

RESUMES

Resumés of papers read at the Ecological Society Conference, 1974, are presented (except for those papers presented in full elsewhere in this issue). For the complete programme of papers read at this conference please refer to the Annual Report appearing on pp. 125-127.

THE FOOD OF THE OPOSSUM
(*Trichosurus vulpecula* Kerr)

IN THE ORONGORONGO VALLEY, NEAR WELLINGTON

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The diet of a population of opossums from an area of 2.25 ha in the Orongorongo Valley near Wellington was investigated, using faecal analyses to identify the cuticles of the leaves eaten.

Because of the variation in the digestibility of the leaf cuticles of the different species [the cuticle of hangehange (*Geniostoma ligustrifolium*) is twelve times more digestible than that of climbing rata (*Metrosideros fulgens*)] it was necessary to calculate an index of digestion for each of the tree species known to be eaten in quantity. These indices were determined by feeding captive opossums with known amounts of the leaf species eaten in the wild, and then measuring the relative frequency of the specific cuticle in the faeces. This factor was then used to correct the observed frequencies of each species occurring in the faeces. Implicit in the calculations to determine the index is a computation to include the weight per unit area of the leaf, which allows the corrected results to be compared using proportional weights rather than areas.

Faeces from 25-35 opossums routinely live-trapped in the study area each month were combined and prepared for microscopic examination. Five hundred and fifty identifications of abaxial cuticle were made from each monthly combined sample.

The results from the four years' analysis, May 1969 to April 1973 showed that two species, kamahi (*Weinmannia racemosa*) and northern rata (*Metrosideros robusta*) comprised about 60% of the total leaf intake. Climbing rata (*Metrosideros fulgens*) and supplejack (*Ripogonum scandens*) contributed a further 15-16% but occurred seasonally, most climbing rata being eaten during the spring and early summer, and supplejack in winter. Of the further ten species contributing regularly to the diet, mahoe (*Melicactus ramiflorus*), hangehange (*Geniostoma ligustrifolium*), five finger (*Pseudo-*

panax arboreum) and tawa (*Beilschmiedia tawa*) occurred most commonly. Some other species were present intermittently.

Foods other than leaves are also eaten by opossums; from the frequency of occurrence of different types of fragments in the faeces, it was found that leaves contributed about 60-70% of the diet. The rest comprised other types of food, e.g. flowers, fruit, seeds, bark, and petiole. Bark fragments were present consistently though in varying amounts throughout the period, but it is not known if bark biting fulfils a nutritional or social need.

Though hinau (*Elaeocarpus dentatus*) leaves were not present often in the diet, the opossums browsed on the developing flower buds of hinau from March, when they first appeared, until they expanded into flowers, which were also eaten in November-December. In addition opossums also ate unripe hinau fruit which the trees carried well into the winter months.

Fruit of other species was also eaten; pigeonwood (*Hedycarya arborea*) and supplejack with fruit ripening over a three to four month period, and horopito (*Pseudowintera axillaris*) and kaikomako (*Pennantia corymbosa*) both with a short fruiting season. Flowers and fruit of other species were also eaten, as well as other types of food but more work is required to determine the contribution that these supplementary foods make to the diet.

GRAZING PRESSURES OF GRASSHOPPER
POPULATIONS IN ALPINE TUSSOCK GRASSLANDS

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The following model has been used to assess grasshopper grazing pressures in alpine tussock grasslands throughout the South Island of New Zealand:

Given that members of a herbivore population may be grouped into k consumer classes (e.g. insect

instars) each consuming a quantity of plant tissue c and destroying a further quantity d ,

$$\text{Population damage} = (c_1 + c_2 + \dots + c_k) \\ + (d_1 + d_2 + \dots + d_k)$$

where

Class consumption,

c = consumption per member per unit feeding interval

× number of active feeding intervals in a life span

× population size of the class

As the class consumption equation inter-relates feeding performances and population behaviour throughout full life spans of known environmental conditions, it incorporates a detailed knowledge of weather conditions, grasshopper activity thresholds and feeding thresholds. For example, the number of "active" feeding intervals (see the second term) represents a summation of all favourable feeding opportunities based on the known feeding regimen and on the observed non-limiting weather conditions throughout the modal life-span of the class. Appropriate behavioural and environmental data were collected for three grasshopper species at one tussock grassland site and population damage levels were then expressed as grazing pressures by relating dietary preferences to the availability of relevant vegetation species. Full details are presented by White, 1974, *N.Z. Journal of Agricultural Research* 17: 357-372.

