annuals deserves further testing (Prof. A. S. Crafts, personal communication).

## IV. Animal Performance in Relation to Species and Botanical Composition

### A. Some Preliminary Considerations

Much has been written in the Californian and Australian literature about the need to encourage perennial grasses, and to discourage "weedy annuals" in annual-type pastures, by appropriate management techniques (B. J. Jones and Love, 1945; Heady *et al.*, 1963; Bentley and Talbot, 1948; Love and Williams, 1956; D. W. Cooper, 1960; Heady, 1956b; M. B. Jones *et al.*, 1961; Tiver, 1954; Gross, 1963). Similar views have been expressed in Israel (Miles, 1952; Naveh, 1960). An extreme example, in respect to perennials, appears in Cooper's paper, where a plea is made for the promotion of "champagne" grasses (especially *Danthonia californica*) by reduced stocking rates combined with a deferred-rotation grazing system. Emphasis is placed on controlling animal movements "according to plant growth requirements." But another, perhaps equally extreme, example may be given. On deep sandy soils around Perth, Western Australia, the very palatable perennial grass *Ehrharta calycina* grows without difficulty, provided grazing pressure is very low. On an established *E. calycina*–clover pasture, even with 2 months autumn deferment and rotational grazing, Rossiter (1952) found that the perennial grass had virtually disappeared after grazing for 3 years at stocking rates ranging from 2.7 to 4 sheep per acre. However, even at the higher stocking rate, the animals performed well, although the pasture consisted essentially of subterranean clover and capeweed. The author questioned the role of grasses, even annual grasses, in clover pastures in Western Australia.

Some of these problems, as Love (1961) has pointed out, stem from the use of principles from "traditional" ecology (e.g., the key importance of climax vegetation as the most productive and desirable range condition) as a guide to pasture research and management. Heady (1956b) realized that there were "certain inconsistencies between grazing value and successional tendencies," e.g., with ripgut bromegrass on the one hand, and clovers on the other. Nevertheless, Heady's statement that the management of pastures to favor *Erodium* spp. and clovers usually involves "a sacrifice in total production" is open to serious question—on the bases both of plant dry matter yield under heavy grazing (see Section V below), and also of animal production per unit area of pasture.

Almost all the dominant species in annual-type pastures have been reported as possessing undesirable properties, albeit to differing degrees: this applies even with *Erodium* spp., medics, and subterranean clover, the latter because of "clover disease" (Moule *et al.*, 1963). Moreover, *Hordeum leporinum* and especially *Bromus rigidus*, which are usually regarded as undesirable, both have the virtue of high growth rate in autumn; and even medusahead (*Taeniatherum asperum*) may not be as unpalatable as commonly believed (Lusk *et al.*, 1961). It may be wise, therefore, to discontinue the use of the qualifications "desirable," "undesirable," and "weedy" for annuals, except in extreme cases.

### B. Chemical Composition

The chemical composition of annual-type pasture, especially in connection with seasonal changes, has been well documented in early literature (Hart *et al.*, 1932; Richardson *et al.*, 1931; Underwood *et al.*, 1937; Gordon and Sampson, 1939). In the Californian analyses, annual grasses, together with *Erodium botrys*, showed a decline in N content from 3.5 per cent in the early vegetative growth stage to 0.8 per cent at the dry mature stage. The corresponding figures for bur medic were about 4.5 per cent N and 2.4 per cent N, the latter high value being due in part to inclusion of bur material. In addition, crude fiber contents were markedly higher, at all growth stages, in grasses than in broadleaved herbs, though potassium and calcium were lower. The more recent data for subterranean clover (Beck, 1952; Rossiter, 1958), are in general agreement with the N pattern already mentioned for bur medic. During the growing season in Western Australia, N contents for capeweed and annual grasses are, in general, almost identical (Beck and Lapsley, 1939; Rossiter, 1958).

Throughout the dry summer months, there is often, but not inevitably, a slight downward trend in percentage of N content with time. There are also marked differences, both between species and between sites, some indication of which is given by Allden (1959) for southern Australia. The ranges were as follows:

| | |
|---|---|
| Subterranean clover | 1.1% N to 3.0% N |
| Annual grasses | 0.9% N to 1.6% N |
| *Phalaris tuberosa* | 0.6% N to 1.1% N |

Further and more recent summer data, showing the range of values be-



tween years, on a clover pasture at "Glen Lossie" Field Station, Kojonup, Western Australia, are of interest for comparison:

| | |
|---|---|
| Subterranean clover | 1.3% N to 2.0% N |
| Capeweed | 1.3% N to 1.7% N |
| Erodium | 0.5% N to 0.8% N |
| Annual grasses | 0.6% N to 0.8% N |

The lower N contents for annual grasses are of interest in relation to Allden's figures, and may be due to differences in soil N supply. At Wongan Hills, Western Australia, the N contents of both grasses and capeweed during summer were higher in the presence of subterranean clover than in its absence (Rossiter and Shier, unpublished).

Virtually no seed was present in the dry herbage samples from Kojonup, the analyses of which are given above. But seed (and bur) contain substantial N contents, e.g., 1.5 per cent N to 2.0 per cent N for grass seeds (Gordon and Sampson, 1939); 4.8 per cent N and 1.4 per cent N for *E. botrys* seeds and seeds + beaks, respectively (Gordon and Sampson, 1939); and 4.5 to 6.5 per cent N for clover and medic seeds, but only 2.5 to 3.5 per cent N for whole burs (M. C. Franklin and Powning, 1942; H. C. Franklin *et al.*, 1964).

### C. Digestibility and Voluntary Intake

#### 1. *Growing Season*

For mixed annual pasture at Roseworthy College, South Australia, Hutchinson and Porter (1958) obtained a value of *c.* 75 per cent for D.M.D. (dry matter digestibility) in the spring period. With a mixed pasture of Wimmera ryegrass and subterranean clover also under grazing, Pearce *et al.* (1962b) at Werribee in Victoria found a slight rise in percentage of O.M.D.[4] (organic matter digestibility)—from <80 to >80 per cent—during the spring period, followed by a dramatic fall from mid-October. In the following winter O.M.D. was slightly <70 per cent. With pen feeding, Vercoe *et al.* (1962) observed *maximum* voluntary intakes by sheep of *c.* 1000 g. organic matter per day. In Portugal, Azevedo *et al.* (1963) examined two sown and two cultivated pastures, using Reid's "chromogen" method. Estimated values for O.M.D. of the mixed pastures during the growing season ranged from 70 to 81 per cent.

Few data are available for individual species components. Results

[4] Some authors have expressed digestibility results on an organic matter basis only, others on a dry matter basis only. Where figures are available for comparison, per cent O.M.D. is usually 1 to 3 units higher than per cent D.M.D.

rom pen feeding experiments with sheep for grass and subterranean clover (Fels *et al.*, 1959) and capeweed (H. L. Davies, 1966) are given.

| O.M. basis | Grass (Sept.) | Clover (Sept.) | Grass (Oct.) | Clover (Oct.) | Capeweed (Aug. to Sept.) |
|---|---|---|---|---|---|
| Digestibility (%) | 79 | 82 | 69 | 73 | 83 |
| Voluntary intake (g.) | 1040 | 1030 | 585 | 855 | 744 |

At comparable stages of growth, differences in digestibility between species were relatively slight. H. L. Davies (1962) found that the organic matter intake of capeweed was low compared with a mixture of grass/clover harvested at the same time (744 g. per sheep per day compared with 1210 g. per sheep per day); the low intake was associated with low dry matter content.

