BIOTIC ASPECTION IN THE COAST RANGE MOUNTAINS OF NORTHWESTERN OREGON*

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INTRODUCTION

From the fall of 1932 to the spring of 1938, the author conducted an ecological investigation of a Douglas fir-hemlock community in the Coast Range Mountains of northwestern Oregon. Biotic and environmental observations, collections, and instrumental data were recorded weekly within a restricted portion of the forest. Information was obtained on the fundamental structure, organization, and interrelationship of animal communities in a typical forest of this area. This paper, however, will concern itself only with an aspectional interpretation of the data secured.

Acknowledgment is made to the late Dr. R. H. Wolcott, for suggesting the project, and to Dr. I. H. Blake for his guidance. The University of Nebraska, the Pacific Northwest Forest and Range Experiment Station, and Linfield College loaned equipment and the college also provided the services of research assistants. Tektronix Inc. of Portland, Oregon gave generous financial assistance for completing this publication. The continuity of this study resulted from efforts of many individuals, several of whom were unpaid. D. McKey-Fender has been the chief contributor to the compilation and editorial phases and Mary Comber Miles deserves credit for the graphs, charts and photographs.

Determinations of specimens were made by the following authorities: C. P. Alexander (Tipulidae); L. C. Altman (Megascolecidae); F. C. Baker (Mollusca); Wm. W. Baker (Rhynchophoridae); Nathan Banks (Acarina, Phalangida, Psocidae, and Mecoptera); R. H. Beamer (Cicadellidae); W. A. Bell (Enchytraeidae); Bernard Benesh (Lucanidae); J. Bequaert (ectoparasites, Leptidae, Tabanidae, and Vespidae); Adam G. Boving (coleopterous larvae); F. M. Carpenter (Neuroptera); J. C. Chamberlain (Pseudoscorpionida); R. V. Chamberlain (Myriapoda); Q. D. Clarkson (spermatophytes); J. A. Comstock (Macrolepidoptera); J. F. Gates Clarke (Microlepidoptera); S. E. Crumb (lepidopterous larvae); C. H. Curran (Diptera); R. A. Cushman (Ichneumonidae); Kathleen C. Doering (Cercopidae); John Davis (Cicadellidae); E. O. Essig (Aphididae); E. P. Felt (Cecidomyidae); M. H. Hatch (Staphylinidae); Kenneth M. Fender (Coleoptera and Lepidoptera); Geo. R. Ferguson (Serphoidea); T. H. Frison (Plecoptera and Apidae); Harriet Exline Frizzell (Araneida); A. B. Gahan (Chalcidoidea); C. M. Gjullin (Culicidae); C. T. Greene (dipterous larvae); Kenneth Gordon (Amphibia); A. B. Gurney (neuropterous larvae); Carl Heinrich (lepidopterous larvae and Microlepidoptera); Ralph Hopping (Coleoptera); T. H. Hubbell (Rhaphidophorinae); H. G. James (Collembola); S. G. Jewett (Mammalia and Aves); H. H. Kieffer (Microlepidoptera); Karl V. Krombein (Sphecidae); M. C. Lane (Elateridae); Hugh B. Leech (Staphylinidae); S. F. Light (Isoptera); E. G. Linsley (Andrenidae); J. O. Maloney (Isopoda); D. McKey-Fender (spermatophytes and miscellaneous invertebrates); C. F. W. Muesebeck (Aleyrodidae, Ichneumonidae, and Braconidae); G. Riegel (Braconidae); E. S. Ross (Histeridae); H. H. Ross (Trichoptera, Tenthredinidae, including larvae); V. D. Roth (Araneida); H. C. Severin (Orthoptera); F. R. Shaw (Fungivoridae); James R. Slater (Amphibia); H. R. Smith (Formicidae); Roger C. Smith

*Studies from the Department of Zoology, University of Nebraska, No. 299.

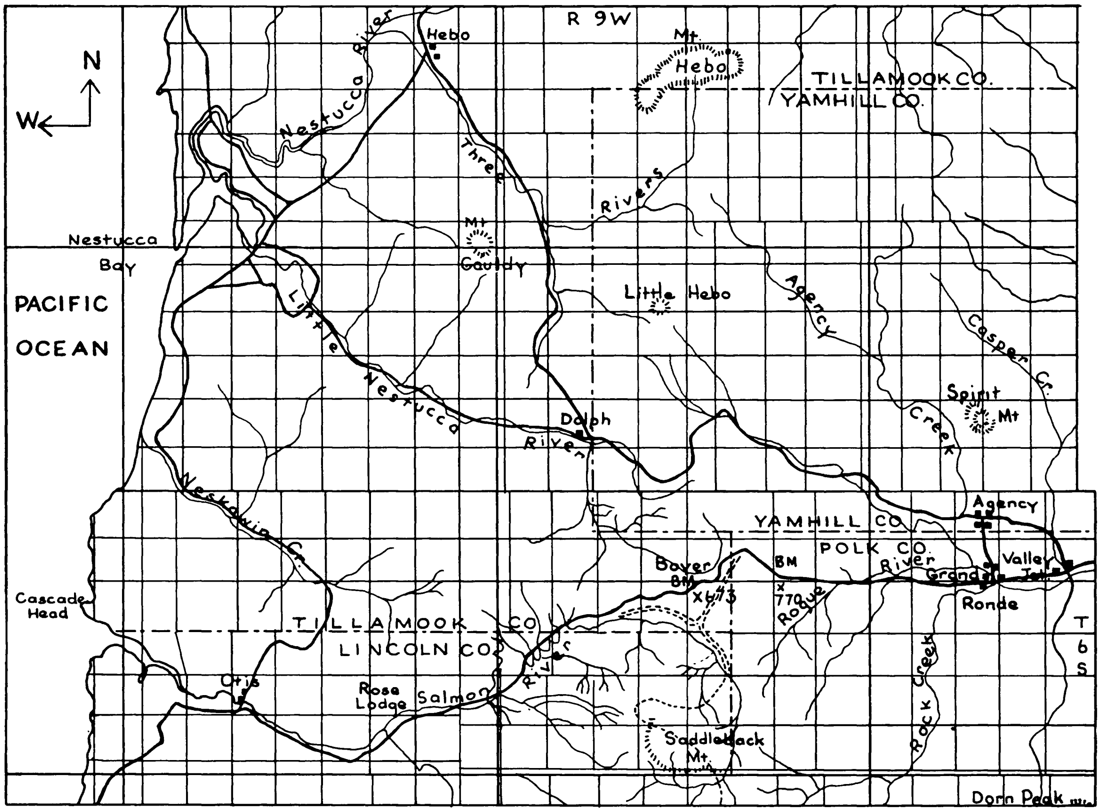

FIG. 1. Map of region, adapted from Forest Service map of Hebo Ranger District, Siuslaw National Forest.

(Neuroptera); T. E. Snyder (Isoptera); G. Spencer (Thysanura); L. H. Weld (Cynipidae); A. Wetmore (dipterous larvae); Katherine A. Wolfe (mosses); and E. P. Van Duzee (Hemiptera).

Accuracy of the account of the geology of the region was very kindly checked by Ralph S. Mason of the Department of Geology and Mineral Industries of the State of Oregon and Ruth Hopson of Portland State College.

DESCRIPTION OF AREA

The site studied was located in the southwest quarter of Section 24, Township 6 south, Range 9 west in the extreme northeast corner section of Lincoln County, Oregon. The area was on a terrace-like ridge sloping gently toward the north from Saddleback Mountain, which is a basic igneous intruded mass. Saddleback is one of the more massive mountains of the Coast Range, the bulk of the mountain proper occupying more than two sections. It lies in the adjoining corners of four topographic maps, the Nestucca Bay, Spirit Mountain, Euchre Mountain, and Valsetz quadrangles, the ridge on which this research was conducted being in the southwest corner of the Spirit Mountain quadrangle. This mountain appears as Saddle Mountain on Forest Service maps and is called Saddlebags locally, distinguishing it from the well known Saddle Mountain in Clatsop County as well as other mountains of the same name. Its elevation is 3359 ft above sea level, while the research area, which became known as "the station," was located at an elevation between 1400 and 1500 ft. The instruments were situated, and most of the observations and collections were made, at about 1420 ft. The area was only accessible by a trail which extended from Boyer southwestward approximately 4 mi to the study area and thence to the top of the mountain. Boyer was a service station situated 6 mi west of Grand Ronde on the Salmon River Highway, i.e., Oregon 18 (Fig. 1).

GEOLOGY

According to Souza (1927), the Coast Range of Oregon consists of gentle, truncated folds trending generally to the northeast, the relationships of which are such as to constitute an anticlinorium. The very regular level to which the mountains have been eroded, averaging 1500 ft, can be explained by normal processes of erosion in the well-developed stream system characteristic of this humid region. Igneous intrusions in the form of sills and dikes have been important in the history and physiography of the region. Saddleback Mountain, as well as Mount Hebo to the north (Fig. 2), owes its height to the protection of a thick cap of gabbro over the softer sedimentary strata (Baldwin & Roberts 1952). The ridge on which the study was made, together with other spurs to the east of the station area, ends abruptly in a steep slope extending down to the Salmon River and its tributaries, which lie in a low, broad valley or pass traversing the Coast Ridge, geologically a shallow fault trough. It was through this low pass at a maximum elevation of 730 ft that the Salmon River Highway was constructed only 2 yrs before this study was begun. While the silhouetted profile of the ridge very much resembles that of an uplifted sea terrace, its contours are explained by the presence of a rather thick dike at about the level of the research station (Fig. 3). It is this dike and attendant faulting that forms the southern scarp of the pass referred to above. The contours of this scarp are much softened by erosion, and at the time of this research were clothed in forest.

FIG. 2. View from near summit of Saddleback Mt. toward north, showing the topography of the Coast Range Mountains and the nature of the forest cover of this region. View is directly across the gap through which the Salmon River highway runs. Mt. Hebo, whose geological relationships are similar to those of Saddleback, can be seen in the middle distance. Photo by Howard Daniels, April 8, 1934.

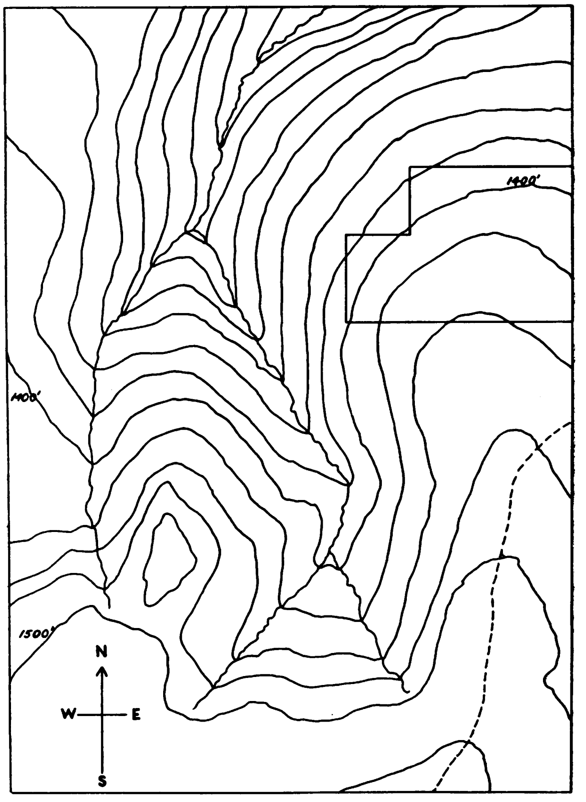

FIG. 3. Contour map of the research area. Contour interval equals 25 ft. Area enclosed in heavy lines is reproduced in detail in Figure 4.

SOIL

The soil was rusty-brown in color and of a crumby texture on the surface. The darker surface layer extended to a depth of 4-6 in., below which a lighter brown or dark yellow silty clay subsoil of considerable depth was encountered. Pits of 1.5-2.0 ft in depth were dug without striking parent rock beneath. Probably in this location the depth of soil had been augmented by washing and sliding of material from higher levels over the top of the decomposed residual soil.

The soil apparently belongs to the pedalfer group and is an imperfectly podzolized type originating from basic volcanic rock. Large boulders are found scattered throughout the soil and on the surface. The soil survey of Yamhill County, Oregon, places this type among the brown or rusty-brown soils of the Olympic series (Kocher 1920).

HISTORY

The influences of civilization upon the Saddleback Mountain area had not been extensive up to the time of this research. Previous to 1910 apparently the only disturbing factors were visits to the region by trappers and hunters. Probably few, if any, permanent shelters or buildings were erected and no clearings were made. A square of logs may be seen in the eastern part of the hectare illustrated in Figure 4 which may be the foundation of a shelter, or more likely a bear trap belonging to this period. About 1910 this territory was opened up to those desiring to file on timber claims. Many clearings were made, each of an acre or two in extent, in which cabins and barns were erected. At least 5 or 6 of these clearings were within 1 mi of the research station. A road over which freight was hauled to the cabins extended up the mountain and ended about a quarter of a mile above the station. After the road was abandoned, it served as a pack trail, which wound up the mountain, crossing the ridge on which the station was situated a few hundred yards south of the research area. During the short period when timber claims were being established, the district was fairly well populated and the effect of trapping and hunting on wild life was undoubtedly marked. It was probably at this time that the few martens remaining in the area were eliminated, as well as elk herds that used to roam over the district.

About 1912 the timber claims were abandoned as dramatically and suddenly as they had been taken up. Cabins were left almost intact by their owners. In many instances the sheds were full of fuel wood, some provisions were left, and much household furniture remained. The owners had been handsomely rewarded by the sale of their timber to large logging companies such as the Miami Logging Company of Grand Ronde, Oregon, and others. The new owners sent in

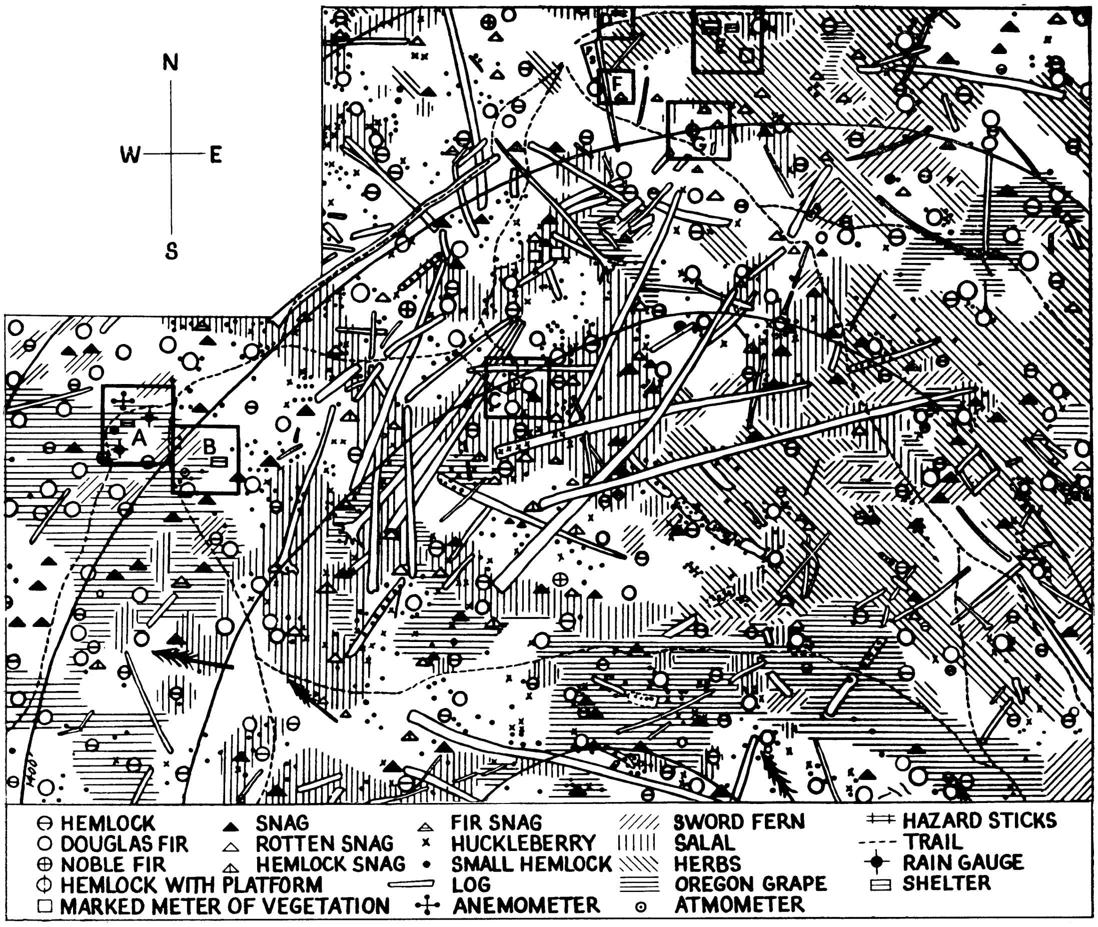

FIG. 4. Vegetation map of the area studied intensively, restricted research area (about 1¼ hectares) being shown in considerable detail. Symbols indicate type and extent of the vegetation (see key below map). Each study location is designated by letter and enclosed by heavy lines. (Orientation in relation to larger research area is shown in Fig. 3.) Adapted from Dirks, 1941.

crews to destroy some of the cabins and discouraged hunting or trapping in the area for fear of fires. Trails and roads were allowed to become blocked by fallen trees and soon became overgrown with salmonberry bushes and bracken fern. This in itself discouraged travel in the region, and the primeval wilderness soon reasserted itself. Due to the resultant inaccessibility, the area proved to be an ideal location for ecological research.

The vegetation was practically untouched. Clearings of the settlers had largely grown up into young hemlocks, firs, bracken fern, salal, and salmon-berry bushes. Aside from a few hunters in the fall, a few fishermen, and an occasional trapper or timber cruiser, the area was undisturbed. Even these intruders confined their activities largely to the main trails and water courses, as is evidenced by the fact that no instruments used in this research were molested until the last week of the investigation.

VEGETATION*

At the time of this investigation, virtually the entire area was covered by coniferous forest. There were occasional large natural openings occupied by a rank growth of bracken fern (*Pteridium aquilinum pubescens*), salal (*Gaultheria shallon*), and thimbleberry (*Rubus parviflorus*), and the small clearings made by settlers were filled with young trees and shrubby vegetation. The forest consisted primarily of an even-aged canopy of Douglas fir (*Pseudotsuga taxifolia*) with an understory of hemlock (*Tsuga heterophylla*) of varying ages. Occasionally at the 1400-1500 ft elevation isolated noble firs (*Abies nobilis*) added some variety to the canopy and very rarely a spindling broadleaf maple (*Acer macrophyllum*) was added to the understory. At the elevation where the instruments were located and the major part of the collecting done, a count was made of tree rings on stumps after the area was logged off, in 1939-40. The Douglas fir averaged approximately 250 yrs in age and two stumps of noble fir were the same age. The larger hemlocks varied from 95 to 270 yrs. This would indicate that no large forest fires had occurred here for at least that length of time, which was borne out by the lack of fire scars on the trees or in the

* Terminology of higher plants throughout this paper is after Abrams, *Illustrated Flora of the Pacific States.*

stumps. Across a ravine to the west many of the trees were much younger, as a fire had burned most of the larger timber some 50-100 yrs previously. The date was not established.

In the immediate vicinity of the research station the large Douglas firs and noble firs formed a canopy at an approximate height of 250-300 ft with the lower living limbs located at about 150 ft. The diameter of the trunks at breast height averaged 4 ft. The larger hemlock trees formed an understory with their first live branches usually beginning at a height of approximately 75 ft and the tops reaching up to the level of the lowest living Douglas fir limbs at 150 ft (Fig. 5). This timber was somewhat past its prime and every year took toll of a few giant firs or hemlocks which had been weakened by fungus and were blown over in a storm. These fatalities left openings in the canopy and eliminated root competition enabling a second generation of hemlocks to gain a foothold. This second understory was very irregular in height and size of trees. Some of the largest were tall enough to reach up to the lower, large hemlock limbs and had a d.b.h. of 1 ft or more. Others were mere seedlings. Figure 4 shows these trees scattered more or less throughout the area but concentrated along the summit of the ridge. There they formed such a dense understory that the surface of the soil was barren of all herbaceous and shrubby growth.