In turn, these data were extended to a survey of grasshopper grazing pressures at different sites by relating consumption and damage to the following intersite variables: population density, consumer body size, vegetation composition, percentage living ground cover and site aspect. Variations in grazing pressure of up to 25-fold were demonstrated between sites, as discussed by White, 1975, *N.Z. Journal of Agricultural Research* 18: 73-85.

CRECHING BEHAVIOUR AND SURVIVAL OF SHELDUCKLINGS

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An often-recorded feature of the European Shelduck's (*Tadorna tadorna*) family life is that some broods, during the course of their development, contain ducklings of different ages. In contrast to many other species of waterfowl which occasion-

ally amalgamate two or three broods, shelduck "creches" may contain as many as 100 ducklings. The formation of creches and behaviour of the ducklings and adults involved was studied during 1970-72 on the Ythan estuary, Scotland. Not all of the broods in the study area were involved in creching; approximately one-third of the 65 broods observed remained as true family units. The largest creche contained 19 ducklings.

Ducklings transferred from small to large broods whenever broods intermingled on the feeding areas or whenever broods were left unattended whilst their guardian adults fought. Adults which lost some or all of their ducklings made no attempt to regain them while adults gaining ducklings seldom attempted to drive them away unless they were of a conspicuously different size to their own young. Most of the ducklings (84%) which transferred from a brood to a creche, or from creche to creche, did so in their first week of life. Movements between broods and creches was followed by marking some day-old ducklings with coloured rubber leg bands. This showed that some ducklings passed through at least three different creches during their eight-week long development and that some creches contained ducklings from at least four different broods. Only one pair of adults guarded each creche and they were all successful breeding adults. Because of the movements of ducklings some of these pairs eventually guarded creches which contained none of their own progeny.

Ducklings fledged from both family broods and creches in each year of study. Combining data for all years, family broods initially contained 126 ducklings of which 43 (34.2%) fledged, whilst those broods which at some time were involved in creching fledged 69 (22%) of their initial 313 ducklings. However, not all mortality in creches occurred at or subsequent to creching, therefore mortality curves were calculated as follows: for all ducklings involved in creching during their first five days of life, their mortality over the subsequent five days was calculated. Similarly for all ducklings involved in creching in the first 10 days, their mortality from day 11 to day 15 was calculated and so on to the 40th day. Mortality rates were similarly calculated for family broods. Ducklings reared in family broods survived significantly better than those reared in creches.

Although the amalgamation of young into creches has been described in other groups of birds such as penguins, pelicans, terns and flamingos, the phenomenon is clearly not the same in all species and it is important to distinguish between the cause and the

function of such gatherings. In shelducks the mixing of broods may be considered the result of firstly the mutual attraction which ducklings show toward each other and secondly, the necessity of a number of broods to utilise a common feeding area. The function of creching is not related to the adult's moult migration as has been suggested by Hori (Wildfowl 20: 5-22, 1969). Creching can be demonstrated to be the major proximate cause of duckling mortality so why does an obviously disadvantageous habit persist? Ducklings which amalgamate into large creches spend much longer feeding than those remaining in small groups and, as a result, fledge sooner. There is an obvious advantage in this. This advantage may extend to ensuring a greater probability of survival in the post-fledging period which may, on balance, offset the higher mortality associated with creching.

This paper has now been published in full. The reference is: Williams, M., 1974. Creching behaviour of the Shelduck *Tadorna tadorna* L. *Ornis Scandinavica* 5: 131-143.