The decline in nutritive value of annuals which supervenes during reproductive growth and seed development can be illustrated by data for *Bromus tectorum* (C. W. Cook and Harris, 1952) (see tabulation).

| Growth stage | Lignin (%) | D.M.D. (%) | D.M.I. (g. sheep/day) |
|---|---|---|---|
| Boot | 4.1 | 67 | 1500 |
| In head | 4.4 | 65 | 1270 |
| Dough | 6.3 | 51 | 1040 |
| Early shattering | 8.4 | 46 | 950 |
| Plants dry | 10.4 | 39 | 910 |

The relationship of percentage of D.M.D. to lignin content lends support to the recent ideas of Armstrong *et al.* (1964) on the predictive value of percentage of lignin for assessing nutritive value.

## 2. *Summer Period*

Early Californian studies were directed to the dry feed period, especially to the losses in quality following exposure to rain. Hart *et al.* (1932) reported 50 per cent D.M.D. and 40 per cent D.M.D. for dried, bleached samples of grass and *Erodium cicutarium*, respectively. In the case of bur medic, D.M.D. fell from 64 per cent to 56 per cent after exposure to sun and rain, a decrease due apparently to loss of soluble nutrients (Guilbert and Mead, 1931). It may be noted that appreciable amounts of bur were included in the medic samples.

Hutchinson and Porter (1958) stated that a 45 per cent D.M.D. had been commonly recorded in digestibility trials with mature summer pasture residues in South Australia. However, marked differences have been found both within and between species components in Western



Australia. For December, Fels *et al.* (1959) reported 57 per cent O.M.D. for grass, and 43 per cent O.M.D. for subterranean clover. Subsequent results from Kojonup (Fels, unpublished data) for the summer period were as follows:

| | Grass | Capeweed | Sub. clover |
|---|---|---|---|
| O.M.D. (%) | 48 | 47 | 52 |

These may be more typical figures for average summer conditions. However, I have found much higher D.M.D. (55 to 60 per cent) for both capeweed and bur-free subterranean clover collected at the beginning of summer at Perth.

Voluntary intakes (for sheep) are usually low, *c.* 400 g. to 600 g. organic matter per day at the lower digestibility values. On the other hand, intakes as high as 800 g. to 900 g. organic matter per day were obtained when digestibility exceeded 55 per cent. Yet anomalies occur, e.g., with Wimmera ryegrass grown at Canberra (H. L. Davies, 1966), as shown by the following data:

| | Sub. clover | Phalaris | Wimmera ryegrass |
|---|---|---|---|
| O.M.D. (%) | 54 | 47 | 56 |
| O.M. intake (g.) | 680 | 840 | 395 |

The wide differences, within species, for percentage digestibility of dry mature herbage present problems of both practical and theoretical interest. Attention was drawn to this in connection with subterranean clover by Fels *et al.* (1959). Whether these differences are related to lignin contents is not known; but the structural and biochemical changes during lignification of maturing plant tissues may be worth exploring further, as one approach. Evidence for a rapid increase in lignification during wilting is available for the Dwalganup strain of *T. subterraneum* (Hardwick, 1954), yet the general topic has not been pursued.

In view of the practical emphasis often placed on the value of clover bur and medic bur, it might be expected that digestibilities (and intakes) would be high. Some years ago, I obtained a mean value of 52 per cent D.M.D. for whole Dwalganup subterranean clover bur, and a voluntary intake of 650 g. dry matter per sheep per day. This suggests that clover bur is not superior to dry clover herbage in nutritive value. For barrel medic bur, Vercoe and Pearce (1960) reported high voluntary intakes (>900 g. dry matter per sheep per day) but a remarkably low value of 32 per cent O.M.D.

Vercoe *et al.* (1961) considered that the point at which digestible N becomes limiting corresponds to a crude protein content in the organic matter intake of grazing sheep of c. 9.5 per cent. This in turn corresponds to a level of c. 1.1 per cent N in the available pasture. From the data already given in Section IV, B, it is evident that N contents are frequently lower than this critical level during the summer months, more especially on pastures dominated by annual grasses and/or erodium.

### D. Field Performance

Estimates of actual intakes of annual-type pasture, in the field, have been made using "local regressions" based on pen feeding experiments (e.g., Hutchinson and Porter, 1958; Fels *et al.*, 1959; Vercoe *et al.*, 1961; Pearce *et al.*, 1962a; Arnold *et al.*, 1964). In many instances, stocking rates have been sufficiently low to permit voluntary intakes; but clearly, *voluntary* intake cannot be assumed in all cases. The influence of stocking rate (2, 4, and 6 sheep per acre) on intake was examined in an annual grass–subterranean clover pasture by Arnold *et al.* (1964). An intake of 1000 g. organic matter per day for sheep of 100 pounds liveweight was found on abundant green pastures: this figure, as the authors point out, is close to other estimates reported in the Australian literature for other types of pasture. Intake was frequently highest at the high stocking rate. However, as the authors point out, the fact that no relation was established does not mean that intake was not affected by the availability of the pasture. Moreover, the errors attached to the estimation of intake by the "local regression" technique are not adequately known. Intake frequently declines when the amount of green pasture on offer is < 900 pounds of dry matter per acre (Arnold, 1964a), but as Arnold has pointed out, the relationships between pasture on offer, intake, and animal performance are complex.

Forage intake by sheep and by cattle, on dry mature pasture, was measured by Van Dyne and Meyer (1964) at Hopland Field Station, California. Several methods, including lignin ratio and procedures based on micro- and macrodigestion, were used to estimate intake in the field. Their results are summarized (as pounds per acre) in the tabulation.

| Period | Early July | Early August | Early September |
|---|---|---|---|
| Dry matter available | 1490 lb./ac. | 1220 lb./ac. | 420 lb./ac. |
| Sheep | | | |
| Mean intake/day (g. D.M.) | 770 | 990 | 770 |
| 24-hr. shrink weight (lb.) | 102 | 98 | 96 |
| Cattle | | | |
| Mean intake/day (kg. D.M.) | 4.81 | 5.63 | 5.95 |
| 24-hr. shrink weight (lb.) | 699 | 710 | 700 |



The authors considered that the intakes for sheep were greater than those usually obtained in dry lot trials on annual dry mixed forage. An interesting feature of the data was the absence of any pronounced decline in intake in late summer, even when the amount of pasture on offer was <450 pounds dry matter per acre.

The general pattern of liveweight change for sheep on Mediterranean annual-type pasture is well established (J. G. Davies *et al.*, 1934; Donald and Allden, 1959; H. L. Davies and Humphries, 1965). Briefly, this comprises a period of increasing liveweight during winter and, more especially, spring; a period of approximately constant liveweight during early summer; and a period of declining liveweight during mid- to late summer and extending into the autumn after the "break" of season. The specific patterns for particular field situations will be dependent on environmental influences, and particularly stocking rate (Davies and Humphries, 1965). If one assumes an approximate figure of 500 to 550 g. digestible organic matter per day (based on many estimates, both in Australia and elsewhere) for maintenance in the field of 100 pounds liveweight Merino sheep in store condition, then the general pattern described above could be anticipated from intake and digestibility data already presented. The submaintenance diet of dry mature summer herbage was shown to be deficient in both protein and available energy by Donald and Allden (1959) and Allden (1959). In practice, however, as Donald and Allden have stated, "a balance must be struck between the physiological capacity of the sheep to adapt itself to a lowered nutritional status and the economic value of feeding a supplement." The retarded growth of weaner sheep appeared to be of no permanent significance to ultimate size, per se, because of the mechanism of "compensatory gain" (Allden and Scott Young, 1964). However, generalization on this point for all Mediterranean environments may be inadmissible (Bradford *et al.*, 1961). Although the picture has been outlined for sheep only, a broadly similar pattern seems to apply for cattle (Wagnon *et al.*, 1942; Bentley and Talbot, 1951; Davenport, 1958).

