A Ten-Year Study of Vegetational Changes Associated with Biological Control of Klamath Weed[1]

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The introduction of the effective leaf-beetle, *Chrysolina quadrigemina* (Rossi), into the United States for the control of Klamath weed, or St. Johnswort (*Hypericum perforatum*), was first accomplished in February, 1946 (Holloway and Huffaker, 1951). During the 12 years which have elapsed since this introduction, data on the composition of rangelands previously heavily infested with this weed have been obtained. It is the purpose of this paper to discuss these data as they bear upon two important questions: (1) To what degree has the weed been reduced by this biological control in the areas studied, and (2) what has been the economic nature of the changes in composition of the vegetation on these ranges?

At the request of the senior author the California State Department of Agriculture initiated a survey in 1951 of the Klamath weed infestations in the State, projected as prior to control by bettles, which control was at that time just getting under way. The county agricultural commissioners estimated a total of 2⅓ million acres of Klamath weed infested ranges (Pryor, 1952). This indicates the seriousness of the original problem.

In a study of this kind it is necessary to ponder the possible improvement even if maximal success in reduction of the weed were attained. Clements and Shelford (1939: 285-293) considered that three-fourths of the land south of Mt. Shasta and from the Coast to the foothills of the Sierra Nevada in Northern California was originally perennial climax grassland, and that replacement by annuals was largely due to overgrazing. Hormay and Fausett (1942) state that annuals now make up 90 to 100 percent of the forage on such ranges, and Sampson (1944), Jones and Love (1945), and Bentley and Talbot (1948) conclude that general re-establishment of perennials cannot be expected on some ranges, nor would such necessarily be desirable.

The present work accents the role which insects may exert with respect to the composition of natural vegetation. Range ecologists have given prominent position to the role of the large herbivores and rodents in determining the composition of range vegetation. They have paid practically no attention to the role of the much more selective grazers among the plant feeding insects which abound on those same ranges. They are, in fact, largely unaware of the high degree of restriction in diet of many of these forms (Huffaker, 1957).

The present effort is limited to the period from 1947 to 1957 at specific study-areas in three of the important infested counties in California—Humboldt, Shasta, and Placer. The data are indicative of results generally, although the specific changes in vegetation vary greatly in time and place.

The results form an essential part of the general evidence and confirm this program as one of the striking world-wide examples of biological control of a weedy species.

Methods

The data were obtained in two ways. First, the ranges and specific sites on which the beetles were first released were studied at four locations by use of an intensive method of sampling, and these results are presented separately for the Loftus site (Shasta County), the Loomis site (Placer County), the Blocksburg site (Humboldt County), and the Fort Seward site (Humboldt County). The second method of study was used to follow the general progress of control of Klamath weed and changes in plant composition over a much more extensive area, but this method of study sacrificed accuracy in determining specific composition, particularly as represented by plant species of purely secondary importance. These latter results are included under the topic, "Vegetation of the Ten Mile Sequence Quadrats." This designation is used because the data embrace the changes occurring in a region extending 10 miles from the point of the original colonization of beetles at the Blocksburg site to a position about 3 miles south of Alderpoint. Twenty-seven range areas were sampled at this sequence of locations. They are not designated except by distance from the point of beginning.

The more intensive study was designed to give an accurate picture of the detailed changes in vegetative composition associated with the action and densities of the two leaf-feeding

[1] *This work was conducted as part of a cooperative project with the Agricultural Research Service, U.S. Department of Agriculture. The entomological aspects of this work have appeared in various journals. The program was initiated by the late Professor H. S. Smith.*

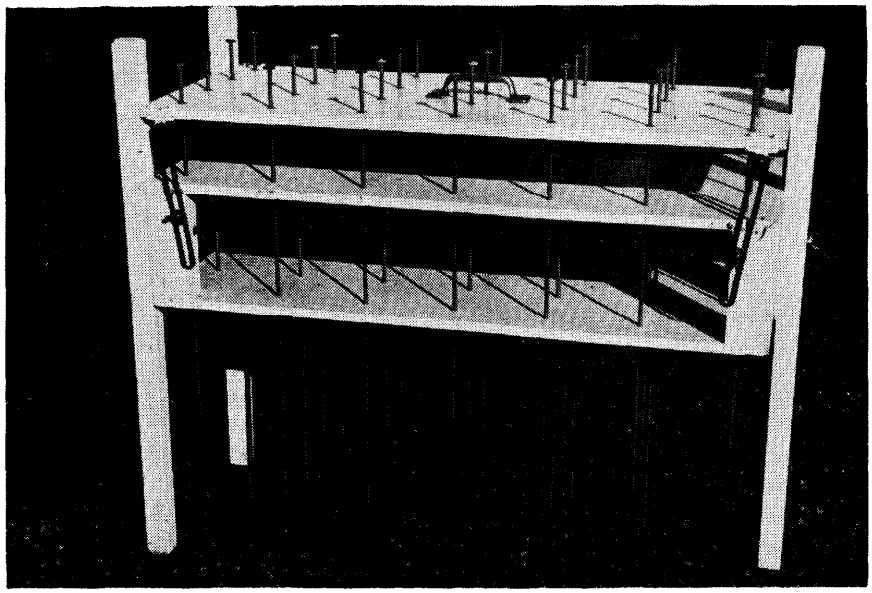

FIGURE 1. Range plant sampling frame used in this study. Each rod marks the center of a micro-position 2 inches in diameter. The plant species of greatest development in the microplots were recorded at each pin.

beetles, *Chrysolina quadrigemina* (Rossi) and *C. hyperici* Forst. Consequently, counts of the beetle populations as well as the plant densities were taken. Excepting for the Loftus site, the method used at these four study areas was described by Huffaker and Holloway (1949) and Huffaker (1951). A sampling frame (Figure 1) one-fourth square meter in area and having 28 rods as microplot designators was used. The plant species of greatest development within a radius of 1 inch (all levels considered) was recorded at each rod. The frame made possible a rapid determination of the dominant plants, with a considerable degree of sensitivity to species which were dominant only at small micro-areas in a quadrat. The method reflects what is implied—the proportions of micro-positions two inches in diameter dominated by the different species. Parker (1948) developed a similar method. Four distance zones were used at the Loftus site in Shasta County—at the center, or beetle release zone, and at ½ mile, 1 mile, and 3 mile distances. The first sampling was done in 1951. Seven permanent quadrats at each distance zone were used. It is significant that the Loftus areas were not typical of infested ranges in that county or generally. The location was chosen because it was at that time the only chance of studying the natural movement of beetles from the center zone to the farthest distance. Thus, this study made it possible to infer natural dispersion and control of the weed, but it did not represent typical, sun-exposed range under normal grazing management, such as was the case for the other sites.

No description has been published of the second method of sampling. In the 10-mile sequence area, time did not permit the detailed method that was used at the four original beetle release sites. Only the three predominant plant species present in each quadrat were listed as to estimated coverage. Beginning at the original beetle colony site at Blocksburg in Humboldt County, positions southward toward Alderpoint were established at each quarter-mile, up to and including 10 miles, except as such positions were occupied by heavy timber, barren river beds, lumber camps, or other terrain on which Klamath weed had no possibility of characteristic success. This study is therefore representative of the ranges in that region, independent of whether the weed ever existed there for whatever reasons except that of obvious unsuitability. The results reveal the extent of previous infestations by this weed, the degree of control, and the pattern of vegetative improvement during the course of beetle action over the past 12 years.

At each distance, three quadrats, each of 1 square meter area, were staked out, and these were: (1) about 5 yards within the range area from the roadside, (2) 50 yards straight in perpendicular to the road, and (3) 100 yards in the same direction. These samples inadequately represented any given field, but collectively, they provided a dependable estimate of the range condition for the region. Table 6 shows the proportions of the total coverages that were typically included by the three predominant species in each quadrat. The remaining coverage was in each case unassigned, but was occupied by miscellaneous species. Actually, in many of those quadrats where a generally dominant species did not occupy a position as one of three predominants, it nevertheless was present as an important element among the miscellaneous representatives. Hence, on the average the figures listed for each species are probably lower than would have been the case had a more complete sampling been done.

All Klamath weed plants were listed whether or not this species was predominant, as were all perennial grasses. This was done so as to follow any progressive changes in perennials.