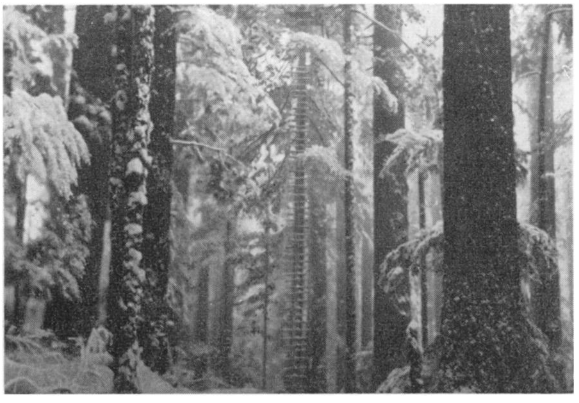

FIG. 5. View from the south showing Location G (the "high hemlock") and environs during the hibernine sector. Ladder on the trunk of the large hemlock may be seen in the central background leading to the platform at an elevation of 80.5 ft (upper center). Photo by Charles Sanford, Feb. 6, 1937.

Associated with the small hemlocks, but also scattered elsewhere throughout the area, were shrubs about 3-10 ft tall. Most of the taller ones were red huckleberries *(Vaccinium parvifolium)*. There were also several dense patches of salal from 8 or 10 to a maximum of approximately 50 ft in diameter and about 3 ft in height. A few very weak and inconspicuous vine maples *(Acer circinatum)* were also present (Fig. 6).

Where the upper canopy was more continuous and young hemlocks and large shrubs therefore largely absent, the soil supported a scattered growth of the ever-

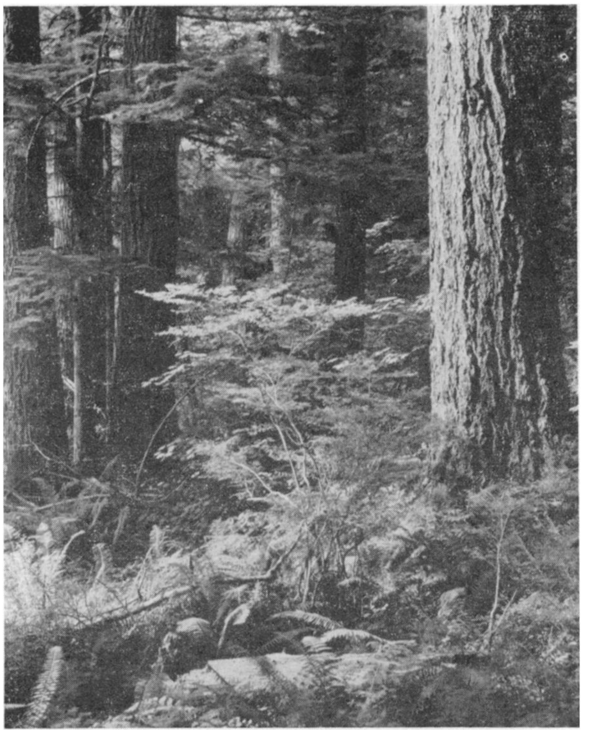

FIG. 6. General view of forest in autumnal aspect showing red huckleberry, vine maple and sword fern. Douglas fir at right measures 3 ft d.b.h. Picture taken Sept. 19, 1954, in Van Duzer Wayside State Park, an area a few miles distant, but typical of the study area before it was logged. Photo by Howard Daniels.

green Oregon grape *(Mahonia nervosa)* and sword fern *(Polystichum munitum)*.

In the spring and early summer the herbaceous layer appeared, including a rather dense growth of vanilla-leaf *(Achlys triphylla)* with more scattered specimens of false Solomon's-seal *(Smilacina sessilifolia)*, wild lily-of-the-valley *(Maianthemum dilatatum)*, fairy bells *(Disporum smithii)*, cool-wort *(Tiarella trifoliata)*, *Trillium ovatum*, and wood-rush *(Luzula parviflora)*. Patches of *Clintonia uniflora* and *Oxalis oregana* formed carpets, and where the sun could penetrate, violets *(Viola sempervirens)*, twayblade *(Listera caurina)*, *Dentaria tenella*, and *Moneses uniflora* were throughout the area. Even under the dense shade of the young hemlocks an occasional saprophytic orchid *(Corallorhiza mertensiana* and *C. maculata)* might be found and more rarely a specimen of Indian pipe *(Monotropa uniflora)* (Fig. 7). Mosses *(Rhytidiadelphus loreus* (L.) Hedw. and *Hylocomium splendens* (Hedw.)) covered the logs, the bases of tree trunks, upper surfaces of fallen limbs, and carpeted the ground wherever other vegetation was not too dense (Fig. 8). The only place where they were absent was in the densest shade of closely growing young hemlocks.

Covering the soil was a litter and humus layer, which in most places approximated 2 in. in thickness, and consisted of needles and branches in all stages of decay, bound together by fungal threads. Where an

FIG. 7. Detail of herb layer in the serotinine sector of the autumnal aspect. Picture taken Aug. 15, 1954, 15 yrs after the area had been logged, yet typical of much of the area at the time it was studied. Plants include Oxalis, Trientalis, vanilla-leaf and sword fern. Twigs of a small hemlock appear at upper border and a small salal appears at right. Photo by Howard Daniels.

FIG. 8. Detail of ground stratum showing mosses, chiefly *Hylocomium splendens* (Hedw.). Typical of north part of Hectare 17 (Fig. 4). Photo by Howard Daniels, Sept. 19, 1954.

old snag or log had decayed, this humus layer would be as much as 6 in. or even more in depth.

CLIMATE

The climate of the Coast Range mountains is extremely humid. According to Wells (1941), "There are some localities on the west slope of the Coast Range (in Oregon) that have heavier precipitation than has been recorded in any other State except in some corresponding areas in Washington. . . . In general precipitation increases from the coast to a belt near the summit of the Coast Range." This location, while exposed to the direct sweep of fog and rain-bearing winds from the Pacific Ocean, did not show an annual precipitation as high as reported for areas farther north on the Coast Range, partly because rain gauges sometimes ran over during heavy mid-week storms. Nevertheless, average recorded annual precipitation was in excess of 89 in. It is a country of very wet winters and dry summers. Most of the precipitation at this level falls in the form of rain. Snow is seldom very deep and usually does not stay long except on the summits of the mountains. Some winters there is practically no snow. An appreciable amount of precipitation occurs in the forest in the form of "Nebel-reisen" or horizontal precipitation caused by condensation of moisture on trees from saturated winds. This drips to the ground beneath and often wets it when outside the forest the soil and vegetation are perfectly dry.

Most of the moisture falls from October to April borne by moisture-laden winds from the southwest or west. These winds are usually light to moderate, but occasionally lash the coast and mountains with such fury as to flatten the more weakly anchored forest trees, and the accompanying floods of water turn streams into raging torrents. Northeast winds are more prevalent during the summer and bring the humidity down abruptly. They generally do not blow for many days at a time, but even in the winter cause the forest to become decidedly dry on the rare occasions when they continue for a week or two. Northeast winds also bring subnormal to freezing temperatures in the winter and abnormally high temperatures in the summer. The wind velocity is greatly reduced within the forest but the accompanying humidity and temperature produce very definite changes in the environment of the forest floor. Wind velocity seldom averages more than 50 mi/day, as recorded by an anemometer at low shrub level, even in the highest gales.

The temperature of this region is famed for its moderation. Within the forest this characteristic is even more evident than in open areas. The average mean temperature for 4 yrs. at this location was approximately 50° F. Temperatures above 70° were very rare and the maximum recorded temperature was 89° F. On the other hand, low temperatures were just as rare. No temperatures close to zero were encountered, the lowest being 11° F. Often when the soil was frozen hard outside the forest, no signs of freezing would be found upon entering the timber. The soil rarely froze beneath the trees. Low temperatures within the forest were usually accompanied by a snowfall or a glaze of sleet. Occasional freezing periods without snow were produced by a strong northeast wind. In the fall the temperatures at this elevation remained considerably above those in the valleys until late in the season, while in the spring, temperatures on the mountain lagged behind those in the lower, open country.

METHODS OF STUDY

Observations, collections and instrumental records were taken weekly from September 18, 1932 to January 9, 1938. A preliminary reconnaissance covering several sections of forested land was conducted to find a suitable location in mature timber. This survey was based on data gathered from County Assessors' offices, from local residents, and from the Pacific Northwest Forest and Range Experiment Station in Portland, Oregon. During this period, field records were kept of all faunal activity and some invertebrates were collected. The vegetation was studied with special care. Information concerning timber cruises, section corner locations, old cabin sites, etc., was checked in the field before a definite location was selected. This phase of the work occupied from September 18, 1932 to February 25, 1933.

INSTRUMENTS

January 21st, 1933, observations were started on the ridge about one-eighth of a mile above the restricted area finally selected for study. On that date a maximum-minimum thermometer was set up 5 ft above the ground level on the north side of a large Douglas fir tree where it remained until June 3, 1933. On February 25th, 1933, a Friez hygrothermograph, an anemometer, and a cylindrical atmometer were installed at the research station. On March 4th, two Forest Service rain-gauges and a set of maximum-minimum thermometers were added, thus completing the battery of instruments installed in the early phase of the study.

At the beginning of the project, the plan was to use stratal data, hence instruments were distributed through as many strata as possible. One of the principal strata was formed by a canopy of Douglas fir crowns 250 ft or more in height. However, the equipment necessary to sample this stratum adequately was unobtainable. Instruments were placed at seven minor locations which have been designated in the order of their establishments at A, B, C, D, E, F and G. These locations are indicated in Figure 4.

The area occupied by Locations D, E, and F lay east of the grove of young hemlocks, on the summit of the ridge, in open timber free from tall shrubs, young trees, or other undergrowth. It was even comparatively free from low shrubs or herbs, and the soil was generally covered with a light growth of mosses over the needles and twigs. This area was exposed to the morning sun and north, east, and south winds, but was protected to some degree from the afternoon sun and west or southwest winds by the young hemlock stand. It was in this vicinity that most of the collections and observations were made.

A fire shelter (FS, Fig. 4), or lean-to, facing west, in front of which fires were built in cold weather, was located about 150 ft northeast of Station C (Fig. 9). Location D was established 20 ft farther north down the ridge where hazard sticks were set up at a level 6 in. above the soil surface, among sword fern and vanilla-leaf and on the east side of a large Douglas fir tree. Location E was 60 ft east of the lean-to and at the same elevation. An instrument shelter was erected to enclose the Taylor recording thermometer, the bulb of which was buried near by, 2 in. beneath a heavy carpet of moss covering a low mound, the result of an old windfall. At location F, Wynne photometer readings were made at an elevation of 3.5 ft, by placing the instrument 4 ft south of the fire shelter on a log which supported that structure (Fig. 4).

FIG. 9. View toward east from in front of the fire shelter during the vernine sector, showing the open character of the forest in this study center. Locations E (thermograph shelter) and F (site of photometer readings) are indicated by letters. Location G is hidden by the large Douglas fir to the right of the shelter, while the herb quadrat at Location E is obscured by the left-hand corner of the fire shelter (see Fig. 4). Photo by M. R. Edmunds, Apr. 24, 1935.

COLLECTING METHODS

The data from the soil layer have not been included in this paper. Regular quantitative counts and surface observations of the humus and moss layer were made over areas which varied in size, depending upon the abundance and size of specimens.

The shrub layer was sampled by a number of methods, each of which produced good results for some part of the population. Random sampling was carried on regularly by means of sweep nets of various sizes and by individual hand-picked collections, in an attempt to obtain representative specimens of the common animals for identification. The specimens were counted in the net after being killed or immobilized by placing the tip of the net for a few minutes in a large cyanide jar. A third method was that of beating the shrubs over 1 sq m of canvas held horizontally by crossed sticks inserted into pockets in the corners. Specimens were then picked off the canvas before they could run or fly away. This was especially successful in obtaining spiders and slow-moving insects on cool days. A fourth method was that of closely examining marked square meters of vegetation for a given length of time—usually about 15 minutes. No collections were made from these marked quadrats.

The low hemlock layer was sampled by all of the methods enumerated for the shrubs and herbs. The beating method was most satisfactory in this layer. Collections were also made of insects lighting or flying across the low hemlock platform.

The high hemlock layer was sampled least successfully. Random collections were made from the bark and boughs, as well as on the platform. Also, some aerial counts were made. A sweep net was used but only random collecting was possible.

The rotting logs, snags, stumps, and other down timber were sampled by examining at random and by collecting and counting specimens over a certain area.

For amphibia, pitfalls were found to be an effective method of collecting. These were formed by smoothing the vertical sides of pits made in using the soil-sample counting chamber. Birds were studied by noting their various calls and by estimating the size of flocks or number of nests over a given area. A few specimens were shot outside the area for specific determination. Small mammals were caught by snap traps placed in runways, near holes, and by stumps, logs, or in other favorable locations. Poisoning was tried off the area but with little success. Molehills and runways were counted over a definite area. Tracks, "sign" and other evidences were used to obtain information on larger mammals.

In addition to collections and observations over this restricted area, regular observations and some collections were made along the trail each week during the trip to and from the research station. Since these were, for the most part, at a lower elevation, they were not strictly comparable with results at the station but produced a good deal of supporting evidence from the aspectional standpoint. Occasional trips were also made to the top of Saddleback Mountain for additional information and observation.

Soft-bodied specimens were preserved in alcohol. Insects were put in vials, pillboxes, or cellophane envelopes to be transported to the laboratory where they were sorted, pinned, and sent to specialists for identification. Amphibia were taken to the laboratory alive where they were killed and preserved in alcohol and formalin. Birds and mammals were shot or trapped, measured, and study skins made for identifications. Their stomach contents were regularly preserved.

A survey was made of the area used for this investigation. Starting from the southwest section-corner, the area intensively investigated was divided into hectares and contour lines were run at 25-ft intervals as shown in Figs. 3 & 4. The hectare corners and contour lines were marked with white and colored rags so that collections could be definitely located as to elevation and hectare. Hectare 17, which included Stations C, D, E, F, and G, was divided into dekameter squares to permit even more accurate location in this area. Hectare 17 and part of hectare 16 were then mapped for location, distribution, and types of vegetation, as shown in Fig. 4.

ASPECTION

HISTORY AND CRITERIA

Aspection may be defined as the seasonal rhythm of the presence and activities of conspicuous organisms within a community. It is equivalent to *seasonal succession* (Allee *et al.* 1949). Aspection as a phase of ecological interest has not attained the degree of importance which it deserves. In the field of botany it enjoyed a period of popularity under the term *phenology*. In the latter part of the 19th century, a number of articles were published on the development of buds, leaves, flowers, fruits and defoliation of trees. Some of the early publications on phenology also considered the seasonal effects on animals (Hough 1864, Robertson 1895). Also there were attempts to correlate phenological and meteorological phenomena (Mikesell 1883). This phase of interest in seasonal phenomena reached a high point in the "Calendar of Leafing, Flowering, and Seeding of the Common Trees of the Eastern United States" (Lamb 1915). Hopkins & Murray (1932), on the basis of a few selected woody plants, established botanical criteria that have been utilized in a number of ecological studies. Shelford (1929) applied the term phenology to the study of correlations between periodic phenomena exhibited by plants and migrations of animals and birds. In 1935, the committee on nomenclature of the Ecological Society of America defined phenology as that science that deals with the time of appearance of characteristic periodic events in the life cycles of organisms under natural conditions, especially those influenced by temperature, latitude and altitude, among other influences in the physical environment. Thus, the term phenology has taken on a wide meaning, the terms "phenological" and "seasonal" being considered equivalent. Huberman (1941) summarized North American phenological efforts, classifying studies in three groups; the construction of calendars and charts without regard to meteorological factors, the correlation of plant and animal activities with meteorological factors, and the applications of the principals of bioclimatology. Glendenning (1943) has termed phenology "the most natural of sciences" and pointed out the value of seasonal studies. During the last decade, several notable phenological studies have appeared, one of the most comprehensive being that of Leopold & Jones (1947), in which were tabulated and analysed 328 seasonal events during the decade 1935-1945 in Wisconsin. Phenological observations have found practical applications in a number of recent studies such as those of Costello & Price (1939) on determining grazing periods on mountain range, Lathrop & Dirks (1944) on timing the seasonal cycles of insects and Penfound *et al.* (1945) on mosquito control. Elsewhere in the world, studies of seasonal phenomena under the term phenology have experienced a mild resurgence in recent years. Among such works may be cited those of Batista Diaz (1942), Rosenkranz (1947, 1948), Marcello (1947, 1950), Voigts (1949), Ledesma (1949), Kurauchi (1951), Kontkanen (1950), Linnavuori (1952) and the reports of phenological observations in the British Isles appearing in the Quarterly Journal of the Meteorological Society, London (*e.g.* Gunton 1943). Many if not most of these works appear to be of a practical nature.

Interest in aspection among North American ecologists originated with Pound & Clements (1898), who recognized "a vernal and an aestival-serotinal aspect" in the prairie. These authors later expanded their concept of seasonal societies, for Wolcott (1918) refers to Pound & Clements' (1900) division of the flowering periods of plants into prevernal, vernal, estival and serotinal aspects. In botanical ecology, the study of aspection was long restricted to the description of seasonal or aspectional societies indicated by the conspicuous subdominant flowering plants of the various seasons. This concept of aspection probably reaches a climax in the description of the seasonal aspects of the prairie by Weaver & Fitzpatrick (1934) who indicated approximate aspectional dates for prevernal, vernal, aestival, autumnal, and hiemal societies but gave no correlation with specific environmental data. Wolfe *et al.* (1949) established botanical criteria based on both floral and vegetational phenomena, and correlated with environmental factors. This study has invited use and commentary by others, notably Cantlon (1953) who studied vegetation and microclimates as particularly applied to topography. Ellison (1954) dates aspection in subalpine vegetation in terms of days from snow melt.

Zoologists have also made numerous contributions to the fund of aspectional information. Adams (1913) noted in his bibliography seasonal succession as recognized by European naturalists. In the same year, Shelford (1913) gave a brief account of seasonal succession, citing definite dates of observation. Wolcott (1918) wrote on seasonal changes in southeastern Nebraska, stressing the correlation of specific physical factors with the biotic phenomena represented in the four seasons of spring, summer, fall and winter. He indicated that environmental and biotic evidence would start these seasons about two or three weeks ahead of the astronomical dates for seasonal limits and pointed out faunal evidences of seasonal activity.

This introduction to faunal aspection was followed by publications of Shelford (1918) and Sanders & Shelford (1922) on seasonal occurrences in animals. Weese (1924b) recognized the adjustment of characteristic insects in a deciduous forest to climatic rhythm and the effect of environmental factors of moisture and temperature in stimulating seasonal migrations. In 1928, V. G. Smith published a definitely dated list of seasonal "socies" for a deciduous forest community in which she recognized vernal, aestival, serotinal, autumnal and hiemal societies. This paper represented the first attempt at organization of an entire fauna, from an aspectional standpoint, through a complete annual cycle. The data were graphically represented in a cyclic arrangement, but no attempt was made to correlate the seasons with environmental fluctuations. This was followed by the report of Shackleford (1929) in which environmental factors were considered, in addition to the fauna, through the various seasons of an annual cycle.