Unfortunately, there are few good experimental data, as far as I am aware, in which animal performance has been compared on different annual-type pastures in a given environment. McKeown (private communication) at Muresk, Western Australia, has compared pastures sown to Dwalganup subterranean clover, Geraldton subterranean clover, and barrel medic for sheep performance. No outstanding treatment differences were found. At "Glen Lossie" Field Station, Kojonup, Western Australia, I found slight differences, for wool growth, and liveweight change during summer, in favor of pastures sown to Yarloop and also Bacchus Marsh were ascribed to higher intakes of clover tops during the summer. Pasture sampling revealed no significant intake of clover bur during summer, a finding which is supported by results of I. F. Davis (1964) in Victoria, using esophageal fistulas. Clover bur may well be useful when dry herbage supplies are exhausted; but whether it "provides a reserve of feed of great value," as claimed by Drake and Elliott (1960) in Victoria, is at least open to question. Supporting evidence for improved animal performance on the Yarloop strain (and also Mt. Barker) compared with Dwalganup is available from South Australia (Day, 1965).

Forage preferences have been demonstrated for annual-type pastures in California by means of the esophageal fistula technique. Heady and Torell (1959) and Weir *et al.* (1959), from studies at Hopland Field Station with sheep, concluded that grasses (mainly *B. mollis*) and to a lesser extent *Erodium* spp. were selected during winter; in May (near maturity) bur medic was preferred; while in July (dry stage) most of the diet consisted of *Erodium*. Subsequent observations (Van Dyne and Heady, 1965) confirmed the fact that *Erodium* seed heads lying on the soil surface were consumed during summer. Van Dyne and Heady (1965) examined interrelations of botanical and chemical dietary components on dry annual range, and interpreted some of their data as illustrating changing dietary selectivity with changing herbage availability. On a Wimmera ryegrass–subterranean clover pasture at Werribee in Victoria, I. F. Davis (1964) could detect no clear preference in the green stage (October). However, in early summer (December) there was a clear preference for grass, while in mid-late summer (February) the sheep preferred the dry clover tops. Moreover, Arnold (1966) observed no marked differences in preference between subterranean clover and annual grasses during most of the growing season. Preference rankings under free choice conditions may show no significant correlations with intake when choice is disallowed (Arnold, 1964b). The importance of differences in forage preference between species and strains, in relation to animal production, is far from clear. The continued cohabitation of several species in a pasture where growth rates are very approximately equal, as stated earlier, may well depend on lack of strong selectivity by the animal, and/or differential and self-balancing preferences throughout the grazing season. Extremes of preference or rejection would tend to elimination or dominance, respectively, both of which are "undesirable."

A final illustration of the need to clarify ideas on species in connection with grazing management and animal performance is provided by the paper of Love and Williams (1956). On a bur medic pasture, these workers found that production of bur was increased from 640 to 2260 pounds per acre by protection from grazing for a 63-day period during the flush of flowering and seed development. Lamb gain, as pounds per acre, was *reduced* by deferment, yet continuous grazing was not advocated because of the reduced bur production per se. Pasture species, as well as management techniques, need to be evaluated in terms of animal performance in the field. And as yet our knowledge of the particular factors contributing to real value in pasture species is very inadequate.



## V. General Discussion

### A. Productivity Levels

The notions of ecological system (or ecosystem), food chain, and biological productivity are now familiar among ecologists (Odum, 1954). Primary productivity has been defined by Odum (1954) as the rate at which energy is stored by producer organisms (chiefly green plants) in the form of organic substances which can be used as food materials. Here, I wish to consider further this question of primary productivity, in respect of annual pastures.

Throughout this review I have placed the emphasis on floristic composition, and changes therein, rather than on total pasture yield. One reason for this will have become clear, viz., species changes are a frequent, if not invariable, consequence of alterations to the ecosystem (e.g., by additions of nutrients, plant species, animals). Total yield changes are then confounded with floristic changes. The other reason is perhaps more significant, viz., the difficulties of measuring yield or primary production *under grazing conditions*, especially with set-stocked management systems. In the past, it has been common practice to obtain dry matter yields from exclosures protected for varying periods, sometimes the entire growing season. This usually gives a quite unrealistic picture for botanical composition; e.g., percentage clover can be grossly underestimated.

One example in which pasture productivity was measured fortnightly using matched "open" and "closed" quadrats (McIntyre, 1946) under a set-stocked system, was reported by Rossiter (1958). The pasture was comprised almost entirely of three species—subterranean clover, capeweed, and ripgut bromegrass—and was stocked at 2.7 sheep per acre. The estimated total dry matter yield per growing season was 440 g./m.$^2$, almost certainly lower than the total yield would have been with some protection from grazing. However, Carter (personal communication) at Adelaide, South Australia, has evidence that total dry matter yields may be lower at low stocking rates than at moderately high rates. The study by Sharkey *et al.* (1964) on a Wimmera ryegrass—subterranean clover pasture in southern Victoria also deserves mention. Here, production was assessed essentially in terms of seed reserves and plant density. The pasture carried 3 sheep per acre successfully, but at 6 sheep per acre the two sown species had virtually disappeared after 3 years of grazing. The so-called "crashpoint" must inevitably come, but it would be interesting to know whether the presence of other strains of *T. subterraneum* might alter the outcome.

Total pasture production could conceivably be increased by the presence of a perennial grass component. One of the few experiments of some relevance on this point was conducted by Neal Smith (1942) at Kybybolite, South Australia, in which *Phalaris tuberosa*–subterranean clover was compared with *Lolium rigidum*–subterranean clover. Mean total yields over a 5-year period, based on exclosures cut at the end of the growing season, were in fact slightly lower for the perennial grass pasture (740 g./m.$^2$ as against 830 g./m.$^2$), despite reasonable persistence of the perennial component. By present-day standards, the pastures were probably understocked, but mean carrying capacities also differed little for the two pasture types (3.8 sheep per acre and 3.9 sheep per acre for the annual and perennial pastures, respectively). At Werribee, Victoria, Sharkey and Hedding (personal communication) compared an annual-type pasture with *Phalaris tuberosa* (density of 1 plant/ft.$^2$), together with subterranean clover and volunteer annuals. At moderately high stocking, total fleece weights per acre were almost identical for the two types of pasture. Amounts of pasture available were always slightly higher in the annual type. Whether the outcome would be affected by a higher plant density of *P. tuberosa* is not yet known.

A clear case of increased pasture productivity from the use of a perennial grass was observed by Humphries and Rossiter (unpublished data) on a deep sandy soil at Perth. Inclusion of *Hyparrhenia hirta* almost doubled total pasture yields and carrying capacity also. Nevertheless, wherever the growing season is <8 to 9 months, the prospects of effecting significant increases in total pasture production, on an extensive scale and *under high stocking rates,* by the inclusion of perennial grasses do not at present seem encouraging. More than 30 years have elapsed since Trumble and Davies (1931) put forward arguments for the use of perennials rather than annuals for many parts of the Mediterranean zone of southern Australia.