Results

Beetle Densities and Control

The action of *Chrysolina quadrigemina*, and to a lesser degree,

C. hyperici, in controlling Klamath weed in California was reviewed in some detail by Holloway and Huffaker (1951), and Huffaker (1951, 1953). Typical of their action generally, in the present study the critical action was the feeding of the larvae, which keeps the plants defoliated over a long period at a time when the food reserves in the root system are low. Mass destruction of plants from this action was common, whereas adult feeding, voracious as it is, was extended over too short a period for effective results.

The larvae fed actively at warm periods throughout the winter and early spring on the prostrate, leafy winter growth. By midwinter and early spring when the larvae reached near-maturity, the destruction was very intense after sufficient time had elapsed at a given site for the building up of a large population. A large proportion of these plants, which were heavily fed upon and continuously stripped of foliage from midwinter to spring, failed to put out growth and died. Some of the most vigorous ones, as well as those which were, during a given year, less damaged, sent out new growth; and these, as well as others distant from the heavy populations, were later destroyed or weakened by the adults. Adult activity is most conspicuous at the period of flowering in late spring.

The graphs of weed and beetle densities presented by Huffaker (1951), covering the first few years' results, showed (1) the rapid control of the weed, (2) the associated mature insects issuing each year, and (3) the decline of the beetles themselves following depletion of their own food. The decline in weed densities, zone by zone, followed a course explicable only, and directly accomplished, by larval feeding.

However, the sampling of mature or nearly mature beetles gave a poor reflection of the populations accomplishing the control. The size of the mature brood is an indication of destruction to come rather than that previously accomplished, because the larvae of the following generation represent the actual controlling factor. Only rarely do the larvae occur in numbers just sufficient to control the weed and yet have adequate food to mature. Starvation usually reduces them prior to maturity to a small proportion of those which accomplish the destruction.

The work at Loftus was initiated in 1951 and sampling of immature populations was done in order to correct for the inadequacy of the earlier method.

Figure 2 shows the zone by zone pattern of beetle and Klamath weed densities. The main weed decline occurred in the center zone in 1951-52 as a result of the winter feeding of the large number of larvae — 291 per ¼ square meter. The next year there was a slight resurgence of the weed as the beetles moved into adjacent, more lush weed areas. These weeds were destroyed by the large population per plant the next year. The beetles attained controlling densities at the ½-mile zone during the winter of 1952-53, and sharp decline of the weed followed. At this mildly shaded location the weed persisted every year at a very low density, and beetle larvae were recorded every year except 1956.

Progress at the 1-mile and 3-mile zones was similar, except that larger populations were required to achieve the result at the shaded, 1-mile location. Beetles were first observed in both zones in 1952, although the build-up of larval populations was rapid in the sunny zone and retarded in the shaded one. Nevertheless, during 1953 and 1954 the weed began declining and this continued for three or four years — the control being much less sudden and dramatic

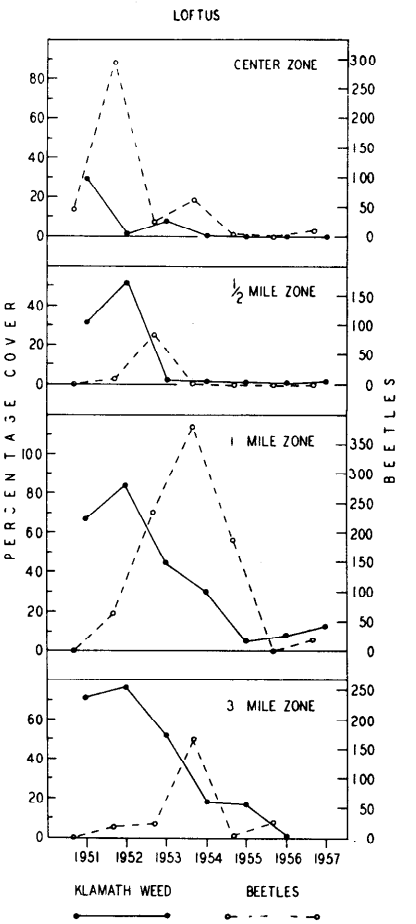

FIGURE 2. The zone-by-zone pattern of reduction in Klamath weed and the corresponding populations of immature beetles per ¼-square-meter quadrat at the Loftus site.

than is characteristic for Humboldt County, for example, but, nevertheless, ultimately satisfactory.

From this study it was shown that even in areas such as the Fort Seward and Blocksburg sites, where Klamath weed remained at an exceedingly low level during the entire period subsequent to its destruction, the beetles maintained themselves at very low densities each winter in or near the quadrats, even though no established, mature plants were present for several years (Tables 2 and 3).

During the progress in years, the seed crop of this weed is gradually depleted. At first hundreds of seedlings per square foot were present, and, although

Table 1. Dominance of range plant species at micro-plot positions in quadrats at the Loftus beetle sites, expressed as percentages of total positions—28 positions per quadrat and 7 quadrats at each of 4 zones.

Species and Category	1951	1952	1953	1954	1955	1956	1957
Klamath Weed	51.3	52.0	26.4	12.5	5.6	2.9	4.6
Other Weeds:							
*Bromus rigidus***	5.0	8.0	4.1	7.4	4.7	3.6	6.1
Centaurea solstitialis	0.0	0.0	0.3	1.3	1.1	3.1	3.9
Agoseris spp.	0.0	0.4	0.1	0.0	0.3	2.0	2.4
Hemizonia, Madia, Calycadenia (tarweeds)	0.8	0.0	0.0	0.1	0.0	1.7	2.4
*Pteridium aquilinum****	0.1	0.3	0.0	0.1	0.4	0.3	1.4
Scleranthus annus	4.2	0.9	0.4	0.8	1.0	0.5	0.9
*Salvia sonomensis****	0.0	0.1	0.3	0.0	0.5	1.4	1.4
Grindelia sp.	0.0	0.0	0.1	0.3	0.0	0.0	0.7
Elymus caput-medusae	0.0	0.0	0.0	0.0	1.6	0.0	0.2
Trichostema lanceolatum	0.0	0.0	0.0	0.0	0.8	0.0	0.0
TOTAL Other Weeds	10.1	9.7	5.3	10.0	10.4	12.6	19.4
Legumes: †							
Lotus spp.	4.8	6.8	7.4	11.9	6.6	6.6	14.3
Trifolium spp.	0.3	0.5	0.4	0.6	0.8	0.3	0.5
Lupinus spp.	0.0	0.0	0.0	0.1	0.4	0.0	0.0
TOTAL Legumes	5.1	7.3	7.8	12.6	7.8	6.9	14.8
Forage Grasses**:							
Bromus mollis	7.8	10.8	19.8	25.8	27.7	29.6	28.1
Bromus tectorum	1.2	3.4	6.5	5.5	4.6	1.9	4.6
Aira caryophyllea	2.3	3.2	8.3	15.6	2.3	1.7	3.6
Festuca megalura & *F. myuros*	0.0	0.0	1.6	2.9	1.1	0.5	0.7
Briza minor	0.0	0.0	0.1	1.1	0.0	0.0	0.0
TOTAL Forage Grasses	11.3	17.4	36.3	50.9	35.7	33.7	37.0
Forbs:							
Erodium cicutarium	2.2	3.5	2.3	0.6	10.1	10.7	4.9
Galium spp.	1.5	0.4	1.6	0.5	3.9	1.0	2.0
Convolvulus fulcratus	0.7	0.3	0.3	1.1	1.6	3.6	3.2
Plantago spp.,†† chiefly *lanceolata*	0.0	0.0	0.0	1.3	0.9	0.0	0.0
Stellaria media	0.7	0.1	0.4	1.7	2.2	0.5	1.2
Eschscholtzia californica†††	0.4	0.4	0.8	0.5	1.4	0.0	0.0
Potentilla congesta	0.1	0.1	0.4	0.3	0.0	0.9	0.9
Ranunculus spp.	0.0	0.1	0.1	0.1	0.4	0.3	0.5
Erodium botrys	0.0	0.0	0.0	0.0	0.5	1.9	0.0
Daucus carota	0.0	1.3	0.1	0.5	0.1	0.0	0.0
Total Forbs	5.6	6.2	6.0	6.6	21.1	18.9	12.7
Miscellaneous Species	0.4	0.2	0.2	1.2	1.5	2.1	0.6
Bare Ground	16.1	7.0	18.2	5.9	18.9	22.8	10.9
Total Forage Species	22.0	30.9	50.1	70.1	64.6	59.5	64.5

* The quadrats at the three mile zone were missing in this sample—destroyed by construction. This accounts in part for the increase in *percentage* of weedy species, compared with 1955 (see text).