Subsequent faunal investigations by animal ecologists have shown a tendency to recognize seasonal societies as a definite part of the community structure. Bird (1930) listed seasons for two successive years in the aspen parkland of Canada, based on the fluctuating animal population, with special emphasis on the vertebrates. Davidson (1930) listed definitely dated seasons without indicating any precise basis for their determination. Brown (1931) compared the seasons in Missouri and Oklahoma oak-hickory forests showing a correlation of the curves of animal population with temperature and precipitation. Seasonal societies also were emphasized in the faunal investigations of Davidson (1932) and Shackleford (1935). In 1936, four ecological publications appeared, all of which recognized the aspectional distribution of the fauna. Carpenter (1936a, b) suggested that the winter population might be divided into hiemal and hibernal societies (socies). Daubenmire (1936) dates the seasons for the "big woods" of Minnesota, and Williams (1936) gave an excellent description of aspectional changes in a beech-maple climax community. Williams included not only faunal population changes but correlated these with floral aspection and environmental changes, as well as with altered physiological activity of faunal inhabitants. His work apparently was based chiefly on general observation of environmental phenomena, as no instrumental records were reported. Carpenter (1939) considered aspection on a mixed grass prairie in Oklahoma, including observations of both plants and invertebrates, and Shackleford (1942) also worked in Oklahoma, designating the seasons as expressed by invertebrate populations of herbs in poorly-drained, overgrazed grassland. McClure (1943) wrote on the biotic communities of the Churchill area, Manitoba, basing his concept of aspection upon the flowering dates of plants. He gave population records for the fauna, as well as environmental records, which could be correlated with the plant aspection, but no definite seasonal societies were delineated. Twomey (1945), in a study of the bird population of an Illinois elm-maple forest delineates seasons, using meteorological records as well as faunal and vegetational data. Dowdy (1944) found that seasonal concepts held for invertebrates in disturbed forest in Ohio and described (1950) the seasonal features of stratal societies in an oak-hickory association. Jones (1946) considered the effect of climate upon aspection and annuation in an elm-maple forest in Illinois (the same woods studied by Twomey 1945). Dirks-Edmunds (1947) included aspection and annuation in a comparison of biotic communities in Illinois oak-hickory and Oregon Coast Range cedar-hemlock associations. Fichter (1954), in a quantitative study of invertebrate fauna of grassland and shrub savanna in eastern Nebraska, considered faunistic, floristic, and environmental expressions of seasonal concepts.

Thus we see the gradual growth and maturation of the aspectional concept, as recognized and used by American ecologists, from its beginnings in a purely floristic phenology, through recognition of faunal aspection, to correlation of seasonal phenomena with environmental factors. Yet it seems probable that further refinement of seasonal concepts, criteria, and terminology is desirable.

As shown above, seasonal phenomena in plants and animals have long been recognized by biologists who have appreciated the fact that there were seasonal effects on living things that did not coincide with equinoxes and solstices, and that the activities of living organisms were the best indicators of such changes. Botanists have used the flowering of subdominant plants, usually confined to the herb layer, as the indicators of aspection or seasonal effects. This led to the use of the terms *hiemal* for winter, *vernal* for spring, *aestival* for summer and *serotinal* for fall seasons. Recently, *prevernal* has been used for a season of earliest blossoms and *autumnal* has been placed after serotinal as a late fall aspect.

With the exception of Wolcott (1918), who attempted to state exact limits of seasons by reference to temperatures, early investigators tended to express environmental criteria for seasons in rather general terms. Even yet, in few papers are seasonal criteria clearly expressed. In accord with the assertion (Vestal 1914) that the animal selects an environmental complex composed of three phases: physical, plant and animal, the author has attempted to designate the seasons by meteorological, botanical and faunal criteria.

Aspectional Analysis

Fluctuations in faunal constituents were considered of prime importance in obtaining a picture of aspection in this community, although analyses of physical environmental factors, flora, and fauna have all been considered.

Population Changes

Many of the faunal collections were of a random character. It is therefore felt that the proportion of individuals of each species to the total population could not be accurately determined in an area including such varied and often comparatively inaccessible habitats and minor biotic communities, even though a representative sample of the common animals active at the time of observation was obtained. This was especially true of the vertebrates. Insects were the most abundant faunal group active in the community and were quite thoroughly collected and identified, hence the population has been analyzed from the standpoint of fluctuation in variety of insects. This procedure also follows the precedent set by Adams, Smith, Shackleford, Davidson and Brown. In determining the character of the total population throughout the year, or what might be termed the "faunal spectrum," an ideal record would be based on all species present in the habitat. In this project such an ideal could not be attained for several reasons. Some species could not be determined even by the specialists. It was often impossible in the field to differentiate similar species. Exact determination of every species was probably ecologically unimportant. Within a given family, related species more often than not appeared to be biological equivalents, occupying much the same niches, using the same type of food, and often present during the same season of the year. For these reasons, and in order that there might be a definite basis for comparison with work of other investigators, the family was used as an arbitrary unit indicating variety of insect population. The total number of insect families collected or observed in the aerial strata of the community on each date the area was visited was calculated and graphed (Fig. 10, solid lines).

In addition to the above analysis of the insect population at the family level, compilation of the occurrence of common and conspicuous insects was made and their seasonal distribution tabulated. In order to be included in this phase of the population analysis, an insect must have been present on more than one of the collecting dates during the season in question for at least 3 out of the 5 yrs studied. While some of the species remain nameless because of the incomplete state of our knowledge of the fauna of the region, determinations are in general reliable and at the species level. (Tables 2, 4, 6, and 8, Fig. 15 and the columnar portion of Fig. 10 are based on the aforementioned data.)

One of the most obvious results of any analysis of the population is the recognition that certain species, or groups of species, suddenly become an integral part of the community while others dwindle to a position of unimportance or as suddenly disappear. This is occurring continually and gives rise to the feeling that the change in the complexion of the fauna from week to week is due to a gradual infiltration of new species and a gradual disappearance of others which in a relatively short time builds up an entirely different community structure. To represent the changing composition of the population a columnar graph was superimposed on the curve of population showing the number of distinctive and common insects appearing for the last time and the number appearing for the first time in each collecting period (Fig. 10). This not only indicates the expected continuous and gradual replacement of faunal units but also shows that on fairly definite dates an upheaval or turnover of animal species occurs producing a new faunal aspect as a result of new species being ushered into the active life of the community and others dropping out. As might be expected, the aspects that follow the winter period of low population are marked by a greater influx of new groups of insects than disappearance of those already present, while the aspects late in the summer are marked by more species dropping out than are added. Since either a decrease or increase of animals indicates a change, the sum of positive and negative results gives the total amplitude of change affecting the population. Because an exceptional waxing and waning of population indicates a surge in the even flow of the seasonal tide of population variety, such points appear to indicate the approximate seasonal limits. It is certain that a comparison of the fauna composing the population before

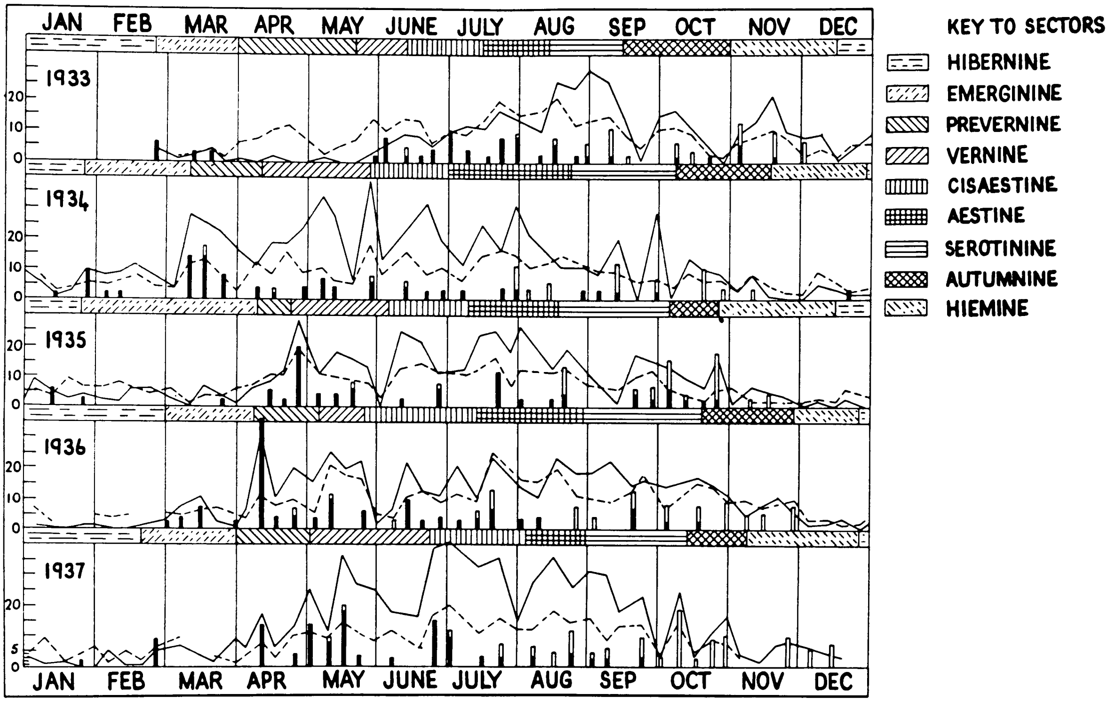

FIG. 10. Correlation of population and environmental factors. Solid line shows the number of families of insects active in the layers of the community above the soil surface on each collecting date: Scale—1 unit equals 1 family of insects. Broken line was produced by plotting a factor obtained by averaging the vapor-pressure deficit for time of observation, light intensity for that afternoon, and mean daily maximum vapor pressure deficit for the week preceding each trip: Scale—1 unit equals .020 of the environmental factor. Solid columns indicate the number of species of common insects appearing for the first time during the year on each date. Open columns indicate the number of species of common insects which appear for the last time during the year on each date. Scale—2 units equal 1 species. Seasonal limits are shown by shaded blocks on upper margin of each annual graph: key appears to the right.

and after one of these periods of fluctuation discloses an appreciable change in population structure. The boundaries of certain seasons for some years (*e.g.*, vernal, 1935) seem to be sharply marked by a sudden change in the population, while in other years, the same season is not so clearly set off (*e.g.*, vernal, 1934). Apparently these changes in population occur more abruptly in some years than in others. The most striking fluctuations occurred in 1937, either because collections were more consistent and more efficiently conducted in that year, or because a late spring shortened the active period. One possible weakness in the investigation that may have prevented the seasonal fluctuations from being more sharply defined is the psychological difficulty of making positive observations on negative phenomena. The dates on which animals became conspicuous by their absence were not consistently noted in the field records. If this information had been more carefully kept, it might have added somewhat to the height of the columns in the early seasons. As it is, these are marked chiefly by the appearance of new animals.

Correlation of Population with Environmental Data

The question that next arises pertains to the reason for such population differences as are shown in Figure 10. As a result of reviewing the effect of seasonal changes on animal life in the vicinity of Lincoln, Nebraska, from 1881 to 1917, Wolcott (1918) stated that the most obvious factor in seasonal changes is that of temperature. Further on he added, "Of the climatic factors (temperature, precipitation, sunshine and cloudiness, wind, humidity, soil moisture and barometric pressure) enumerated above, temperature and moisture have by far the most pronounced direct effect on animal life, not only in determining in a general way the character of the fauna of a locality but also in exerting a considerable control over the time of appearance of many species, as well as the abundance of many forms." Shelford (1913) states, "Seasonal succession is the succession of species or stages in the life histories of species over a given locality due to heredity and environic differences in the life histories (time of appearance) of species living there." The factor of heredity does not lie within the province of this investigation but that of "environic differences" does. Weaver & Clements (1938) emphasize the environmental factor, stating that seasonal aspects are determined primarily by the seasonal march of habitat factors, of which temperature and length of day are most important. Their conclusions deal primarily with plant life, in which length of day has been demonstrated to exert a controlling influence, especially upon flower production. The gradual alteration of length of day is now known to have an effect upon animals (Allee *et al.* 1949) but has not been directly investigated in this study. Among fluctuating factors, the role of temperature is especially eligible for consideration. The direct effect of temperature is not its only effect. Sums of temperature have been shown to exert a controlling influence upon both plant and animal life (Artz & Ludwig 1949, Headlee 1941, Rosenkranz 1948). Besides temperature, Shackelford (1942) considered relative humidity, and to a certain extent precipitation, as factors influencing the occurrence of seasonal changes in invertebrate animal populations.

An inverse ratio between seasonal variations in animal population and variations in the evaporating power of the air in an elm-maple forest was found by Weese (1924). Brown (1931) also showed correlation of curves of animal population with temperature and precipitation in a deciduous forest. Adams (1941) reported, "The correlation coefficients indicate increases of animals with temperature increases and decreases with temperature decreases in all strata, and, in general, increases of animals with relative humidity decreases, or vice versa." He also considered the effect of evaporation but indicated no particular correlation.

The observation that the more modern, active insects tend to appear in environments of high energy intensity (midday, midsummer and the tropics) and the more primitive insects in environments of low intensity has been termed the Kennedy trend (Kennedy 1928). Whittaker (1952), in evaluating the application of this trend to various stations in the Great Smoky mountains, concluded that "the primary correlation of modernity is with the drying power of the atmosphere." On the basis of similar calculations for the Saddleback Mountain area, it was found that the highest modernity index of the year is in the early fall, which is also the season of highest evaporation and very low rainfall.

According to Shelford (1937), we are warranted in concluding that the evaporating power of the air is probably the best index of environmental conditions of land animals. The suggestion that as a measure of the evaporating power of the air vapor pressure deficits "are ecologically more significant than humidity values" was made by Weaver & Clements (1938). These authors refer to the work of Anderson (1936) in which the advantages of vapor pressure deficit measurements over relative humidity are summarized. Anderson concludes, "It is desirable that vapor pressure deficits be recorded in experimental work with organisms rather than relative humidities." Since vapor pressure deficit is the "difference between the saturation vapor pressure for the current temperature (dry bulb) and the saturation pressure for the temperature of the current dew point" (Weaver & Clements 1938), it is influenced by both the temperature and moisture content of the air. In addition Anderson (1936) states, "Vapor pressure deficit alone does give an indication of evaporation rates." Anderson's statement has been criticized by Leighly (1937) who concluded that his analysis and conclusions were untenable and that evaporation is proportional, not to vapor pressure deficit, but to the vapor pressure gradient between the evaporating surface and the air. Thornthwaite (1940) enlarged upon this view and concluded that conventional methods of measuring atmospheric moisture were inadequate and attempts to correlate simple functions of atmospheric moisture were futile. Nevertheless, Huffaker (1942) found a correlation between vegetational distribution and vapor pressure deficit and relative humidity values in zonation of vegetation types in the United States, concluding that vapor pressure deficit provided a superior correlation, the general correspondence between vegetational and vapor pressure deficit lines being too great to be coincidental or even secondary.

Despite, or perhaps because of, the above conflicting views, it was decided to attempt vapor pressure deficit and population correlations in this study. It may be noted that in recent studies, others continue to use vapor pressure deficit values in biotic studies (*e.g.* Kucera 1954, Barnes & Barnes 1954).

Accordingly, vapor pressure deficits for the dates of collection were calculated and graphed from records taken at the low shrub level. The resulting curves were compared with the curves of population diversity shown in Figure 10. Correlation was apparent at once. As the vapor pressure deficit rose the variety of insects increased and as the vapor pressure deficit fell the number of insect groups usually became smaller. This curve was constructed from vapor pressure deficits calculated from hygrothermograph records for the time at which collections and observations were made. As a rule this was about 3:00 p.m. The vapor pressure deficit was usually quite stable during the afternoon while insects were most active; accordingly a figure selected for approximately the time of collection was representative.

At several points this correlation between vapor pressure deficit and complexity of faunal structure broke down. It seemed reasonable that perhaps the trend of vapor pressure deficit for the preceding week might in some cases exert an effect which would not be apparent when vapor pressure deficit for the time of collection was considered alone. Because the minimum vapor pressure deficit was very low for the entire year and fluctuated only slightly, it was not used. The mean daily maximum vapor pressure deficit for the preceding week, however, formed a curve with marked oscillations and these were of such a nature that in most cases, when averaged with the vapor pressure deficit reading at the time of collection, the resulting curve much more closely approximated that of population variability. A curve constructed from the mean vapor pressure deficit for the preceding week gave less favorable results because, while the graph was not materially changed, the fluctuations were too moderate to be effective. A final reason for the use of the maximum reading is that a high vapor pressure deficit, through its correlation with greater environmental stress, would be likely to indicate a more stimulating effect on insect life in this environment than the mean vapor pressure deficit.

In a few points in the graph, even the use of the above-mentioned data did not produce as close correlation as might be desired. In casting about for an additional factor which could eliminate discrepancies it was discovered that the light intensity had an effect which would bring the environmental curve of vapor pressure deficit more nearly into line with the population curve. The light intensity, however, had to be determined from several sources. Wynne photometer readings were available at shrub level through most of the period from December 8, 1934, to June of 1937, and from October, 1937, to January, 1938. A Weston illuminometer was used during the summer of 1937. For the collecting dates on which no photometer or illuminometer records were available, weather observations were found to be consistent enough to provide a reasonable interpretation of the light intensity based on comparisons with similar days on which instrumental records were available. Since the photometric data were more extensive and were in terms of the percent of full sunlight, the illuminometer records and interpretations from type of day were reduced to the same basis of percentage.

To illustrate the procedure by which a combined factor was obtained by averaging the figures for the vapor pressure deficit and light intensity for the collecting date with mean maximum vapor pressure deficit for the preceding week, the following example is offered. On July 21, 1935, the mean daily maximum vapor pressure deficit for the preceding week was .332; the vapor pressure deficit for the collecting period was .287; and the factor of light intensity for that afternoon was 40% of full sunlight. Thus, averaging .332 plus .287 plus .400, a value of .339 is obtained. This calculation was performed for each collecting date. By comparing the type of environmental curve which would be produced on a graph, such as that shown in Figure 10, if only vapor pressure deficits were considered, with a graph in which a light factor is also averaged, the latter was found to conform more nearly to the population trend.

Even this combination of factors does not produce perfect correlation throughout. For many of the discrepancies, no adequate explanation can be advanced at present. Inadequate sampling of the population on some dates, undue emphasis on certain phases of the collecting, or environmental influences that escaped notice previous to the collection, can explain most correlation failures. Variation in skill of personnel assisting in the research on successive collecting dates accounts for poor correlation in the vernal aspect of 1934. When the temperature is low in the early spring and late fall and there is snow, the light intensity may be high, though the vapor pressure deficit on the collecting day is very low. This causes a comparatively high environmental curve to be maintained while at the same time the population curve drops to a low point. If the temperature is near the freezing point, even a bright sun, since it fails to reach many individuals below the canopy, is unable to produce much activity in the insect or arachnid population, while the physical effect of the snow is no doubt a deterrent to normal invertebrate activity. A situation of this kind is very clearly shown on November 2, 1935. On the other hand, on the last preceding collecting date, October 26, 1935, the light intensity was much lower, the vapor pressure deficit at the time of collection was somewhat higher, the temperature higher and the vegetation not extremely wet nor snow-covered. The environmental factor plotted for October 26th does not differ greatly from that of November 2nd, yet the population diversity, as well as total population, on the earlier date was quite high. Variation in response of different insects to the environmental factors considered affects the correlation at certain points. In the serotinine sector of each year such a correlation failure occurs, the vapor pressure deficit-light factor being low but the population high. This appears to be due to the sudden influx of families responding positively to increased humidity (Fungivoridae, Psychodidae, Trichoceridae, Tendipedidae, etc.), even though the occurrence of these same insects later corresponds to the environmental curve in the usual way. It also may be assumed that some environmental factors vary in their effect on variety of insect fauna, depending upon the relationship of those factors to several other undetermined factors, while others (*e.g.* temperature), are undoubtedly cumulative in effect. Additional factors that are known to affect fluctuations of populations but which were not directly considered, are ultraviolet radiation (Shelford 1951) and length of day (Allee *et al.* 1949).

Thus for this investigation the biotic aspects were first determined roughly by noting the dates when the curve of population and the curve of vapor pressure deficits and light (Fig. 10) indicated extreme fluctuation. By referring to the columnar portion of the graph, it was possible to determine whether this fluctuation was due to addition or loss of groups of animals or both. Field notes were then consulted to determine whether the general picture of faunal population, vegetational development and environmental conditions indicated a change at this point. The hygrothermograph records were found to be a valuable index for setting dates of meteorological departure from a normal seasonal pattern. Each season appeared to have a unique relationship between temperature and humidity as illustrated for typical periods (Figs. 11 & 12). The pattern for each season was easily recognizable, in spite of variations and temporary departures from the normal. When this pattern changed distinctly, it was usually possible to discover a correlated alteration in the composition of the population. In the fall of the year more difficulty is encountered in establishing definite dates for the terminations of seasons than at any other periods.