### B. Efficient Utilization of Environmental Resources

#### 1. *Annual-Type Pastures*

Some years ago (Rossiter, 1958) I assessed the fate of dry matter produced by an annual-type pasture. Total production was given in the preceding section, but the way in which this was partitioned, for a 12-month period, can now be summarized (see tabulation).



| Parameter | Dry matter g./m.$^2$ | Dry matter % |
|---|---|---|
| Animal consumption | 215 | 49 |
| Losses from trampling and summer rains | 105 | 24 |
| Seed "losses" | 45 | 10 |
| Maturation losses | 25 | 6 |
| End-of-summer plant residues | 50 | 11 |
| Total production | 440 | 100 |

The relative utilization (almost 50 per cent) was similar to that found for some strip grazing systems. Also, two of the components were regarded as "necessary debits" against the annual-type pasture per se. The seed "losses" are in part required to regenerate the pasture each year; in part also they represent a real loss, via breakdown and decay, etc. The end-of-summer residues may benefit the regenerating sward (Heady, 1956a) and possibly offer some protection against soil erosion. Slightly higher stocking rates may well have improved utilization, but subsequent investigations suggested that the "crashpoint" for the system was *c.* 4 sheep per acre.

A major source of loss from the above system was from trampling, fragmentation of dry plant material, and (to a lesser extent) summer rains. For the 12-month period, these losses totaled about 50 per cent of the amount eaten. Ratliff and Heady (1962) found large losses of dry matter from annuals during the dry season in ungrazed pasture, and they pointed out that the "normal seasonal weight losses" should not be confounded with forage eaten by stock. Their weight losses seemed unduly high at the conclusion of summer—*E. botrys* lost nearly all its yield and *B. rigidus* lost >80 per cent, presumably due in part to seed "losses." The importance of fragmentation losses, especially in plants such as capeweed, is still unclear. It is commonly assumed among graziers that capeweed is normally subject to high losses from this source, but our field measurements through the summer do not support this.

The use of higher stocking rates in southern Australia has revealed differences in pasture productivity between fields on individual farms or properties. Such differences, hitherto obscured by undergrazing, are connected with soil type, topography, etc. An obvious way of improving overall efficiency is to adjust stocking rates in accordance with such site differences. However, this point has been appreciated by Californian workers (Bentley and Talbot, 1951), and to some extent by many graziers.

Some overall improvement in efficiency of the ecosystem based on the annual-type pasture might be expected from autumn deferment (or "autumn saving"). In the study cited above, evidence for benefits from this practice was rather equivocal, except in seasons where a false "break" or a late "break" occurred: total pasture production was then substantially increased by deferment. Further deferment studies with annual-type pastures may be worthwhile, especially in view of encouraging results from a current experiment at Werribee, Victoria (Sharkey, personal communication). Another procedure, which originated in Western Australia, is the "mowing and leaving" of spring pasture *in situ* (Davenport, 1957). The basis for this practice is retention of quality (as digestible energy and nitrogen) for the summer grazing period. However, with current emphasis on high stocking rates, excessive grass dominance is unlikely to be as widespread as previously, so that the argument for "mowing and leaving" loses much of its force. There is, nonetheless, a strong case for seeking adapted annuals, the dry mature residues of which possess consistently high nutritive value. Indeed this may be the most important means by which improved animal production can be achieved.

Further efforts should be directed to ways of improving primary productivity in an annual-type pasture ecosystem. The underlying physiological mechanisms whereby good pasture plants continue to produce leaf surface under high stocking rates are not known. The importance of mineral nutrition cannot be ignored here. And, until this field is explored, we shall remain ignorant on basic pasture plant physiology and shall lack guidance as to what characteristics to seek for improved species and strains. Events during initiation of growth of annuals are also not properly understood. Further studies in this field also seem well justified, and the practical outcome could be the development of plant species capable of giving high seedling densities, and high early growth rates, yet possessing mechanisms which protect against vagaries of seasonal "breaks." Much yet remains to be done on the nutritional requirements of defoliated and/or grazed annuals: some, if not most, of the presently available information on pasture plant nutrition may not be relevant to intensively grazed pastures.

### 2. *Deep-Rooted Perennials*

One of the drawbacks of heavily grazed annual-type pastures is the inefficient use of soil water resources (and probably nutrient resources also) consequent on restrictions to plant root development and extension. The incorporation of deep-rooted perennials such as *Hyperrhenia hirta* or *Eragrostis curvula* into the ecosystem might offer a solution in some areas, especially if the perennials were protected from grazing at "critical" periods in their life cycle. *H. hirta* has already been mentioned (p. 46); this grass is well adapted to withstand heavy grazing and in addition possesses a growth pattern largely complementary to that of winter annuals. Unfortunately, it is difficult to establish from seed. The use of special-purpose pastures has not proved encouraging elsewhere in Australia (Wheeler, 1966), but the question still remains open for Mediterranean conditions.



A possible means of improving efficiency is the introduction of perennial legume shrubs or trees, e.g., tree lucerne (*Chamaecytisus proliferus*), into the annual-type pasture. The perennial would require the following characteristics: deep-rootedness; elevation of leaf canopy above grazing height; high leaf production during late spring and early summer; drought resistance; good recovery after cutting; and high nutritive value (including acceptability to the animal) of leaf and young stems. Harvesting, by cutting, could present practical problems, but these need not be insurmountable.

### 3. *Cereal Crops*

In southern Australia, the introduction of subterranean clover has resulted in substantial increases in soil fertility (Donald and Williams, 1954; C. H. Williams and Donald, 1957; Russell, 1960a, b; C. H. Williams and Lipsett, 1960; Russell and Shearer, 1963; Watson, 1963; Watson and Lapins, 1964). The soil N status alone has improved at rates of 40 to 80 pounds N per acre per year. At the conclusion of a study on grass–clover relationships, Willoughby (1954) emphasized the desirability of a cropping phase, both to utilize accumulated soil N and to enable clovers to resume efficient N fixation. Donald and Williams (1954) also have referred to the opportunities for greater diversification of agriculture, consequent on the improved soil fertility.

There seems to be little doubt concerning the theoretical improvement in overall efficiency from periodic cereal cropping in areas of predominantly annual-type pasture. The *practical* advantage of such procedure is, however, another matter and will be dictated to a large degree by economic issues. In areas where cereal cropping is a major farm enterprise, the use of short-term clover leys (or pastures) was supported by Watson (1963). An extreme example of this practice is available from the South Australian mallee soils, where barrel medic pasture alternates with barley cropping in a 2-year rotation (Winn, 1965).

## C. Future Pasture Plants

Beyond the primary level of productivity, pasture plants are energetically inefficient, and this doubtless is the main reason for the general use of crops for direct human consumption in the relatively densely populated Mediterranean Basin (Anonymous, 1951). There are grounds, moreover, for doubting whether *in situ* grazing is likely to remain, in the long run, a generally accepted practice for high level animal production. A disadvantage of grazing in the field is the difficulty of controlling leaf area index (L.A.I.) for the promotion of maximum dry matter yield (Donald and Black, 1958). For subterranean clover in the Adelaide environment, J. N. Black (1964) has argued that the gap, 10 metric tons per hectare, between potential and actual seasonal production is largely due to L.A.I. exceeding the optimum, late in the growing season. Whether, as Black suggests, a large part of this loss can be eliminated by defoliation to manipulate L.A.I. remains to be investigated.