** *Bromus rigidus* produces an abundance of palatable forage during its early growth, and since it can be grazed sufficiently to curtail heavy production of the objectionable seed heads, it is questionably placed as a weed.

*** These two species occupied an expected position at these shaded locations. They are a natural part of such vegetation.

† All species of these genera were considered with the desirable forage species, since although *some* have low palatability, they are not pernicious and all add to soil fertility.

†† Thornber (1910) classed some plantains very important as forage.

††† "Range Plant Handbook" rates this species as fair forage for sheep and states that tests have failed to establish it as poisonous.

varying with the years, there was a marked decline after about five years. In 1955 and 1957 a very greatly reduced number of seedlings was characteristic. The beetles fed actively on the seedlings, deposited eggs on them, and a very rare larva developed to maturity by moving from seedling to seedling to feed. Thus, the beetles survived, though widely dispersed in proportion to numbers, and synchronous with any focal points of weeds which would otherwise become mature, flower, and produce seeds.

Another reason the beetles are able to survive and control their host plant at very low weed densities is that they do not achieve full success under shade (Table 1). This is commonly observed in this country, and is reported by Clark (1953) and Parsons (1954) as a reason why they gave inadequate control in Australia, where, contrary to the status in California, important infestations occur in partially wooded areas. However, differences in summer rainfall are also involved. When laying eggs, the beetles shun heavy shade for sunnier locations. The grazing value of such shaded rangelands in California is very small in proportion to the extensive open ranges where control is complete; and these shaded areas furnish "marginal" survival, maintaining a better distribution of the beetles against the potential localized resurgence of the weed on the important open ranges.

Vegetation at The Loftus Site, Shasta County[2]

Table 1 and Figure 2 show the control of Klamath weed and the changes in cover for other plants

2 *The authors express their thanks to Mrs. Margaret K. Bellue of the California State Department of Agriculture and to staff members of the Herbarium, University of California, for making some of the plant determinations.*

at the Loftus site. In 1951, Klamath weed was dominant in all zones, although deervetch *(Lotus americanus)*, soft chess *(Bromus mollis)*, and ripgut brome *(B. rigidus)* were, collectively, important in the center zone. Klamath weed was the sole dominant at the other three zones, and bare spots between the clumps of weeds were common, as were certain substratal forms. The weed decline and beetle action, zone by zone, is shown in Figure 2.

The beetles had been released in 1948, but their results were slight through 1951. By 1952, they had destroyed nearly all the weed in the central zone, and soft chess, ripgut brome and *Lotus* spp., then predominated. Yet, there was an increase in the weed's importance in the other zones, as the beetles had not attained high densities there. This accounts for the fact (Table 1) that Klamath weed was just as important, as a whole, in 1952 as in 1951. By 1953, the beetles had removed the weed at the ½-mile zone, and there was some reduction at the other two zones, the greater reduction being at the one-mile zone. By 1954, the weed in the two closest zones had been brought under good control, and a marked reduction achieved at the distant zones.

Combining the zones (Table 1), Klamath weed was reduced by 1953 to 26.4 percent; by 1954, to 12.5 percent; and by 1955 to 5.6 percent. In 1956 and 1957 there was no appreciable further decrease. This is contrary to experience nearly everywhere in California except in shaded locations, and many of these quadrats were in partially shaded areas. Thus, these areas, as previously stated, are not typical of the former economic problem.

As the weed was reduced, the space vacated was taken by species previously present. Only in 1957 was the proportion of "other" weedy species much greater than in 1951 when Klamath weed was abundant. This abundance of other weeds in 1957 is partially due to the fact that the quadrats at the 3-mile zone were no longer present, and that location had been more typical range with a better class of forage developing there. Hence, of the remaining three zones, only one was in fairly open, typical range, the other two being shaded and less suitable to good range species such as soft chess and filaree *(Erodium* spp.). In spite of this, there was only a minor increase in other weeds, and the pattern has not been one of increasing claim by pernicious species. For example, ripgut brome, the predominant among the weedy species, had the same coverage when Klamath weed was abundant as later. Also, it is questionably placed as a weed, as it is good forage when young and is controlled by moderate grazing.

The serious weed, medusa head, *(Elymus caput-medusae)*, occupied a small area adjacent to one of the quadrats since 1953, but it spread very slowly and hardly disturbingly at this location. The same situation has existed for 7 years near one of the study areas in Humboldt County.

Also, yellow starthistle *(Centaurea solstitialis)* came in with the reduction of Klamath weed at this location. Here it was favored by an oak leaf cover which hindered germination and establishment of good forage species less than it did the thistle, which is a summer annual and germinates after substantial decomposition of the leaves. This thistle remained low in abundance but did reach a level of 4 percent in 1957. Seedlings of tarweed *(Madia glomerata)* were also of variable occurrence. Bracken fern *(Pteridium aquilinum)* and sonoma salvia *(Salvia sonomensis)* are perennials which increased slightly in spots where they had been present, even when Klamath weed was abundant.

Forage grasses, legumes and forbs claimed the major part of the space vacated (Figures 2 and 3). By 1954, the grasses reached the level previously occupied by Klamath weed, and yielded some of that predominance in 1955, 1956, and 1957, mainly to species of legumes and forbs. The years 1954 and 1957 were comparatively good "legume years," while 1955 and 1956, on the other hand, were favorable years for filaree *(Erodium cicutarium)*. The pattern of total forage species was 22.0, 30.9, 50.1, 70.1, 64.6, 59.5 and 64.5 percent, respectively, and 1951 through 1957 (Table 1). The total for all forage species was highest in 1954, and slightly less in 1955 and 1957. The amount of bare ground has been quite variable and it is caused by many factors — excessive litter, rocks, hoof disturbances, manure chips, rodent action, or vehicle disturbance.

Vegetation at the Fort Seward Site, Humboldt County

Table 2 and Figure 3 show the changes in vegetation for this site from 1947 through 1957. In 1946, the year the beetles were introduced, this site had Klamath weed uniformly as the principal dominant, but the plants were sufficiently spread so that grasses and forbs, collectively, shared about equally with it in total predominance at the micro-positions. By 1948, the beetles had reduced the density of the weed in one of the sampled zones (Huffaker, 1951), and thus its general abundance was reduced to 22.5 percent, with a corresponding increase in total forage species. By 1949, the weed was further reduced to 15.6 percent, and at no time since then has it attained dominance at any micro-position sampled; hence, the zero levels from 1950 through 1957.

Total forage associated with the control at this location has

Table 2. Dominance of range plant species at micro-plot positions in quadrats at the Fort Seward beetle sites, expressed as percentages of total positions—28 positions per quadrat and 7 quadrats at each of 4 zones.

