BURIED, VIABLE SEEDS IN TWO CALIFORNIA BUNCHGRASS SITES AND THEIR BEARING ON THE DEFINITION OF A FLORA

by

Jack Major & William T. Pyott

Davis, U.S.A.

Of the ecological factors which determine the differences between two kinds of vegetation, the most frequently neglected is a difference in the two floras. We define the flora as a factor independent of climate, soil parent material, relief, the rest of the biota, fire, and time. In theoretical terms the flora is the assemblage of different kinds of plant disseminules reaching the site. The effective flora includes those kinds of plants which can survive at the levels of the other factors obtaining in the ecosystem throughout the development of the vegetation and soil on the site in question (Jenny, 1941 & 1958; Major, 1951; Crocker, 1952).

An immediate objection to any idea that the flora *can* be an independent factor in vegetation or soil development is that floristic regions coincide with climatic regions (Sjörs, 1955: 159), and that in detail the areas of distribution of different kinds of plants coincide with soil or petrological boundaries. It is a first assumption of all ecology that each biotype fits within the environmental spans of its biotope. However, this is only a necessary condition for the biotype's occurrence there; it is not sufficient for, depending on an ecosystem's history, any one of several kinds of plants could occur there.

Since the flora is already determined as of time zero, it cannot be a function of only climate and/or soil as Robinson (1949: 110) maintained. Crocker points out that ". . . the basic segregation of plant species into regional floras preceded soil formation and plant, succession time zero" (1952: 15).

The flora *can* be independent of the other site factors named above; it certainly not always is independent. Given the same set of site factors other than the flora in two regions which differ in their historical development, the floras often differ between these two regions [1]. For example, the areas with mediterranean climates in California, Chile, South Australia, South Africa and southern Europe contained examples of matching environments with dissimilar floras when in pristine condition. Proof of the ecological similarities is afforded by the present vegetation which now has

---

[1] Taxonomy and nomenclature follow Munz & Keck (1959).

very many elements in common in all these regions (FOURNIER, 1946; MUNZ & KECK, 1959; OBERDORFER, 1960). Man has destroyed the former isolation of these regions from one another, and he has mixed their floras. Many of the introduced plants occupy seral or even weedy habitats, but others are in what appears to be stable vegetation.

We do not neglect plant competition as a factor in determining vegetation. The flora is a measure of potential competition in a particular locale.

The theoretical definition of a flora is useful in arranging our ideas on why plants grow where they do in general. In specific cases, a specific flora needs to be determined. This is seldom done, and rarely explicitly. The determination is difficult for seeds are small, are widely dispersed from the parent plant and, although adapted to specific means and methods of dispersal, are scattered in more or less random directions from the parent plant. Too, the frequency distributions of dissemination distances must differ enormously among various species.

HEIMANS (1954a & b) has discussed the necessity of introducing into phytogeography the idea of accessibility of a given spot to plant diaspores. He mentions that plant sociologists expect to find the same combination of characteristic species in each spot where a particular plant association occurs, and they are surprised when this is not so. "However, this absence quite simply is because a given species has not yet been able to arrive on the spot. The locality can be too isolated and the means of dissemination of the species in question can be insufficient" (1954b: 142). He suggests as a measure of accessibility the distance to the next station of the species. This measure would take into consideration one aspect of the problem, another being efficiency of dispersal. HEIMANS uses the idea of accessibility in discussing the unique Violetum calaminariae on the zinc rich soils of central and western Europe (1961: 57). These considerations, among others, lead him to the conclusion that the association is an old, relic one, and this conclusion in turn supports, and is supported by, his taxonomic interpretations of the peculiar species concerned. HEIMANS notes how important accessibility is in maintaining small nature reserves in an intensively cultivated country. In a varying environment many species need repeated re-introduction into a site to persist. He suggests that the rate of migration of new species into a habitat such as an isolated pond may be slower than the rate of succession. Two ponds would therefore differ in successional status as measured by species composition simply because of their differences in accessibility. Again, the disjunct distributions in presently continuously and well-forested regions of many periglacial plants adapted to raw soils is explicable on the basis of drastic changes in the accessibility of such sites to adapted plants since the melting of Pleistocene ice. The forests. which presently bar access of the pioneer plants to such sites, formed late in the history of the disjunct sites. HEIMANS makes other interesting points.

Although HEIMANS' discussion is the most thorough, other ecologists have recognized accessibility or the nature of the available flora as a factor in determining the nature of vegetation. Unfortunately the recognition has usually been theoretical. It has not always found the practical application necessary. That is, a regional vegetational monograph should define the flora just as it must define the levels of such ecological factors as climate if other ecologists are to use the description.

TANSLEY (1914: 198) included the accessibility of a site to propagules and its historical conditioning as a determinant of the make-up of plant associations. GLEASON (1917: 467) distinguished two sets of factors, namely the nature of surrounding populations and the environment, as determining the plants which successfully invade a given area, and NICHOLS (1923: 18) agreed. PRAEGER (1923: 115) phrased the problem in this way: "It is clear that before we can have a plant society, the plants have to get there, and the successive changes in our plant societies are as much the result of migrations from without as of extermination within; so it is clear that plant dispersal is the dynamic influence which is behind every progressive change of vegetation."

GODWIN (1923) was able to show that ponds resulting from railroad construction differed in their floras, although sites frequented by waterfowl are supposed to have an excellent chance of having a homogenized flora. The number of species per pond was a clear function of age of pond. And (p. 163) " . . .the paper will have attained its end . . . if it renders any ecologist one whit less facile in his too frequent assumption that when a plant is not growing in a certain area, it is mainly because it cannot".

These clear statements did not persuade later ecologists that the principle was too obvious to mention. CAIN said (1947: 193) that ". . . in different geographical localities there will be different (plant) associations, even though the climate and edaphic situations are very similar, because the component species must be drawn from different regional floras." The local significance of characteristic species was pointed out by the founders of the Zürich-Montpellier school of phytosociology (BRAUN-BLANQUET 1925: 144; KOCH 1926: 10). TUOMIKOSKI (1942: 181—2) also discussed the limitation of a particular plant community to a particular florestic region. ETTER (1943: 9, 43—45) repeatedly appealed to "the historical floristic possibilities" to explain some of the presences or absences of particular species from particular regional plant associations. SOCHAVA's "fratriae of plant formations" (1945) represent ecologically equivalent, but divergently evolved at the species level, associations of plants in similar habitats in different floristic regions. CROCKER & WOOD (1947) used the events during the geological history of the South Australian flora to help explain the floristic composition of the Australian vegetation. In summary, the idea that a taxon must be able to disseminate propagules to a biotope to enter the plant association there is usually not stated in so many words, but many phytosociologists have used it instinctively.

How can we determine the flora of a given biotope? JENNY suggested a floristic list for the area including the biotope in question as a first approximation (1941: 203). A many -season catch of seeds would be a closer approximation if the plants could be identified and if the seasons sampled were representative. We have tried to use the content of buried viable seeds in the soil.

PROBLEMS IN DETERMINING BURIED VIABLE SEED NUMBERS

The method using buried viable seeds has several defects.

The first is that many species in perennial plant communities evidently reproduce mostly vegetatively, or at least very little from seed. Swards dominated by such perennial grasses as *Molinia caerulea* (L.) MOENCH., *Brachypodium pinnatum* (L.) BEAUV., *Nardus stricta* L., *Bromus erectus* HUDS. (= *Zerna e.* (HUDS.) S. F. GRAY), *Scirpus caespitosus* L. (= *Trichophorum c.* (L.) HARTMAN), *Festuca rubra* L., *F. ovina* L. (at least at high altitudes, not in peat soils), *Deschampsia caespitosa* (L.) BEAUV., etc. in England and Wales (CHAMPNESS & MORRIS 1948: 156; CHIPPINDALE & MILTON 1934; MILTON 1936, 1939, 1943) and *Phalaris arundinacea* L., *Agropyron repens* (L.) BEAUV., and *Bromus inermis* LEYSS. in Russian floodplain meadows (RABOTNOV 1956: 488) were found to have no seeds at all in the soil. RABOTNOV also (1956: 488—9) lists a number of forbs which are prominent in the vegetation of his meadows, but whose seeds were not found in the soil (*Veratrum lobelianum* BERNH., *Geum rivale* L., *Sanguisorba officinalis* L., *Lysimachia vulgaris* L., *Symphytum officinale* L., etc.). ZELENCHUK (1961: 83) corroborates these data and adds other species. GOLUBEVA (1962) adds a number of dominant, perennial, steppe grasses to his group, including *Stipa* spp., *Koeleria gracilis* PERS., *Agropyron intermedium* (HOST.) BEAUV., *Helictotrichon* spp., etc. HARBERD (1958, 1961, 1962) has suggested on other evidence that many populations of the perennial English grasses, *Festuca rubra* and *F. ovina*, are actually clones of very great age, and the evidence from the absence of their buried viable seeds in soils supports his idea.

Another problem of very great importance results from the selective germination imposed on any soil's seed population when the system is transferred to the greenhouse. Seeds differ greatly in germination requirements so whatever single test condition be used, it will not fit the requirements of some seeds. These will continue in dormancy. Many plants produce a proportion of hard seed, fire stimulated seed, etc., and these kinds of seeds which are difficult to germinate accumlulate in a soil. Most determinations of buried viable seeds have necessarily continued the counting over many months, even several growth seasons. SNELL (1912) however found that 90% of his seeds germinated the first year, although BRENCHLEY & WARINGTON (1930) continued their germination runs over 3 years. This last procedure has been followed by most later investigators. As is evident from BRENCHLEY & WARINGTON's data and, as ROBERTS (1958: 761), RABOTNOV (1958: 1580—1) and others note, third year germinations are few. However, BRENCHLEY had earlier (1918) showed induced dormancies of 58 years, and natural dormancies of 10+ years were shown by BRENCHLEY & WARINGTON (1933).