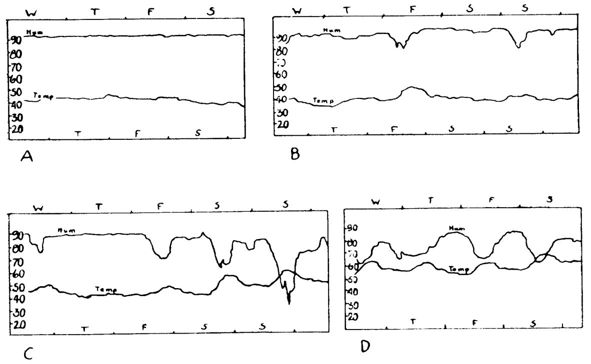

FIG. 11. Sample hygrothermograph records showing typical seasonal patterns. A. Record for the period from Dec. 7, 1936 to Dec. 10, 1936, showing the uniformly high humidity and moderately low temperature, with extremely slight diel fluctuation, characteristic of the hiemine sector. B. Record for the period from March 10, 1936 to March 15, 1936, showing the high humidity and moderately low temperature, with slight diel fluctuation, characteristic of the emerginine sector. C. Record for the period from May 4, 1936 to May 9, 1936 illustrating the increasing daily fluctuation in humidity and temperature, with lowered humidity and increased temperature, characteristic of the transition from the prevernine to the vernine sector of the vernal aspect. D. Record for the period from July 15, 1936 to July 19, 1936, indicating the characteristic diel alternation in the aestival aspect, from high temperature and low humidity to low temperature and high humidity.

The faunal fluctuations at that time of the year are much smaller and representatives of the population drop out at various points. Hardier types of animals are not taken during unfavorable periods and reappear later when the weather moderates. Meteorological factors in the autumn are subject to wide fluctuations and in some years of this study the seasons passed almost imperceptibly into the succeeding stage of aspection. Hence, it is felt that some of the attempts to date the termini definitely may be rather arbitrary, especially in view of the fact that collections and observations were made a week or more apart.

The seasons tentatively determined by these data were then checked against graphs of temperature, humidity and precipitation, an attempt being made to determine whether a unity or continuity of character was shown by these separate factors, and, if not, whether adjustments in seasonal limits might be made which would improve the seasonal picture.

BIOTIC ASPECTS IN THE OREGON COAST RANGE FOREST

As a result of the above-mentioned considerations of environmental and biotic data, it has been possible to piece together a panorama of the seasonal changes by means of a combination of environmental, vegetational and faunal analyses. These seasonal changes include both major and minor biotic divisions. The four *aspects* or major biotic seasons are termed the hiemal, vernal, aestival and autumnal aspects. Nine biotic subdivisions or seasonal societies of the four major aspects are found. These subdivisions are termed *sectors,* the names of which are given the suffix-*ine* in preference to the -*al* suffix which heretofore has been used to designate both major and minor biotic seasons. The winter or hiemal aspect consists of three sectors, hiemine, hibernine and emerginine; the spring or vernal aspect includes the prevernine and vernine sectors; the summer or aestival aspect shows a division into early (eisaestine) and late (aestine) sectors; while the fall or autumnal aspect includes the serotinine and autumnine sectors.

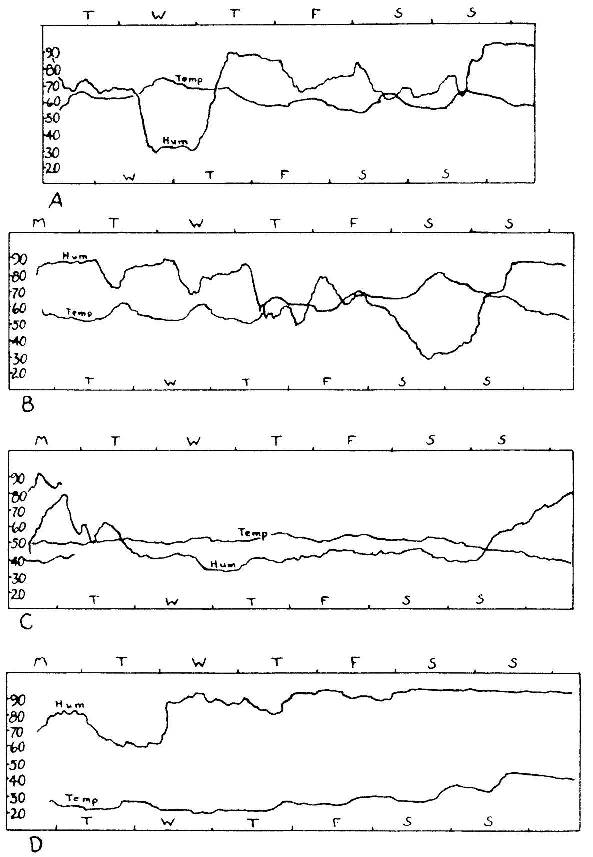

FIG. 12. Sample hygrothermograph records showing typical seasonal patterns. A. Record for the period from Aug. 27, 1936 to Sept. 2, 1936, showing a short period of very low humidity on Aug. 28, such as is often characteristic of the change from the aestival to the autumnal aspect (serotinine sector). B. Record for the period from Aug. 28, 1934 to Sept. 4, 1934, illustrating the unstable moisture conditions, with fluctuations extending over several days, which are characteristic of the autumnine sector, *i.e.*, a period of low humidity extending over several days, with a return to humid conditions of similar duration. E. Record for the period from Nov. 21, 1936 to Nov. 29, 1936, showing the type of fluctuation characteristic of the autumnine sector, *i.e.* a period of low humidity extending over several days, with a return to humid conditions of similar duration. D. Record for the period from Feb. 15, 1936 to Feb. 22, 1936, showing the characteristic hibernine pattern, *i.e.*, a cold, dry spell, with return to high humidity and higher temperature.

TABLE 1. Dates of seasonal limits.

Year 1st	2nd	3rd	4th	5th	6th
HIEMAL ASPECT					
Hiemine Sector					
Start Oct. 30, '32	Nov. 1, '33	Nov. 17, '34	Oct. 26, '35	Nov. 28, '36	Nov. 8, '37
End	Dec. 15, '33	Dec. 28, '34	Dec. 15, '35	Dec. 26, '36	Dec. 19, '37
Hibernine Sector					
Start	Dec. 15, '33	Dec. 28, '34	Dec. 15, '35	Dec. 26, '36	Dec. 19, '37
End Feb. 25, '33	Jan. 25, '34	Jan. 24, '35	Mar. 1, '36	Feb. 20, '37	Jan. 9, '38
Emerginine Sector					
Start Feb. 25, '33	Jan. 25, '34	Jan. 24, '35	Mar. 1, '36	Feb. 20, '37	Studies
End Apr. 1, '33	Mar. 10, '34	Apr. 9, '35	Apr. 7, '36	Mar. 30, '37	Terminated
VERNAL ASPECT					
Prevernine Sector					
Start Apr. 1, '33	Mar. 10, '34	Apr. 9, '35	Apr. 7, '36	Mar. 30, '37	
End May 20, '33	Apr. 10, '34	Apr. 23, '35	May 5, '36	May 1, '37	
Vernine Sector					
Start May 20, '33	Apr. 10, '34	Apr. 23, '35	May 5, '36	May 1, '37	
End June 12, '33	May 27, '34	June 5, '35	May 25, '36	June 24, '37	
AESTIVAL ASPECT					
Cisaestine Sector					
Start June 12, '33	May 27, '34	June 5, '35	May 25, '36	June 24, '37	
End July 15, '33	July 1, '34	July 9, '35	July 8, '36	Aug. 4, '37	
Aestine Sector					
Start July 15, '33	July 1, '34	July 9, '35	July 8, '36	Aug. 4, '37	
End Aug. 13, '33	Aug. 22, '34	Aug. 17, '35	Aug. 28, '36	Aug. 30, '37	
AUTUMNAL ASPECT					
Serotinine Sector					
Start Aug. 13, '33	Aug. 22, '34	Aug. 17, '35	Aug. 28, '36	Aug. 30, '37	
End Sept. 15, '33	Oct. 7, '34	Oct. 5, '35	Oct. 19, '36	Oct. 13, '37	
Autumnine Sector					
Start Sept. 15, '33	Oct. 7, '34	Oct. 5, '35	Oct. 19, '36	Oct. 13, '37	
End Nov. 1, '33	Nov. 17, '34	Oct. 26, '35	Nov. 28, '36	Nov. 8, '37	

Dates for the seasonal limits of these aspects and seasons are given in Table 1. The biotic aspects generally precede the calendar seasons and are affected by climatic conditions which shorten or lengthen their duration. The opening dates of the vernal aspect in this location fluctuated about the date of the spring equinox while the aestival aspect started before the summer solstice in every year but 1937. Acceleration of biotic seasons is also shown by the opening of the serotinine sector of the autumnal aspect approximately one month before the autumnal equinox and by the beginning of the early sector of the hiemal aspect which started, on the average, a month and a half ahead of the winter solstice.

Hiemal Aspect

The winter, or hiemal aspect as a whole, is the period of unfavorable physical factors of the environment with a correspondingly restricted biota. Though moderate and with transitional phases at either end, the winters in this community are rather extensive, being over four months in length. The hiemal aspect usually begins in late October or mid-November and ends around the first of April. The invertebrate population consists chiefly of a characteristic group of Trichoceridae, Fungivoridae, Psychodidae and spiders all of which have been elements of the autumnal fauna. It is low both in number of individuals and diversity of species during the hiemine sector and becomes very restricted in the hibernine sector of this aspect, but awakens to greater activity in the late or emerginine sector when it is considerably augmented by a group of animals destined to become a part of the fauna of the vernal aspect. Table 2 and Figure 13 show that only 25 species of insects are characteristic of the hiemal aspect. Of these species none begins its activity in the hiemine sector, one begins in the hibernine sector and twelve in the emerginine, the remainder having been a part of the autumnal fauna. None of these is restricted to the hiemine nor hibernine sector and only three (12%) are restricted to the emerginine sector. Diptera represent 44% and Coleoptera 20% of the hiemal fauna. The hiemine sector has a more varied population than the hibernine, which is the low point for the year, while the emerginine has the greatest population of the winter. Temperatures lie almost entirely below the average annual mean of 50° F (Fig. 14), and humidity is high (75-90%). Vapor pressure deficits therefore are low, the weekly maxima averaging less than .100

TABLE 2. Seasonal distribution of insects characteristic of the hiemal aspect (winter). E, emerginine sector; PV, prevernine sector; SV, vernine sector; CA, cisaestine sector; SA, aestine sector; S, serotinine sector; A, autumnine; H, hiemine sector; Hi, hibernine sector; X, characteristic of a given aspect; --, present but not in significant numbers. The seasonal distribution of each insect considered is tabulated throughout the year but is not repeated on any other chart unless characteristic of that season, *i.e.*, was collected more than once during a given season for at least three of the five years studied.

Sector	E	PV	SV	CA	SA	S	A	H	Hi
Collembola									
Entomobryidae: *Tomocerus flavescens* Tullb.	X	X	X	X	--	X	X	X	
Sminthuridae: *Ptenothrix* sp.	X	X	X	X	--	X	X	X	
Homoptera									
Aleyrodidae: gen. et sp. indet.	X	X	X			X	X	X	--
Coccoidea: indet.	X						X	X	X
Hemiptera									
Pentatomidae: *Elasmothethus cruciatus* Say	X								X
Lygaeidae: *Ischnorrhynchus resedae* Pans.	X								
Gastrodes pacifica Prov.	X								
Coleoptera									
Staphylinidae: *Anthobium subcostatum* Maekl.		X					X	X	
A. pictum Fauvel		X					X	X	
Cerambycidae: *Plectrura spinicauda* Mann.		X	X	X	X	X	X	X	
Curculionidae: *Nemocestes incomptus* Horn		X	X	X	X	X	X	--	
Sciopithes obscurus Horn		X	X	X	X	X	X	--	
Diptera									
Trichoceridae: *Trichocera pallens* Alex.	X						X	X	X
Psychodidae: *Psychodes* sp.	X	X	X			X	X	X	X
Culicidae: *Culiseta incidens* (Thoms.)	X	X	X	X	X	X	X		
Fungivoridae: *Exechia* sp.	X	X					X	X	X
Fungivora sp. 1	X	X				X	X	X	
Diadocidea borealis Meig.	X	X							
D. ferruginosa Meig.	X	X							
Mycomya sp.	X	X							
Monoclona sp.	X								
Phoridae: *Triphleba* sp.	X						X	X	X
Anthomyiidae: *Pegomya* sp.	X	X					X		
Lepidoptera									
Gracilariidae: *Cameraria gaultheriella* (Wlshm.) larvae	X	X					X	X	X
Hymenoptera									
Belytidae: *Xenotoma* sp.	X	X	X		X	X	X		
Total	20	18	9	6	7	10	18	15	8

mm Hg. The light intensity is also very low, averaging less than 25% of full sunlight. Precipitation is high, averaging 2-3 in. per week.

Hiemine Sector: This subseason or sector of the winter season may be characterized as the portal for entrance into the dormant phase of winter. It generally starts about the first week in November, the extremes being October 26, 1935 and November 23, 1936. The average duration is approximately one month, terminating in December. The hiemine sector of winter has very little botanical evidence of a positive nature to distinguish it. Leaves have disappeared from all deciduous shrubs and trees leaving only the evergreen foliage of salal, Oregon grape,

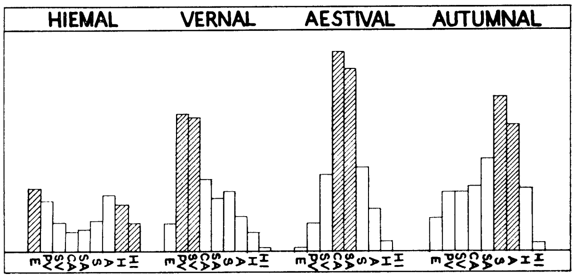

FIG. 13. Totals of common species of insects characteristic of each aspect (shaded columns) and their seasonal distribution throughout the remainder of the year (unshaded columns). Compiled from tables of seasonal occurrence of insects by D. McKey-Fender.

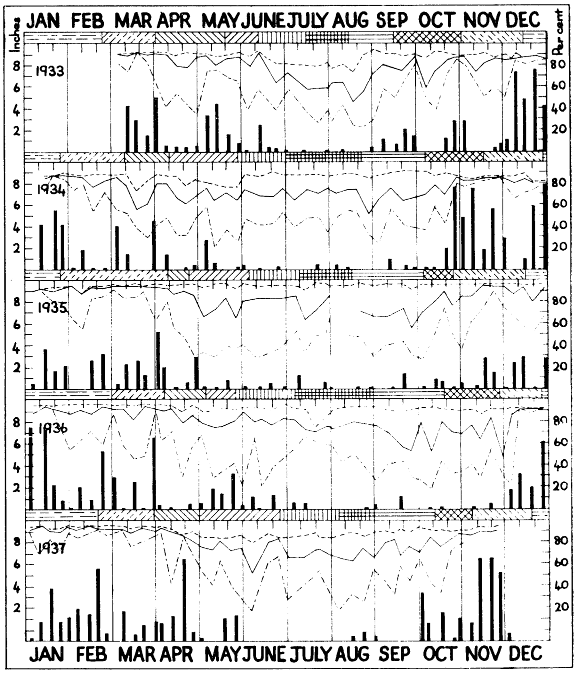

FIG. 14. Weekly maximum, mean and minimum relative humidity and total weekly precipitation. Broken (short dash) line—maximum humidity; dot-dash line—minimum humidity; solid line—mean humidity. (This figure was obtained by averaging readings arbitrarily selected at 12-hour intervals for the week preceding each collecting date). Scale—1 unit equals 2% of relative humidity. Columns show weekly precipitation as measured by the rain gauge located beneath an opening in the canopy at Instrument Location A. Scale—5 units equal 1 inch of precipitation. Seasonal limits indicated as in Figure 10.

sword fern, deer fern and conifers, bringing out the basic evergreen character of the vegetation of this community. Mosses and lichens brighten up and some mosses produce capsules at this time.

A sharp drop in variety of insects is associated with the end of the autumnine and beginning of the hiemine sectors. The hiemal aspect begins when all hymenoptera, most diptera and most coleoptera disappear, leaving only a few families of insects which are active consistently. Fungivoridae, Psychodidae and Trichoceridae are particularly characteristic. Aleyrodidae occur quite generally but are not active and decline in numbers as the sector wears on. Collembola *(Tomocerus flavescens* Tullberg and *Ptenothrix* spp.) characterize the hiemine sector by appearing in considerable numbers on the shrubs and hemlocks, even having been collected in the top of the large hemlock designated Location G (Figs. 4 & 5). Except for the cerambycid beetle *Plectrura spinicauda* Mann. and two weevils *(Nemocestes incomptus* Horn and *Sciopithes obscurus* Horn) the insects are all very small. Work of the salal leaf miner larvae *(Cameraria gaultheriella* (Wlshm.)) is noticeable at this time (Table 2). Adult spiders are present but are only active on warm days. They remain under leaves in a semidormant condition most of the time. Slugs still occur occasionally on the forest floor. Amphibia are sluggish and not frequently encountered.

This is the only sector in which no new species of insects are added to the population, which is low in number of individuals and variety of species, the graphed population line (Fig. 10) descending toward its winter low. Thirteen species of insects are recognized as common in this sector, all of which remain through to its end (Table 2). *Hylemya alcathoe* Walk., *Vespula vulgaris* L., several beetles and several of the Ichneumonidae characteristic of the autumnal aspect terminated their activity early in the hiemal aspect in some years, but the autumnal fauna in general disappeared at the beginning of the hiemal aspect.

Flocks of red-breasted nuthatches *(Sitta canadensis* L.), Sitka red crossbills *(Loxia curvirostra sitkensis* L.), Pacific varied thrushes *(Ixoreus naevus* (Gmelin)), chickadees (*Parus rufescens* (Townsend) and *P. atricapillus occidentalis* Baird), kinglets *(Regulus satrapa olivaceus* Baird and *R. calendula grinnelli* (Palmer)) and California creepers *(Certhia familiaris occidentalis* (Ridgway)) are common at this time. Western pileated woodpeckers *(Dryocopus pileatus picinus* Bangs), Oregon gray jays (*Perisoreus canadensis obscurus* Ridgway) and juncos *(Junco hyemalis oregonus* Townsend and *Junco hyemalis shufeldtii* Coale) which are present during the hiemine sector, migrate to lower levels toward its close, appearing this high on the mountain only in warm periods of the succeeding (hibernine) sector. The population of permanent resident birds becomes noticeably decreased at the close of this sector.

From a meteorological standpoint the opening of the hiemal aspect seems to correlate well with the descent of weekly minimum temperatures to the vicinity of 40° F. Sometimes this drop immediately precedes the opening of the aspect. Within the hiemine sector the weekly minimum may temporarily rise above this level. On the whole, minimum temperatures remain well below 40° F during the hiemine sector. The maximum temperature is generally quite consistent, the seasonal means of maximum temperature ranging near 50° F, whereas the mean minimum shows much greater variation. The maximum temperatures are so stable that one might say a lid or ceiling has been placed on the temperature allowing very little fluctuation at the upper limits but placing less restriction on the lower levels. The mean temperatures for the sector varied very little from year to year averaging 43.5° F. The hiemine sector appears to terminate when the temperature range becomes practically restricted to a zone between 50° and 30° F (Fig. 15). Precipitation varies widely, from a weekly average of 0.77 in. in 1933 to a maximum weekly average of over 5.41 in. in 1937 (Fig. 14). The humidity in general is high, the 5-year average of the seasonal mean being 86% (Figs. 11a, 14). Wind direction is from all points of the compass, but predominantly from the southwest with north and northeast winds occurring frequently. The wind velocity is in general moderate, although southwesterly gales lasting a few days may occur. The weather is predominantly cloudy during this season, interspersed with clear periods of a few days' extent. Vapor pressure deficit descends during this sector to the low level of the winter and in most years remains relatively stable throughout the season (Table 3).