SPECIES	1947	1948	1949	1950	1951	1953	1955	1957
Klamath Weed	36.6	22.5	15.6	0.0	0.0	0.0	0.0	0.0
Other Weeds:								
Hypochoeris glabra	6.1	11.4	7.6	3.2	13.6	1.3	6.6	2.2
Hordeum gussoneanum and *H. murinum*	1.5	0.0	0.0	1.9	0.9	0.7	0.0	1.3
*Bromus rigidus**	0.0	0.0	0.0	0.0	0.0	0.3	0.1	1.1
Agoseris spp.	0.0	1.2	0.0	1.7	0.0	1.4	0.4	0.1
Amsinckia douglasiana	0.0	0.3	0.0	0.8	0.0	0.5	0.1	0.1
Eremocarpus setigerus	0.0	0.0	0.0	0.1	0.4	0.1	0.0	0.1
Micropus spp.	0.5	0.1	0.1	0.1	0.0	0.0	0.0	0.1
Total Other Weeds	8.1	13.0	7.7	7.8	14.9	4.3	7.2	5.0
Legumes:								
Lotus spp.	0.1	2.0	1.7	11.6	6.2	3.4	0.5	8.7
Trifolium spp.	2.3	6.4	0.0	17.4	1.9	8.3	0.4	5.6
Lupinus spp.	0.0	0.1	0.0	0.5	0.3	0.0	0.0	1.0
Total Legumes	2.4	8.5	1.7	29.5	8.4	11.7	0.9	15.3
Forage Grasses:*								
Bromus mollis	14.8	6.4	34.1	20.3	23.7	29.7	44.1	23.5
Danthonia californica	2.9	0.5	2.8	1.6	3.1	0.4	5.9	9.2
Aira caryophyllea	4.8	3.8	10.3	3.9	3.2	14.3	2.3	11.1
Avena fatua	4.7	1.7	0.8	0.6	2.7	4.2	2.7	2.9
Festuca megalura & *F. myuros*	2.3	1.0	2.4	0.6	1.0	3.0	4.6	0.9
Briza minor	0.1	1.9	0.0	3.6	0.5	7.0	0.7	0.3
Elymus glaucus	0.0	1.0	0.4	0.8	0.4	0.3	0.4	0.4
Total Forage Grasses	29.6	16.3	50.8	31.4	34.6	58.9	60.7	48.3
Forbs:								
Erodium spp. chiefly *botrys*	9.9	21.0	11.7	11.8	28.0	13.2	27.4	20.1
Plagiobothrys canescens	0.3	0.9	0.0	0.8	2.4	0.4	0.4	4.4
Linanthus bicolor	0.1	3.3	0.3	0.8	1.0	1.0	0.3	2.6
Geranium dissectum and *G. molle*	0.5	1.4	1.3	3.6	2.8	3.0	1.0	2.1
*Baeria chrysostoma***	0.6	3.8	0.7	2.7	2.4	5.1	0.7	1.4
Galium spp.	0.0	0.1	0.5	1.3	0.1	0.1	0.1	0.3
Stellaria media	0.0	0.0	0.0	0.6	0.3	0.3	0.3	0.1
Ranunculus spp.	0.0	0.6	1.2	0.3	0.0	0.0	0.1	0.3
Orthocarpus, Cordylanthus, Castilleia	0.8	2.2	0.1	2.3	0.3	0.1	0.1	1.1
Total Forbs	12.2	33.3	15.8	24.2	37.3	23.2	30.4	32.4
Miscellaneous Species	1.5	0.7	1.3	2.0	2.0	1.3	0.6	0.3
Bare Ground	9.7	5.6	7.4	5.1	2.8	0.3	0.7	0.4
Total Forage Species	44.2	58.1	68.3	85.1	80.3	93.8	92.0	96.0

* *Bromus rigidus* is questionably placed as a weed (see note, Table 1).

** Although this species is conspicuous because of its relatively large and showy flowers, it has not been classed as noxious. Also, it was a characteristic component of the climax vegetation, having evolved with it. Since it is also grazed, it is classed with the forbs.

been very good. Subsequent to complete control of the weed, only during 1951 did total forage fall below 85 percent, and during the years of the last three samplings, the levels were over 90 percent—96 percent in 1957. The lower level in 1951 was due to an increase in a single weedy species, hawkbit *(Hypochoeris glabra)*, which forms a tight winter rosette effectively reducing competition when conditions for its germination give it advantage.

One species may compensate for the low importance of another, and of course this may apply to a weed or a forage species. Fortunately, the compensation experienced was usually between grasses, forbs, and legumes of some forage value. In 1950 and 1951, the grasses increased very little over their status when Klamath weed was abundant, but during 1950 the legumes were at their greatest development at 29.5 percent, while in 1951 filaree *(Erodium botrys)* reached its highest density. The lower level of the forage grasses in 1957 is compensated by a high level of legumes at 15.3 percent, and a good level of forbs, mainly filaree, at 32.4 percent.

An attempt to correlate years of abundance of certain of the annual species with meteorlogical data was not fruitful.

The best annual grass in this region, soft chess, consistently was predominant after removal of Klamath weed, except in 1951 when filaree exceeded it. The rather inferior silver hairgrass *(Aira caryophyllea)*, is nearly always present, and its dominance at micro-positions varies with the changeable success of more robust competitors. Its highest level was in 1953, when filaree did not succeed to its usual degree. The other annual grasses also varied from year to year, as is characteristic on such ranges (Bentley and Talbot, 1948). This applies also to the forbs. Of these the wild geraniums predominated, with filaree very abundant and *Geranium dissectum* and *G. molle* commonly encountered. Branchy goldfields *(Baeria chrysostoma)* was both common and conspicuous by its color.

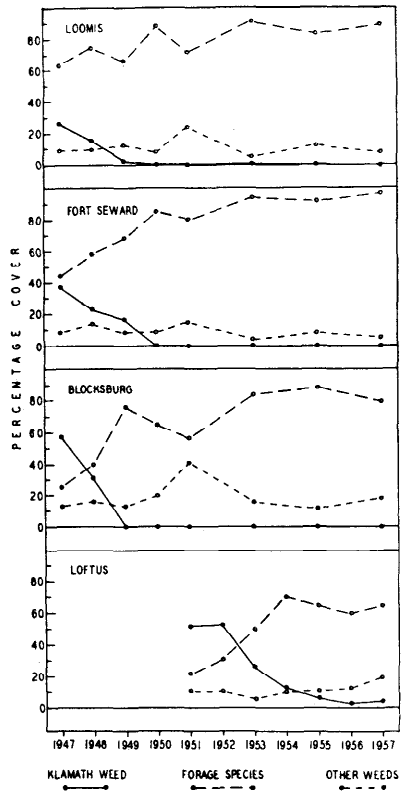

FIGURE 3. Changes in cover of Klamath weed, other weeds, and forage species from 1947 through 1957 associated with continuous control of Klamath weed by beetles at the Loomis, Fort Seward, Blocksburg, and Loftus sites.

Only two perennial grasses were dominant at any time. These were California oatgrass *(Danthonia californica)*, the dominant climax species of this region, and blue wildrye *(Elymus glaucus)* the latter of only minor but stable occurrence. The changes in California oatgrass were encouraging. Before 1955, it occurred sparingly on this range. It existed in the quadrats only at the center zone. In such areas where it was initially present, it has greatly increased during the past ten years.

Not only has it increased where it originally occurred, but it has appeared within the past three years in other quadrats representing three of the four distance zones. Other data (see "Blocksburg site" and "Ten-Mile Sequence Quadrats") show that once established in a local area, it may increase moderately fast if conditions are favorable. Subsequent to Klamath weed removal, no noxious species has shown consistent inroads. Only hawkbit amounted to anything, and it only in 1951.

Vegetation at the Blocksburg Site, Humboldt County

In 1946, when the beetles were introduced, and in 1947 prior to much beetle activity, this range was a solid stand of dense Klamath weed. The dominance shown in Table 3 and Figure 3 for 1947 illustrates the degree to which the importance of Klamath weed is compromised by the method of sampling, which favors minor substratal associates present in the inter-spaces. Pictures taken at this location (Figure 4) show the denseness of the weed. In June or July, it characteristically attained sole dominance and almost complete coverage, although in Table 3 it is listed at only 57.6 percent in 1947. This is because the samples were taken in May prior to its attainment of full dominance. This was in one sense desirable, since such sampling gave a measure of the substratal associates, many of which assumed greater importance upon removal of the weed; but it constitutes an "under-rating" of the former importance of the weed, which is inherent to the method of sampling.

Considering the denseness of the weed formerly, and noting from Table 3 that by 1949 it was not present at any micro-position, and only in 1955 did it reappear at a 0.1 percent level, the perfection in control is obvious. Forage species increased markedly, including return of the climax bunchgrass, California oatgrass (Huffaker, 1951). The data demonstrate that at such locations oatgrass may steadily increase once established in local areas, and at the same time spread more slowly to greater distances. It occurred at only 9.2 percent when Klamath weed was dominant in 1947, mainly in wet areas and along cattle paths. It increased to 22.7 percent in 1949, the year the weed was removed, and, subsequently, to 23.4, 28.9, 30.3, 52.6 and 45.0 percent, respectively, for 1950-51-53-55-57. The differences between 1955 and 1957 are probably due to phase of growth and variable robustness of associated plants and do not necessarily mean its actual disappearance anywhere. It is not yet as completely dominant as was Klamath weed initially, but it is the principal species, and still increasing.

Aside from California oatgrass, the increase in other forage grasses was at first substantial, but these have given way somewhat to oatgrass, and, during 1951, to hawkbit, which reached a level of 40 percent that year. Here, hawkbit is commonly present and if unfavorability exists for more robust plants, it fills in the void; but it has not shown persistent aggressiveness or dominance generally. Soft chess was the dominant annual grass, but silver hairgrass was about equal with it. Two other perennial grasses were present, Halls bentgrass *(Agrostis hallii)* and Pacific panicum (*Panicum pacificum*), but neither was aggressive during this study.