Another difficulty is that plant seeds are aggregated in general about mother plants, for distances of seed dispersal are short in relation to the spacing of individuals of specific taxa and inefficient in general. Aggregated populations are difficult to sample satisfactorily since mathematical statistics usually necessarily assumes random distibution of variates. A square root transformation will help to normalize the variates and stabilize variance (ROBERTS 1958: 765), but is makes interpretation of results difficult.

Unfortunately, as RABOTNOV (1958: 1572, 1964) points out, appropriate sizes (areas) of samples have not been investigated. Sizes of soil corers used have varied from 3.1 cm diameter (MILTON 1939) or even 2.3 cm diameter (ROBERTS 1958, et seq.) to 10 × 10 cm (RABOTNOV 1956; ZELENCHUK 1961), or even 400 cm^2 (MALINOVSKI 1955, cited from RABOTNOV 1958) to 1 ft^2 (929 cm^2) (OLMSTED & CURTIS 1947; SUMNER & LOVE 1961). The size of sample area should obviously be adapted to the pattern in the vegetation, but it is difficult to find generalizations in this field to use as guides (GREIG-SMITH 1964).

The number of samples necessary has been discussed by CHAMPNESS (1949a) and RABOTNOV (1958 & 1964). CHAMPNESS found that for her 25 cm^2 soil cores, the variance was roughly equal to 3 × the mean number of seeds per core for individual species. Therefore, she concluded that to stay statistically within 10% of the mean number, it would be necessary to take 300/mean number of cores. The total numbers of seeds per core ran from 3 to 10, so the number of cores necessary for the statistical reliability mentioned is much too large to be practicable. For total number of seeds she would have needed 70 cores to stay within 10% of the mean, and for the most abundant species, *Ranunculus repens* L., 200. All investigators have certainly taken too few cores. The obvious solution is to lower the demands placed on statistical reliability, but part of the trouble is inherent in the application of statistics applicable to normal populations to populations which are not in fact, and could not be expected to be, normally distributed but quite obviously are aggregated. RABOTNOV (1958) made a thorough analysis of his 1956 data from a Russian river floodplain and concluded that for his 100 cm^2 cores, with a mean viable seed content of 58.8 and standard deviation of 23.1, from 4 to 15 cores were necessary to stay within 20% to 10% respectively of the mean number. However, for individual species the number varied from 13 for the single species of 100% frequency (*Glechoma hederacea* L. avarage number of seeds 30.0, standard deviation 16.5) to 705 for *Plantago major* L. (average 0.16, s.d. 0. 64)to stay within 15% of the mean. For ±20% of the mean the numbers necessary were 7 and 397. Cores numbering 100 would give average numbers within 15% of the mean for only 7 species out of 42. Of these 42 species 24 occurred in $<$ 10% of the cores; only 4 species were in $>$ 50% of them.

The depth distribution of seeds in soils is usually unknown, but some seeds may be very deeply buried, and others may be only in the litter layer and not in the sampled mineral soil. PEYRONEL (1953: 261), RABOTNOV (1956: 496), SNELL (1912) and CHIPPINDALE & MILTON (1934) all showed approximately logarithmic decreases of numbers of seeds with depth in the soil, but numbers were still appreciable at 30—50 cm. SNELL (1912) had shown substantial nubers of seeds were present to 1 m depth.

An extreme may be the record in Lakeland sand of North Carolina of the tiny (3.78×10^{-3} mg) seeds of *Striga asiatica* (L.) D. KUNTZE to 60 in. depth (150 cm). The content at this depth per 6 in (15 cm)vertical interval was $140—16 \times 10^6$ per acre or 36,000 to 4,000 per m^2 according to ROBINSON & KUST (1962). According to RABOTNOV (1958: 1578) some 64—99.6% of all pasture seeds were found in the 0—10 cm layer of soil. He points out that in most of his meadow types the number of seeds in the 2—10 cm layer is greater than in the 0—2 cm layer. Deep burial induces dormancy whereas a surficial position leads to rapid germination for many seeds. Both trampling of livestock (RABOTNOV 1956: 497) and activities of earthworms bury seeds deeply (CHIPPINDALE & MILTON 1932, 1934: 513—4, MILTON 1939: 155). Peaty soils in Britain under *Molinia, Nardus, Festuca-Agrostis* and *Calluna* dominated vegetation have few seeds below the very surface layers of soil and have few earthworms (CHIPPINDALE & MILTON 1932).

In ZELENCHUK's (1916) neutral, meadow peaty soils of the Lvov (Lemberg) area of the northwestern Ukraine buried seeds were confined to the upper 20 cm of soil. The vegetation was characterized by *Molinia caerulea*, *Deschampsia caespitosa*, or *Schoenus nigricans* L. Some was mown for hay, some pastured, some protected. In soils of high water table such as these, mixing of soil horizons is shallow at most.

As to other effects of soil type, soil texture and associated poor draining must also be considered in comparing results from different areas. MILTON (1948: 173; 1943: 163; 1939: 154; 1936: 68), CHIPPINDALE & MILTON (1934: 516; 530), and CHAMPNESS & MORRIS (1948: 169) found that wet and/or clayey soils induced dormancy and preservation of viable seeds at depth. PRINCE & HODGDON (1946:7) found a statistically significant 30% greater content of viable seeds in clayey than in light soils.

Finally, seedlings are not easy to identify, especially when grown under greenhouse conditions. Most of our plants were spindly and rank compared with field-grown specimens.

AREA STUDIED

The area sampled is at 38° 30 1/2′ N and 122° 02 1/2′ W in western Yolo Country, California at the mouth of Putah Creek on the eastern side of the inner Coast Range. It includes an ungrazed roadside lying about 3 m above the asphalted road itself and an adjacent, fenced off, recently lightly sheep-grazed, unimproved pasture. Apparently neither area has ever been plowed. Elevation is 185 ft (56 m), slope is 5 to 10° W, and physiographically the site occupies the toe of an alluvial fan against the neighboring hills.

The soil is a Non-Calcic Brown (HARRADINE 1963) gravelly clay of the Laughlin series, developed from argillaceous sandstone under a continentally tinged, mediterranean climate.

The regional climate for our ecosystem (MAJOR 1951) will be described mainly in terms of the balance between supply and need for water during the course of an average year (MAJOR 1963a). Average yearly precipitation is 484 mm, and average yearly calculated potential evapotranspiration is 876 mm. These quantities are exactly out of phase in monthly distribution. As a result, the area has summer drought and winter excess of water. Average calculated annual actual (as contrasted to potential) evapotranspiration is only 304 mm with a spring peak of monthly water use of 59 mm in April and a fall peak of 30 mm in November. Average yearly accumulated summer water deficit is 572 mm and average runoff 180 mm. All water balance calculations are according to THORNTHWAITE, MATHER & CARTER (1957) and assume 100 mm of available soil water storage of decreasing availability as water is used.

Average monthly temperatures run from a low of 7.3° C in winter to a high of 25.3° C in summer. The town of Winters weather station mean maximum temperatures of 12.5 to 36.1° C and mean minima of 1.2 to 14.8° C in winter and summer respectively, with absolute maxima and minima of 23 to 44 and —8 to 9° C, are probably very nearly valid for our site (see below). Average monthly precipitation is from a high of 100 mm per month in winter to 1 mm per month in summer.

Monthly climatic data for our site were interpolated from two nearby stations, namely that of Winters 4 miles (6½ km) *east* of our site at 135 ft (41 m) elevation and another on the shore of an arm of the Lake Berryessa reservoir formed behind Monticello Dam a little over 4 miles (7 km) *west* in the mountains at 505 ft (154 m) elevation. The climatic record at Winters was averaged over the last 20 years from U.S. Weather Bureau summaries. That for Monticello Dam covered the last 5 years plus one month. These 61 monthly average temperature and precipitation values were plotted against the corresponding values for Winters, linear regression lines were drawn, and theoretical 20-year average values for Monticello Dam were obtained from the regressions at the 20-year average values for Winters.

Climatic differences between Winters and Monticello Dam are not great, and the climate at our site was assumed to be more similar to the former. Thus, yearly average precipitation for Winters and Monticello Dam is 454 versus 565 mm with differences from 18 mm a month in winter down to 3 mm or so in summer when Winters had no precipitation in July and August. Annual temperatures are 16.5 and 15.9° C respectively, essentially confirming the commonly used lapse rate of —0.6° C/100 m rise in elevation. Monthly differences vary from 0.2 in winter to 1.0° in summer.

These average climatic figures of course give an incomplete picture of this variable climate. While temperatures do not vary much as to yearly pattern in different years, precipitation does. Using the Winters climatic record, in about half the years of record the summer drought is at least partially broken by some precipitation. The amount may be as low as 2 mm or as high as 26 mm per month. The average is about 7 mm. Such amounts would usually come in one storm. These quantities are probably not significant for plants (Major 1963a: 490) except in the rare cases of more than 10 mm precipitation or so which would wet a significant depth of soil and prolong the growth period for estival plants. Depth of wetting for such a storm would be more than 7 to 10 cm since available water is about 15 to 10% by volume in these soils. Of undoubtedly more inportance to plants than the sparse summer rains are the winter droughts. In 80% of the years of record at Winters a winter drought with down to zero precipitation per month occurs. The median value is about 13 mm for the drought month, the average figure 18 mm. These amounts would be concentrated in only part of the month, leaving the rest without incoming water and exposed to potential evapotranspiration of some 15 mm of water or more in an absolutely dry month. In other words, the "usual" precipitation pattern is for fall rains adequate to germinate the annual plants making up most of the flora (see below), followed by a drought with less than 20 mm of precipitation for the month, followed by normal, excessive precipitation which decreases to zero from spring to summer—although in some years the summer drought for estival plants is temporarily broken.