BEHAVIOURAL PROCESSES AND POPULATION REGULATION IN THE CINNABAR MOTH

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Tansy ragwort (*Senecio jacobaea* L.), a biennial weed, is eaten, and occasionally defoliated over large areas, by larvae of the cinnabar moth (*Tyria jacobaeae* (L.)) Nonetheless such outbreaks do not eradicate the plant. How does so vulnerable a plant manage to persist and, how can a herbivore that devastates its food supply persist after population crashes?

Conclusions to the second question only are presented in this particular paper. Both plant and herbivore are native to Europe and man-introduced to other countries, including Vancouver Island, British Columbia, where the field work was done.

Female moths usually lay each of several clusters of 30-60 eggs on a different plant. The surviving larvae from an average sized cluster eat most of the biomass of the average tansy ragwort; hence the spacing of clusters is adaptive, and at low moth densities promotes efficient use of the food resource. At high densities, however, the distribution of clusters is contagious, since moths prefer ovipositing on large plants, and fail to discriminate against plants that already have clusters on them. Consequently

many plants are overloaded (i.e., the larval food requirements exceed the plant biomass), whereas some plants have no clusters on them, and thus become food refuges.

These food refuges are important, I suggest, for maintaining the moth when populations crash through starvation, since they provide adequate food for the dispersing larvae that find them. Dispersal in the fifth instar is density-dependent, and is associated with an antagonistic "head-flicking" behaviour. Larvae also disperse when food is plentiful, however, for in one population over 75% of the larvae dispersed once during the fifth instar. In that particular study larvae that dispersed had, on average, more food after dispersal than before, although the risk of not reaching a plant was sometimes high. As with the egg-laying behaviour of female moths, dispersal behaviour in the larval stage can benefit the individual. Yet at high densities the consequences of these behaviours may increase mortality rates.

From these observations I conclude that under some conditions populations of the cinnabar moth can regulate their own numbers before all the host plants are stripped, but that under other conditions they cannot do so, and crash through starvation. A necessary condition for an outbreak seems to be that larvae suffer little mortality during dispersal, a condition that is satisfied when plant density is high. Data on plant density from 11 outbreak areas are consistent with this idea. The essential features of the regulatory mechanism proposed for the cinnabar moth could be identified in other insect species. Outbreaks in these species were also associated with high host-plant densities.

ROOKS (*Corvus frugilegus frugilegus* L.)

HIDING NUTS IN HAWKE'S BAY

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Observation of individually marked rooks near Hastings in 1968-70 showed that 30-50% of feeding time in autumn and winter was spent in locating, eating or hiding nuts (Purchas, 1973). Walnuts and sometimes acorns were collected from trees or the ground below and carried singly in the bill to open areas of ground 25-300 m away. The nuts either were eaten immediately (after being hammered open with the tip of the bill) or were hidden singly in tufts of grass or in crevices between clods of ploughed soil. Stored nuts were covered with pieces

of dry dung, uprooted turf or soil. Rooks often moved the nuts to four or five different places before finally hiding them, particularly when other rooks were nearby.

Throughout the winter rooks frequently searched for and recovered hidden nuts which they ate or transferred to new positions. There was no difference between the rate at which nuts were found in 1968 and 1969; the average discovery rate for autumn and winter was 5.8 minutes per nut. However, the rate was faster in autumn than in winter when nuts were more scarce.

Records from 43 marked rooks sighted at least four times, showed that during autumn individual birds fed on only certain parts of the feeding area available. Statistically, this preference was highly significant. A sample of 17 birds, sighted at least six times showed that individuals again returned to their favoured feeding areas in the second half of autumn when hidden nuts were sought and recovered. Again, the trend was highly significant.

REFERENCE

- PURCHAS, T. P. G. 1973. The feeding ecology of the rook (*Corvus frugilegus frugilegus* L.) in the Heretaunga Plains, Hawke's Bay. Ph.D. thesis, Victoria University of Wellington, New Zealand. 125 pp.