Total forage was fairly high, but depressed somewhat by the prevalence of hawkbit, particularly in 1951. Total forage was dominated by the grasses, but legumes contributed 12.4 percent in 1953 and lesser amounts during other years. Total forbs were commonly low in importance, never exceeding 9 percent and usually at 7 or 8 percent, with *Plantago* spp. slightly surpassing others.

Vegetation at Loomis Site, Placer County

The data for this site are presented in Table 4 and Figure 3. Beetles were introduced in 1946. Initially, there was a "patchy"

Table 3. Dominance of range plant species at micro-plot positions in quadrats at the Blocksburg beetle sites, expressed as percentages of total positions—28 positions per quadrat and 7 quadrats at each of 4 zones.

SPECIES	1947	1948	1949	1950	1951	1953	1955	1957
Klamath Weed	57.6	31.1	0.0	0.0	0.0	0.0	0.1	0.0
Other Weeds:								
Hypochoeris glabra	12.9	15.4	11.7	18.8	39.9	9.4	3.4	12.5
Cynosurus echinatus	0.0	0.0	0.0	0.0	0.9	5.0	4.7	5.0
Agoseris spp.	0.0	0.0	0.0	0.1	0.0	0.4	1.9	0.6
*Bromus rigidus**	0.0	0.0	0.4	0.8	0.3	0.3	0.3	0.1
Rumex spp.	0.4	0.4	1.5	1.0	0.4	0.3	0.4	0.0
Eremocarpus setigerus	0.0	0.0	0.0	0.0	0.0	0.1	0.3	0.0
Total Other Weeds	13.3	15.8	13.6	20.7	41.5	15.5	11.0	18.2
Legumes:								
Trifolium spp.	0.8	0.8	0.1	2.9	0.9	8.0	0.6	4.5
Lotus spp.	0.0	0.9	0.8	2.3	2.2	4.3	0.5	1.4
Lupinus spp.	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Total Legumes	0.8	1.7	0.9	5.2	3.1	12.4	1.1	5.9
Forage Grasses:								
Danthonia californica	9.2	13.3	22.7	23.4	28.9	30.3	52.6	45.0
Bromus mollis	4.9	10.1	18.5	16.2	7.9	8.2	5.6	8.5
Aira caryophyllea	5.9	3.7	23.6	7.1	6.5	14.6	17.9	7.9
Briza minor	0.0	4.3	0.3	2.8	2.4	9.3	1.5	3.1
Avena fatua	0.0	0.0	0.0	0.0	1.7	0.5	0.1	0.4
Agrostis hallii	0.5	1.5	2.3	1.1	0.0	0.0	0.1	0.3
Panicum pacificum	0.7	0.3	0.4	0.3	0.3	0.8	0.5	0.0
Total Forage Grasses	21.2	33.2	67.8	50.9	47.7	63.7	78.3	65.2
Forbs:								
Plantago spp.** chiefly *lanceolata*	1.7	2.4	0.7	0.5	2.5	2.4	2.5	2.8
Orthocarpus, Cordylanthus, Castilleia	0.1	0.3	0.0	0.4	0.9	0.5	0.6	1.9
Sisyrinchium bellum, Brodiaea spp.	0.0	0.0	1.4	1.2	0.4	0.1	2.3	1.0
Filago gallica	0.0	0.4	0.2	0.2	0.1	1.5	0.0	1.1
Linanthus bicolor	0.3	0.7	0.0	0.1	0.0	0.4	0.3	0.3
Ranunculus spp.	0.0	0.1	0.4	0.3	0.3	0.3	0.1	0.1
Luzula, Juncus, sedges	0.0	0.4	1.3	0.9	0.0	0.1	0.7	0.6
Daucus carota	0.5	0.1	1.2	0.0	0.0	0.3	0.1	0.5
Chlorogalum pomeridianum	0.3	0.4	0.3	0.4	0.0	0.1	0.5	0.3
Galium spp.	0.1	0.3	2.1	3.6	0.8	1.1	0.5	0.0
Prunella vulgaris	0.4	0.4	0.5	0.5	0.5	0.3	0.4	0.0
Geranium dissectum	0.3	0.1	0.1	0.7	0.3	0.4	0.0	0.0
Total Forbs	3.7	5.6	8.2	8.8	5.8	7.5	8.0	8.6
Miscellaneous Species	0.4	0.6	0.7	2.1	0.3	0.6	0.5	2.0
Bare Ground	3.5	12.4	8.8	12.8	1.7	0.1	0.8	0.5
Total Forage Species	25.7	40.5	76.9	64.9	56.6	83.6	87.4	79.7

* *Bromus rigidus* is questionably placed as a weed (see note, Table 1).

** Thornber (1910) classed some plantains very important as forage.

distribution of Klamath weed, but in those areas where it occurred, heavy growth of plants up to 4 feet in height was characteristic, but these were not so close together as at Blocksburg, for example. Although again an underestimate of reality, the weed in 1947 prior to injury by beetles, is shown at 26.1 percent. This is partly because the zones and quadrats were laid out without regard to the patches of weed and represented the open range, generally, as was so at each site. These robust plants of a "bunched" habit of growth have some years individually supported large numbers of beetles, and yet a small percentage of the plants would partially recover following even fairly prolonged defoliation, after the beetles ceased feeding and entered aestivation. Observations showed that specific plants invariably succumbed the next year except in the one quadrat among the 28 which was shaded. Even in the open areas a few new plants appeared occasionally, sufficiently dispersed to escape destruction until after their maturity and seeding, but a shifting sequence in time and place at a low density of weeds and beetles was characteristic.

This example is intermediate between the Loftus site on the one hand and the Fort Seward and Blocksburg sites on the other, but with the economic result much closer to the latter. Economically, it is of little moment that the weed persisted at 0.1 to 0.3 percent representation.

Ripgut brome was the only weedy species of importance, although fiddleneck (*Amsinckia douglasiana*) occurred at about the one percent level in 1950, 1953 and 1957, and at 2.3 percent in 1955. This is about equal to the presence initially in 1947 and 1948 of both species, except that in 1951 ripgut brome was about three times as important as commonly.

Ripgut brome is much inferior to soft chess, but it is doubtfully considered a weed on such ranges, although in other situations it may be highly objectionable and aggressive. It rarely attains importance and seems to yield readily to better forage on moderately grazed ranges. Its foliage is readily taken by livestock until the long-awned, barbed seed heads form.

In general, this range im-

Table 4. Dominance of range plant species at micro-plot positions in quadrats at the Loomis beetle sites, expressed as percentages of total positions—28 positions per quadrat and 5 quadrats at each of 5 zones.

SPECIES	1947	1948	1949	1950	1951	1953	1955	1957
Klamath Weed	26.1	15.4	2.1	0.1	0.1	0.3	0.1	0.0
Other Weeds:								
*Bromus rigidus**	6.1	6.9	10.3	7.1	21.4	3.0	8.4	3.9
Amsinckia douglasiana	1.9	1.0	0.0	0.9	0.1	0.8	2.3	0.9
Hordeum gussoneanum and *H. murinum*	0.1	0.9	0.0	0.0	2.1	0.0	0.0	1.7
Hypochoeris glabra	0.0	0.0	0.0	0.1	0.3	0.6	0.0	1.4
Rumex spp.	0.5	0.4	0.0	0.1	0.3	0.1	1.0	0.1
Agoseris spp.	0.0	0.0	0.0	0.0	0.0	0.4	0.3	0.1
Eremocarpus setigerus	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0
Total Other Weeds	8.6	9.2	11.7	8.2	24.2	4.9	12.0	8.1
Legumes: **								
Trifolium spp.	0.1	0.0	0.0	3.8	1.0	13.0	1.3	9.1
Lupinus spp.	6.7	5.9	0.0	17.6	3.0	14.1	1.6	6.1
Medicago hispida	0.0	1.3	0.0	0.6	1.4	2.8	0.1	3.3
Lotus spp.	0.6	1.6	0.1	1.1	1.8	7.7	0.6	2.3
Total Legumes	7.4	8.8	0.1	23.1	7.2	37.6	3.6	20.8
Forage Grasses: *								
Bromus mollis	14.3	34.1	50.9	36.3	47.7	18.0	36.3	43.6
Festuca megalura and *F. myuros*	6.0	11.2	9.0	0.4	4.1	5.0	11.3	3.7
Aira caryophyllea	1.0	2.4	0.1	0.3	1.3	0.3	2.4	2.0
Briza minor	0.0	0.0	0.0	0.3	0.1	2.3	0.7	0.0
Total Forage Grasses	21.3	47.7	60.0	37.3	53.2	25.6	50.7	49.3
Forbs:								
Erodium botrys	32.1	15.1	4.8	20.6	10.3	21.4	25.7	17.6
Plagiobothrys canescens	2.1	0.4	0.0	4.7	0.1	2.4	1.6	1.0
Geranium dissectum	0.1	0.3	0.4	1.0	1.0	1.6	0.8	0.4
Torilis nodosa	0.1	1.7	0.3	0.4	0.0	0.3	0.1	0.1
Stellaria media	0.0	0.1	0.4	1.0	0.0	1.6	0.6	0.0
Galium spp.	0.0	0.1	0.0	0.0	0.0	0.4	0.4	0.0
Daucus carota	0.1	0.0	0.0	0.0	0.3	0.1	0.3	0.0
Total Forbs	34.5	17.7	5.9	27.7	11.7	27.8	29.5	19.1
Miscellaneous Species	0.2	0.2	0.2	0.2	0.1	2.6	2.2	1.3
Bare Ground	1.7	0.7	18.7	3.1	3.1	0.4	1.3	0.0
Total Forage Species	63.2	74.2	66.0	88.1	72.1	91.0	83.8	89.2