VEGETATION

The vegetation on our adjacent, investigated sites is Valley Grassland in the area of the Foothill Woodland (MUNZ & KECK 1959: 17). It can be described by stand surveys made 30 April 1960 (Table I). Cover and sociability for each species were described by BRAUN-BLANQUET's scales (1951). Parenthized species have been found in the stands in later years. The stand area in each case was 200 m^2, and this area, as shown by concentrically enlarged plots, is well beyond the minimal area for these kinds of plant associations. At the time of sampling the plant cover was about 65% where ungrazed and 20% where grazed. Litter was more abundant where ungrazed.

TABLE I.

Stands of vegetation found in the ungrazed area outside the fence and in the grazed area inside. Abundance and sociability are recorded for each species according to BRAUN-BLANQUET's scales (1951). Life forms follow RAUNKIAER's scheme (BRAUN-BLANQUET 1951: 29—39).

Species Name	Ungrazed	Grazed	Life Form	Native or Introduced
GRASSES:				
Stipa pulchra	3.2	2.2	H	Native
Aristida hamulosa	.	1.2	H	Native
Avena barbata	r.1	r.1	Th	Intro.
A. fatua	+.1	.	Th	Intro.
Bromus mollis	1.1	+.1	Th	Intro.
B. rigidus	r.1	r.1	Th	Intro.
Festuca megalura	r.1	.	Th	Native
F. dertonensis	(+.1)	(+.1)	Th	Intro
Gastridium ventricosum	.	r.1	Th	Intro.

Table I (continued)

Species Name	Ungrazed	Grazed	Life Form	Native or Introduced
Legumes:				
Lotus subpinnatus	+.1	r.1	Th	Native
Lupinus nanus	r.1	r.1	Th	Native
Medicago hispida	r.1	.	Th	Intro.
Trifolium tridentatum	.	r.1	Th	Native
Forbs:				
Brodiaea laxa	r.1	.	G	Native
Br. pulchella	r.1	(+.1)	G	Native
Clarkia purpurea ssp. quadrivulnera	.	r.1	Th	Native
Convolvulus arvensis	(r.1)	.	G	Intro.
Erodium botrys	1.1	1.1	Th	Intro.
E. cicutarium	(r.1)	+.1	Th	Intro.
E. obtusiplicatum	1.1	+.1	Th	Intro.
Forbs:				
Filago gallica	(+.1)	r.1	Th	Intro.
Gilia tricolor	r.1	r.1	Th	Native
Linanthus bicolor	(r.1)	.	Th	Native
Lomatium utriculatum	r.1	.	H	Native
Navarretia pubescens	(r.1)	r.1	Th	Native
N. tagetina	(r.1)	.	Th	Native
Orthocarpus purpurascens	r.1	.	Th	Native
Sanicula bipinnatifida	+.1	.	H	Native
S. bipinnata	.	r.1	H	Native
Silene gallica	r.1	r.1	Th	Intro.
Tillaea erecta	(r.1)	r.1	Th	Native
Trichostema lanceolata	.	r.1	Th	Native
Wyethia augustifolia	r.2	.	H	Native
Ruderals:				
Centaurea solstitialis	r.1	r.1	Th	Intro.
Hypochoeris glabra	.	r.1	Th	Intro.
Hordeum vulgare	.	r.1	Th	Intro.
Dry Site Plants:				
Eriogonum latifolium ssp. nudum	1.1	r.1	H	Native
Plantago hookeriana	r.1	+.1	Th	Native
Bromus rubens	r.1	(1.1)	Th	Intro.
Total no. spp.	31	28	39	22 Native

The ungrazed area was last burned in the fall of 1957. The grazed area evidently would not carry a fire.

This vegetation is subject to marked changes in aspect. On 18 March 1961 the grazed area had a vegetation cover of about 50%, mostly *Erodium obtusiplicatum* and *Gilia tricolor* in the plot sampled. In early spring *Erodium botrys* and *E. obtusiplicatum* are usually most prominent. On otherwise bare areas *Tillaea erecta* and *Gilia tricolor* may be abundant and prominent. *Stipa pulchra* and *Bromus mollis* are dominant in late spring. In summer, if grazing has been sufficiently heavy to markedly reduce the transpiring leaf surface, *Trichostema lanceolata* can be abundant. After the litter of the ungrazed area was burned, the annual fescues were abundant between the bunchgrass clumps.

Thus, most of the annual species can occur on either side of the fence. The differences in the ungrazed and grazed areas are expressed primarily by the presence in the grazed area of the unpalatable *Aristida hamulosa* which is usually found on cobbly, apparently infertile soils and by species which indicate the presence of residual, available soil water, namely *Trichostema lanceolata* maturing in full summer, *Clarkia purpurea* ssp. *quadrivulnera* maturing in early summer, and *Gastridium ventricosum* maturing in late spring. The grazed area is further unique in having such introduced ruderals as *Hypochoeris glabra* and *Hordeum vulgare*. We would expect *Medicago hispida*, which is ordinarily found on heavy, compacted soils and is early in the plant succession in the California annual grassland, to occur in the grazed area. Instead it was found only in the grazed. The grazed area lacks a few native forbs such as *Linanthus bicolor*, *Lomatium utriculatum*, *Orthocarpus purpurascens*, *Sanicula bipinnatifida*, and *Wyethia angustifolia*. Other differences in species presence between the stands we either do not regard as significant or cannot correlate with ecological conditions.

MATERIAL AND METHODS

Soil samples were collected 19 October 1963 from 10 randomly spaced points in each vegetation area. The core had a circular area of 21.5 cm^2, and sampling depths were 0—1 and 1—2 inches (0—2½ and 2½—5 cm) in the mineral soil. The soil samples were stored in a cold room at ca. 0° C for 16 days until 5 November. They were then spread on top of sterilized soil in 8 inch pots, placed in the greenhouse, and watered as needed. The soil samples were therefore reduced in depth by a factor of 15.1 times for germination.

As seedlings were identified they were removed, except that some were left to flower to check identifications.

Germination was allowed to continue for approximately 6 months. During this time no plants recorded in the pots were setting seed in the vicinity of the greenhouse.

RESULTS

Under the greenhouse conditions grasses germinated faster than forbs with the exception of *Erodium botrys* (with which we have included *E. obtusiplicatum*). Some viable *Avena* seeds appeared charred and are probably, therefore, 7 years old.

Some seeds had already germinated when the soil samples were collected as a result of the 52 mm (2.06) in of rain that came 12—13 Sept. 1963 (12 mm), 5—11 Oct. (34 mm), and 16 Oct. (6 mm).

TABLE II.

Numbers of seeds germinating in a total of ten 21.5 cm^2 surface soil samples from each site, by depths. To convert these total figures to numbers of seeds per m^2 multiply by 46.5, to number per acre by 188.6×10^1.

Species	Numbers of seeds						Grand Total	Presence (No. of Soil Cores
	Ungrazed			Grazed				
	0–1	1–2	Total	0–1	1–2	Total		
PLANTS FOUND IN VEGETATION OF BOTH AREAS:								
Avena fatua & barbata	8	0	8	3	2	5	13	5
Bromus mollis	25	7	32	33	3	36	68	14
Erodium botrys & obtus.	1	2	3	4	0	4	7	6
Festuca megalura & dertonensis	16	2	18	58	1	59	77	11
Filago gallica	1	–	1	98	4	102	103	8
Lotus subpinnatus	0	0	0	1	0	1	1	1
Silene gallica	3	1	4	5	2	7	11	7
Tillaea erecta	77	34	111	28	10	38	148	18
PLANTS FOUND IN GRAZED AREA ONLY:								
Medicago hispida	0	0	0	1	1	2	2	1
Trichostema lauceolata	0	0	0	1	0	1	1	1
Trifolium tridentatum	0	0	0	4	0	4	4	2
PLANTS FOUND IN NEITHER AREA:								
Capsella bursa-pastoris	0	0	0	1	1	2	2	2
Lolium multiflorum	0	0	0	2	0	2	2	1
Sagina apetala	0	0	0	1	0	1	1	1
Totals	131	46	177	240	24	264	441	20
No. of species	7	5	7	14	8	14	14	

Table II shows the numbers of buried, germinable seeds of each species in the two areas, by depths.

Whereas only 7 species were found as seeds in the soil of the ungrazed area, 14 occurred in the grazed. In each case the variety of species at the lower soil depth was less than in the surface soil. On neither site was a species found in the 1—2 inch depth but not in the 0—1 inch. Finally, all the kinds of plants found as seeds occurred in the grazed area, only half of them in the ungrazed.

Fewer buried seeds were found in the ungrazed area than in the grazed. The total numbers from the 10 sample cores, having a ground area of 215 cm^2 (0.213 ft^2) were 177 in the ungrazed area and 264 in the grazed. These are numbers of 8,230 and 12,290 per m^2 (33.4 and 49.8 × 10^6/acre). Note that 10,000 seeds per m^2 is one seed per cm^2. The average numbers per sample of 17.7 and 26.4 seeds had standard deviations of 10.9 and 22.9. They are therefore not significantly different. Ranges were 6 to 64 ungrazed and 1 to 17 grazed in the various cores.