SOME ADAPTIVE MECHANISMS AFFECTING THE DISTRIBUTION OF BUMBLEBEES IN NEW ZEALAND

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All four species of bumblebees now present in New Zealand were introduced from England. Two species *Bombus terrestris* (L.) and *B. ruderatus* (Fab.) were liberated near Christchurch in 1885 and soon spread throughout the North and South Islands. Their initial spread was, however, assisted by man. Two more species *B. hortorum* (L.) and *B. subterraneus* subsp. *latreillellus* (Kirby) were introduced in 1906 and again liberated near Christchurch. Because of the difficulty for a layman to distinguish between these species and those already established, it is unlikely that nests or queens of the new species would be sent off to other parts of New Zealand by private individuals as was done with those species initially established. The spread of these two latter species, therefore, can safely be assumed to be natural and unassisted by man.

In the 1950's and 60's the pattern of distribution

of bumblebees in the South Island was shown to be: *B. terrestris* and *B. ruderatus* throughout; *B. hortorum* was confined to the eastern side of the main divide south of Amberley and was recorded from 59 different localities embracing Canterbury, Otago and Southland; *B. subterraneus* was found only on the eastern side of the main divide south of Lincoln and was recorded from 20 different localities. *B. subterraneus* is mainly an upland species and is restricted to the sub-alpine basins on the drier side of the Southern Alps. It is found in numbers only in Mackenzie Country and the Wanaka-Hawea Flat areas of Central Otago. Even within these districts its abundance is strikingly variable from locality to locality.

Some possible adaptive mechanisms affecting the distribution of bumblebees, especially *B. subterraneus* were discussed. It was contended that the rigorous climatic conditions in the sub-alpine regions would be the most potent selection pressure that determined the relative abundance of species in those areas. It would work in two ways; by determining the flowering season of food plants, and the weather conditions in which the bumblebees could fly to collect their food. This places a premium on the thermo-regulatory mechanisms of the species. It is observable that *B. subterraneus* can fly in more inclement weather conditions (colder and windier) than the other three species and this indicates a more efficient thermo-regulatory ability.

The morphological adaptations that would facilitate this capacity in *B. subterraneus* are:

- (a) both the queens and the workers are large, especially the first formed workers, thus minimising surface heat loss;
- (b) the dense coat of short hairs which consists of a plumose underfelt and a scaly set of guard hairs form a very efficient insulating mechanism, retaining the heat produced by biochemical mechanisms in the thoracic flight muscles—a process which, it has recently been postulated, raises the internal thoracic temperature to the 30°C necessary for the flight muscles to operate.

The behavioural adaptations that favour *B. subterraneus* in sub-alpine conditions are:

- (a) late emergence from hibernation, thus ensuring emergence when its food plants are in flower and when weather conditions are more settled;
- (b) it has a foreshortened life cycle, with a large first brood, and the nest reaches climax quickly with early queen production. The young queens are thus fertilised and safely hibernated before the onset of cold weather.

The other species, *B. terrestris*, *B. ruderatus* and *B. hortorum* have a long season on the wing and consequently in the sub-alpine conditions face all the hazards of the early spring and late autumn. In the milder conditions of the lower level habitats this character is to their advantage because they can establish nests and flourish before the late emerging *B. subterraneus*.

It was contended that the adaptations discussed were the major determinants of the uneven distribution patterns of the four species in the South Island.

DISTRIBUTION, ECOLOGY AND PHOTOSYNTHESIS OF ALPINE RANUNCULI IN WESTERN NORTH AMERICA

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Snowbank plant communities (Fig. 1), at or above treeline in the mountains of western North America, from the Aleutian Islands of Alaska to southern California and New Mexico, usually contain one or



FIGURE 1. A snowbank habitat on the Olympic Peninsula, Washington, where *Ranunculus suksdorfii* subspecies *suksdorfii* occurs.

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more species of *Ranunculus*. In this paper the distribution, ecology and photosynthesis of six species of these snowbank *Ranunculi* are described.