Hibernine Sector: This is the comparatively severe portion of the winter and is designated as the period of deepest dormancy from a biotic standpoint. Heretofore authors have used the terms hibernal and hiemal more or less synonymously, but, in view of the need for a refinement of aspectional terminology disclosed by this author's studies, it seems best to allocate the term hiemine to the sector of the winter season in which animals are going into hibernation and to use hibernine for the sub-season or sector in which hibernation is at its maximum. Because of the moderate winters in this region a small group of invertebrate species may be active even in the hibernine sector of the hiemal aspect. In winters of extreme cold and during the coldest weather of mild winters, all invertebrates above ground are in a dormant state.

Usually this sector begins in the middle of December and ends in mid-February. It is a rather long subseason, averaging seven weeks. The shortest hibernine sector was in 1934 when it lasted only four weeks.

Higher plants are all dormant and there is no particular evidence of any activity in the lower types.

The hibernine sector is primarily the dormant season of the invertebrate population above ground at this location. With the beginning of this sector, 8 of the hiemine species drop out altogether (Table 2), while the only invertebrate typically added to the population during this period is a pentatomid bug *(Elasmothethus cruciatus* Say) which was obtained from hemlock boughs even when they were loaded with snow. In common with the other characteristic hibernine species, this bug extends into the emergine sector.

There are no animals entirely confined to this sector. Those discussed as being especially characteristic of the hiemine sector are also characteristic of the hibernine sector. The difference lies in the fact that in the hibernine sector these insects are barely main-

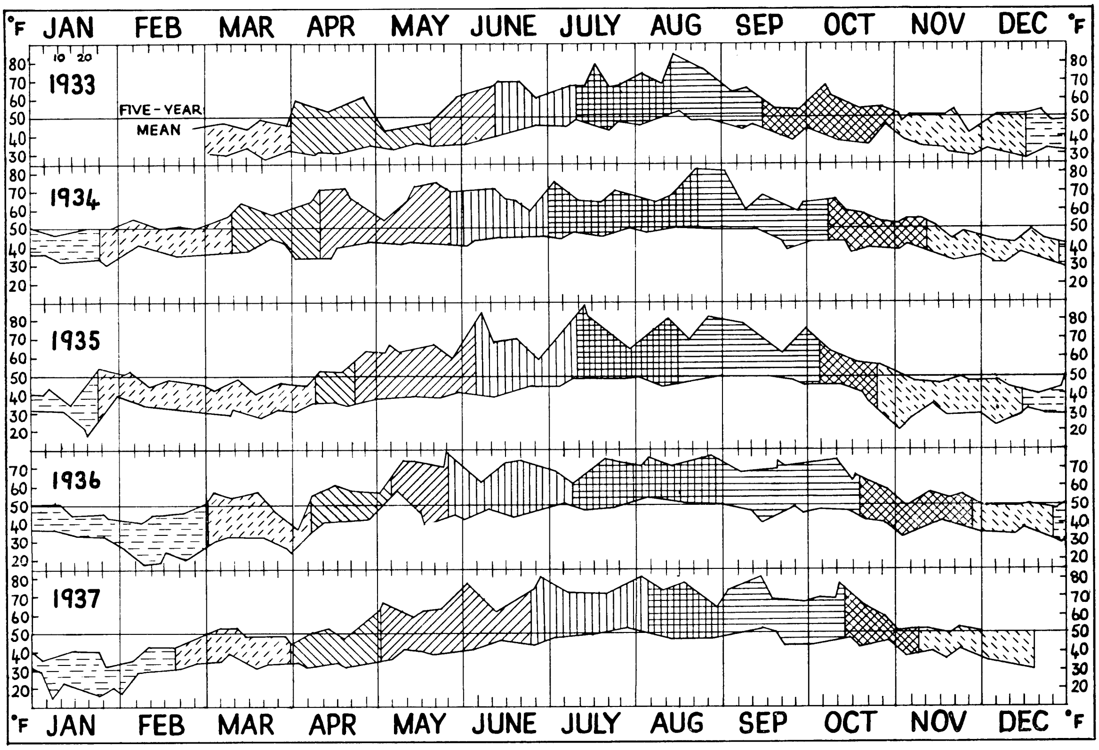

FIG. 15. Weekly maximum and minimum temperatures, from Weather Bureau maximum and minimum thermometers in the shrub level. Upper line—maximum; lower line—minimum. Shading between the two lines indicates the seasonal limits as shown by the key accompanying Figure 10. A five-year mean, which is approximately the mean annual temperature for each of the five years, is indicated by a light solid line at the 50° F level.

taining an existence and activity is at a low ebb. The Fungivoridae, Trichoceridae, Aleyrodidae and Psychodidae so characteristic of the hiemine sector, are usually found in apparent hibernation during the hibernine sector quietly hanging beneath salal leaves and only flying rather sluggishly on rare occasions when the temperature permits limited activity. During this sector several types of invertebrates are absent which are present in every other season; these include collembola and mollusca. Only eight species of insects are at all common during this sector, the active population above ground on any one collecting day consisting of only two or three families of insects. Amphibia, chipmunks and bears are known to hibernate during this period. Tracks of rabbits, the snow-shoe hare (*Lepus americanus washingtonii* Baird) and the brush rabbit (*Silvilagus bachmani ubericolor* (Miller)), bobcat (*Lynx rufus fasciatus* Raf.), cougar (*Felis concolor oregonensis* Raf.), civet cat (*Spilogale phenax latifrons* Merriam) and white-footed deer mice (*Peromyscus maniculatus rubidus* Osgood) and other mice were noted during snowy periods. Tracks of the Columbian black-tailed deer (*Odocoileus hemionus columbianus* (Rich.)) were seen, but not so frequently as later.

Environmentally, this sector of winter is characterized by cold, rainy weather and occasional heavy snows. Predominantly cloudy weather may be interspersed with brief spells of clear, frosty days (Fig. 12d). The sector seems to be initiated by a drop in temperature immediately preceding or following the opening date. The range of temperatures may be very wide, a variation of more than 25° within the week being not uncommon. The lowest temperatures of the year are recorded during this season, maxima and minima both being low. Minimum temperatures may drop considerably below freezing, but usually hover around 30° F. The maximum temperatures generally range between 40 and 50° F. In the years under consideration, the close of the season was marked by a definite rise in temperatures, both maximum and minimum. At either end of the sector, the trend of temperature appears to be more significant than the actual temperatures recorded (Fig. 15). The average precipitation is higher than during the hiemine sector and does not show so much variation. The seasonal average varies from 1.35 to 4.00 in./wk, making it the season of heaviest precipitation, much of which in most years is in the form of snow. Humidity is high, averaging 92%. Low humidity may occur during clear weather (Fig. 12d). Wind velocity shows extreme variation from very light breezes to gales. The predominating wind comes from the southwest. East winds are more frequent than in the hiemine sector, and are associated with low temperatures. The low light intensity averages much the same as in

TABLE 3.* Seasonal averages of meteorological data for the hiemal aspect.
H—hiemine sector; Hi—hibernine sector; E—emerginine sector; T—entire hiemal aspect.

	First Winter	Second Winter				Third Winter				Fourth Winter				Fifth Winter			Sixth Winter			Averages		
	E '33	H'33	Hi'33 -'34	E'34	T	H'34	Hi'34 -'35	E'35	T	H'35	Hi'35 -'36	E'36	T	H'36	Hi'36 -'37	E'37	T	H'37	H	H	E	T
Temperature																						
Maximum	46.6	51.8	50.0	51.3	50.9	47.4	41.0	48.0	46.0	50.0	45.4	49.4	47.7	51.0	39.1	47.8	44.7	51.4	50.3	43.6	48.6	47.3
Minimum	31.6	34.7	33.6	37.1	35.1	36.0	28.5	31.0	32.0	29.2	32.6	29.2	30.9	34.2	21.8	33.7	28.0	36.4	34.2	27.6	32.5	31.5
Mean	39.1	43.1	42.3	44.2	43.0	42.7	34.7	39.5	39.5	43.9	36.9	39.2	39.4	42.9	30.5	40.5	36.6	43.9	43.5	35.8	40.5	39.5
Range	15.0	16.8	16.3	14.1	15.1	11.4	12.0	17.0	12.8	20.8	17.5	20.0	19.1	16.7	17.1	14.5	15.6	15.4	16.7	15.8	16.1	15.3
Relative Humidity																						
Maximum	....	92.2	89.4	90.0	90.7	87.5	90.5	94.9	91.8	96.0	95.2	95.6	95.6	97.7	94.8	95.5	94.5	95.0	92.6	92.4	94.0	93.1
Minimum	....	71.4	85.2	72.0	73.2	78.0	86.5	78.9	80.1	66.0	76.5	66.0	70.0	60.8	85.5	85.0	79.4	90.8	73.3	83.4	75.4	75.6
Mean	....	87.7	89.4	82.0	87.7	85.2	85.5	90.9	88.7	88.7	91.8	90.1	90.2	80.6	92.3	93.0	89.7	94.3	86.6	89.7	90.5	86.5
Range	....	20.5	4.2	18.0	14.6	9.0	4.0	16.1	13.7	30.5	17.5	29.6	25.1	32.2	9.2	10.6	15.0	4.1	19.1	8.7	18.5	17.8
Precipitation	2.87	1.60	4.77	1.63	2.61	2.70	1.35	2.05	2.56	2.16	2.92	2.03	2.18	1.79	2.58	2.28	1.93	5.41	2.73	2.90	2.17	2.32
Light	11.8	30.0	22.5	25.0	25.0	21.0	30.0	28.9	27.4	10.0	21.8	26.6	19.5	21.2	25.7	28.0	21.5	20.0	20.4	25.0	24.0	24.2
Evaporation	....	1.27	....	1.04	....	0.75	....	1.48	....	....	....	2.80	....	2.89	....	....	....	0.48	1.34	....	....	....
Vapor Pressure Deficit																						
Maximum	....	.099	.046	.072	.063	.060	.047	.053	.059	.074	.048	.097	.068	.077	.022	.049	.040	.....	.077	.040	.067	.057
Mean	....	.036	.026	.035	.032	.041	.023	.021	.026	.029	.019	.024	.025	.058	.013	.018	.025	.039	.040	.020	.024	.029

*Sources of meteorological data are as follows: *Temperature* (F°), from Weather Bureau maximum and minimum thermometers: Figures given are means of maximum, minimum, median and range as read each week. *Relative humidity* (%), from hygrothermograph: Figures are means of weekly readings of maximum, minimum and range, mean from daily median. *Precipitation* (inches), from rain gauge under opening in canopy: Figures given are means of weekly totals. *Light*: Figures given are means of % of full sunlight on the day observations were made. *Evaporation*, from Livingston cup atmometer: Figures given are means of cubic centimeters water evaporated daily. *Vapor pressure deficit* (inches Hg.), from hygrothermograph records: Figures given are means of maximum, minimum and median weekly vapor pressure deficit readings. *Wind velocity*, from cup anemometer readings: Figures given are means of miles recorded per day. All readings were at the shrub level.

the hiemine sector, while vapor pressure deficit, though low, varies more widely. This variation of the vapor pressure deficit is apparently correlated with the periods of clear, cold weather characteristic of this season (Table 3).

Emerginine Sector: At this location and elevation there is a definite stirring of activity and emergence from dormancy on the part of the animal life before blossoms appear on any plants. The term *vernal* was introduced by botanists to indicate the flowering stage of spring flora. *Prevernal* was added to separate the blooming period of the very earliest plants from the more typical spring flowers. Thus the terms vernal and prevernal have come to have a definite association with blossoming of certain plants. It is proposed therefore that the term *emerginine* be adopted where it is necessary to designate a sub-season or sector of winter in which hibernation is definitely in the process of breaking up, the hiemine fauna have renewed their activities and some animals have become active in anticipation of their role as typical prevernine species. This proposal would be in recognition of the fact that flowers are not the first indicators of the approach of spring.

This sector is typically 5 weeks in length, although in 1935 it lasted 10 weeks, establishing the earliest opening date, January 24, and the latest closing date, April 9 (Table 1, Fig. 16). The period covered by the emerginine sector is extremely variable, as are the meteorological and faunal characteristics of this season (Fig. 10).

An emerginine sector is indicated vegetationally by a greener tinge in the bark of deciduous trees, by swelling buds and sprouting herbs and shrubs. No flowers are yet in evidence.

The initiation of the emerginine sector is not definitely characterized by the activity of any one species of invertebrate. Several species were used in attempting to fix approximate opening dates but all failed in one or more years because of insufficient specimens to form a complete record. This sector proved a difficult one in which to obtain satisfactory data. The weather at this time of the year is so variable that organisms could be active between collecting dates and yet unavailable on the date of collection because of low temperatures, high humidity, snow or rain. This, coupled with the paucity of insect life even under the best of conditions, caused the records to be incomplete. The rain barrel mosquito *(Culiseta incidens* (Thoms.)) was the best indicator except in 1936, when it was not noted until the close of the aspect. Tendipedidae and a lygaeid bug *(Ischnorrhynchus resedae* Pans.) initiated the sector very consistently except in 1935. In that year they occurred before the beginning of the emerginine sector which was definitely established by the environmental data and general collection records. An anthomyid fly *(Pegomya* sp.) was collected at the beginning of the sector in 1936 and 1937. To obtain an opening date for the emerginine sector, it was necessary therefore to strike a mean point between the first occurrence of several of these forms, taking the environmental records also into account. Although this sub-season is a definite unit, more careful collecting is needed to establish dependable faunal indicators for its initiation. Sporadic evidences of activity of moles *(Scapanus o. ora-*

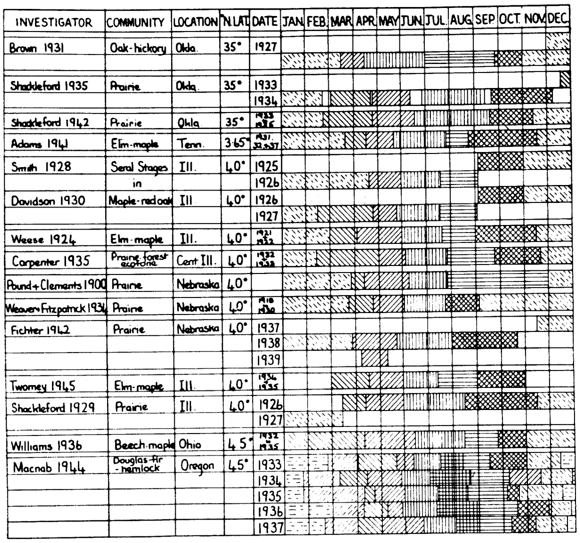

FIG. 16. Seasonal limits. Aspectional studies of various authors in the United States brought together, making possible a comparison of the period covered by each season in each year for the several communities and geographic locations involved, as well as a comparison of the terminology used in each case. Geographic location, biotic community, latitude and dates of observation are specified for each. Sectors of this author are keyed as in Figure 10. In the case of authors having an undivided prevernal-vernal aspect only one of the vernal sector symbols is shown; the symbol for the hiemal sector of this author (diagonal broken lines) is used for the winter aspect of other authors, whether termed hiemal or hibernal; the symbol for the early sector of the aestival aspect (vertical lines) is used for the aestival aspect of others.

rius True), shrews *(Sorex t. trowbridgii* Baird), mice and an occasional chipmunk *(Eutamius t. townsendii* Bachman) were encountered throughout this sector. Pacific varied thrushes were present singly or in pairs rather than in flocks. Gray and Stellar jays, pileated woodpeckers and juncos returned to the area.

The Trichoceridae which are found in the hibernine sector are characteristic and abundant here. Several species of Fungivoridae are present. A group of hemiptera are especially characteristic and frequently collected, although never abundant. These animals hibernate as adults in cracks of bark and other sheltered places during the hiemine and hibernine sectors but are collected very infrequently in these sectors. Not more than twelve and usually only five or six different families of insects were active in the shrub level on any one collecting day during the emerginine sector. The total number of individuals active in this sector is also low. A few insects characteristic of the vernal aspect begin their activity within the emerginine sector. Among these are occasional muscoid flies, Geometridae, a few Staphylinidae and occasional Ichneumonidae.

The close of the emerginine sector is marked by the absence of the hemiptera as well as Trichoceridae and by the appearance of *Calliphora vomitoria* L., Lycidae, a number of Staphylinidae and the geometrid moth *Mesoleuca gratulata* Walk. (Table 2.)

Generally the emerginine sector is cloudy and rainy with snow falling occasionally at this elevation. The sector starts environmentally when the maximum temperatures first rise above the annual mean of 50° F in the spring regardless of whether they drop below this point later in the season. The minimum temperatures do not seem to be significant, as they may drop well below freezing during the sector without permanently affecting the insect population. The close of the season is marked by a rise in maximum temperatures which often reach at least 60° F. The weekly minimum temperatures also rise permanently above 30 F around which they previously oscillated, although their rise tends to lag behind the rise in maximum temperatures (Fig. 15). The weekly average precipitation for the sector in all years dropped below 2.5 in. (Table 3). Rains are not as heavy as in the hibernine sector. Winds are light to moderate with southwest winds predominating. Northeast winds occur frequently. Humidity is high, having averaged 90.5% during this sector for the duration of the records. There is an increased range in relative humidity during this sector. Average light intensity is low, being practically the same in the emerginine as in the hibernine sector. There is a pronounced though slight rise in vapor pressure deficit at the beginning of this sector, which is maintained with little fluctuation throughout the emerginine sector. A still more pronounced rise in vapor pressure deficit at the close of the emerginine initiates the vernal aspect.

VERNAL ASPECT

In line with the plant ecologists' policy of confining the term prevernal to the dates of earliest spring flowers and vernal to the later more typical spring flowers, the flowering plants of this community show quite clearly two distinct vernal sectors. Division of the vernal aspect into two subseasons or sectors is also shown by an influx of new invertebrate species between the two subdivisions, materially altering the composition of the population of the later sector. The meteorological factors also show a break in the environmental transition, from wet to dry, and cold to warm weather, which accentuates the division into early and late sectors. The faunal records as a whole bind the two vernal sectors rather closely, however, so that the picture obtained is that of a single season rather than two seasons. It seems best, therefore, to designate the prevernal and vernal aspects of other authors as early and late *subseasons* rather than seasons. This being the case, the terms *prevernal* and *vernal* are not as desirable as *prevernine* and *vernine* sectors which are two parts of a unit called the spring or *vernal aspect*.

The vernal aspect is characterized as the season when unfolding buds add a fresh tinge of green to plants of the shrub layer and when the growth of herbs covers the forest floor with a carpet of green leaves and flowers.

The vernal aspect is generally quite extensive, averaging about eight weeks in extent. The opening date is generally early in April (Table 1). The earliest termination was May 25, 1936 and the latest June 24, 1937. Both the early and late sectors exhibited considerable variability in duration from a minimum of two weeks for both subseasons in 1935 to around 7 weeks for the prevernine sector in 1933 and 7 weeks for the vernine sector in 1934 (Fig. 16).

The occurrence of numerous pollenophagous insects is correlated with the presence of blossoming herbs. Coleoptera characterize the vernal aspect by their abundance, at least 40 species having been collected more than once in this season during the 5-yr period, 34.3% of common vernal insects belonging to this order. Diptera also reach a peak of abundance and variety during this period, 53 species having been collected, which indicates the dipterous nature of this community. Only 19 species occurred commonly enough to be included on the charts of common insects (36.2% of the total). Craneflies of the family Tipulidae replace the smaller Trichoceridae characteristic of the winter aspect. Tendipedidae, Simuliidae and Psychodidae are abundant. Muscoid flies are very common while Syrphidae and Bibionidae are only slightly less abundant. Geometridae emerge in numbers. Hymenoptera, which represent 14.5% of the vernal species, show a greater variety than at any other season except the autumnine (late autumn), when they are also abundant, but then chiefly represented by the smaller parasitic species (Table 4). Of the 55 species of insects occurring commonly in the vernal aspect, most (80%) begin their activities during the aspect, the remaining species having been part of the hiemal fauna. Nearly half (43.6%) of the species are restricted to the vernal aspect, 16.3% being restricted to the prevernine sector and only 9% to the vernine. Over half of the vernal species (54.5%) occur in both sectors of the aspect, 23.4% being present in the prevernine sector but not in the vernine and 21.8% in the vernine but not the prevernine sector. In general, the vernal aspect population drops suddenly at the beginning of the cisaestine sector and then dwindles away gradually through the remainder of the year. The greater height of the serotinine column over the aestine (Fig. 13, vernal) is due to a resurgence of insects responding positively to increased moisture.