In New Zealand, Mitchell (1960) has drawn attention to the self-limiting nature of *in situ* grazing with respect to yield potential and has raised the question of utilizing tall-growing, high-yielding plants which permit efficient light interception at high L.A.I., under a cutting system. This concept warrants further consideration by pasture research workers, although economic considerations may restrict its use. In the immediate future, at least, significant advances are likely to accrue from research within currently accepted ecosystems.

## References


Adams, A. B. 1931. *J. Agr., W. Australia* [2] 8, 227.
Aitken, Yvonne. 1955a. *Australian J. Agr. Res.* 6, 212-244.
Aitken, Yvonne. 1955b. *Australian J. Agr. Res.* 6, 258-264.
Aitken, Yvonne, and Davidson, B. R. 1954. *J. Australian Inst. Agr. Sci.* 20, 253-256.
Allden, W. G. 1959. *Australian J. Agr. Res.* 10, 219-236.
Allden, W. G., and Scott Young, R. 1964. *Australian J. Agr. Res.* 15, 989-1000.
Amor, R. L. 1965. *J. Australian Inst. Agr. Sci.* 31, 25-35.
Anderson, A. J. 1942. *J. Australian Inst. Agr. Sci.* 8, 73-75.
Anderson, A. J., and Thomas, M. P. 1946. *Council Sci. Ind. Res. Australian Bull.* 198, Part I.
Andrew, W. D. 1962. *Australian J. Agr. Res.* 13, 212-219.
Andrew, W. D. 1963. *Australian J. Biol. Sci.* 16, 281-283.
Andrew, W. D., and Hely, F. W. 1960. *Australian J. Agr. Res.* 11, 705-714.
Andrew, W. D., and Milligan, R. T. 1954. *J. Australian Inst. Agr. Sci.* 20, 123-124.
Anonymous. 1951. "Pasture and Fodder Development in Mediterranean Countries." Organization for European Economic Co-Operation, Paris.
Argyle, D. B. 1962. *J. Agr., W. Australia* [4] 3, 333-341.
Armstrong, D. G., Blaxter, K. L., and Waite, R. 1964. *J. Agr. Sci.* 62, 417-424.
Arnold, G. W. 1964a. *In* "Grazing in Terrestrial and Marine Environments" (D. G. Crisp, ed.), pp. 133-154. Blackwells Sci. Publ., Adlard and Son, Ltd., England.
Arnold, G. W. 1964b. *Proc. Australian Soc. Animal Prod.* 5, 258-271.
Arnold, G. W. 1966. In press.
Arnold, G. W., McManus, W. R., and Bush, I. G. 1964. *Australian J. Exptl. Agr. Animal Husbandry* 4, 392-403.
Ashby, W. C., and Hellmers, H. 1955. *J. Range Management* 8, 80-83.
Ashby, W. C., and Hellmers, H. 1959. *Botan. Gaz.* 120, 151-157.
… J. F. 1966. In press.





Asher, C. J., and Ozanne, P. G. 1961. *Australian J. Agr. Res.* 12, 755-766.
Azevedo, J. P. de, Costa, M. J. D. S., and Chicau, J. M. 1963. *Melhoramento* 16, 111-137.
Bailey, E. T. 1961. C.S.I.R.O. Plant Industry Divisional Report No. 21.
Ballard, L. A. T. 1958. *Australian J. Biol. Sci.* 11, 246-260.
Ballard, L. A. T. 1961. *Australian J. Biol. Sci.* 14, 173-186.
Barrett-Lennard, R. A., and Gladstones, J. S. 1964. *Australian J. Agr. Res.* 15, 895-904.
Beck, A. B. 1952. *J. Agr., W. Australia* [3] 1, 1-4.
Beck, A. B., and Lapsley, R. G. 1939. *J. Agr., W. Australia* [2] 15, 422-426.
Bennett, H. W. 1959. *Agron. J.* 51, 15-16.
Bennetts, H. W., Underwood, E. J., and Shier, F. L. 1946. *Australian Vet. J.* 22, 2-12.
Bentley, J. R., and Green, L. R. 1954. *J. Range Management* 7, 25-30.
Bentley, J. R., and Talbot, M. W. 1948. *Ecology* 29, 72-79.
Bentley, J. R., and Talbot, M. W. 1951. *U. S. Dept. Agr., Circ.* 870.
Bentley, J. R., Green, L. R., and Wagnon, K. A. 1958. *J. Range Management* 11, 133-140.
Berry, L. J. 1958. *Proc., Ann. California Weed Conf.* 10, 3-6.
Biddiscombe, E. F., Cuthbertson, E. G., and Hutchings, R. J. 1954. *Australian J. Botany* 2, 69-98.
Biswell, H. H. 1956. *J. Range Management* 9, 19-24.
Biswell, H. H., and Graham, C. A. 1956. *J. Range Management* 9, 116-118.
Black, J. N. 1956. *Australian J. Agr. Res.* 7, 98-109.
Black, J. N. 1960. *Australian J. Agr. Res.* 11, 277-291.
Black, J. N. 1963. *Australian J. Agr. Res.* 14, 206-225.
Black, J. N. 1964. *J. Appl. Ecol.* 1, 3-18.
Black, M. 1959. *Can. J. Botany* 37, 393-402.
Bradford, G. E., Weir, W. C., and Torell, D. T. 1961. *J. Animal Sci.* 20, 281-287.
Carlin, B. F. 1958. *J. Agr., W. Australia* [3] 7, 185-188.
Carter, E. D. 1958. *J. Dept. Agr. S. Australia* 61, 401-408.
Cocks, P. S. 1965. *Australian J. Exptl. Agr. Animal Husbandry* 5, 203-207.
Collis-George, N., and Sands, Jocelyn E. 1959. *Australian J. Agr. Res.* 10, 628-636.
Collis-George, N., and Sands, Jocelyn E. 1961. *Nature* 190, 367.
Conrad, J. P., Hall, H. L., and Chaugule, B. A. 1947. *Soil Sci. Soc. Am. Proc.* 12, 275-277.
Cook, C. W., and Harris, L. 1952. *J. Range Management* 5, 331-337.
Cook, L. J. 1942. *J. Dept. Agr. S. Australia* 45, 420-423.
Cooper, D. W. 1960. *J. Range Management* 13, 203-205.
Cooper, J. P. 1950. *J. Brit. Grassland Soc.* 5, 105-112.
Crawford, E. J. 1962. *J. Dept. Agr. S. Australia* 65, 268-271.
Crocker, R. L., and Tiver, N. S. 1948. *J. Brit. Grassland Soc.* 3, 1-26.
Cumming, B. G., and Hay, J. R. 1958. *Nature* 182, 609-610.
Cuthbertson, E. G. 1965. *Agr. Gaz. N. S. Wales* 76, 333-336.
Davenport, N. 1957. *J. Agr., W. Australia* [3] 6, 393-411.
Davenport, N. 1958. *J. Agr., W. Australia* [3] 7, 341-346.
Davidson, J. L., and Donald, C. M. 1958. *Australian J. Agr. Res.* 9, 53-72.
Davies, H. L. 1962. *Proc. Australian Soc. Animal Prod.* 4, 167-171.
Davies, H. L. 1966. Ph.D. Thesis.
Davies, H. L., and Humphries, A. W. 1965. *J. Agr., W. Australia* [4] 6, 409-413.
Davies, J. G., Scott, A. E., and Frazer, K. M. 1934. *Council Sci. Ind. Res. Australia Bull.* 83, 1-76.