* *Bromus rigidus* is questionably placed as a weed (see note, Table 1).
** All these legumes were considered beneficial (see note, Table 1).

proved in direct proportion to the reduction in Klamath weed (Figure 3). Levels of forage from 72.1 percent in 1951 (low because of the high level of ripgut that year) to 91.0 percent in 1953 and 89.2 percent in 1957 were attained. The low level of 66.0 percent in 1949 was due mainly to an excessive amount of bare ground. This was caused by a very heavy mat of litter from the unusually vigorous growth the previous year, which deterred germination and prevented proper growth of seedlings.

Again, 1953 and 1957 were very favorable for the annual legumes, these totalling 37.6 percent in 1953 and 20.8 percent in 1957. The fluctuating fortunes of the legumes, edible forbs and "other weeds," mainly ripgut brome (of doubtful weedy status), caused the forage grasses to vary considerably year to year, the scarcity of these during a given year being compensated by increases in legumes and forbs.

Vegetation of the Ten-Mile Sequence Quadrats

The sites of this study were one-quarter mile apart, except where timber or other non-range land existed, and extended from the original beetle colony (1946 release) near Blocksburg to beyond Alderpoint, Humboldt County. The 27 locations are representative of the range improvement in the county resulting from control of Klamath weed by beetles.

Table 5 presents the densities of Klamath weed both before control and subsequently through 1957, as well as densities of the perennial grasses. Of the 27 ranges randomly established, 25 were infested with Klamath weed at the beginning of the study. The average coverage by Klamath weed was 37 percent, and the infested fields varied from a low of 10 percent to a high of 60 percent. This included quadrats either too wet or too dry for this weed, as well as those on ideal slopes.

Control was complete at this site in the practical sense. By 1950 the beetles had controlled the weed within 5 miles from the release site. At some sites beyond that distance the weed increased in importance. There were other scattered areas more distant which had been controlled by secondary, disjunct colonies of beetles; and there were still other areas where there was little change in the importance of the weed that year. The average density was about 10 percent. In 1951 beetle action was decisive. At only one micro-area was any Klamath weed dominant, and it was recorded there as a trace.

From 1953 through 1957 observations every year and the specific quadrat data every-other-year showed that the weed reappeared, but not in significant

numbers. Only in the shaded or disturbed soil areas did the weed establish itself beyond the position of a trace. Its average importance for the years, 1951, 1953, 1955 and 1957 was less than 0.2 percent, compared with 37 percent originally.

Because of its importance among the perennials, California oatgrass is listed separately. Other perennials are recorded, but their identities are shown only by footnotes.

At only 12 of the 27 locations were such perennials originally present. By 1957 or previously, at 22 of the 27 locations perennials were to some degree locally dominant. The average combined importance of all species of these desirable perennials was low, at 8.2 percent, initially in 1950, and increased to 11.0, 16.0, 19.1, and 23.2 percent for the years 1951, 1953, 1955 and 1957, respectively.

Of this increase, California oatgrass was the major contributant. It had a density of 7.8 percent in 1950, 9.3 in 1951, 11.3 in 1953, 15.8 in 1955, and 20.0 percent in 1957—still only 2½ times its original abundance generally. However, on some ranges its progress was very promising, and this was generally associated with favorable grazing management (see also Murphy, *et al.*, 1954). Where this perennial was present in 1950 but at a low level due, among other things, to competition by Klamath weed, it increased rapidly with beetle control of the weedy competitor. At the 4-mile distance, it was then

Table 5. Change in percentage composition of Klamath weed and desirable perennial grasses coincident with biological control of Klamath weed on 27 ranges in a series from the beetle release center near Blocksburg to a distance 10 miles southward—with ¼ mile between places (excluding non-range areas).*

Distance in miles of places originally infested	Klamath Weed: Pre-beetle density 1949	1950	1951	1953	1955	1957	Perennial Grasses: First year of beetle effect 1950 Danthonia	1950 Other	1951 Danthonia	1951 Other	1953 Danthonia	1953 Other	1955 Danthonia	1955 Other	1957 Danthonia	1957 Other
Release center	60	0	0	0	0	0	24	1[2]	29	T[3]	30	1[3]	52	1[4]	45	T[5]
¾	15	0	0	0	0	0	15	0	13	0	9	8[6]	23	0	43	0
1	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1¼	35	0	0	0	T	0	0	0	0	0	0	0	1	0	0	0
1½	0	0	T	0	0	0	0	0	0	0	0	13[6]	0	0	0	0
1¾	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0
2	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2¼	40	0	0	0	T	0	0	0	0	0	0	0	0	0	0	0
3¼	40	0	0	0	0	0	40	0	40	0	30	0	53	1[7]	68	T[7]
3½	40	0	0	0	0	0	37	0	52	0	47	0	43	0	60	0
3¾	52	0	0	0	0	0	0	7[8]	0	7[8]	0	7[8]	0	8[8]	0	10[8]
4	37	0	0	0	0	0	1	0	1	0	1	6[6]	4	0	12	0
4¼	28	0	0	0	0	0	13	0	17	2[9]	26	2[9]	50	16[10]	45	10[9]
4½	52	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4¾	52	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	58	0	0	0	0	0	3	0	3	0	3	0	5	0	5	12[5]
6	23	28	0	0	3**	0	21	0	18	3[6]	30	5[6]	15	30[6]	20	18[6]
6¼	27	2	0	0	0	0	0	0	3	0	0	0	1	0	0	1[5]
6½	28	0	0	0	0	0	0	0	0	0	0	0	0	3[8]	0	2[8]
6¾	23	12	0	0	0	0	0	0	0	3[6]	0	32[6]	0	6[6]	35	2[6]
7	37	15	0	0	0	0	10	0	17	17[6]	50	20[6]	52	7[6]	65	0
7¼	47	2	0	7†	0	0	0	0	0	0	0	0	12	0	5	0
8	38	38	0	0	0	0	2	0	6	0	13	0	25	0	30	0
8¼	35	70	0	0	(sawmill)		0	0	0	5[11]	0	3[11]	(sawmill yard—logs)			
8¾	38	38	0	T	0	0	0	0	0	0	3	0	0	0	0	0
9	52	40	0	2**	T	4**	5	0	5	0	7	7[11]	10	0	5	0
9¾	23	27	0	0	0	0	0	0	0	0	0	0	0	0	0	12[12]
Average	37	11	0	0.4	0.1	0.2	7.8	0.4	9.3	1.7	11.3	4.7	15.8	3.3	20.0	3.2
Combined average							8.2		11.0		16.0		19.1		23.2	

* On five of the twenty-seven ranges perennials were never sampled.

** Marshy area and/or partially shaded.

† Seedlings on disturbed area.

T—Trace.

[1] *Danthonia californica;* [2] *Agrostis hallii* - 1.1 and *Panicum pacificum* - 0.3; [3] *Panicum pacificum;* [4] *Agrostis hallii* - 0.1 and *Panicum pacificum* - 0.5; [5] *Agrostis hallii;* [6] *Holcus lanatus;* [7] *Poa scabrella;* [8] *Stipa pulchra;* [9] *Elymus glaucus;* [10] *Elymus glaucus* - 8.3 and *Agrostis hallii* - 8.3; [11] *Lolium perenne;* [12] *Lolium perenne* - 10.0 and *Elymus glaucus* - 2.0.

present at the 1 percent level. By 1955 it had crept up to 4 percent, and by 1957 to 12 percent—a twelve fold increase. At the 4¼ mile distance a threefold increase occurred during that period; at the 7-mile distance, an increase from 10 percent in 1950 to 65 percent in 1957; and at the 8-mile distance, from 2 to 30 percent. At a few locations there was a very minor increase.