The two depths did differ significantly in buried viable seed content as shown by an analysis of variance. Trampling by sheep did not mix seeds deeply into the soil, judging by our data. On the contrary, our data suggest that trampling could have compacted the soil, so seeds were not buried.

Quantitatively the numbers of seeds found in the soil are considerable. This is not unexpected in predominantly annual vegetation such as this. Some of the common annual plants have buried seed populations consistent with their abundance and constancy in this kind of vegetation. For example, there are ca. 1500 *Bromus mollis* seeds per m^2, 300 wild oats per m^2, 800—2500 annual fescues, 200—300 *Silene gallica*, 5000—7000 *Tillaea erecta*, etc. The *Bromus mollis* and *Silene gallica* are ubiquitous in this annual grassland, but the *Bromus* is usually abundant while the *Silene* is scattered. Wild oats are present if grazing is not too heavy; their growth depends strongly on soil fertility level. The annual fescues may form patches of very great abundance following disturbance. The high numbers of buried seeds help explain this behavior. The diminutive *Tillaea* is almost always present in tiny open spots, on shallow soil, etc. *Filago gallica* is a colonial plant, and the 5,000 seeds per m^2 in the grazed area must mean the samples were taken from such a facies.

However, the buried seed populations by no means correlate well with the vegetation on the sites. The *Erodium* spp. are both ubiquitous and abundant in the vegetation, but they had few buried seeds (150—300/m^2). Some may have already germinated in the early fall rains noted. Of the perennials none had buried seeds, yet *Stipa pulchra* and *Aristida hamulosa* are the dominants in the vegetation investigated. Obviously seed reproduction by perennials is less vital to population maintenance than seed reproduction by annuals, even though the latter evidently do usually depend on soil stored seeds to carry them over a few unfavorable seasons. CHAMPNESS & MORRIS (1948) also found that perennials had a disproportionately low representation in the buried seed population as compared with annuals.

Qualitatively the results are also interesting. Of the 19 species found in the vegetation of both sites (Table I), only 8 had seeds which germinated in our samples. These species did not: *Brodiaea pulchella*, *Bromus rigidus*, *Br. rubens*, *Centaurea solstitialis*, *Eriogonum latifolium* ssp. *nudum*, *Erodium cicutarium*, *Gillia tricolor*, *Lupinus nanus Navarretia pubescens*, *Plantago hookeriana*, and *Stipa pulchra*. The *Bromus rubens* might not have been identified even if it had occurred (cf. *Bromus mollis*).

Many of these species are common, and we would expect the soil to contain their seeds. It is probably significant that of the 10 perennial species found in either area none had germinable seeds in the soil. Five of these perennials are confined to the ungrazed area, but 3 more are found in both grazed and ungrazed areas.

Only one of the 8 species found exclusively in the vegetation of the ungrazed area had germinable seeds in the soil samples, namely *Medicago hispida*. As noted above this is anomalous since its two seeds germinated from the grazed soil.

Of the 8 species found only in the grazed area, 6 did not show up in our soil samples. The seedlings identified as *Trifolium tridentatum* could have included the common, prevernal *Tr. depauperatum* which we would expect in both areas.

Of the 3 species which had not been seen in our vegetation areas but which proved to have seeds in the soil, *Sagina apetala* is another, prevernal annual, and all could be moved about via sheep and deer feces (HEADY 1954 and personal communication). These 3 are all introduced plants, and all occurred only in the grazed area.

These data were analyzed by the methods of WILLIAMS & LAMBERT (1959, 1960) for associations between species, i.e., a hierarchial subdivision was looked for based on presence and based on either positive or negative association. In the analysis, species occurrence in more than 90 and less than 10% of the samples did not subdivide the samples by species composition or were indeterminate respectively. The remaining species (Table I) which were used in the analysis included *Avena fatua-barbata*, *Bromus mollis*, *Erodium botrys-obtusiplicatum*, *Festuca megalura-dertonensis*, *Filago gallica*, and *Silene gallica*. Briefly, only a subdivisioon based on presence or absence of *Filago gallica* was significant. Unfortunately we cannot, as WILLIAMS & LAMBERT found they could for their species, correlate an ecological difference with the presence or absence of *Filago gallica* seeds in the soil. As is demonstrated below from the literature, there is abundant evidence that buried viable seeds are better floristic than ecological or vegetational indicators. The patterned distribution of buried viable seeds of *Filago gallica* is probably related to lack of distant seed dispersal from the mother plant. *Filago gallica* occurs in patches, so do its seeds. The correlation is not necessarily ecological, i.e. related to habitat.

DISCUSSION

Our buried viable seed study was intended both as a contribution to theoretical ecology in helping to define the flora of a given ecosystem and as a description of some aspects of a bunchgrass area in California. Still, the number of seeds contained in soils of different ecosystems has other theoretical and applied connotations.

As BRAUN-BLANQUET has observed (1951), in many plant communities competition in the early stages of the life history of many species is so drastic that few individuals survive. This early struggle for existence would seem to be an advantageous focus for much evolutionary study. Competition between mature plants is obviously of secondary importance so far as survival of a taxonomic unit in a particular ecosystem is concerned. The role of competition of course must first be recognized (MASON & STOUT 1954: 255; MAJOR 1958: 359; WALTER 1960: 16—26). A prerequisite for this needed re-direction of evolutionary study is knowledge of the qualitative and quantitative make up of the seed populations entering various ecosystems. This factual basis is largely lacking. A good deal of the existing literature of this kind is reviewed in this paper.

For the data on potential competition to be comparable. the ecosystems to which they apply must be defined. Unfortunately in North America this primary vegetation survey is incomplete (MAJOR 1959, 1963b). The biosystematist can always fall back on HARSHBERGER's survey of 1911 of the vegetation of North America or, in special cases, on an adequate state or regional survey as in Wisconsin, southern Illinois, the eastern forests, the prairies, etc., on local phytosociological studies, or 8 pages in a local flora (MUNZ & KECK 1959). KNAPP (1957) has written a modern survey which is notable for its unfortunate lack of use in the area it describes. His recent book (KNAPP 1965) is a much-needed botanical tool.

In practical terms the seed content of soils is of obvious importance in attempts to modify vegetation. Thus, in California SUMNER & LOVE (1961) have complained that the huge populations of seeds of resident plants make difficult the establishment of reseeded species. The complaint is certainly just, but probably misplaced. The presence of several 10's of pounds of seeds per acre of such desirable range plants as *Bromus mollis*, *Lolium* spp., *Medicago hispida*, and various clovers in California's range soils (SUMNER & LOVE 1961) is a valuable insurance against failure of reseeding attempts. These can backfire since the necessary soil preparation leaves the site open to weed invasion if the reseeding is not successful. *Halogeton glomeratus*, e.g., has been immensely aided to its present prominent position on Nevada rangelands by unsuccessful attempts to replace sagebrush with wheatgrasses.

The same point that seed mixtures for pasture establishment apply much less seed than is already contained in the soil has been made by MILTON (1936: 66—8), PRINCE & HODGDON (1946: 8) and CHAMPNESS & MORRIS (1948: 171). ZELENCHUK (1961: 86) emphasizes the heavy competition the seedlings of desirable pasture grasses must face.

On the other hand AMELIN (1947) has celebrated the heavy seed production by plants of the deserts of Uzbekistan as a stabilizer of the range resource. Seed production of both annuals and perennials amounted to 3,000 to 33,000 per m². In the North American central grassland BROWN (1943) measured the seed yield in various habitats over a 3 year period which included a severe drought year and followed by only 4 years dustbowl conditions which decimated many grasslands. Seed yields varied from 720 to 53,200 mg per m² different years in the most xeric shortgrass (*Bouteloua gracilis* (HBK) LAG. ex STEUD. — *Buchloe dactyloides* (NUTT.) ENGELM.)type, from 4510 to 40,100 mg per m² in the *Andropogon scoparius* MICHX. type, from 0 to 118,900 mg per m² in the most mesic *Andropogon gerardi* VITMAN type, 3,470 to 47,006 mg per m² in revegatitang areas, and 10,000 to 187,900 mg per m² in a heavily dusted area. The seeds concerned may weigh around 1 mg each, although those of *Sporobolus cryptandrus* (TORR.) A. GRAY according to data quoted by BROWN (p. 88) weigh only 0.07 mg each. ZELENCHUK's (1961: 79) plant communities produced from 7000 seeds/m² in mown areas to 113,000 in reserves.

TABLE III.

Average numbers of plants × 10³ per m² in December from 40 1-in² (6.45 cm²) quadrats taken in 3 grassland sites in each of 5 seasons at the Hopland Field Station in the North Coast Ranges in California. From HEADY (1958: 406).

Species	Sites		
	I.	II.	III.
Bromus mollis	6.4	6.2	2.3
Br. rigidus	1.7	0.3	0.2
Erodium botrys	0.3	2.2	1.2
Legumes	0.3	0.9	1.6
Other forbs	8.1	7.8	9.1
Other grasses	0.9	6.0	25.6
Totals	17.1	23.4	40.0

Data on seed numbers from ecosystems similar to ours have been obtained in California. In a study of the annual grassland vegetation near Hopland, some 100 mi (150 km) north of San Fransisco in the Coast Ranges, HEADY (1958) found from 9,910 to 54,200 seedling plants per m^2 in December as the averages from 40 1-in^2 (6.45 cm^2) quadrats studied in each of 5 seasons. The overall average numbers and species composition are given in Table III.