The vernal aspect is a season of transition from wet to dry and cold to warm environment (Table 5). The factors of moisture and temperature are, in general, intermediate between winter and summer but are progressing with fluctuations toward the conditions typical of summer. The minimum temperature averages well above the freezing point, although occasional frosts do occur. The maximum for the vernal aspect averages around 60° F and the seasonal mean 40° F. Wind direction for the vernal aspect is characterized

TABLE 4. Insects characteristic of the vernal aspect (spring). Explanation as in Table 2.

Sector	E	PV	SV	CA	SA	S	A	H	Hi
Collembola									
Entomobryidae: *Tomocerus flavescens* Tullb.	X	X	X	X	--	X	X	X	
Sminthuridae: *Ptenothrix* sp.	X	X	X	X	--	X	X	X	
Homoptera									
Aleyrodidae: gen. et sp. indet.	X	X	X			X	X	X	--
Cicadellidae: *Errhomus oregonensis* Baker		X	X						
Coleoptera									
Carabidae: *Scaphinotus angusticollis nigripennis* Roesch.			X	X		X	X		
Staphylinidae: *Anthobium subcostatum* Mackl.		X					X	X	
A. pictum Fauvel		X					X	X	
Pelecomalium testaceum Mann.		X							
Lycidae: *Dictyopterus simplicipes* (Mann.)		X							
Cantharidae: *Podabrus piniphilus* (Esch.)			X	X					
Elateridae: *Ctenicera mendax* Lec.			X						
Byrrhidae: *Listemus acuminatus* (Mann.)		X							
Nitidulidae: *Epurea* sp.		X	X						
Melandryidae: *Prothalpia holmbergi* (Mann.)		X	X	X					
Cerambycidae: *Evodinus vancouveri* (Csy.)		X	X						
Chrysomelidae: *Timarcha intricata* Hald. larvae		X	X						
Curculionidae: *Nemocestes incomptus* Horn		X	X	X	X	X	X	X	
Stremneus tuberosus Boh.		X	X	X	X	X			
Scolytidae: *Pseudohylesinus grandis* Sw.		X	X	X	X				
P. sericeus (Mann.)		X	X	X	X				
Gnathotrichus sulcatus (Lec.)			X	X	X	X			
Dendroctonus pseudotsugae Hopk.		X	X						
Diptera									
Tipulidae: *Limonia infuscata* (Doane)		X	X						
Simuliidae: *Prosimulium* sp.		X	X	X					
Prosimulium fulvum Coq.			X	X					
Psychodidae: *Psychodes* sp.	X	X	X			X	X	X	X
Culicidae: *Culiseta incidens* (Thoms.)	X	X	X	X	X	X	X		
Fungivoridae: *Diadocidea borealis* Meig.	X	X							
D. ferruginosa Meig.	X	X							
Fungivora sp. 1	X	X				X	X	X	
Fungivora sp. 2		X							
Boletina sp.		X	X						
Bibionidae: *Bibio* sp		X	X						
Empidae: *Iteaphila* sp.			X						
Rhamphomyia sp.			X						
Clythiidae: gen. et sp. indet.			X						
Syrphidae: *Syrphus opinator* O. S.		X	X	X	X	X	X		
Anthomyidae: *Pegomya* sp.	X	X							
Hylemya alcathoe Walk.		X	X	X	X	X	X		
Hydrotea militaris Mg.			X	X	X	X			
Calliphoridae: *Phormia terraenovat* Desv.			X	X	X	X			
Calliphora vomitoria L.		X	X	X	X	X			
Lepidoptera									
Geometridae: *Melanolophia imperfectaria* Walk.		X	X						
M. imitata Walk.		X	X						
Mesoleuca gratulata Walk.		X							
Trichodesia californiata Pack.			X						

TABLE 4 (Cont.)

Sector	E	PV	SV	CA	SA	S	A	H	Hi
Hymenoptera									
Tenthredinidae: *Tenthredo* sp.		X							
Pristola macnabi Ross		X							
Ichneumonidae: *Ephialtes ellopiae* (Harr.)			X	X	X				
Belytidae: *Xenotoma* sp.	X	X	X		X	X	X		
Vespidae: *Vespula vulgaris* L.		X	X	X	X	X			
V. rufa var. *consobrina* (Saus.)		X	X	X	X	X			
Bombidae: *Bombus sitkatensis* Nyl.		X	X	X	X	X			
B. flavifrons dimidiatus		X	X	X	X	X			
Total	9	43	43	24	18	20	3	8	1

by more frequent north and east winds, although the predominating wind direction is still from the southwest. Wind velocity is moderate, though averaging higher than that in any other season. Light intensity averages 35% of full sunlight, a marked increase over that of any of the winter seasons. Average weekly precipitation is below that of the emerginine sector. An increase of evaporation rates in the vernal aspect is to some degree correlated with decreasing humidity. Vapor pressure deficits are increasingly high, average weekly maxima in general being greater than .200 mm Hg.

Prevernine Sector: The prevernine (early) sector is characterized by the blossoms of skunk cabbages *(Lysichiton camtschatensis)*, violets *(Viola sempervirens)*, Oxalis, huckleberries and trilliums.

The aspect opens with evidences of increased vertebrate activity. Tracks and sign of deer were noted more frequently. The rufous hummingbird *(Selasphorus rufus* (Gmelin)) was the first spring migrant bird noticed. Bears *(Ursus americanus altifrontalis* (Elliot)) become active at the same time that the skunk cabbages blossom. Chipmunks at this elevation are regularly first heard about this time, following some three months of almost complete dormancy. Moles and Microtus become consistently active near the surface of the soil. Higher temperatures permit the amphibia to become active; the discoglossid toad *(Ascaphus truei* Stejneger) and salamanders *(Ensatina eschscholtzii* Gray and *Plethodon vehiculus* Cooper) appearing frequently on the forest floor.

Molluscs, represented by humped slugs *(Prophysaon* spp.) and the Columbia snail *(Polygyra columbiana pilosa* (Henderson)), are first consistently recorded on the humus surface during this sector. A white geometrid moth *(Mesoleuca gratulata* Walk.) is particularly conspicuous in this sector. Psychodidae here attain a peak in abundance and then suddenly disappear from the records during the late sector. Tenthredinidae are present during the prevernine sector, and their larvae become noticeable in the late sector. Aleyrodidae imagoes disappear during the prevernine sector, while Pegomya closes its period of activity at this time to reappear in another brood in the late autumn.

The vernal aspect begins when the average maximum weekly temperatures jump from the vicinity of 50° F, or below, to the vicinity of 60° F, or above (Fig. 15). A leveling off or an actual slump in temperature occurs subsequent to the first ascent, and when the temperature rises the second time a weather change brings in the vernine sector. Precipitation averages 1.35 in./wk, considerably less than that of the emerginine sector of winter. Wind velocity during the prevernine sector is the highest of the year, but varying within the season as well as from year to year.

Vernine Sector: The vernine sector or late sector of the vernal aspect brings false Solomon's-Seal, Oregon grape, salmonberry *(Rubus spectabilis)*, vanilla-leaf, twayblade and devil's club *(Oplopanax horrida)* into bloom.

This sector is usually marked by the appearance of summer resident birds. Their arrival may possibly be characteristic of the entire vernal season although the exact arrival dates were hard to determine. In some years the first records of some species were in the prevernine sector. The more important summer resident birds of this locality are the russet-backed Swainson thrush *(Hylochichla ustulata* (Nuttall)), the western wood pewee *(Myiochanes richardsoni* (Swainson)), Pacific western flycatcher *(Empidonax difficilis* Baird), the hermit warbler *(Dendroica occidentalis* (Townsend)) and the Pacific band-tailed pigeon *(Columba fasciata monilis* Vigors). Birds are nesting and mammals are rearing families during this sector.

The beginning of this late sector of the vernal aspect is quite clearly indicated by the first appearance of the large, snail-eating carabid *Scaphinotus angusticollis nigripennis* Roesch. A larger white geometrid *(Trichodesia californiata* Pack.) takes the place of Mesoleuca, blue-bottle flies become very conspicuous and Empidae appear consistently and in numbers (Table 4). The myriapod *(Harpaphe haydeniana* (Wood)) reaches a peak of abundance on the humus surface in this period.

The vernine maximum weekly temperature averages at least 60° F. It may briefly be considerably higher, but tends to range near that point. Precipitation averages 1.03 in./wk. Wind velocity is less than during the prevernine sector and predominantly southwest. Light intensity is higher in the vernine than in the prevernine sector, while vapor pressure deficits are also usually higher.

AESTIVAL ASPECT

The aestival aspect is the last one which can be characterized in this coniferous region by the blossoming of plants, and is also distinguished by the fruiting of a number of herbs and shrubs. The aestival aspect is 2-2.5 months in length. The dates at which the season begins and ends are somewhat variable, the extremes for the beginning date being May 25, 1936 and June 24, 1937, with August 13, 1933 the earliest, and August 30, 1937 the latest, dates marking the termination.

TABLE 5.* Meteorological data for the vernal aspect—seasonal averages. PV—prevernine sector; SV—vernine sector; T—entire aspect.

	1933			1934			1935			1936			1937			Average		
	PV	SV	T	PV	SV	T	PV	SV	T	PV	SV	T	PV	SV	T	PV	SV	T
Temperature																		
Maximum	51.3	61.5	53.5	61.4	68.5	65.5	47.6	64.1	55.9	58.3	73.3	64.7	48.2	65.0	58.9	53.3	66.5	59.1
Minimum	33.1	36.0	33.7	39.4	40.9	40.2	32.0	38.1	35.0	39.2	40.0	38.2	33.0	39.2	37.0	35.4	38.8	36.8
Mean	42.2	48.3	43.5	51.4	54.7	53.5	40.6	51.1	45.9	48.7	56.8	52.2	41.0	52.1	48.0	44.9	52.7	48.5
Range	18.1	25.5	19.7	22.0	27.7	25.3	15.2	26.0	20.2	19.0	33.0	25.0	15.0	25.0	21.8	17.4	27.4	22.4
Relative Humidity																		
Maximum	93.4	93.7	93.6	86.8	84.5	85.5	96.0	95.6	95.7	90.0	91.0	90.4	92.4	85.4	88.3	90.8	89.4	90.2
Minimum	67.1	61.7	65.9	45.0	41.0	42.8	63.5	37.1	45.8	57.0	36.0	48.0	74.4	45.4	58.3	55.3	43.7	49.8
Mean	87.4	89.5	88.1	73.3	70.8	72.0	90.3	77.6	81.8	80.5	77.4	79.3	89.6	85.2	87.1	83.2	76.7	79.8
Range	25.6	32.0	26.0	28.0	43.5	42.2	32.6	58.5	49.8	33.0	55.0	42.4	27.4	42.5	33.9	34.3	45.6	40.1
Precipitation	2.07	0.80	1.71	1.71	0.70	1.06	0.35	0.69	0.61	0.24	2.15	1.06	2.71	0 74	1.56	1.35	1.03	1.20
Light	34.2	33.3	34.0	32.0	30.8	32.0	....	28.0	....	32.5	53.3	41.4	28.0	32.8	31.5	31.6	35.6	34.6
Evaporation	....	....	....	4.50	5.29	4.90	5.14	5.78	5.35	2.12	5.16	3.43	....	5.98	....	....	....	....
Vapor Pressure Deficit																		
Maximum	.121	.188	.141	.266	.345	.311	.133	.331	.271	.205	.336	.270	.081	.286	.200	.161	.297	.238
Mean	.032	.026	.029	.107	.109	.108	.025	.046	.041	.065	.086	.074	.025	.093	.064	.048	.060	.059

*See notes for Table 3.

From a faunal standpoint, the aestival and vernal aspects are similar, with a large variety of species, many of which are common to both. The aestival aspect has, however, its own distinctive fauna. Scorpion flies (Mecoptera) were recorded only from this aspect, Cercopidae *(Philaenus leucophthalmus)* also characterize the period, while aphids attain their peak of abundance and variety. Cicadas also seem to be characteristic here, as they were heard trilling in the tree tops, though none was collected. Coleoptera are less abundant than in the vernal aspect, constituting only 29.4% of the common species. The aestival insects are preponderantly diptera (44.4%). Several species of diptera common to the vernal aspect were forced to drop out or become insignificant in the aestival aspect, while 20 genera, with over 27 species, were added, producing a decided increase in the variety of diptera represented in the aestival as compared with the vernal aspect. The increase was especially noticeable in the predaceous and blood-sucking groups, 12 out of the 35 common species of diptera in this aspect being haemophagous, contrasting with the pollenophagous species characteristic of the vernal aspect. The Anthomydae, Calliphoridae, Muscidae and Tipulidae increased in diversity. Geometrid moths were represented by two genera peculiar to the aestival season. The variety of organisms active in the upper layers during the season was high. As many as 35 important families of insects were taken on one collecting date, with an average of 15-20 for each collection period during the season (Fig. 10). 78 species of insects were common and conspicuous during the aestival aspect. Half of these species were restricted to the aestival aspect, occurrence of the remaining 50% being distributed in both directions from the aestival peak (Fig. 16, aestival), 30.7% of aestival species occurring in the vernal aspect and 32% in the autumnal aspect. Over half (56.4%) of the aestival species occurred in both sectors, 24.4% occurring only in the cisaestine sector and only 18.1% being restricted to the aestine sector. The cisaestine sector has the highest total of characteristic insects for the year, 64 species. A few species (14.1%) first appear in one of the aestival sectors and continue into the autumnal aspect or beyond. These are mostly diptera. Few of the aestival species occur in the hiemine and none occurs in the hibernine sector. The large red mites of the humus surface (Trombidae) are the only characteristic invertebrates other than insects. Amphibia apparently aestivate during this aspect as they were not observed moving about on the surface.

The aestival aspect as a whole is a season of high temperatures and vapor pressure deficits, with a correspondingly high population curve. Meteorologically, this season gives a false impression of stability. The range of temperatures is wider at this season than at any other, even though temperatures fluctuate at a high level and show comparatively little variation in either maximum or minimum levels. Precipitation during the aestival aspect reaches the lowest point for the year, averaging 0.2 in./wk for the 5 years. The humidity is much higher than the low precipitation would seem to warrant, the mean maximum averaging 98% for the 5 yrs and the mean minimum 46%. Wind velocity is low during this aspect with northwest and southwest, light to moderate winds equally represented. Light intensity averages higher than in the vernal aspect (39%). Vapor pressure deficit reaches a very high point during this aspect, weekly maxima averaging over .350 mm Hg. Evaporation in general is maintained at a high level. Hygrothermograph records are especially distinctive during this aspect, the diel rhythm of temperature and humidity fluctuations being very regular (Fig. 11d).

TABLE 6. Insects characteristic of the aestival aspect (summer). Explanation as in Table 2.

Sector	E	PV	SV	CA	SA	S	A	H	Hi
Neuroptera									
Hemerobiidae: *Hemerobius conjunctus* Fitch				X	X				
Mecoptera									
Panorpidae: *Brachypanorpa oregonensis* McLach.				X	X				
Corrodentia									
Caeciliidae: *Caecilius aurantiacus* Hgn.					X	X	X		
C. quillayute Chap.					X	X	X		
Homoptera									
Cercopidae: *Philaenus leucophthalmus*				X	X				
Aphidae: *Macrosiphum solanifolii* (Ashm.)				X	X				
M. scolopii Essig				X	X				
Amphorophora rubicola (Oestl.)				X	X				
Coleoptera									
Carabidae: *Scaphinotus angusticollis nigripennis* Roesch.			X	X		X	X		
Cantharidae: *Podabrus piniphilus* Esch.			X	X					
Silis pallida Mann.				X					
Cephaloidae: *Cephaloon pacificum* Van D.				X					
C. bicolor Horn.				X					
Mordellidae: *Anthobates* sp.				X	X				
Elateridae: *Ctenicera umbripennis* (Lec.)			X	X					
C. sylvatica (Van D.)					X				
Athous rufiventris Esch.					X				
A. vittiger Lec.					X				
A. pallidipennis Mann.					X				
Megapenthes stigmosus (Lec.)					X				
Lucanidae: *Platyceroides laticollis* (Csy.)				X					
P. aeneus (Van D.)				X					
Cerambycidae: *Plectrura spinicauda* Mann.		X	X	X	X	X	X	X	
Chrysomelidae: *Syneta simplex* Lec.				X					
Luperodes sp.					X				
Curculionidae: *Sciopithes obscurus* Horn.		X	X	X	X	X	X	--	
Nemocestes incomptus Horn		X	X	X	X	X	X	--	
Dyslobus lecontei Csy.			X	X	X	X			
Stremneus tuberosus Boh.			X	X					
Scolytidae: *Pseudohylesinus grandis* Sw.			X	X	X	X			
Gnathotrichus sulcatus (Lec.)			X	X	X	X			
Diptera									
Tipulidae: *Cylindrotoma splendens* Doane				X	X				
Limnophila oregonensis Alex.			X	X	X				
Tipula macnabi Alex.			X	X	X	X			
Simuliidae: *Prosimulium fulvum* Coq.			X	X					
Tendipedidae: *Chasmattonotus univittatus* Lw.				X	X				
Heleidae: *Culicoides* sp.				X	X	X	X		
Culicidae: *Aedes varipalpus* Coq.				X	X	X			
Culiseta incidens (Thoms.)	X	X	X	X	X	X	X		
Fungivoridae: *Platyura* sp.				X	X	X			
Euphrosyne sp.				X	X				
Tabanidae: *Tabanus californicus* Marten					X				
T. captonis Marten					X				
T. sonomensis O. S.					X				
T. atrobasis McD.					X				
Chrysops proclivus O. S.				X					
C. pertinax Will.				X					
Rhagionidae: *Rhagio costalis* Lw.				X	X				
Leptidae: *Symphoromyia plumbea* Ald.				X	X				
S. kincaidi Ald.				X	X				
Cyrtidae: *Eulonchus sapphirinus* O. S.				X					
Syrphidae: *Stenosyrphus rectoides* Cur.			X	X	X				
Syrphus opinator O. S.		X	X	X	X	X			
Melanostoma angustatum Will.				X	X	X			
Piophilidae: *Mycetaulus costalis* Mel.				X	X				
M. bipunctatus Fall.				X	X				
Helomyzidae: *Suillia assimilis* Lw.				X	X	X	X		
Anthomyidae: *Hylemya alcathoe* Walk.		X	X	X	X	X	X		
Allocostylus diaphana Wd.				X	X	X	X		
Helina lysinoe Walk.				X	X	X	X		
Fannia incisurata Zett.				X	X				
Fannia ochrogaster Mall.				X	X				
Hydrotea militaris Mg.			X	X	X	X			
Muscidae: *Mesembrina latriellae* Desv.					X	X	X		
Calliphoridae: *Phormia terraenovat* Desv.		X	X	X	X	X			
Calliphora vomitoria L.		X	X	X	X	X			
Lepidoptera									
Geometridae: *Ceratodalia queneata* Pack.				X	X				
Hydriomena oedenata Swett				X					
H. captata Swett				X					
Hymenoptera									
Belytidae: *Pantoclis* sp.				X	X				
Ichneumonidae: *Ephialtes ellopiae* (Harr.)			X	X	X				
Amblyteles russatus (Cress.)				X					
A. astutus (Hgn.)				X					
A. semissis (Cress.)				X					
Vespidae: *Vespula vulgaris* L.		X	X	X	X	X	X		
V. maculata (L.)		X	X	X	X	X			
Bombidae: *Bombus sitkatensis* Nyl.		X	X	X	X	X			
B. flavifrons dimidiatus		X	X	X	X	X			
Total	1	12	25	64	59	28	14	3	0

The aestival aspect, like the other aspects, is divided into sectors, though not quite so clearly. The break between the cisaestine and aestine sectors comes at about the middle of the aestival aspect but varies considerably from year to year, the extremes being July 1, 1934 and August 4, 1937.