These six species, previously classified as varieties of the single species *R. eschscholtzii* Schlecht., have three ploidy levels. There are three species with the diploid level ($2n = 16$), *R. oxynotus* Gray, *R. suksdorfii* Gray, and *R. macauleyi* Gray. *R. adoneus* Gray and *R. eximius* Greene are tetraploid ($2n = 32$), and *R. eschscholtzii* is hexaploid ($2n = 48$). (Although not discussed here, a count of $2n = 96$ was obtained for a seventh species *R. nivalis* L.). A detailed description of the biogeography of these species is published in Fisher et al. (1973).

All the species, with the exception of *R. eschscholtzii* have almost mutually exclusive geographical distributions (Fig. 2). *R. oxynotus* (Fig. 3a) is confined to the higher mountains of California and central Nevada. It has glaucous grey leaves and occurs in exposed, dry sites, often in the shadow of rocks. Unlike *R. eschscholtzii* it seldom occurs within the forest margin.

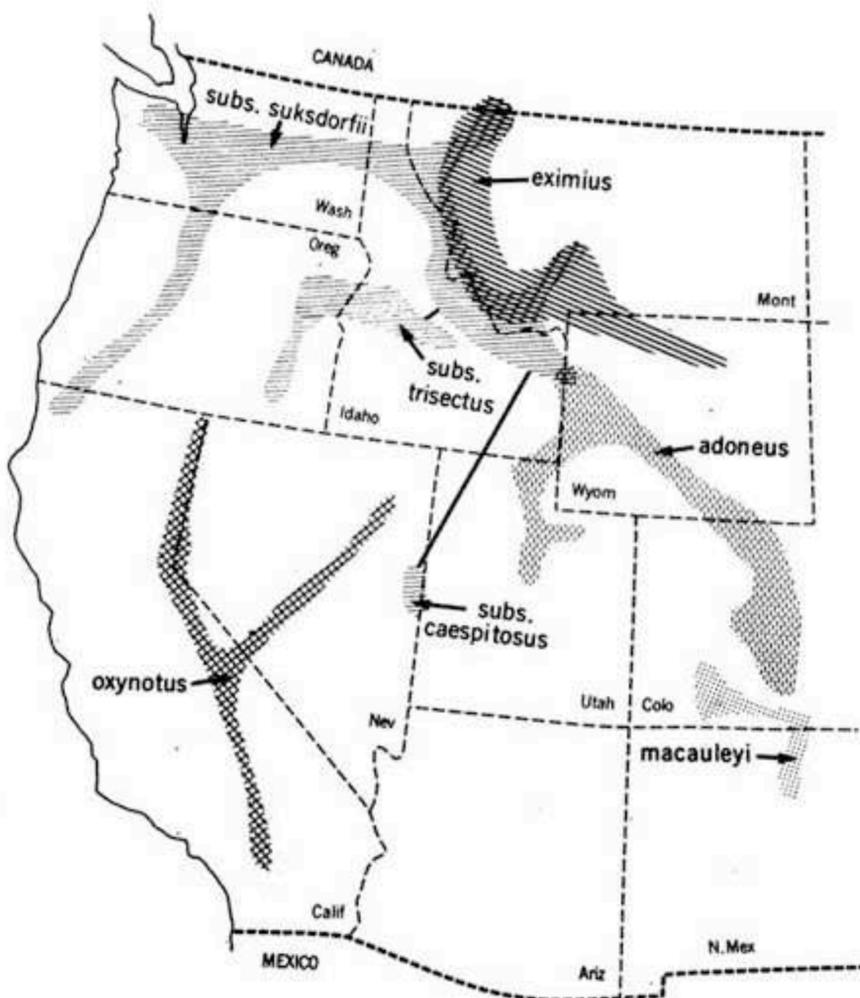


FIGURE 2. Distribution map of the diploid and tetraploid species: *R. oxynotus*, *R. suksdorfii*, *R. macauleyi*, *R. adoneus* and *R. eximius*.