The sampling of California rangeland soils for their seed content by SUMNER & LOVE (1961) used a unit of 1 ft^2 (929 cm^2) of surface soil, with 3 replications. Coefficients of variation were generally greater than 100% for individual species, but ca. 50% for total numbers of seeds. The two areas in Sonoma County in the Coast Range and one in Mariposa County in the Sierra Nevada foothills showed 15,200, 20,100 and 22,700 seeds per m^2. That for a dust blow area in arid Kings County had only 322, of which 80% were *Bromus rubens* and 20% *Erodium cicutarium.*

In a later study in the Hopland area mentioned above HEADY & TORELL (1959) partially scalped the litter and mulch off 3 plots, seeded them to *Bromus mollis*, *Erodium cicutarium*, and *Medicago hispida*, and later sampled them to ¼ inch (6 mm) depth with 10 1-$inch^2$ (6.45 cm^2) plots for germinable seeds. A fourth plot was unseeded. The effects of the seeding are not apparent in the data except for *Medicago hispida* which was increased from 150 seeds per m^2 to roughly 6 times this number. Total numbers of seeds found for the 4 treatments varied from 2,000 to 5,670 per m^2.

TABLE IV.

Numbers of seedlings $\times 10^3$ per m^2 in dense patches of annual vegetation at the San Joaquin Experimental Range in the Sierra Nevada foothills of California. Data from BISWELL & GRAHAM (1956: 117).

Dominant species	Numbers of seedlings of					
	Dominant sp.		Other spp.		Totals	
	1st yr	2nd yr	1st yr	2nd yr	1st yr	2nd yr
Festuca megalura	224.8	168.1	—	3.6	—	171.7
Bromus mollis	187.7	93.0	—	4.7	—	97.7
Erodium botrys	11.3	13.0	17.2	11.1	28.5	24.1
Trifolium variegatum	—	71.6	—	26.5	—	98.1

BISWELL & GRAHAM (1956) had found that 0.04 ft^2 (37.2 cm^2) plots located in the densest patches of various California annual grassland species gave from 225,000 for annual fescues to 24,000 for filaree seedlings per m^2 (Table IV). The first is an immense number and surpasses others in the literature.

In other ecosystems quite different from those in California the buried viable seed contents of arable lands (SNELL 1912; BRENCHLEY 1918; BRENCHLEY & WARINGTON 1930, 1945; WARINGTON 1958; MILTON 1943, 1948; KOTT 1947; ROBINSON 1949; PEYRONEL 1953; BUDD, CHEPIL & DOUGHTY 1954; ROBERTS 1958, 1962, 1963), pastures (BRENCHLEY 1918; CHIPPINDALE & MILTON 1934; MILTON 1936, 1939, 1943, 1948; CHAMPNESS 1949b; CHAMPNESS & MORRIS 1948; DORE & RAYMOND 1942; LIPPERT & HOPKINS 1950; HARRIS 1959; RABOTNOV 1956; GOLUBEVA 1962; MUEGGLER 1956; ZELENCHUK 1961) or haylands (BLAKE 1935; ZELENCHUK 1961), and forests (OOSTING & HUMPHREYS 1940; OLMSTED & CURTIS 1947; KARPOV 1960; SNELL 1912) have all been investigated.

The importance of soil-contained weed seeds to agriculture is obvious. Unless weed control is to be a continuing cost, reductions of soil-contained weed seeds would seem to be a proper measure of the success of weed control efforts.

The ecologically most diverse summary of weed seeds in agricultural fields is given by KOTT (1947: 25—27) with data from fields from the Black Sea and Fergana to the Leningrad and Irkutsk regions within the Soviet Union, from North America and Western Europe, and with very detailed data from a series of fields in the Moscow area. Numbers of soil-contained seeds are in general greater in the more southern regions, being 300,000 seeds/m^2 in the Dnepropetrovsk area and 100,000 seeds/m^2 not unusual in the Ukraine and nearby areas. However, these figures are for total numbers of seeds, many of which are not viable. In the Moscow region the numbers were 32,780 to 117,528 seeds per m^2, with about 1/4 viable.

In English arable soils numbers of buried viable weed seeds have been in the range of 40,000 to 75,000 per m^2 both for field crops (BRENCHLEY & WARINGTON 1930: 243 as an average for several fields and a maximum) and row crops (ROBERTS 1962: 805). ROBERTS began one experiment with a minimum of 19,800 and a maximum of 175,000 buried viable seeds per m^2 in his plots (1958: 766), but he has shown (1963) that vegetable fields under good care may have populations of only 4,000 to 15,000 buried viable seeds per m^2. The last figure represents mostly a 13 times increase in population of *Poa annua* as the results of one wet summer favorable to the weed and unfavorable to its control. ROBINSON (1949) found in Minnesota agricultural areas 1000 to 40,000 weed seeds per m^2. In grainlands of arid southwestern Saskatchewan, with quite a different set of weeds such as *Thlaspi arvense*, *Salsola kali*, *Sisymbrium altissiumum*, etc. as compared to mesic western European or northeastern U. S. environments, BUDD et al. (1954) found from 5,000 to 23,000 buried viable weed seeds per m^2

(to 15 cm depth). A year's fallow generally reduced the numbers by 30—80%, the reduction being inversely proportional to original numbers, but a year's wheat generally at least doubled the fallow field's weed seed population.

Brenchley & Warington (1945) for English field crops and Roberts (1962) for row crops have also shown that fallowing can markedly reduce buried viable weed seed populations. Roberts generalized the data as showing that fallowing produced a logarithmic decrease in numbers of such seeds with a yearly reduction of about 50%. The rapid downward trend indicated by this short half life of one year can be drastically reversed by an accident which lets weeds compete on favorable terms with the crop for even one season. Still, Warington (1958) was able to show that a single year of fallowing in a 5-year crop cycle would not only reduce the weed population temporarily but hold it low. Almost a 50% reduction to 17,000 seeds per m^2 was achieved on the Broadbalk wheat field from 1930 to 1945. A few species did increase, or maintain their numbers.

The persistence of seeds of arable weeds in the soil, variations between species in period of dormancy, and variations between different species in amounts of seed produced all mean little correspondence can be expected between the present vegetation of arable fields and their buried viable seed populations. Since the phytosociology of cultivated crops and their weeds has been neglected until recently, it is not usual to find detailed, even qualitative comparisons between actual vegetation and buried weed seed populations of arable fields.

Such data are more common for pastured lands. In the prairies of the Great Plains Blake (1935) and particularly Lippert & Hopkins (1950) showed mostly low numbers of buried viable seeds, and most were ruderals such as *Poa pratensis*, *Bromus tectorum*, *Hordeum pusillum*, etc. Disturbed areas had many buried seeds. *Sporobolus cryptandrus* alone had over 20,000 buried viable seeds per m^2 in one denuded and burned pasture versus 3400 per m^2 in another not burned. A degraded pasture corner had 15,000 buried viable seeds per m^2 of such nitrophilous species as *Amaranthus retroflexus*, *A. graecizans*, *Monolepis nuttalliana*, etc. The native, perennial grasslands had only from 300 to 800 seeds per m^2, of which the majority were still weedy annual grasses or forbs, or zoochores. The high proportion of seral species may have reflected the drastic opening up of these grasslands during the drought of the 1930's.

Some Quebec pasture data (Dore & Raymond 1942) gave rather low soil seed content figures although the variety of species involved was large, namely 56. Average numbers of buried viable seeds per m^2 varied from 2180 to 7250 in 4 pastures and averaged about 5500. Species found as seeds but not in the vegetation numbered 16. On the other hand, 15—20 of the species found in each pasture were not found as seeds in the pasture soils.

Data from English grazing lands are abundant. A constant note is the presence of seeds of species of arable land in most pastures. The history of land use is thus reflected in the buried seed populations.

Champness (1949b) investigated newly grassed areas at the end of their first growth season. Although an ungrazed ley had some 19,000 seeds per m^2 at the end of the first season, leys which were grazed and therefore in which weeds had less chance to replenish the seed supply had only 5,000 to 10,000 buried viable seeds per m^2. She concludes that replenishment by new plants is a major factor controlling buried weed seed populations. Milton (1936: 61—2) also showed that older swards had fewer buried seeds of arable species than young swards.

Champness & Morris (1948) investigated a great variety of grazed lands. In general the numbers of buried viable seeds per m^2 were low in such specialist communities as *Eriophorum* (2500/m^2) and *Molinia caerulea* (2000/m^2) and were higher in *Nardus stricta* (7500/m^2), heather (*Calluna vulgaris*), and grassland (5500 to 17,500) to rushes (*Juncus*, 9,000 to 15,300). Old pastures had seeds of such plants as *Plantago* spp., *Senecia vulgaris*, and *Urtica dioica* although these plants did not occur in the turf. A *Molinia* area had 9 species which occurred as buried seeds but not in the turf and 6 in the turf but not as buried seeds. Champness & Morris list a number of plants having more seeds in the soil than in the turf. Those showing the opposite are mostly perennials.

Milton (1943) in a study of calcareous pasture soils in Britain found that they had a much higher proportion of buried legume seeds than did the acid pastures (Chippindale of Milton 1934; Milton 1936, 1939). Again discrepancies both qualitative and quantitative between sward and buried viable seed populations were noted. Milton (1948) provides some data allowing calculation of total numbers of buried viable seeds per m^2 following various cultivation treatments. He shows that ploughing of pasture land and cropping to potatoes may raise the number of viable seeds from as low as 7,000 per m^2 for dry grasslands to 36,000 for wet to a high of 55,000 seeds per m^2. Prompt reseeding to pasture species reduced buried seed numbers from some 6,000 per m^2 to half or less. The persistance of seeds of *Ulex europaeus* and *Juniperus communis* in cropped soils is notable, but so is the presence of seeds of weeds of arable lands in the uncultivated grasslands.