Davis, I. F. 1964. *Proc. Australian Soc. Animal Prod.* 5, 249-250.
Davis, L. A., and Laude, H. M. 1964. *Crop Sci.* 4, 477-480.
Day, H. R. 1965. Kangaroo Island Research Centre Annual Report, 1964-1965.
Donald, C. M. 1946. "Pastures and Pasture Research." University of Sydney, Australia.
Donald, C. M. 1958. *Australian J. Agr. Res.* 9, 421-435.
Donald, C. M. 1960. *Herbage Abstr.* 30, 81-90.
Donald, C. M., and Allden, W. G. 1959. *Australian J. Agr. Res.* 10, 199-218.
Donald, C. M., and Black, J. N. 1958. *Herbage Abstr.* 28, 1-6.
Donald, C. M., and Williams, C. H. 1954. *Australian J. Agr. Res.* 5, 664-687.
Drake, F. R., and Elliott, N. M. 1960. *J. Agr. (Victoria)* 58, 645-655.
Dunne, T. C. 1936. *J. Agr., W. Australia* [2] 13, 67-69.
Dunne, T. C., and Elliott, H. G. 1950. *J. Agr., W. Australia* [2] 27, 115-117.
Evans, L. T. 1964. *In* "Grasses and Grasslands" (C. Barnard, ed.), p. 126. Macmillan, New York.
Evans, R. A. 1960. *Ecology* 41, 305-310.
Evenari, M. 1965. *Proc. Intern. Seed Testing Assoc.* 30, 49-71.
Ewart, A. J. 1930. "Flora of Victoria." Govt. Printer (for University Press).
Fels, H. E., Moir, R. J., and Rossiter, R. C. 1959. *Australian J. Agr. Res.* 10, 237-247.
Fitzpatrick, E. N., and Dunne, T. C. 1956. *J. Agr., W. Australia* [3] 5, 321-326.
Franklin, M. C., McInnes, P., and Briggs, P. K. 1964. *Australian J. Exptl. Agr. Animal Husbandry* 4, 129-131.
Franklin, M. C., and Powning, R. F. 1942. *J. Council Sci. Ind. Res. Australia* 15, 191-200.
Fryxell, P. A. 1957. *Botan. Rev.* 23, 135-233.
Gibson, A. H. 1962. *Australian J. Biol. Sci.* 16, 28-42.
Gladstones, J. S. 1958. *Australian J. Agr. Res.* 9, 171-181.
Gladstones, J. S. 1960. *J. Australian Inst. Agr. Sci.* 26, 19-25.
Gladstones, J. S., and Barrett-Lennard, R. A. 1964. *J. Australian Inst. Agr. Sci.* 30, 258-262.
Gladstones, J. S., Leach, B. J., Drover, D. P., and Asher, C. J. 1964. *Australian J. Exptl. Agr. Animal Husbandry* 4, 158-164.
Gordon, A., and Sampson, A. W. 1939. *California, Univ., Agr. Expt. Sta., Bull.* 627, 1-95.
Grant Lipp, A. E., and Ballard, L. A. T. 1959. *Australian J. Agr. Res.* 10, 495-499.
Grant Lipp, A. E., and Ballard, L. A. T. 1962. *Australian J. Biol. Sci.* 16, 572-584.
Greenway, H., and Andrew, W. D. 1962. *Australian J. Exptl. Agr. Animal Husbandry* 2, 234-235.
Gross, F. C. 1963. *J. Dept. Agr. S. Australia* 66, 252-257.
Guenzi, W. D., and McCalla, T. M. 1962. *Soil Sci. Soc. Am. Proc.* 26, 456-458.
Guilbert, H. R., and Mead, S. W. 1931. *Hilgardia* 6, 1-11.
Hagerstrom, R. C. 1964. *J. Dept. Agr. S. Australia* 67, 308-315.
Hardwick, Nancy E. 1954. *Australian J. Agr. Res.* 5, 383-391.
Harlan, J. R. 1945. *Am. J. Botany* 32, 142-148.
Harper, J. L., Williams, J. T., and Sagar, G. R. 1965. *J. Ecol.* 53, 273-286.
Harris, G. S. 1961. *New Zealand J. Agr. Res.* 4, 253-260.
Hart, G. H., Guilbert, H. R., and Goss, H. 1932. *California, Univ., Agr. Expt. Sta., Bull.* 543, 1-62.
Heady, H. F. 1956a. *Ecology* 37, 798-812.
Heady, H. F. 1956b. *J. Range Management* 9, 25-27.



Heady, H. F. 1958. *Ecology* 39, 402-416.
Heady, H. F. 1961. *J. Range Management* 14, 182-193.
Heady, H. F., and Torell, D. T. 1959. *J. Range Management* 12, 28-34.
Heady, H. F., Cooper, D. W., Rible, J. M., and Hooper, J. F. 1963. *J. Range Management* 16, 51-54.
Hellmers, H., and Ashby, W. C. 1958. *Ecology* 39, 416-428.
Hely, F. W. 1962. *Australian J. Agr. Res.* 13, 801-811.
Hely, F. W., and Brockwell, J. 1964. *Australian J. Agr. Res.* 15, 50-60.
Hervey, D. F. 1949. *J. Range Management* 2, 116-121.
Hiesey, W. M., and Milner, H. W. 1965. *Ann. Rev. Plant Physiol.* 16, 203-216.
Hilder, E. J., and Spencer, K. 1954. *J. Australian Inst. Agr. Sci.* 20, 171-176.
Hironaka, M. 1961. *J. Range Management* 14, 263-267.
Hoglund, O. K., Miller, H. W., and Hafenrichter, A. L. 1952. *J. Range Management* 5, 55-61.
Horn, E. E., and Fitch, H. S. 1942. *California, Univ., Agr. Expt. Sta., Bull.* 663, 96-129.
Hoveland, C. S., and Elkins, D. M. 1965. *Crop Sci.* 5, 244-246.
Howard, W. E. 1950. *J. Range Management* 3, 291-298.
Hulbert, L. C. 1955. *Ecol. Monographs* 25, 181-213.
Humphries, A. W., and Bailey, E. T. 1961. *Australian J. Exptl. Agr. Animal Husbandry* 1, 150-152.
Hutchinson, K. J., and Porter, R. B. 1958. *Proc. Australian Soc. Animal Prod.* 2, 33-41.
Jensen, H. L. 1943. *Proc. Linnean Soc. N. S. Wales* 68, 207-220.
Jones, B. J., and Love, R. M. 1945. *California Agr. Extension Serv. Circ.* 129.
Jones, M. B. 1960. *J. Range Management* 13, 188-192.
Jones, M. B. 1963a. *Agron. J.* 55, 251-254.
Jones, M. B. 1963b. *Agron. J.* 55, 254-257.
Jones, M. B. 1964. *Agron. J.* 56, 235-237.
Jones, M. B., and Evans, R. A. 1960. *Agron. J.* 52, 459-461.
Jones, M. B., Martin, W. E., Berry, L. J., and Osterli, V. P. 1961. *J. Range Management* 14, 146-148.
Jones, M. B., McKell, C. M., and Winans, S. S. 1963. *Agron. J.* 55, 44-46.
Juhren, M., Went, F. W., and Phillips, E. 1956. *Ecology* 37, 318-330.
Kleinig, C. R. 1965. *Australian J. Agr. Res.* 16, 311-319.
Knight, W. E., and Hollowell, E. A. 1958. *Agron. J.* 50, 295-298.
Knight, W. E., and Hollowell, E. A. 1962. *Crop Sci.* 2, 124-127.
Knowles, P. F. 1943. *J. Am. Soc. Agron.* 35, 584-594.
Köppen, W. 1923. "Die Klimate der Erde." de Gruyter, Berlin.
Laude, H. M. 1956. *J. Range Management* 9, 126-129.
Laude, H. M. 1957. *J. Range Management* 10, 37-38.
Laude, H. M., and Chaugule, B. A. 1953. *J. Range Management* 6, 320-324.
Laude, H. M., Kadish, A., and Love, R. M. 1957. *J. Range Management* 10, 116-120.
Lewis, H., and Went, F. W. 1945. *Am. J. Botany* 32, 1-12.
Litav, M., Kupernik, G., and Orshan, G. 1963. *J. Ecol.* 51, 467-480.
Love, R. M. 1961. *J. Brit. Grassland Soc.* 16, 89-99.
Love, R. M., and Williams, W. A. 1956. *Proc. 7th Intern. Grassland Congr., Palmerston, New Zealand, 1956* pp. 509-518. Dept. Agr., Wellington, New Zealand.
Lusk, W. C., Jones, M. B., Torell, D. T., and McKell, C. M. 1961. *J. Range Management* 14, 248-251.
McIntyre, G. A. 1946. *Council Sci. Ind. Res. Australia Bull.* 201, 70-83.