Cisaestine (L. *cis*, on this side, and L. *aestus*, summer) *Sector:* The cisaestine or early sector of the aestival aspect is characterized by the blooming of Clintonia, salal, Coralorrhiza and false Solomon's-seal. Salmonberries mature in this sector and are practically gone before the end of the aspect.

Scaphinotus remains active during the cisaestine sector, disappearing at its close, while a group of beetles including the Cantharidae, Lucanidae and Cephaloidae are limited to this sector. In the diptera, Tabanidae of the genus Chrysops and the Cyrtidae (*Eulonchus sapphirinus*) are restricted to this

TABLE 7.* Meteorological data for the aestival aspect—seasonal averages. CA—cisaestine sector; SA—aestine sector; T—entire aspect.

	1933			1934			1935			1936			1937			Average		
	CA	SA	T	CA	SA	T	CA	SA	T	CA	SA	T	CA	SA	T	CA	SA	T
Temperature																		
Maximum	68.8	72.4	70.0	67.0	69.1	68.3	70.0	79.0	72.8	70.8	72.4	71.6	75.2	77.3	76.1	70.0	74.0	71.7
Minimum	44.3	47.2	45.7	44.0	48.7	47.0	42.2	48.6	45.7	46.0	48.8	47.5	48.5	48.0	48.2	45.0	48.2	46.8
Mean	56.2	60.8	58.5	55.0	59.0	57.7	56.2	62.7	57.6	58.5	61.3	60.0	61.6	62.6	62.0	57.4	61.2	59.1
Range	22.5	26.0	24.2	23.0	20.0	21.3	28.0	30.4	29.3	24.8	22.1	23.1	26.7	29.3	27.5	25.0	25.5	25.0
Relative Humidity																		
Maximum	84.5	83.0	83.1	90.0	90.0	90.0	95.0	95.5	95.5	93.3	90.1	91.7	86.5	88.0	87.0	89.8	88.2	89.2
Minimum	53.0	39.8	43.5	44.6	48.8	47.0	41.0	50.4	47.6	43.1	55.6	50.4	46.8	28.0	41.6	46.1	44.5	46.1
Mean	70.6	64.2	66.4	72.0	71.5	73.4	84.3	75.0	79.7	82.0	75.7	79.1	72.7	69.0	71.3	74.3	71.7	73.9
Range	31.5	43.2	39.8	45.4	41.1	42.9	54.0	44.6	55.1	48.1	34.5	41.3	39.6	60.0	46.4	43.7	46.6	43.1
Precipitation	0.61	0.04	0.32	0.14	0.08	0.12	0.35	0.11	0.23	0.61	0.10	0.33	0.45	0.35	0.42	0.42	0.13	0.28
Light	26.0	42.0	34.0	36.0	32.0	34.0	57.0	27.4	40.0	32.0	60.0	46.0	40.0	43.3	41.1	38.3	40.9	39.0
Evaporation	....	10.8	....	6.02	4.82	5.31	7.67	8.07	7.97	4.22	7.07	5.75	8.32	8.19	8.27	....	....	....
Vapor Pressure Deficit																		
Maximum	.349	.396	.376	.353	.309	.325	.369	.420	.396	.324	.326	.325	.386	.344	.372	.354	.359	.358
Mean	.056	.173	.139	.122	.119	.120	.092	.120	.106	.072	.131	.101	.129	.134	.132	.094	.135	.119

*See notes for Table 3.

sector. The cisaestine sector has a somewhat greater total of characteristic insects than the following (aestine) sector (Table 6 and Fig. 13). It is in general cooler and cloudier than the aestine sector but the evaporation rates and vapor pressure deficits do not differ significantly.

Aestine (L. *aestus,* summer) *Sector:* About the middle of the aestival aspect, the false Solomon's-seal and Clintonia fruits add a touch of color to the forest herb layer. Leptidae, psocids and Hemerobiidae are characteristic of the late sector of this aspect, their appearance usually coinciding with the opening date. The Leptidae disappeared consistently with the close of the aspect. The russet-backed Swainson thrush, western wood pewee, hermit warbler and Pacific bandtailed pigeon leave during the aestine sector.

The aestine sector is characterized by high temperatures and low humidity, high vapor pressure deficit, low precipitation and high light intensity (Table 7). It usually draws to a close with an extremely hot, dry period in which the temperatures frequently reach or exceed 80° F and humidity descends to 40% or even 30%. This is usually succeeded by attainment of high maximum humidity (sometimes accompanied by the first light, fall rains), and continued high maximum temperatures as the serotinine sector of the autumnal aspect begins.

Autumnal Aspect

As the aestival aspect closes, the accompanying population shift initiates the autumnal decline toward the limited population of winter. By this time, the annual destiny of plant life has been fulfilled. Most fruits have formed and expendable vegetative parts are deteriorating. During the autumnal aspect the meteorological transition toward the unfavorable physical conditions of winter begins, with decreasing light intensity and increasing humidity being the earliest expression of their approach. The autumnal aspect as a whole occupies 2-2.5 months, beginning some time in August and ending in late October or mid-November in most years.

The autumnal aspect in this community, like other aspects, consists of more than one subseason. Most investigators of faunal aspection agree with the conclusion that the fall season is composed of two phases which they have called the serotinal and autumnal. There are indications that certain authors have interpreted a serotinal season as starting about where the mid-aestival break in population occurred in this study, so it is difficult to tell whether the term serotinal as they have used it refers to a late summer or early fall season. Their term autumnal clearly applies to the fall aspect as a whole. The early sector of the *autumnal aspect* is here designated as the *serotinine* and the later sector the *autumnine*.

A drop in faunal population at the close of the aestival aspect initiates the autumnal aspect (Fig. 10). The serotinine and autumnine sectors are closely related biotically. The difference in faunal composition of these two sectors is much less than that between the aestine and serotinine sectors, especially as to diversity of insects (Tables 6 and 8). 67 species of insects are characteristic of the autumnal aspect, 55% appearing for the first time within the aspect and 15% reappearing after a period of inconspicuousness or complete absence. 25% of autumnal insects occur only in the autumnal aspect, 18% being limited to the serotinine sector and 12% to the autumnine sector. Much of the autumnal population is also found in other aspects (Fig. 13, autumnal). The vernal fauna includes 27% of the autumnal species, as does the aestival population, while 22.2% of the autumnal insects occur also in the hiemal aspect. The nature and activities of the vertebrate population also unite the serotinine and autumnine sectors into a fall aspect. The summer resident birds have departed and permanent residents and fall migrants tend to occur in flocks in both fall sectors. The smaller mammals are more active than during the middle of the summer. The larger mammals indicate restlessness by roaming through the forest before being limited by the more rigorous weather of the winter. Amphibia are active in both sectors. While the autumnal sectors are clearly two parts of a single season, the differences between the two are somewhat greater than those between the sectors of most other aspects (Table 9).

Serotinine (L. *Serotinus,* late ripe) *Sector:* The average length of the serotinine sector is only 5 weeks, usually starting late in August and giving way to the autumnine sector in early October. There is a tendency for it to be abbreviated in those years in which the autumnine sector is long.

The serotinine is the sector in which the last fruits become ripened. Oregon grape and salal mature at this elevation early in the sector and the last red huckleberries ripen. False Solomon's-seal also bears fruit well into this sector. The herbs show aging by yellowed, ragged leaves which are being attacked by mildew and other fungi (Fig. 7).

The renewed fall activity of Scaphinotus probably provides as good a positive index to the early phase of the autumnal aspect as any part of the faunal picture. Cicadellidae *(Empoasca* sp. and *Conodonus flavicapitatus* Van. D.), were also good indicators of the beginning of this season. The first fall records of Aleyrodidae approximated the opening dates in the last two years of the study, when the most careful observations were made. Termites were recorded as emerging in their nuptial flights at this time in the two years in which the winged forms were observed. The serotinine sector is the first in which more invertebrates drop out of the population than are added to it. This decrease in variety principally affects the diptera and coleoptera. The insects present appear to be hardy types that find conditions suitable for constant activity; accordingly the population curve representing the variety of families stays at a high level. Coleoptera, which were so abundant in the vernal and aestival seasons, become very limited in variety in the serotinine sector. Diptera continue to dominate the field in variety. Among the lepidoptera, geometrids are active in the serotinine as in the aestine sector, but all are unfamiliar genera and species. The pine-white butterfly *(Neophasia menapii* Feld.) and the hemlock looper moth *(Nepitia phantasmaria* Stkr.) are species of potential economic significance. The former is characteristic of the first few days and the latter of the entire sector. Yellow-jackets reach a peak in abundance and activity during this sector and toward its close become very irritable and inclined to sting. Mosquitoes are also troublesome and numerous at this time. An abundance of adult spiders characterizes the serotinine sector; they are at the height of their predatory activity (Table 8).

The vertebrate fauna is characterized by renewed

TABLE 8. Insects characteristic of the autumnal aspect (fall). Explanation as in Table 2.

Sector	E	PV	SV	CA	SA	S	A	H	Hi
Collembola									
Entomobryidae: *Tomocerus flavescens* Tullb.	X	X	X	X	--	X	X	X	
Sminthuridae: *Ptenothrix* sp.	X	X	X	X	--	X	X	X	
Isoptera									
Kalotermitidae: *Zoötermopsis angusticollis* Hgn.						X			
Corrodentia									
Caeciliidae: *Caecilius aurantiacus* Hgn.				X	X	X			
C. quillayute Chap.				X	X	X			
Neuroptera									
Hemerobiidae: *Hemerobius bistrigatus* Bks.				X	X				
H. pacificus Bks.				X	X				
H. humili L.				X	X				
H. conjunctus Fitch				X	X				
Homoptera									
Coccoidea: indet.	X						X	X	X
Aleyrodidae: gen. et sp. indet.	X	X	X			X	X	X	--
Fulgoridae: *Catonia nemoralis* Van D.						X	X		
Cicadellidae: *Empoasca* sp.						X	X	X	
Empoasca filamenta DeL.							X	X	
Colladonus flavicapitatus (Van D.)						X			
Coleoptera									
Carabidae: *Scaphinotus angusticollis nigripennis* Roesch.			X	X		X	X		
Staphylinidae: *Anthobium pictum* Fauvel		X					X	X	
A. subcostatum Maekl.		X					X	X	
Derodontidae: *Peltastica tuberculata* Mann.							X		
Derodontus trisignata Mann.							X		
Elateridae: *Hemicrepidius morio* Lec.						X			
Cerambycidae: *Plectrura spinicauda* Mann.		X	X	X	X	X	X	X	
Curculionidae: *Sciopithes obscurus* Horn.		X	X	X	X	X	X	--	
Nemocestes incomptus Horn.		X	X	X	X	X	X	--	
Scolytidae: *Gnathotrichus sulcatus* (Lec.)		..	X	X	X	X			
Diptera									
Tipulidae: *Tipula macnabi* Alex.			X	X	X	X			
Ormosia fusiformis (Doane)						X	X		
O. perspectabilis Alex.						X	X		
Psychodidae: *Psychodes* sp.	X	X	X			X	X	X	X
Heleidae: *Culicoides* sp.				X	X	X	X		
Culicidae: *Aedes varipalpus* Coq.				X	X	X			
Culiseta incidens (Thoms.)	X	X	X	X	X	X	X		
Fungivoridae: *Lycoria* sp.					X	X			
Bolitophila sp.					X	X	X		
Exechia sp.	X	X					X	X	X
Fungivora sp. 1	X	X				X	X	X	
Polyxena sp.							X		
Anisopidae: *Anisopus alternatus* Say							X		
A. punctatus Fab.							X		
Empidae: *Hormopeza nigricans*						X	X		
Syrphidae: *Syrphus opinator* O. S.		X	X	X	X	X			
Helomyzidae: *Suillia assimilis* Lw.				X	X	X	X		
Anthomyidae: *Pegomya* sp.	X	X					X		
Hylemya alcathoe Walk.		X	X	X	X	X	X		
Alloeostylus diaphana Wd.				X	X	X	X		
Helina lysinoe Walk.				X	X	X	X		
Muscidae: *Mesembrina latriellae* Desv.					X	X	X		

TABLE 8 (Cont.)

Sector	E	PV	SV	CA	SA	S	A	H	Hi
Calliphoridae: *Calliphora vomitoria* L.		X	X	X	X	X			
Phormia terraenovat Desv.			X	X	X	X			
Tachinidae: *Arctophyto sarcophagina* Coq.					X	X			
A. wickhami					X	X			
Phoridae: *Megaselia* sp. 1						X	X		
Megaselia sp. 2						X	X		
Lepidoptera									
Pieridae: *Neophasia menapii* Feld.						X			
Geometridae: *Nepytia phantasmaria* Stkr.						X			
Tortricidae: *Peronia brittania* Kearf.						X			
Graciliariidae: *Cameraria gaultheriella* Wlsh. adult						X			
C. gaultheriella Wlsh. larvae	X	X					X	X	X
Hymenoptera									
Belytidae: *Xenotoma* sp.	X	X	X		X	X	X		
Miota sp.						X			
Vespidae: *Vespula vulgaris* L.		X	X	X	X	X	X		
V. maculata L.		X	X	X	X	X			
V. rufa consobrina (Saus.)		X	X	X	X	X			
Ichneumonidae: *Thaumatotypidea* sp.							X		
Braconidae: *Apanteles longicornis* (Prov.)							X		
Eulophidae: *Tetrastichus* sp.							X		
Polyneura sp.							X		
Total	11	21	19	21	30	50	44	12	3

activity of amphibia in response to the higher humidity and early fall rains. The summer resident birds are gone and varied thrushes, red crossbills, chickadees and kinglets occur in flocks which pass over and through the forest in waves of intense activity. Renewed activity of moles and Microtus becomes evident as they throw up fresh mounds of earth and make ridges in the humus. Chipmunks are more frequently heard and seen.

The close of the serotinine sector is marked sharply by the disappearance of the large muscid fly *(Mesembrina latriellei* Desv.) which coincides with the end of this sector in each of the 5 yrs. Other blue-bottle flies *(Phormia* spp.) also disappear at the close of this sector. The activities of the yellow-jackets *(Vespula vulgaris* L.) also tend to diminish at this time. The treehole mosquito *(Aedes varipalpus* Coq.) usually ceased being bothersome at the close of the serotinine sector.

In the serotinine sector the average of temperatures for five years is slightly higher, and the minimum temperatures slightly lower, than those of the aestival aspect (Table 10). The apparent stability of aestival temperatures is breaking down. Though the weekly maximum drops lower than in the aestival aspect, there are frequently records of over 80° F early in this aspect. The average minimum temperatures, which during the aestival aspect and early serotinine sector fluctuate close to the annual mean of 50° F, fall permanently below that level toward the latter part of the serotinine sector (Fig. 15). Precipitation increases again in this sector, especially toward its close, leading into the rainy autumnine sector. There is a tendency toward great oscillation in the curves of mean and minimum humidities, short humid periods alternating with exceptionally dry intervals. Wind velocity is practically the same as in the aestival aspect and predominantly southwest. Light intensity is lower throughout the autumnal aspect than in the aestival, due to the smoke of forest fires and haze characteristic of the serotinine sector, and the effect of clouds and fog in the autumnine sector, when it is even lower. Records for evaporation rates and vapor pressure deficit indicate that there is not much difference in the desiccating effects of the aestine and serotinine sectors, in spite of the increased humidity and precipitation in the latter. Hazard stick data also show that the increased precipitation and humidity of the serotinine sector has not built up the moisture content of the logs. The close of this sector appears to be governed more by a drop in temperatures than by any other physical factor.

Autumnine (L. *autumnus,* autumn) *Sector:* In extent, this sector is the most abbreviated of all. It generally begins early in October and lasts to approximately the first week of November.

The increased dampness of this sector brings out fungus fruiting bodies and their associated mycetophagous fauna in humus and decaying wood. It is the season of falling leaves. The herb layer, which in the serotinine had begun to die, in this sector has lost any vestige of life. The leaves instead of being yellow have become mottled dark brown with decay. All of the deciduous shrubs and trees lose their leaves at this time. The vine maples, especially, lose their leaves in steady showers as the sun strikes them in the morning following a frost. Even the conifers join in showering the forest floor with wornout needles.

Consistent with the opening of the autumnine sector are the appearance of a brown scale (not identified) on the leaves of salal and Oregon grape and the occurrence of fresh leaf-miner tunnels in salal leaves. In spite of the brevity of this sector, its population is distinctive. There is enough dry, sunny, warm weather to produce considerable activity among hardy types of insects. Braconidae, Ichneumonidae and Vespidae are particularly noticeable. Otherwise, diptera dominate the community as usual. Several types of coleoptera are present, including the mycetophagous Derodontidae and Staphylinidae. The Trichoceridae return (Table 8). The disappearance of Scaphinotus marked the end of the season in all years except 1935. In that year an unusually early snowfall accompanied by exceptionally low temperatures brought the aspect to a close abruptly. Rising temperatures later brought out two isolated specimens that were probably only indicative of a potential extension of the autumnal season.

The bird population is rather stable during the autumnine sector, consisting wholly of permanent residents, except for the flocks of juncos (mostly *Junco hyemalis oreganus* (Townsend)), which drift through

TABLE 9.* Seasonal averages of meteorological data for the autumnal aspect. S—serotinine sector; A—autumnine sector; T—entire aspect.

	1933			1934			1935			1936			1937			Average		
	S	A	T	S	A	T	S	A	T	S	A	T	S	A	T	S	A	T
Temperature																		
Maximum	77.0	61.5	67.0	71.0	58.3	64.6	73.1	66.3	70.8	71.4	57.0	65.4	70.5	63.2	67.6	72.6	61.2	67.1
Minimum	50.1	42.8	45.5	56.5	40.3	43.4	49.0	44.3	47.4	46.7	38.8	43.4	48.5	43.5	46.4	48.1	41.9	45.0
Mean	63.6	52.4	56.3	58.7	49.4	54.0	61.0	55.3	59.1	59.0	47.9	54.4	58.0	53.4	56.1	60.0	51.6	56.1
Range	26.7	18.5	21.5	24.5	17.6	21.0	24.1	22.0	23.3	24.7	16.2	22.0	22.0	19.2	15.4	24.4	19.1	21.8
Relative Humidity																		
Maximum	90.8	92.6	91.9	90.2	89.0	89.5	95.2	95.6	95.3	92.2	91.2	91.0	91.4	91.7	91.5	91.9	92.0	91.8
Minimum	42.0	67.0	55.5	41.5	63.7	51.8	42.6	51.3	43.5	34.8	41.0	37.4	51.5	68.0	56.6	42.5	58.2	49.5
Mean	67.5	81.0	68.7	62.7	80.0	73.1	71.5	80.5	77.5	68.6	73.9	70.8	77.6	84.3	81.5	69.5	79.9	74.3
Range	47.2	25.0	35.5	49.2	25.3	34.9	52.8	44.3	49.6	57.4	50.2	54.4	39.8	23.7	34.0	49.2	35.7	41.6
Precipitation	0.36	1.47	0.80	0.24	3.60	2.07	0.28	0.59	0.38	0.20	0.14	0.17	1.04	1.41	1.19	0.42	1.44	0.92
Light	37.5	26.6	31.0	21.0	24.2	23.3	35.0	10.7	21.6	30.0	40.0	32.6	15.0	21.6	35.0	33.7	24.6	30.3
Evaporation	9.53	3.30	6.12	6.46	2.36	4.22	8.96	3.16	4.23	5.80	4.68	3.37	5.64	2.15	4.35	7.27	3.13	4.45
Vapor Pressure Deficit																		
Maximum	.458	.147	.197	.462	.129	.280	.420	.158	.333	.377	.227	.321	.330	....	....	.409	.165	.282
Mean	.178	.071	.110	.191	.077	.122	.155	.045	.153	.143	.086	.112	.097	.061	.087	.152	.069	.116

*See notes for Table 3.

TABLE 10. Meteorological data summarized by aspects—averages for the period of the study.