A different kind of pastured meadow vegetation was investigated by Rabotnov (1956), namely floodplain meadows of the Oka river near Moscow. Alluviation each year is substantial to none depending on the terrace level. The soils are turfy, rich in humus, and in a podsolizing zone. Reference has already been made to some of the plant species present in these meadows. The perennial, grassy dominants had few seeds in the soil, but there was still a great variety of species present. Many constant or abundant species are familiar weeds or pasture plants (*Phleum pratense*, *Deschampsia caespitosa*, *Trifolium hybridum*, *Tr. pratense*, *Chenopodium album*, *Glechoma hederacea*, *Plantago major*, *Ranunculus acer*, *R. repens*, etc.). Total numbers of buried viable seeds to 10 cm depth varied from a low of 2540 per m^2 in 1948 and 280 in 1950 in a *Bromus inermis* meadow to 16,980 in a *Geranium pratense*-grass meadow in 1948 and 8020 in an *Alopecurus pratensis* L. meadow in 1950. Of the largest number, 11,740 were contributed by *Glechoma hederacea*. Average number over 22 stands was about 5000 buried viable seeds per m^2.

The vegetation investigated over 3 years for buried seeds by ZELENCHUK (1961) was in the southern part of the deciduous forest zone in the northwestern Ukraine. Soils were neutral meadow peats. Vegetation was richly diversified with 56—75 species per association or a total of more than 100 kinds, of which 2/3 were forbs. Average numbers of buried seeds over the 3 years were from 15,000 to 42,000 per m^2. Mowing increased numbers about 30% as compared with reserved areas in the *Molinia caerulea-Deschampsia caespitosa* vegetation. However in *Schoenus nigricans-Molinia-Deschampsia* vegetation mowing decreased seed numbers some 30% as compared with reserves. In both cases sedges and *Juncus* spp. were sharply increased; grasses were decreased by mowing. ZELENCHUK agrees with other investigators on the lack of close correspondence, either qualitatively or quantitatively, between buried viable seeds and vegetation.

The species-rich meadow-steppe investigated by GOLUBEVA (1962) can be characterized by its species composition, of which *Agropyron intermedium*, *Anthoxanthum odoratum*, *Bromus inermis*, *Stipa pennata* L. and such forbs as *Achillea millefolium*, *Artemisia absinthum* L., *Erigeron acer* L., and *Hypericum perforatum* are familiar, by its richness in species (129), and its chernozem soil. Only 2% of the buried viable seeds were of the dominant, perennial grass species. GOLUBEVA (p. 83) ascribes this insignificant number of seeds of the perennial grasses to their great variations in fruiting in different years, to their rapid germination, and to the lack of adaptations in most species to long preservation of viability. Of the seeds found to be present, only those of *Chenopodium album* did not belong to a taxon found in the vegetation.

This meadow-steppe had 18,875 seeds per m^2 where mowed and 19,625 where unmowed. Litter accumulation of 500 g/m^2 therefore did not prevent the penetration of seeds into the soil. In fact, the litter layers had 2400 to 2500 seeds per m^2 in mowed and unmowed sections respectively. The 0—2 cm soil layer of the unmowed area had a possibly significant decrease of 10% less seeds from the 8900 per m^2 found in the mowed area. Qualitatively the species differences (seeds) between the two treatments were negligible.

When treatments are burning versus non-burning, MUEGGLER (1956) has shown that the soil-contained seeds of *Artemisia tridentata* on rangeland of southern Idaho are reduced in numbers almost 5 times in the 0—1/4 in (6 mm) soil layer by burning. No significant reduction took place in the 1/2—1 in (12—25 mm) layer. The latter contained far fewer seeds than the uppper layer.

Finally, there are some data on the buried viable seeds in forest soils. MILTON (1936, 1948) and SNELL (1912) found that seeds of species such as *Digitalis purpurea*, which is characteristic of European woodlands (in a disturbed state at least), persist after clearing and cultivation whereas species of arable soils persist in planted woodlands. OOSTING & HUMPREYS (1940) reviewed much of the previous work on buried seeds and sampled a successional series following old field abandoment in the Piedmont of North Carolina. The succession is from annuals to perennial grass after 5 years, to pines after 15 years, and to hardwoods after some 200 years. From the mineral soil they recovered buried viable seeds in numbers varying from a high of 13,200 per m^2 in the 1-year old stand down to 700 in the 58 year old stand. The 10 stands of different ages had an average of about 5400 seeds per m^2. There was a trend from many in young stands to fewer buried viable seeds in older. The consistent occurrence of species characteristic of early successional stages in the soil of old stands was attributed to storage and prolonged dormancy. OOSTING & HUMPHREYS mention that 18 species of old field herbs were in sites of all age classes through 85 years or more. The conclusion must be that the potential flora of near-climax forests includes species no longer evident in the vegetation. Number of species found as seeds averaged about 35 in each stand, varying from 47 in the 5-year old stand to 29 in both the 33- and 85-year old stands. Analysis of variance showed the most prominent quantitative differences were between open and wooded sites. However, given the opportunity to set seed, almost any of the plants could probably saturate the habitat with disseminules in a very few years.

Soils of northeastern U.S. forest stands were investigated by OLMSTEAD & CURTIS (1947). In 7 different kinds of forests they found by a sieving technique from 2900 to 120 seeds per m^2, although only 1 to 71% were viable. The lack of correlation between vegetation and buried viable seeds was marked. In each stand, seeds of at least 15 species were found for which there were no parent plants. Antithetically, there were many species of plants (a maximum of 29) in each stand from which no seed was found. Conspicuous was the absence of *Rubus* plants in all stands although its buried seeds were the second most abundant in the soils of any plant species.

A more northern forest ecosystem in the Russian southern taiga (*Picea abies* (L.) H. KARSTEN — *Vaccinium myrtillus* L. vegetation, even-aged, over podsolized soils) was investigated by KARPOV (1960). The 100 year old forest is described in detail as to stand structure, ground cover and soil profile. It is typical of a widespread type of boreal vegetation. Numbers of buried viable seeds were 3000 to 5000 per m^2 in Sphagnum low spots, 3600 to 1200 in the level spots, and 1300 on the summits of the nanorelief. Only *Luzula pilosa* (L.) WILLD. of all the species in the spruce forest showed up in the buried seeds count and then to the extent of only 1/2% of all seeds. None of the other species recorded as seeds are mentioned in the description of the stand. The plants represented as buried, viable seeds are such as are characteristic of preceeding successional stages (*Rubus idaeus* L. and *Chamaenerion* (= *Epilobium*) *angustifolium* (L.) SCOP.) and of clearings in the forest (*Deschampsia caespitosa* and *Carex* spp). There is thus an extreme contrast in this taiga forest between the present plant cover and the buried, viable seed content of the soil.

This same theme runs through most of the observations on buried viable seeds in the soils of the various ecosystems described above, namely that the correspondence between the kinds of plants found as buried viable seeds and the kinds of plants found in the vegetation is poor. It may be poor in some cases because the soil stores seeds favored by former agricultural treatments (BRENCHLEY & WARINGTON 1930). In fact, all the arable lands show this. So do those which were once farmed. MILTON (1943: 161) found that fields not cultivated for 20 years still had buried, viable, arable weed seeds. OOSTING & HUMPREYS (1940) found seeds of weeds of freshly abandoned fields present in all successional stages, even including the later forests. Planted forests in Germany had seeds of plants of arable lands even after 50 years (SNELL 1912: 336). KARPOV's forest (1960) had been ploughland. MILTON (1936: 69) did find different species in the hill grazing lands and in the lowland, formerly cultivated grasslands in Britain, and PRINCE & HODGDON (1946) said the correlation between sward and buried seed content was considerable. Most authors have been struck by the discrepancies however. CHIPPINDALE & MILTON

(1934: 526) concluded that "The most remarkable feature of these results is the extreme variation shown by different species of plants in respect of numbers of viable seeds which are in the soil, correlated with this is the complete absence of any close association between the surface vegetation and the seed flora of the soil beneath", and MILTON (1936: 69) later agreed except as noted above. Later he found (MILTON 1943: 162; RABOTNOV 1947: 64) seeds of more leguminous species and fewer calcifuges in calcareous soils than in the acid hill pastures. Marshes differed from upland soils in kinds of buried seeds present (MILTON 1939, 1943: 16). CHAMPNESS & MORRIS (1948: 155—6) found that in English sown grasslands and some types of seral vegetation the correlation between the species composition of the sward and the viable seeds buried beneath it was incomplete. Perennial plants in general were better represented in the turf than in the buried seed population. The discrepancies between species composition of the sward and of the buried viable seeds found by DORE & RAYMOND (1942) have already been mentioned above.

OOSTING & HUMPHREYS (1940) found the seeds of many species not recorded in the vegetation, and vice versa. Even the "germinations from 2-year fields are remarkably unrelated to aboveground observations" (p. 270). Again, "Age classes beyond the establishment of pine show little correlation between naturel vegetation and germinations" (p. 271). Finally, only 16 species of woody seedlings were recorded, with 5 in the terminal oak-hickory site although 6 of the 10 stands were forested. The seeds of some woody species occurred in the seral, herbaceous stands. Two shrubs showed up as buried viable seeds in the 0- to 2-year stands.