McKell, C. M., and Wilson, Alma M. 1963. *Agron. J.* **55**, 134-137.
McKell, C. M., Major, J., and Perrier, E. R. 1959. *J. Range Management* **12**, 189-193.
McKell, C. M., Jones, M. B., and Perrier, E. R. 1962a. *Agron. J.* **54**, 459-462.
McKell, C. M., Robison, J. P., and Major, J. 1962b. *Ecology* **43**, 686-698.
McKell, C. M., Wilson, A. M., and Williams, W. A. 1962c. *Agron. J.* **54**, 109-113.
Mann, A. P. 1959. *J. Agr. (Victoria)* **57**, 489-491.
Marshall, C., and Sagar, G. R. 1965. *Ann. Botany (London)* [N.S.] **29**, 365-370.
Martin, W. E., Pierce, C., and Osterli, V. P. 1964. *J. Range Management* **17**, 67-68.
May, L. H., and Davidson, J. L. 1958. *Australian J. Agr. Res.* **9**, 767-777.
Meadly, G. R. W. 1936. *J. Agr., W. Australia* [2] **13**, 144-147.
Meadly, G. R. W. 1946. *J. Agr., W. Australia* [2] **23**, 85-123.
Meadly, G. R. W. 1947. *J. Australian Inst. Agr. Sci.* **13**, 153-160.
Meadly, G. R. W., and Pearce, G. A. 1955. *J. Agr., W. Australia* [3] **4**, 457-459.
Meadly, G. R. W., and Pearce, G. A. 1957. *J. Agr., W. Australia* [3] **6**, 357-380.
Miles, W. H. 1952. *J. Range Management* **5**, 207-211.
Miller, H. W., Hafenrichter, A. L., and Hoglund, O. K. 1957. *J. Range Management* **10**, 62-66.
Millikan, C. R. 1961. *J. Australian Inst. Agr. Sci.* **27**, 220-233.
Millington, A. J. 1960. *J. Agr., W. Australia* [4] **1**, 137-144.
Mitchell, K. J. 1956a. *New Zealand J. Sci. Technol.* **A38**, 203-216.
Mitchell, K. J. 1956b. *New Zealand J. Sci. Technol.* **A37**, 395-413.
Mitchell, K. J. 1960. *Proc. New Zealand Soc. Animal Prod.* **20**, 82-92.
Mitchell, K. J., and Lucanus, R. 1960. *New Zealand J. Agr. Res.* **3**, 647-655.
Moore, R. M., and Biddiscombe, E. F. 1964. *In* "Grasses and Grasslands" C. Barnard, ed., Chapter 13. Macmillan, New York.
Morley, F. H. W. 1958a. *Australian J. Biol. Sci.* **11**, 261-274.
Morley, F. H. W. 1958b. *Australian J. Agr. Res.* **9**, 745-753.
Morley, F. H. W. 1961. *Advan. Agron.* **13**, 57-123.
Morley, F. H. W., and Katznelson, J. 1966. *In* "Symposium on Colonizing Species" (H. Baker, ed.), p. 269. Academic Press, New York.
Moule, G. R., Braden, A. W. H., and Lamond, D. R. 1963. *Animal Breeding Abstr.* **31**, 139-157.
Munns, D. N. 1965. *Australian J. Agr. Res.* **16**, 757-766.
Myers, K., and Poole, W. E. 1963. *J. Ecol.* **51**, 435-451.
Myers, L. F., and Moore, R. M. 1952. *J. Australian Inst. Agr. Sci.* **18**, 152-155.
Naveh, Z. 1960. *J. Range Management* **13**, 302-306.
Neal Smith, C. A. 1942. *J. Dept. Agr. S. Australia* **45**, 485-496.
Newman, E. I. 1963. *J. Ecol.* **51**, 625-638.
Odum, E. P. 1954. "Fundamentals of Ecology." Saunders, Philadelphia, Pennsylvania.
O'Neil, J. M. 1958. *J. Dept. S. Australia* **61**, 374-377.
Ormrod, D. P., and Williams, W. A. 1960. *Agron. J.* **52**, 229-234.
Ozanne, P. G., Asher, C. J., and Kirton, D. J. 1965. *Australian J. Agr. Res.* **16**, 785-800.
Parker, C. A. 1962. *J. Agr., W. Australia* [4] **3**, 713-716.
Pearce, G. R., Vercoe, J. E., and Freer, M. 1962a. *J. Agr. Sci.* **59**, 397-402.
Pearce, G. R., Vercoe, J. E., and Tribe, D. E. 1962b. *J. Agr. Sci.* **59**, 349-353.
Quinlivan, B. J. 1962. *J. Agr., W. Australia* [4] **3**, 113-125.
Quinlivan, B. J., and Millington, A. J. 1962. *Australian J. Agr. Res.* **13**, 377-387.
Ratcliffe, D. 1961. *J. Ecol.* **49**, 187-203.