	Hiemal Aspect			Vernal Aspect		Aestival Aspect		Autumnal Aspect	
	H	Hi	E	PV	SV	CA	SA	S	A
Temperature (°F.)									
Maximum	50	44	49	53	67	70	74	73	61
Minimum	34	28	33	35	39	45	48	48	42
Mean	44	36	40	45	53	57	61	60	52
Range	17	16	16	17	27	25	25	24	19
Relative Humidity (%)									
Maximum	93	92	94	91	89	90	88	92	92
Minimum	74	83	75	55	44	46	45	43	58
Mean	87	90	91	83	77	74	72	70	80
Range	19	9	19	34	46	44	43	49	34
Precipitation	2.73	2.90	2.17	1.35	1.03	0.42	0.13	0.42	1.44
Light (%)	26	25	24	32	36	38	41	34	25
Vapor Pressure Deficit									
Maximum	.077	.040	.067	.161	.297	.355	.359	.409	.165
Mean	.040	.020	.024	.048	.060	.094	.135	.152	.069
Wind Velocity (mi./day)	18	16	16	23	19	18	19	17	20

the mountains in the course of their southward migration. Chipmunks attain a peak of abundance in our records at this time and amphibia reach a second peak of activity. Deer are mating and bear wander restlessly preceding hibernation.

The autumnine sector is a season of the first fall frosts, heavy rains and strong winds, interspersed with Indian summer weather. The first snowfall may also occur during this sector. Light intensity drops decidedly. Evaporation is slightly less in this season than in the preceding and correlates in a rough way with the precipitation for the various years. The increased precipitation and relative humidity of the autumnine sector definitely lower the vapor pressure deficit (Table 10). A fall in weekly maximum temperature below 55° F, usually accompanied by heavy precipitation—which at this level may be in the form of snow—together with minimum temperatures of 40° F or less, brings the autumnal aspect to a close.

DISCUSSION

SUBSTANTIATION OF SECTOR CONCEPT

Comparison of the seasonal boundaries of faunal and floral aspection established by other investigators with those of the Coast Range is of interest (Fig. 16). The moderate climate of the Pacific Coast greatly abbreviates the dormant stage of the winter aspect, which is marked by transitional stages at both ends, therefore the author has subdivided the hiemal aspect, using the terms, *hibernine* for the dead of winter, *hiemine* for the introductory winter season, and *emerginine* for the transitional stage preceding the spring aspect. Such a subdivision establishes sectors of a duration in harmony with the extent of aspectional subseasons throughout the rest of the year. The length of the hiemal aspect of other authors is quite extensive as compared with the remaining seasons of the year. This season extends from approximately two and a half months as determined by Shackleford (1934) for an Oklahoma prairie, to over five months indicated by Smith (1928) in seral stages of an Illinois forest, by Fichter (1942) for Nebraska prairie, and by Brown (1931) for the oak-hickory forests of Wisconsin. A 5-month hiemal season is quite a contrast to the brevity of their prevernal and vernal seasons which generally last only one month. An extremely long hiemal season is no doubt partly justifiable on the basis of the comparatively long winters characteristic of mid-continental areas. Some interesting evidence for the division of the hiemal aspect into hiemine, hibernine and emerginine sectors, however, appears in the papers of several of the ecologists who have considered aspection in the deciduous forest and prairie biomes.

In spite of the widely separated locations, the usual beginning date for the hiemal aspect occurs in November. The population curve shown by Weese (1924) contains an indication of an early phase of the hiemal aspect (hiemine sector of the present paper) in an elm-maple forest in Illinois. He reports a period of about a month between November 14 and December 19 in which the total population is still declining to its minimum average for the winter. Williams (1936) described November as the time of hibernation for invertebrates and some vertebrates and states that in December, January and February the species list of birds is restricted to the permanent resident and winter visitor groups. The intimation that the bird population is not entirely restricted until December perhaps shows that a pre-hibernal subdivision should be recognized. Adams (1941) also may have indicated something of the same kind when he referred to an abundance of Ptenothrix on November 27 and December 4, 19, and 25 after the hiemal aspect had begun. Shackleford's (1929) curve of weekly mean air temperatures for 1926 shows that air temperatures did not drop much below 32° F until about the middle of December, which should permit enough invertebrate activity above the soil level to mark a season preceding the dead of winter, when hibernation is most nearly complete.

The greater part of the hiemal aspect reported by other investigators correlates well with the season referred to as *hibernine* in this paper. The animals are for the most part in an inactive state, but, as recognized in most reports, a few insects and spiders are active on warm days throughout the winter.

The evidence from other authors that an emerginine sector should be separated from the latter part of the hiemal aspect is even better. The total population curve shown by Weese (1924) does not show it unless it should take the place of his prevernal aspect, which is one month earlier than Weaver & Fitzpatrick's (1934) average prevernal aspect in the prairie at almost the same latitude. The prevernal aspect might then apply to the more rapid increase in population reported by Weese during the early part of April. The appearance of late winter and spring mosses mentioned by Weaver & Fitzpatrick may be a floristic indication of an emerginine sector in the prairie. The notable increase in bird population reported by Twomey (1945) during the latter part of his hiemal aspect is coincident with the beginning of the migration of hibernating insects from beneath the leaves of the ground stratum, and probably represents an emerginine phenomenon. Cantlon (1953) suggests an emerginine type of phenomenon when he refers to Wolfe *et al.* (1949) in stating, "The change from winter to spring has been defined as the period when vegetative activity shows a marked increase near the surface and under the litter." A sudden and sustained increase in *Parasitus* sp., together with *Epitrix fuscula*, and *Gongylidiellum pallidum*, from the latter part of February to early April in Smith's (1928) report probably indicates a potential emerginine sector or at least a prevernal sector, although the latter would probably not be comparable to the length reported by Davidson (1930) and Williams (1936) (Fig. 16).

Weese (1924) reported a rise of the weekly mean air temperatures to between − 2.1 and 8.3° C during March in the latter part of this hiemal aspect, which corresponds to the temperature range between 30° and 50° F reported for the emerginine sector in this paper. Shackleford (1929) also indicates a sharp rise in weekly mean air temperatures above 32° F about the first of February, 1927, which is another evidence of an emerginine sector.

Additional evidence for an emerginine sector is shown in the graphed population and environmental factors for the prevernal season by Davidson (1932), in which the mean air temperature records remained below 30° F until the first part of April. This could mark the close of an emerginine sector. A sharp rise in temperature followed in the latter part of her prevernal season, which brings the average, with one lapse below 32° F, to a figure well above that point. Such a sudden rise in temperature would mark a true prevernal season. Positive evidence of a faunal nature for an emerginine sector is shown in Davidson's data by the early rise of the spider, *Gongylidiellum pallidum* Em., to a peak of abundance between the first of February and the first of April. Renewed activity during this period is indicated for the perennial predominant spiders. Another seasonal spider, *Phrurolithus palustris* Bks., also originates in the middle of her prevernal season. These evidences point to a break in the season she called prevernal, which could be recognized as evidence for an earlier emerginine and a later prevernine season.

The great length of the preverna1 season as reported by Carpenter (1935), Williams (1936), and Davidson (1930) is probably due to the inclusion of an unrecognized emerginine sector. Although Carpenter starts the prevernal on February 15 on the basis of the "arrival of the first spring birds" and "appearance of Peziza cups and budding of the buckeye and elm," he states, "By April 2 the aspection had greatly progressed with the weekly mean temperature rising to 46.5° F as compared with 33° for the preceding week"; and further, "On the later date (April 2) many Diptera were flying and first ground blossoms appeared." Such a statement clearly indicates a cleavage in the middle of his prevernal aspect. The criteria for aspection from a botanical point of view are indicated by Weaver & Clements (1938) in their statement, "Societies in forests are found only beneath the primary layer of trees and their subdominance is obvious." Since Carpenter reports the earliest "ground blossoms" to be those of herbs, April 2 would seem to mark the actual beginning of the prevernal aspect in his studies and would give a seasonal duration for that aspect comparable to that reported by the majority of investigators considered in Figure 16.

Williams (1936) indicates precisely the same phenomenom by stating that the prevernal aspect begins with the month of February, in spite of his statement that "most of its aspects are hibernal." The early part of the prevernal season he characterizes botanically by renewed color of mosses and lichens and faunally by renewed bird activity. He then notes that late in March the earliest flowers come into bloom.

Thus on almost the same dates two investigators (Carpenter and Williams) on different projects, in widely separated localities, indicate that a prevernal season might be recognized as beginning in accord with the plant ecologists' concept, *i.e.,* that the earliest blossoms mark the opening of the prevernal season. The author believes that the hiatus between the dead of winter and the plant ecologists' prevernal season should be recognized and designates it the emerginine sector. This term fits the indications of renewed activity of plant and animal life referred to above (from about the first of February to approximately the last of March). The prevernal aspect of all investigators, except Davidson (1930), who unfortunately did not designate in her paper the bases for dating this season, would then be brought into close approximation as to dates and duration.

The prevernine sector of this Oregon locality corresponds in duration to the prevernal aspect of some other investigators (Fig. 16, Weaver & Fitzpatrick, Pound & Clements, Weese, Shackleford, Twomey, and Adams). Most investigators have reported the vernal season as one of the shortest, though Pound & Clements, as well as Weese and Williams, each allotted two months to it. The research on Saddleback Mountain in the Coast Range reveals a tendency for the early spring (prevernine) and late fall (autumnine) sectors to be pinched down into very brief periods. This is also shown by the serotinal season as reported by Adams.

The aestival aspect compares most favorably in duration and dates included for the locations listed in Figure 16. The effect of the latitude of regions, as well as annual variations in climate, would seem to account for the discrepancies that occur. For example, the aestival aspect is reported by Brown as starting in April in the oak-hickory woods in Oklahoma, the only case in which this season is indicated as starting so early. This locality is about five degrees farther south than the places where seasonal studies were made in Illinois and Nebraska, which could account for the earlier aestival season in Oklahoma. In the study by the author in the Coast Range forests, the aestival aspect includes the greater part of the month of August and begins at a later date than those given to this season by most other investigators. The later dates here can be explained by the fact that the writer's station was located on aproximately the 45th parallel of north latitude. The fact that the elevation selected in the Coast Range mountains is greater than that of Illinois and the central states in general would accentuate the tendency for the seasons to be later at this latitude than in the vicinity of the 40th parallel where most other projects were located. There is little doubt about the aestival character of the season as a whole when compared with the aestival aspects of other authors, even in cases where they do not indicate a subdivision of this aspect.

The fall seasons as illustrated in Figure 16 show that the period Brown (1931) designated as a serotinal aspect coincides with Shackleford's (1934) aestival season (in the same state at about the same latitude). It seems likely that Brown has given a preferable interpretation of the season, since the midportion of her serotinal aspect coincides with dates ascribed to the serotinal aspect by other authors. In her study of an Illinois prairie (1929), Shackleford apparently divided the period others have called a serotinal aspect equally between the aestival and autumnal seasons, as have Muma & Muma (1949) in their study of the spider fauna of three eastern Nebraska communities. The inclusive interpretation of the term *autumnal* as used by recent authors *(e.g.,* Shackleford, Weaver & Fitzpatrick, and Fichter) is antedated by Pound & Clements' (1900) use of the term *serotinal* for the entire fall period. When the serotinal and autumnal seasons of most eastern authors are combined, their total duration of approximately three to four months is roughly comparable. This is from about a week to over one month longer than the combined duration of the serotinine and autumnine sectors of the autumnal aspect in the Coast Range location in Oregon. It appears that the autumns may be of greater length in the central states than on the Pacific Coast.

Tabulations such as Figure 16, though they reveal interesting parallels, also reveal a prevailing lack of agreement upon seasonal dates and terminology, even where the same communities have been studied. It seems likely that many of the differences are not inherent in the communities, *i.e.*, not due to annuation but are subjective, due to differences in the observers and to the relatively indefinite seasonal criteria which have been used.

INTERRELATIONSHIPS OF SEASONS

Examination of Table 10 reveals that the hiemine, hibernine and emerginine sectors are closely united from an environmental standpoint. They have an almost identical average temperature range for the 5 years. A 5-yr average of relative humidities produces about the same result. Precipitation averages show a high rate for all three sectors together. Vapor pressure deficit averages, which have been shown to correlate with the curve of population (Fig. 10), tend to split this winter group of biotic seasons into sectors. The three winter sectors are united biotically by the occurrence of three groups of diptera.

The prevernine and vernine sectors of the vernal aspect are in many ways similar or complementary to the autumnine and serotinine sectors of the autumnal aspect, respectively. In some ways the entire vernal aspect strikes a balance with the autumnine sector of fall. In others the prevernine sector of the vernal aspect compares most favorably with the autumnine sector and the vernine sector with the serotinine sector (Table 10). Certain environmental factors unite the prevernine sector with the summer, while the autumnal aspect also tends to be pulled two ways—toward the summer or toward the winter season. The vertebrate populations of the vernal and autumnal seasonal societies are alike in the peak of activity attained by the amphibia in both seasons. Birds and mammals are also very active in both. The seasons differ, however, in the type of activity exhibited. The birds in the vernal aspect are numerous due to an influx of summer residents. In the autumnal aspect the summer residents are gone, but winter residents are traveling in flocks and surges of bird activity traverse the forest as these flocks pass through. In the vernal aspect the reproductive activities of mammals render the mammalian fauna relatively conspicuous. In the autumnal aspect, especially the late sector, a pre-hibernal restlessness causes local migration of larger mammals, and hoarding activities among many of the smaller ones. Twomey (1945) apparently noted the same phenomenon when he writes that "the vernal and autumnal aspects are comparable in that they both show great fluctuations in the respective animal populations." He refers to the vernal aspect as "one of intense activity" and says that the "most striking phenomenon of the autumnal period is that of movement both in the insects and birds."

Both the environmental line of cleavage and biotic distinctions between the vernal and aestival aspects are striking. Vegetational differences are not as clear as faunal differences, as the herbs and shrubs continue to blossom, and fruits do not appear to characterize this area until the late sector of the aestival aspect. The evidence of a decided change in the biota between the vernal and aestival aspects is supported by the addition of many new families of insects to the aestival aspect. This picture of a major break between the vernal and aestival aspects is also aided by the activities of summer resident birds, their conspicuous courting activity during the vernal aspect contrasting with their quieter nesting activities during the early sector of the aestival aspect, which Twomey (1945) designates as a change "from one of song to silence."

The similarity of the aestival aspect to the serotinine sector of the autumnal aspect is largely environmental. Despite a close relationship of the environmental factors the insect fauna is very distinctive (Tables 6 & 8). The vertebrates, like the insect groups, tend to emphasize the dissimilarity of the aestival and autumnal aspects. A break in the biotic structure of the community, due to simplification of the insect and bird population and revival of mammalian and amphibian activity, marks the end of the aestival and beginning of the autumnal aspects as the point where decline toward the winter season of limited activity and variety of fauna begins.

The organization of the biotic seasonal societies recognized in this study places the aestival aspect in contrast to the hiemal aspect. In many ways the aestival aspect is well qualified to fill this role. It is characterized by the highest minimum temperatures, lowest weekly precipitation and greatest intensity of light. The population in this aspect attains its peak in number and diversity of fauna. As was indicated in the detailed description, there is good evidence that an early and late phase of this biotic season should be recognized. When this is done, and the aestival aspect is divided into early and late sectors, it resembles the spring and fall aspects in being a two-phase biotic unit comparable to the unit formed by the vernal aspect with its prevernine and vernine sectors. The serotinal and autumnal aspects of other authors could be considered to be early and late sectors of a fall aspect, the environmental and biotic characteristics of which are transitional between the summer and winter seasons.

Thus the seasonal relationships revealed by this study, and the classification adopted here serve to emphasize the basic fact of the complementary nature of the aestival aspect (summer, or the growing season) and the hiemal aspect (winter, or the dormant season), as well as the transitional nature of the vernal aspect (spring) and the autumnal aspect (fall). It represents a return to the basic simplicity of the four astronomical seasons of the temperate zone, coupled with a recognition of the inherent complexity of each of the major seasons.

SUMMARY AND CONCLUSIONS

1. A 5-yr aspectional study was conducted from 1933 to 1938 at an elevation of 1400 ft in a subclimax

community of mature, even-aged Douglas fir and hemlock, in a location representative of conditions at an average elevation in the mesophytic coniferous biome along the crest of the Coast Range Mountains.

2. Collections and observations were made at weekly intervals. Continuous records were made of the temperature in the humus layer of the soil surface and temperature and humidity in the low shrub layer, while maximum and minimum thermometers at shrub, low tree and high tree levels, and instruments measuring evaporation, wind velocity, precipitation, light intensity and moisture content of wood in the shrub and herb layers, were read weekly. For this aspectional study only results obtained from the layers above the soil surface have been considered.

3. A curve of population for each of the 5 years of investigation was constructed on the basis of the number of families of insects collected, or observed to be active, in the layers above ground each week. Besides the fluctuating, gradual and continuous increase of the population to a summer maximum, and similar decrease to a winter minimum, striking changes were found to occur at varying intervals, contributing a new aspect to the population. These changes in population were both quantitative and qualititative. The locations of these major fluctuations in the normal curve of population growth or decline were used as indications of seasonal boundaries.

4. Fluctuations of environmental factors, which are not always the same or in the same degree, usually accompany the major biotic fluctuations.

5. An environmental factor derived from averaging the vapor pressure deficit at the time of collection, with the mean daily maximum vapor pressure deficit for the preceding week, and the light intensity of the collection date, correlates well with the curve of diversity of insect population above the ground level.

6. Biotic seasons can and should be determined by means of vegetational, faunal, and environmental criteria. (1) Vegetational criteria include the blooming and fruiting of plants, especially subdominants, the formation of new growth, and the defoliation of the plant community. (2) Of particular importance under faunal criteria, are the shifting composition of the population, peaks of abundance of animals in the various stages of their life histories, reproductive activities, and migrations, both horizontal and vertical. Composition of the insect population is especially important. (3) Among environmental criteria, temperature, humidity, evaporation and precipitation are of classic importance in establishing seasonal limits, while vapor-pressure deficit, which is based on temperature and humidity and hence correlated with the evaporating power of the air, is of particular value. This study revealed a correlation between a combined vapor pressure deficit—light factor and diversity of insect population. The distinctive seasonal patterns of temperature and humidity as recorded by the hygrothermograph are of significant use, while weather in the larger sense, including wind, clouds, barometric pressure, storms, etc., must also be considered.

7. The term *aspect* has been reserved to denote the four major biotic seasons, corresponding roughly to the four astronomical *seasons,* winter, spring, summer, and fall, which are bounded by the equinoxes and solstices. *Sector* designates the biotic subdivisions of the four major aspects, the suffix *-ine* being used in preference to the *-al* suffix heretofore used for both major and minor biotic seasons. The seasons are (1) hiemal aspect (winter) with hiemine, hibernine, and emerginine sectors; (2) vernal aspect (spring) with prevernine and vernine sectors; (3) aestival aspect (summer) with eisaestine and aestine sectors; and (4) autumnal aspect (fall) with serotinine and autumnine sectors. (a) The three sectors of the hiemal aspect are closely related both environmentally and biotically. (b) Hibernine is reserved for the subdivision of the hiemal aspect characterized by deepest dormancy of animals, particularly arthropods, and of all plants, while the hiemine and emerginine sectors are recognized as separate sectors, during which organisms are entering and emerging from dormancy, respectively. (c) The vernal and autumnal aspects exhibited marked biotic and environmental similarity and both are transitional. (d) The vernal and aestival aspects are separated by a major line of cleavage, which is most clearly marked by environmental data, but is also evident biotically. (e) The aestival aspect is divided into two sectors, chiefly on the basis of biotic criteria. Maximum variability of the insect population in the eisaestine sector is correlated with the favorable environmental factors of that period. (f) Environmental correlation of the late aestival (aestine) and early autumnal (serotinine) sectors is very close but a biotic comparison shows great differences between the two. (g) The serotinine sector marks the beginning of the autumnal decline toward environmental and biotic aspects characteristic of winter.

8. The distinctive composition of any sector is produced by the loss of a group of animals characteristic of the close of the preceding sector, the presence of an intrinsic group, and the addition of a group of animals which carries through into the following sector.

9. Interpretations of aspectional criteria can be sufficiently specific to enable comparison of locations varying in elevation, latitude and other topographic or geographic features.

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