In the experiment described by ELLISON (1949: 113) in the subalpine, herbaceous vegetation on the Wasatch Plateau of Utah where seeds found in bare soil, on the edge of patches of vegetation, and within these patches were germinated, neither the species found nor the numbers found correlated with the species composition of the vegetation or the nature of the patchiness of the vegetation. The bare areas, for example, had almost ¼ of the total number of seeds found although they never had more than a very few depauperate annual plants growing in them. The most abundant seeds were from the perennial herb *Oenothera flava* (A. NELS.) MUNZ, a plant not even mentioned in ELLISON's paper.

RABOTNOV (1956: 489) found that both buried viable seed kinds and numbers varied greatly from year to year. And the qualitative differences between sward and seeds was marked. Of 33 species in a meadow's buried viable seed population only 14 were found in the meadow's vegetation. Of the 19 taxa not found in the vegetation analyses 8 were of nearby meadows, 9 of nearby weedy fields, and 2 were entirely foreign meadow plants. The meadow vegetation also had 33 different species of plants, but of these 19 were not found as buried seeds. Only 7 of these were found as seeds in other soils of this kind of meadow. The remainder were of plants whose seeds germinated quickly or of plants existing in the area only vegetatively. Both *Eryngium planum* L. and *Lythrum salicaria* L. occurred as seeds in meadows lacking the plants in the vegetation. The former also showed the reverse situation. The lack of buried viable seeds of the dominant grasses has already been remarked. RABOTNOV concludes that the species composition of the buried viable seeds is more varied than the species composition of the vegetation. It can be richer by 10—19 species (p. 498).

GOLUBEVA (1962: 86) also found discrepancies similar to those described above. Seeds of large-seeded species and the dominant grasses were lacking in the soil.

The conclusion must be that study of the living, above-ground vegetation of a plant community by no means gives us an even qualitative picture of its true composition.

What other meanings have these consistent differences but partial similarities between the species composition of the vegetation on a site and the soil content of buried viable seeds? RABOTNOV's (1956) and GOLUBEVA's (1962) point is well-taken that understanding of the dynamics of a plant community demands knowledge of the buried viable seeds in the soil. These plants are potential competitors of plants already within and those introduced into the community. At the same time, they reflect either real or potential stages in its successional development. By investigating the seed content of the soil we therefore have an operational method of fleshing out JENNY's (1941, 1958), MAJOR's (1951) and CROCKER's (1952) definition of the floristic factor as a determinant factor in plant ecology. Unfortunately it does not give us the whole story, for many plants which are important components of the vegetation are not components at all of the buried viable seed population. Still, the latter enriches what we see in the vegetation. The discrepancy holds particularly where the dominants are perennial grasses and heavy-seeded perennial herbs or woody plants. Annual plants, and particularly annual weedy plants, are especially well-represented among the buried viable seeds of a plant community.

Finally, relative numbers of seeds in the soil and plant individuals in the vegetation are very poorly correlated. Buried viable seed content is no indicator of grazing treatment (this study), mowing (GOLUBEVA 1962 & ZELENCHUK 1961), or even many kinds of agricultural treatments. These treatments may modify absolute numbers of seeds of particular plants — and such modification is obviously important in weed control if in fact it cannot be used as a measure of weed control — but the presence of even a few plants of a weedy species can very quickly saturate the habitat with individuals of that plant (ROBERTS 1963, and others). The definition of the flora of a given ecosystem therefore need not include determination of either relative or absolute numbers of seeds entering that ecosystem.

The contagious distribution of seeds from a particular mother plant makes difficulties in sampling for buried viable seeds. Perhaps this phenomenon could also be used to study seed dispersal, for example, of an introduced plant or an isolated, unique one. The relict nature of disjunct species could be elucidated by such studies over a considerable geographic area.

SUMMARY

A complete description of a plant community must include the buried viable seeds in the soil. The plants occurring in this form are a part of the flora, which helps to determine the community, even though they are not readily evident. The importance of defining an ecosystem's flora is reviewed. When the soil's buried viable seed population is used to help determine the flora, various problems arise since perennial plants reproduce much less abundantly by seed than do annuals, laboratory germination conditions probably do not suit all species, and seeds are not distributed at random so sampling is made difficult. In an investigation of buried viable seeds in two grazed and ungrazed California bunchgrass sites poor correspondence between vegetation and soil seed populations was found. Numbers were 8000 to 12,000 seeds per m^2. Figures of this order or magnitude are general in the periodical literature which describes the buried viable seed populations and the factors which influence them qualitatively and quantitatively in various kinds of arable, mesic pastured or mown, steppe, and forest plant communities.

Not only are the plants evident above ground in a stand of vegetation part of the ecosystem which includes that vegetation, so also are the plant disseminules in the soil.

This paper records a determination of the kinds and numbers of viable seeds in two stands of *Stipa pulchra*, bunchgrass vegetation in the eastern foothills of the central Coast Ranges of California. Such vegetation is variable from year to year, over a climatic cycle of years, and successionally (i.e., it is seral and therefore changes with time, other habitat factors being constant (HEADY

1958). By no means all the species which can occur in this vegetation over a period of several years are evident above ground at one time. We have attempted to use the soil content of buried, viable seeds in the two stands as a measure of this potential flora.

LITERATURE

Amelin, I. S. 1947 — (Securing seeds for revegation of the deserts of central Asia). *Vsesoiuzn. Akad. Selskokhoz .Nauk. im V I. Lenina Dok.* 12, 3: 28—31.

Biswell, H. H. & Graham, C. A. 1956 — Plant counts and seed production on California annual-type ranges. *J. Range Mgt.* 9, 3: 116—118.

Blake, A. K. 1935. — Viability and germination of seeds and early life history of prarie plants. *Ecol. Monogr.* 5, 4: 405—460.

Braun-Blanquet, J. 1925 — Zur Wertung der Gesellschaftstreue in der Pflanzensoziologie. *Vierteljschr. Naturf. Ges. Zürich* 70: 122—149.

Braun-Blanquet, J. 1951 — Pflanzensoziologie. Grundzüge der Vegetationskunde. 2te Aufl. Springer, Vienna.

Brenchley, W. E. 1918 — Buried weed seeds. *J. agr. Sci.* 9: 1—31.

Brenchley, W. E. & Warington, K. 1930 — The weed seed population of arable soil. I. Numerical estimation of viable seeds and observations on their natural dormancy. *J. Ecol.* 18: 235—272.
II. Influence of crop, soil and methods of cultivation upon the relative abundance of viable seeds. *Do.* 21: 103—127, 1933.

Brenchley, W. E. & Warington, K. 1945 — The influence of periodic fallowing on the prevalence of viable weed seeds in arable soil. *Ann. appl. Biol.* 32: 285—296.

Brown, H. R. 1943 — Growth and seed yields of native prairie plants in various habitats of the mixed prairie. *Trans. Kansas Acad. Sci.* 46: 87—99.

Budd, A. C., Chepil, W. S. & Doughty, V. L. 1954 — Germination of weed seeds. III. The influence of crops and fallow on the weed seed population of the soil. *Canad. J. Agr. Sci.* 34: 18—27.

Cain, S. A. 1947 — Characteristics of natural areas and factors in their development. *Ecol. Monogr.* 17, 2: 185—200.

Champness, S. S. 1949a — Notes on the technique of sampling soil to determine the content of buried viable seeds. *J. Brit. Grassl. Soc.* 4: 115—118.

Champness, S. S. 1949b — Notes on the buried seed populations beneath different types of ley in their seeding year. *J. Ecol.* 37: 51—6.

Champness, S. S. & Morris, K. 1948. Populations of buried viable seeds in relation to contrasting pasture and soil types. *J. Ecol.* 36: 149—173.

Chippindale, H. G. & Milton, W. E. J. 1932 — Note on the occurrence of buried seeds in the soil. *J. agr. Sci.* 22: 451—2.

Chippindale, H. G. & Milton, W. E. J. 1934 — On the viable seeds present in the soil beneath pastures. *J. Ecol.* 22: 508—31.

Crocker, R. L. 1952 — Soil genesis and the pedogenic factors. *Quart. Rev. Biol.* 27, 2: 139—168.

Crocker, R. L. & Wood, J. G. 1947—Some historical influences on the development of the South Australian vegetation communities. *Trans. roy. Soc. South Australia* 71: 91—136.

Dore, W. G. & Raymond, L. C. 1942 — Viable seeds in pasture soil and manure. *Sci. Agr.* 23, 2: 69—79.

Ellison, L. 1949 — Establishment of vegetation on depleted subalpine range as influenced by microenvironment. *Ecol. Monogr.* 19: 95—121.

ETTER, H. 1943 — Pflanzensoziologische und bodenkundliche Studien an schweizerischen Laubwäldern. *Mitt. Schweiz. Anst. Forstl. Versuchswesen* 23: 7—132.

FOURNIER, P. 1946 — Le quatre flores de la France. 2nd ed. Lechevalier, Paris.

GLEASON, H. A. 1917 — The structure and development of the plant association. *Bull. Torrey Bot. Club* 44: 63—481.

GODWIN, H. 1923 — Dispersal of pond floras. *J. Ecol.* 11: 160—164.

GOLUBEVA, L. V. 1962 — (Data on the reserves of living seeds in the soil under steppe vegetation). *Biull. Moskov. Obshch. lsp. Prirody Otd. Biol.* 67, 5: 76—89.

GREIG-SMITH, P. 1964 — Quantitative plant ecology. 2nd ed. Butterworths, London. 256 pp.

HARBERD, D. J. 1958 — A spurious significance in genecological trials. *Nature* 181: 138.