Ratliff, R. D., and Heady, H. F. 1962. *J. Range Management* **15**, 146-149.
Reeves, J. T., and Fisher, H. M. 1960. *J. Agr., W. Australia* [4] **1**, 353-354.
Richardson, A. E. V., Trumble, H. C., and Shapter, R. E. 1931. *Council Sci. Ind. Res. Australia Bull.* **49**, 1-47.
Robbins, W. W. 1940. *California, Univ., Agr. Expt. Sta., Bull.* **637**, 1-128.
Ross, M. A. 1963. *J. Dept. Agr. S. Australia* **66**, 258-260.
Rossiter, R. C. 1947. *J. Council Sci. Ind. Res. Australia* **20**, 389-401.
Rossiter, R. C. 1952. *Australian J. Agr. Res.* **3**, 148-159.
Rossiter, R. C. 1958. *Australian Agrostology Conf., Univ. New England, Papers, 1958* Vol. **1**, pp. 56/1-15.
Rossiter, R. C. 1959. *Australian J. Agr. Res.* **10**, 305-321.
Rossiter, R. C. 1961. *Australian J. Agr. Res.* **12**, 821-833.
Rossiter, R. C. 1964. *Australian J. Agr. Res.* **15**, 61-76.
Rossiter, R. C. 1966. In press.
Rossiter, R. C., and Millington, A. J. 1961. *Australian J. Agr. Res.* **12**, 27-39.
Rossiter, R. C., and Pack, R. J. 1956. *J. Australian Inst. Agr. Sci.* **22**, 71-73.
Russell, J. S. 1960a. *Australian J. Agr. Res.* **11**, 902-926.
Russell, J. S. 1960b. *Australian J. Agr. Res.* **11**, 926-947.
Russell, J. S., and Shearer, R. C. 1963. *Australian J. Agr. Res.* **15**, 91-99.
Sampson, A. W., Chase, A., and Hedrick, D. W. 1951. *California, Univ., Agr. Expt. Sta., Bull.* **724**, 1-130.
Sedgley, R. H. 1963. *Australian J. Agr. Res.* **14**, 646-653.
Sharkey, M. J., Davis, I. F., and Kenney, P. A. 1964. *Australian J. Exptl. Agr. Animal Husbandry* **4**, 34-38.
Shier, F. L. 1952. *J. Agr., W. Australia* [3] **1**, 781-784.
Silsbury, J. H. 1964. *Australian J. Exptl. Agr. Animal Husbandry* **4**, 352-356.
Simon, J. F., and Simon, Alicia. 1965. *Australian J. Agr. Res.* **16**, 37-50.
Smith, D. F. 1965. *Herbage Abstr.* **35**, 912.
Squires, V. R. 1963. *Australian J. Exptl. Agr. Animal Husbandry* **3**, 35-38.
Stebbins, G. L. 1957. *Am. Naturalist* **91**, 337-354.
Stechman, J. V., and Laude, H. M. 1962. *J. Range Management* **15**, 98-103.
Stephens, C. G., and Donald, C. M. 1958. *Advan. Agron.* **10**, 167-256.
Stern, W. R., and Donald, C. M. 1962a. *Australian J. Agr. Res.* **13**, 599-614.
Stern, W. R., and Donald, C. M. 1962b. *Australian J. Agr. Res.* **13**, 615-623.
Sumner, D. C., and Love, R. M. 1961. *California Agr.* **15**, 6.
Talbot, M. W., and Biswell, H. H. 1942. *California, Univ., Agr. Expt. Sta., Bull.* **663**, 13-49.
Talbot, M. W., Biswell, H. H., and Hormay, A. L. 1939. *Ecology* **20**, 394-402.
Tiver, N. S. 1954. *J. Dept. Agr. S. Australia* **58**, 49-55.
Tiver, N. S., and Crocker, R. L. 1951. *J. Brit. Grassland Soc.* **6**, 29-80.
Toms, J. 1958. *J. Agr., W. Australia* [3] **7**, 555-557.
Toole, E. H., and Hollowell, E. A. 1939. *J. Am. Soc. Agron.* **31**, 604-619.
Trumble, H. C. 1935. *J. Australian Inst. Agr. Sci.* **1**, 30-31.
Trumble, H. C. 1937a. *Trans. Roy. Soc. S. Australia* **61**, 41-62.
Trumble, H. C. 1937b. *J. Dept. Agr. S. Australia* **40**, 779-786.
Trumble, H. C. 1939. *J. Dept. Agr. S. Australia* **42**, 953-958.
Trumble, H. C. 1949. *J. Brit. Grassland Soc.* **4**, 135-160.
Trumble, H. C., and Cornish, E. A. 1936. *J. Council Sci. Ind. Res. Australia* **9**, 19-28.
Trumble, H. C., and Davies, J. G. 1931. *J. Council Sci. Ind. Res. Australia* **4**, 140-151.
Trumble, H. C., and Donald, C. M. 1938a. *J. Australia Inst. Agr. Sci.* **4**, 206-208.

Trumble, H. C., and Donald, C. M. 1938b. *Council Sci. Ind. Res. Australia Bull.* 116, 1-47.
Trumble, H. C., and Frazer, K. M. 1932. *J. Dept. Agr. S. Australia* 35, 1341-1353.
Trumble, H. C., and Shapter, R. E. 1937. *Council Sci. Ind. Res. Australia Bull.* 105, 25-36.
Underwood, E. J. 1951. *Rept. Australian New Zealand Assoc. Advance Sci.* 28, 81-88.
Underwood, E. J., Shier, F. L., and Harvey, R. J. 1937. *J. Agr., W. Australia* [2] 14, 442-447.
Van Dyne, G. M., and Heady, H. F. 1965. *J. Animal Sci.* 24, 305-312.
Van Dyne, G. M., and Meyer, J. H. 1964. *J. Animal Sci.* 23, 1108-1115.
Vercoe, J. E., and Pearce, G. R. 1960. *J. Australian Inst. Agr. Sci.* 26, 67-70.
Vercoe, J. E., Tribe, D. E., and Pearce, G. R. 1961. *Australian J. Agr. Res.* 12, 689-695.
Vercoe, J. E., Pearce, G. R., and Tribe, D. E. 1962. *J. Agr. Sci.* 59, 343-348.
Wagnon, K. A., Guilbert, H. R., and Hart, G. H. 1942. *California, Univ., Agr. Expt. Sta., Bull.* 663, 50-82.
Wagnon, K. A., Bentley, J. R., and Green, L. R. 1958. *J. Range Management* 11, 177-187.
Waisel, Y., and Adler, Y. 1959. *Can. J. Botany* 37, 741-742.
Walker, C. F., and Williams, W. A. 1963. *J. Range Management* 16, 64-69.
Wallace, M. M. H., and Mahon, J. A. 1952. *J. Australian Inst. Agr. Sci.* 18, 91-94.
Wallace, M. M. H., and Mahon, J. A. 1963. *Australian J. Exptl. Agr. Animal Husbandry* 3, 39-50.
Watson, E. R. 1963. *Australian J. Agr. Res.* 14, 796-807.
Watson, E. R., and Lapins, P. 1964. *Australian J. Agr. Res.* 15, 885-894.
Weir, W. C., Meyer, J. H., and Lofgreen, G. P. 1959. *Agron. J.* 51, 235-237.
Went, F. W. 1949. *Ecology* 30, 1-13.
Wheeler, J. L. 1966. In press.
Whyte, R. O. 1949. *J. Brit. Grassland Soc.* 4, 33-45.
Williams, C. H., and Donald, C. M. 1957. *Australian J. Agr. Res.* 8, 179-189.
Williams, C. H., and Lipsett, J. 1960. *Australian J. Agr. Res.* 11, 473-484.
Williams, W. A. 1956. *Agron. J.* 48, 273-274.
Williams, W. A. 1963. *Crop Sci.* 3, 472-474.
Williams, W. A., and Elliott, J. R. 1960. *Ecology* 41, 733-742.
Williams, W. A., Love, R. M., and Conrad, J. P. 1956. *J. Range Management* 9, 28-33.
Willoughby, W. M. 1954. *Australian J. Agr. Res.* 5, 157-180.
Winn, D. B. 1965. *J. Dept. Agr. S. Australia* 69, 2-17.