The perennials have thus come to dominate the vegetative picture on a portion of these ranges, but they remain at low levels on others. The results suggest that the maximal improvement could be accomplished in this region, to the decided advantage of the rancher, if proper developmental management were employed. The data also suggest that many ranchers are not apt to utilize the necessary caution in degree and timing of grazing.

Table 6 presents the data for all plants, but the post-control years are averaged. Since the perennial Klamath weed and the perennial grasses were presented by years (Table 5), and since annuals vary greatly from year to year, the loss is not great.

Since in each quadrat the method was to record coverage of only the three dominant species, there was for each quadrat a residue of other occupants. This residue was, in quadrat "B," for example, not necessarily distinct from the species which were dominant in quadrat "A." If the "other weeds" constitute a given percentage among the 3 dominants of respective quadrats, presumally they would constitute an approximately equal percentage among the aggregate residue of plants not represented by the 3 dominants in the respective quadrats. Thus, as "corrected" values, the aggregate of residue is prorated to the range types, augmenting those values to a closer approximation than is revealed by the "uncorrected" figures. This technique is not applied by species, so it must be remembered that the percentage figures for each species are lower than they should be. This "correction" is not entirely logical in all respects, but the plus and minus errors tend to cancel out the results being considered closer approximations of the weedy category compared with the forage catagories.

The unaltered figures for "other weeds" varied from zero at the 8¼ mile distance to 47.0 percent at the 1½ mile distance, with the moderately noxious dogtail, or winter annual grass (*Cynosurus echinatus*) far surpassing at most locations the second most abundant weedy species, hawkbit. The value for dogtail was 9.2 percent, and the total for all weeds was 16.2 percent, with hawkbit contributing 2.7 percent. Specialists do not consider either dogtail or hawkbit serious range weeds. The grass is grazed some when young, and it heads and dries later than some of the other more palatable forage such as soft chess, cheatgrass (*Bomus tectorum*), ripgut brome, the foxtail grasses (*Hordeum gussoneanum* and *H. murinum*) the spiny *Navarretia* spp., and the tarweeds, collectively, constituted the bulk of the weedy species. It is worth noting that in this region, studied for ten years, medusa head was not recorded.

The more adequate "corrected" figures for "other weeds" varied from zero to 60 percent, the latter as before, at the 1½ mile distance under heavy grazing by sheep. The average "corrected" figure for weedy species was 21.4 percent, and since more than half of this was by the less serious and partially utilized dogtail, this figure is not so discouraging.

The total forage was also "corrected." The two "corrections" presumably involve errors unprejudiced in either direction. There was a marked improvement after control of Klamath weed. Areas that originally had dense stands of the weed were largely lost to cattle grazing and could be brought back by sheep grazing only slowly, and often to the detriment of range condition. The 37 percent coverage by the weed initially is considered a de-emphasis of the standing of Klamath weed, as an estimate of its harmfulness to the ranchers' interest in this area at that time (Figure 4). Other weeds which increased slightly since the removal of Klamath weed are not of comparable aggressiveness, persistence, or toxicity. Also, this increase was no more than an approximate sharing of the vacated space with the forage species according to each group's respective composition on the range before Klamath weed was brought under control.

Consider now the "uncorrected" categories of forage species. Legumes were of minor occurrence but in the maintenance of soil nitrogen they may be of greater importance than their proportionate presence indicates. The legumes, *Lotus, Trifolium,* and burclover (*Medicago hispida*) totaled only 5.4 percent as an average for all places. The year 1953 was unusually favorable for them, and 1957 somewhat less so. Forage grasses comprised the bulk of the edible types, aggregating 36.1 percent "uncorrected," but it is to be remembered that these figures are low. The principal species was California oatgrass, with 11.7 percent (Table 5). Soft chess was next in value at 7.0 percent, although the inferior silver hairgrass exceeded it in coverage, at 10.0 percent. Orchard grass (*Holcus lanatus*) was fourth at 1.6 percent. The forbs were dominated by filarre (*Erodium botrys* and *E. cicutarium*), principally the former, at 7.7 percent. The only other forbs which reached levels of approximately 1 percent were *Plantago* spp., and pink centaurium (*Centaur-*

Table 6. Average percentage composition by forage species and weeds on twenty-seven ranges subsequent to removal of Klamath weed by beetles 1951-1957.