HARBERD, D. J. 1961 — Observations of population structure and longevity of *Festuca rubra* L. *New Phytol.* 60: 184—206.

HARBERD, D. J. 1962 — Some observations of natural clones in *Festuca ovina* L. *New Phytol.* 61: 85—100.

HARRADINE, F. 1963 — Morphology and genesis of Non-Calcic Brown soils in California. *Soil Sci.* 96, 4: 277—287.

HARRIS, G. S. 1959 — The significance of buried weed seeds in agriculture. Proc. 12th New Zealand Weed Conf.: 85—92.

HEADY, H. F. 1954 — Viable seed recovered from fecal pellets of sheep and deer. *J. Range Mgt.* 7, 6: 259—261.

HEADY, H. F. 1958 — Vegetational changes in the California annual type. *Ecology* 39, 3: 402—416.

HEADY, H. F. & TORELL, D. T. 1959 — Forage preference exhibited by sheep with esophageal fistulas. *J. Range Mgt.* 12, 1: 28—34.

HEIMANS, J. 1954a — L'accessibilité, terme nouveau en phytogéographie. 8th Int. Congr. Bot., Paris, Rapp. et Commun. Sect. 7: 45.

HEIMANS, J. 1954b — L'accessibilité, terme nouveau en phytogéographie. *Vegetatio* 5/6: 142—146.

HEIMANS, J. 1960/61 — Taxonomic, phytogeographic and ecological problems round *Viola calaminaria*, the zinc violet. *Natuurhist. Genootsch. Limburg* 12: 55—71.

JENNY, H. 1941 — Factors of soil formation. McGraw-Hill, New York.

JENNY, H. 1958 — Role of the plant factor in the pedogenic functions. *Ecology* 39, 1: 5—16.

KARPOV, V. G. 1960 — (On the species composition of the viable seed supply in the soil of spruce-*Vaccinium myrtillus* vegetation). *Trudy Moskov. Obshch. Isp. Prirody* 3: 131—140.

KNAPP, R. 1957 — Über die Gliederung der Vegetation von Nordamerika. *Geobot. Mitt.* 4, *Univ. Koln.* 63 pp.

KNAPP, R. 1965 — Die Vegetation von Nord- und Mittelamerika und der Hawaii-Inseln. Gustav Fischer, Stuttgart, XI + 373 pp.

KOCH, W. 1926 — Die Vegetationseinheiten der Linthebene, unter Berücksichtigung des Verhaltens in der nordost Schweiz. *J. St. Gall. Naturf. Gesell.* 61, 2: 1—146.

KOTT, S. A. 1947 — (The biological properties of weedy plants and the struggle against weediness of soils). Ogiz, Moskva. 240 pp.

LIPPERT, R. D. & HOPKINS, H. H. 1950 — Study of viable seeds in various habitats in mixed prairie. *Trans. Kansas Acad. Sci.* 53, 3: 355—364.

MAJOR, J. 1951 — A functional, factorial approach to plant ecology. *Ecology* 32: 293—412.

MAJOR, J. 1958. — Plant ecology as a branch of botany. *Ecology* 39, 2 :352—363.

MAJOR, J. 1959 — A comparison of two different schemes for mapping vegetation.

Review of Moor & Schwarz, Die kartographische Darstellung der Vegetation des Creux du Van Gebietes, 1957. *Ecology* 40, 3: 324.

Major, J. 1963a — A climatic index to vascular plant activity. *Ecology* 44, 3: 485—498.

Major, J. 1963b — Vegetation mapping in California. Bericht über das internationale Symposion für Vegetationskartierung, Bundesanstalt für Vegetationskartierung, Stolzenau/Weser, 23—26 März 1959, ed. R. Tüxen. Cramer, Weinheim. p. 195—218.

Mason, H. L. & Stout, P. R. 1954 — The role of plant physiology in plant geography. *Ann. Rev. Plant Physiol.* 5: 249—270.

Milton, W. E. J. 1936 — The buried viable seeds of enclosed and unenclosed hill land. *Welsh Plant Breed. Bull.* 4, Series H: 58—73.

Milton, W. E. J. 1939 — The occurrence of buried viable seeds in soils at different elevations and on a salt marsch. *J. Ecol.* 27: 149—159.

Milton, W. E. J. 1943 — The buried viable seed content of a midland calcareous clay soil. *Empire J. exp. Agr.* 11: 155—167.

Milton, W. E. J. 1948 — The buried viable seed content of upland soils in Montgomeryshire. *Empire J. exp. Agr.* 16: 163—177.

Mueggler, W. F. 1956 — Is sagebrush seed residual in the soil of burns or is it windborne? U. S. Forest Service, Intermountain For. and Range exp. Sta. Res. Note 35, 10 pp.

Munz, P. A. & Keck, D. D. 1959 — A California flora. Univ. of Calif. Press. Berkeley. 1618 pp.

Nichols, G. E. 1923 — A working basis for the ecological classification of plant communities. *Ecology* 4: 11—23 and 154—179.

Oberdorfer, E. 1960 — Pflanzensoziologische Studien in Chile, ein Vergleich mit Europa. J. Cramer, Weinheim. Cf. *Ecology* 43, 2: 350—1, 1962,

Olmstead, N. & Curtis, J. D. 1947 — Seeds of the forest floor. *Ecology* 28, 1: 49—52.

Oosting, H. J. & Humphreys, M. E. 1940 — Buried viable seeds in a successional series of old field and forest soils. *Bull. Torrey Bot. Club.* 67, 4: 253—273.

Peyronel, B. 1953 — Sulla presenza de semi germinabili a varie profundita nel terreno lavorato e nel terreno incolto. *Allionia* 1: 257—265.

Praeger, R. L. 1923 — Dispersal and distribution. *J. Ecol.* 11,: 114—123.

Prince, R. S. & Hodgdon, A. R. 1946 — Viable seeds in old pasture soils. *New Hampshire Agr. exp. Sta. techn. Bull.* 89. 16 pp.

Rabotnov, T. A. 1947 — (New data on the stock of germinable seeds in the soils of meadow cenoses). *Priroda* 36, 8: 63—65.

Rabotnov, T. A. 1956 — (Some data on the content of living seeds in soils of meadow communities). In: Akademiku V. N. Sukachevu k 75-letiyo so dnia rozhdeniia, Akad, Nauk SSSR, Moskva-Leningrad, p. 481—499.

Rabotnov, T. A. 1958 — (On methods of studying the supply of living seeds in soils of meadows). *Bot. Zhurnal* 43, 11: 1572—1581.

Rabotnov, T. A. 1964 — (Determination of the age composition of species populations in communities). In: (Field geobotany, ed. A. A. Korchagin, E. M. Lavrenko & V. M. Poniatovskaia). III, p. 132—145. Akad. Nauk SSSR, Moskva-Leningrad.

Roberts, H. A. 1958. — Studies on the weeds of vegetable crops. I. Initial effects of cropping on the weed seeds in the soil. *J. Ecol.* 46, 3: 759—768. II. Effect of 6 years of cropping on the weed seeds in the soil. *Do.* 50, 3: 803—813, 1962. IV. Further observations on the effects of different primary cultivations. *Do.* 51, 2: 233—332, 1963.

Robinson, E. L. & Kust, C. A. 1962 — Distribution of witchweed seeds in the soil. *Weeds* 10, 4: 335.

Robinson, G. W. 1949 — Soils — their origin, constitution, and classification.

3rd ed. Murby, London.

ROBINSON, R. G. 1949 — Annual weeds, their viable seed populations in the soil, and their effect on yields of oats, wheat, and flax. *Agron. J.* 41: 513—518.

SJÖRS, H. 1955 — Remarks on ecosystems. *Svensk bot. Tidskr.* 49, 1/2: 155—169.

SNELL, K. 1912 — Über das Vorkommen von keimfähigen Unkräutsamen in Boden. *Landw. Jahrb.* 43: 323—347.

SOCHAVA, V. B. 1945 — (Fratriae of the plant formations of the USSR and their phylocoenogeny). *Dokl. Akad. Sci. USSR* 47, 1: 57—60.

SUMNER, D. C. & LOVE, R. M. 1961 — Seedling competition from resident range cover often cause of seeding failures. *Calif. Agric.* 15, 2: 6.

TRANSLEY, A. G. 1914 — Presidential address. *J. Ecology* 2: 194—202.

THORNTHWAITE, C. W., MATHER, J. R. & CARTER, D. B. 1957 — Instructions and tables for computing potential evapotranspiration and the water balance. *Drexel Inst. Technol., Publ. in Climatol.* 10, 3: 183—311.

TUOMIKOSKI, R. 1942 — Untersuchungen über die Untervegetation der Bruchmoore in Ostfinnland. I. Zur Methodik der pflanzensoziologischen Systematik. *Ann. bot. Vanamo* 17: 1—200.

WALTER, H. 1960 — Standortslehre. 2te Aufl. Ulmer, Stuttgart. 566 pp.

WARINGTON, K. 1958 — Changes in the weed flora on Broadbalk permanent wheat field during the period 1930—55. *J. Ecol.* 46, 1: 101—113.

WILLIAMS, W. T. & LAMBERT, J. M. 1959 — Multivariate methods in plant ecology. I. Association analysis in plant communities. *J. Ecol.* 47: 83—101. II. Use of a computer for association analysis. *Do.* 48: 689—710, 1960.

ZENENCHUK, T. K. 1961 — (The content of viable seeds in meadow peaty soils of the Lvov Region). *Biull. Moskov. Obshch. Isp. Prirody Otd. Biol.* 66, 3: 77—92.