Category / Distance in miles	Center	¾	1	1¼	1½	1¾	2	2¼	3¼	3½	3¾	4	4¼	4½	4¾	5	6	6¼	6½	6¾	7	7¼	8	8¼	8¾	9	9¾	Mean
Klamath Weed				T††	T			T									0.8					1.8			T	1.5		0.2
Others Weeds:																												
*Cynosurus echinatus**	3.7	25.4	30.0	15.0	37.0	26.6	2.1	33.3		2.6			8.4	7.9	10.8	9.5	7.5	4.5		10.8			5.6			8.7		9.2
Hypochoeris glabra	16.3	1.3		0.8			2.1	2.1		2.9	1.3	3.3			5.8	4.1		1.7	1.3	2.1	1.3	6.5			13.3	2.1	5.0	2.7
Hemizonia, Madia Other tar weeds		2.9	2.2	0.8	2.9	0.8	0.4				1.7	7.2	2.1	10.0	4.1	6.7							5.0					1.7
*Bromus rigidus***									0.8				4.4	1.7				2.1				1.3	2.7		2.5	1.7	0.8	0.7
Hordeum gussoneanum & *H. murinum*				3.3		10.0						4.1								0.8								0.7
Navarretia spp.			3.1	1.3	1.3	2.7	2.5	1.1			1.7				0.4			1.3	1.7									0.6
Agoseris spp.		0.8			3.7						0.8												5.0		1.7			0.4
Centaurea solstitialis																											4.1	0.1
Hordeum hystrix				0.4	1.7								1.3															0.1
Eremocarpus setigerus																						1.3						T
Lactuca scariola					0.4																							T
Rumex acetosella																0.8												T
Total "Other Weeds"	20.0	30.4	35.3	21.6	47.0	40.1	7.1	36.5	0.8	5.5	5.5	14.6	16.2	19.6	21.1	21.1	7.5	9.6	3.0	13.7	1.3	9.1	18.8	0.0	17.5	12.5	9.9	16.2
Legumes:																												
Lotus spp.		1.3	3.7	3.3		0.4		4.1	0.5					1.7			8.7		1.3	1.7		3.3	0.8	10.8	11.7		4.1	2.1
Trifolium spp.	3.1			2.1	1.3	2.1	1.7		0.8		1.3	2.5			4.6		2.1	2.5				1.7	5.8		1.3	12.1		1.7
Medicago hispida			4.6			0.8	2.3	5.8															2.9	20.0			2.9	1.5
Vicia spp.														3.3														0.1
Total Legumes	3.1	1.3	8.3	5.4	1.3	3.3	4.0	9.9	1.3	0.0	1.3	2.5	0.0	5.0	4.6	0.0	10.8	2.5	1.3	1.7	0.0	5.0	9.5	30.8	13.0	12.1	7.0	5.4
Forage Grasses:																												
Danthonia californica	39.2	22.0		0.3		0.6			47.9	50.4		4.4	34.5	6.2	2.1	4.1	20.8	1.1		8.7	45.8	4.1	16.9		0.8	5.4		11.7
Aira caryophyllea	11.7	3.2	7.9	9.4	2.1	1.7	9.1	0.8	12.7	15.1	8.3	5.8	11.6	11.2	15.8	17.1	1.3	14.1	11.6	10.0	13.1	24.5	5.0	13.3	22.1	10.0	1.7	10.0
Bromus mollis	7.5		2.1	12.1	4.6	4.1	6.6	2.1	7.7	4.5	6.7	14.9	3.7	10.4	2.5	4.1		13.1	17.9	8.3		3.7	5.6	1.6	5.4	15.0	25.8	7.0
Holcus lanatus		2.1			3.3							1.7					14.1			10.8	10.8							1.6
Festuca megalura & *F. myuros*			2.1						0.8			4.6						0.4				9.1	4.1	1.6	4.6	2.9	5.8	1.3
Lolium perenne & *L. multiflorum*				5.6	2.1	5.8	5.4					2.5												4.0		1.7	2.5	1.1
Briza minor	2.3	0.4	2.1		0.7			1.7	0.4		0.8	0.4		3.7	1.7				0.8		1.3	1.7		2.5		2.9		0.9
Carex, Luzula, Juncus					1.7											1.3	14.9			3.1	2.1							0.9
Avena fatua				1.3			3.9			1.3	0.1				0.8			1.1		2.1					1.3		1.7	0.5
Agrostis hallii													4.1			2.9		0.3										0.3
Elymus glaucus													6.6														0.5	0.3
Stipa pulchra											7.9								1.3									0.3
Gastridium ventricosum			2.1	1.7	1.6			0.6																				0.2
Poa scabrella									0.2																			T
Total Forage Grasses	60.7	27.7	16.3	30.4	16.1	12.2	25.0	5.2	69.7	71.3	23.8	34.3	60.5	31.5	22.9	29.5	51.1	30.1	31.6	43.0	73.1	43.1	31.6	23.1	34.2	37.9	38.0	36.1
Forbs:																												
Erodium spp., chiefly *botrys*		21.6	9.5	5.4	0.8	5.4	36.6	4.6	12.1	7.9	31.7	17.9		0.4	12.5	13.7		13.7	4.1	1.7		2.5		0.8	1.7		2.5	7.7
Centaurium venustum		0.6			5.4	2.7	3.3	3.7										4.6	13.1	4.1	2.8	1.7	0.8		0.8			1.6
Plantago spp.**				0.4									1.7	0.7			1.7					1.7	3.1	12.4		1.3		0.9
Linanthus bicolor									2.5	1.3	3.7	2.1	1.3						0.8						0.4	3.7	1.7	0.7
Geranium spp., chiefly *dissectum*						0.8		1.7			1.3	1.3					0.4	0.8	2.3	0.8							1.7	0.4
Modiola caroliniana							0.4												5.0	1.7		2.5						0.4
Daucus carota & *D. pusillus*											1.3								0.8						2.5	0.8		0.2
Filago, Micropus			1.3									2.1													0.8			0.2
Galium spp.				2.1				1.7										0.4										0.2
Lythrum hyssopifolia			2.1			2.1																						0.2
Anagallis arvensis												0.8										1.3					1.3	0.1
Baeria chrysostoma†			0.8					2.1																				0.1
Cordylanthus, Orthocarpus, Castilleia															0.4													T
Plagiobothrys canescens																											1.3	T
Total Forbs	0.0	22.2	13.7	7.9	6.2	11.0	40.3	13.8	14.6	9.2	38.0	24.2	3.0	1.1	12.9	13.7	2.1	19.5	26.1	8.3	2.8	9.7	3.9	13.2	6.2	5.8	8.5	12.5
Bare Ground				3.3	1.7																							0.2
Remaining Misc. Coverage	16.2	18.4	26.4	31.4	27.7	33.4	27.2	34.6	13.6	14.0	31.4	24.4	20.3	42.8	36.6	35.7	28.5	38.3	38.0	33.3	22.8	32.1	36.7	32.9	19.1	31.7	36.6	29.0
Total Forage Species "Corrected" Total	63.8	51.2	38.3	43.7	23.6	26.5	69.3	28.9	85.6	80.5	63.1	61.0	63.5	37.6	40.4	43.2	64.0	52.1	59.0	63.0	75.9	57.8	45.0	67.1	63.4	55.8	53.5	54.7
Forage Species "Corrected" Total	74.1	60.6	48.4	57.4	30.1	35.4	88.2	38.9	97.2	91.8	82.9	75.9	76.4	53.7	55.2	58.6	82.2	74.8	81.4	84.0	93.2	76.4	61.5	89.2	75.5	73.5	73.1	70.0
Other Weeds	23.2	36.0	44.6	28.4	60.0	53.5	9.0	49.1	1.0	6.3	7.2	18.2	19.5	28.0	28.8	28.6	9.6	13.0	4.1	18.3	1.6	13.3	25.0	0.0	20.8	16.5	13.5	21.4
"Corrected" Misc. Coverage	2.7	3.4	7.0	10.9	8.2	11.2	6.4	12.0	1.9	2.0	9.9	6.0	4.1	18.3	14.1	12.8	8.1	12.3	14.4	7.8	5.2	10.3	13.5	10.8	3.7	10.1	13.4	8.9

* Not palatable but mainly a ruderal and only moderately aggressive. ** See footnote, table 1. † See footnote, table 2. †† T—Trace.

FIGURE 4. Panoramic view showing type of rangeland in the 10-mile sequence study originally infested with Klamath weed. The striking control of the weed by beetles is shown in the upper foreground, and the complete coverage of the weed at the flowering stage in the then uncontrolled area is shown in the immediate foreground. *(Photograph by J. K. Holloway, June 1949).*

ium venustum). Combined forbs, "uncorrected," amounted to 12.5 percent.

Summary and Conclusions

Klamath weed, prior to 1949, was estimated to infest 2⅓ million acres of valuable rangeland in northern California. The failure of other solutions prompted the late H. S. Smith to initiate biological control, a program he had discussed as early as 1928 with the late R. J. Tillyard of Australia. In 1947, a ten-year study was begun on control of this weed by imported beetles, primarily *Chrysolina quadrigemina* (Rossi), relative to degree of control and range plant composition. The data show that a major improvement in the ranges resulted. Control was more effective than hoped for even by enthusiasts. The weed now exists at less than 1 percent of its former occurrence. There was concurrent marked increase in perennial grasses, chiefly California oatgrass in Humboldt County, and there and elsewhere the winter annuals—grasses, legumes and forbs—of fair to good forage value claimed a major portion of the space opened up by decline of Klamath weed. This low level of the weed constitutes no loss whatever, except as it may occasion premature intervention to eradicate it locally.

There was good correlation in the progress in beetle densities with control of Klamath weed when the former were plotted in the immature rather than the mature stage—consistent with an explanation of reciprocal density-dependence in the two populations.

During the course of this study no noxious species have entered the land vacated by Klamath weed to an alarming degree. The vast improvement by biological removal of Klamath weed, with the correlated increase in forage of fair to good value is documented, although many of the annuals are not the most desirable. The principal forage species were California oatgrass, soft chess, and filaree (*Erodium* spp.), in Humboldt County, and the latter two plus *Lotus* spp., in Shasta and Placer Counties.

In general, increase of other weeds following decline of Klamath weed was minor; in many instances no increase at all. The main weeds in Humboldt County were dogtail and hawkbit, while ripgut brome was the predominant in Shasta and Placer Counties. None of these was a serious aggressor on these ranges. In Humboldt County dogtail and hawkbit are extensive in places, but they do not displace or dominate California oatgrass, which was the dominant single species in an area within 10 miles of the beetle release site. Also, both are annuals and neither toxic nor pernicious. Ripgut brome is highly objectionable in grain fields or abandoned areas, but it can be controlled by moderate grazing. It is grazed and of value prior to formation of the barbed seed heads.

Medusa head is a serious claimant, but in the extensive area represented by the Blocksburg, Fort Seward, Alderpoint region of southern Humboldt County, formerly notorious for its Klamath weed, it has made little inroad. It may or may not be significant, but in the equally extensive region westward toward Garberville, where the soils are more shallow and porous and Klamath weed was never a problem, medusa head has during the same period of time increased from a status of rarity to one of continuousness for miles. Thus, we do not know whether climatic and edaphic conditions where Klamath weed was most favored originally offer advantage to medusa head over the desirable forage species, or vice versa. Nor do we know to what degree good range management can influence the result in the right direction.

Abuse by overgrazing or poorly timed grazing will increase the chances that noxious species or those of low value will

come in. Chemical methods of control, no less than biological, are subject to the same unfounded fear that if we control a given noxious weed we may get a worse one in its place!

The rancher should follow progressive management conducive to long term values. Such management should make it possible to gather the maximum reward from the extensive success of biological control of a weed, which during earlier years did much to stymie research toward general range improvement.

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DR. R. L. LANG, acting head of the Department of Agronomy (which includes range management) at the University of Wyoming, holds a hat box while KAREN BEETLE draws the names of the winners of the original oil paintings. The raffle netted $30.50 for the Range Management Scholarship Fund of the Wyoming Section.