There are three subspecies of *R. suksdorfii*. Extending from the mountains of northwest California,

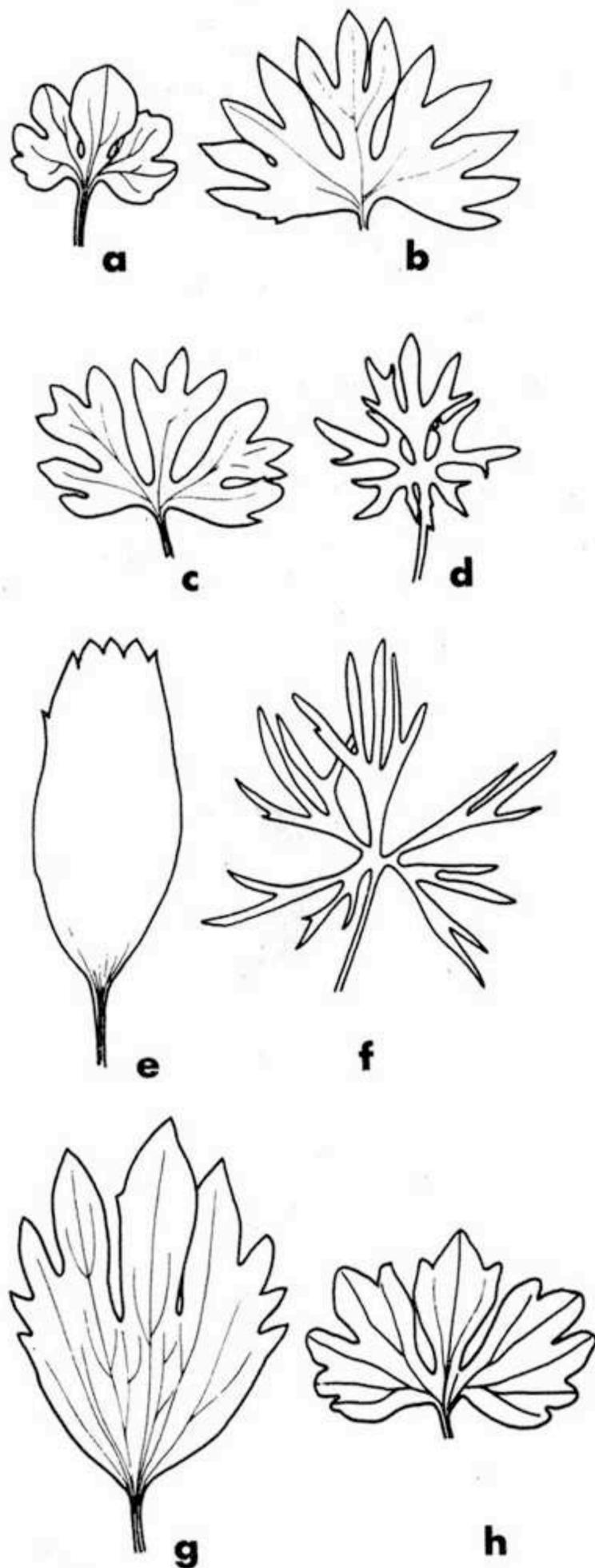


FIGURE 3. Typical leaf shapes of (a) *R. oxynotus*, (b) *R. suksdorfii* subsp. *suksdorfii*, (c) subsp. *trisectus*, (d) subsp. *caespitosus*, (e) *R. macauleyi*, (f) *R. adoneus*, (g) *R. eximius*, (h) *R. eschscholtzii*.

northwards through the frequently cloud-covered mountains of western Oregon and Washington, and eastwards, just south of the Canadian border is subspecies *suksdorfii* (Fig. 3-b). In the drier and less cloud-covered mountains of Idaho and eastern Oregon there is a gradual change to a glaucous and more narrowly lobed leaf form (subspecies *trisectus*, Fig. 3-c). Further south in the even drier and clearer mountains of eastern Nevada is subspecies *caespitosus* (Fig. 3-d), which is also glaucous, with finely dissected leaves. All three *suksdorfii* subspecies occur in exposed alpine herb-fields, close to patches of melting snow.

In the very high parts of the southern Rocky Mountains of southern Colorado and northern New Mexico, *R. macauleyi* (Fig. 3-e) occurs in both the shade of forest margins alongside *R. eschscholtzii*, and out into the open beside snowbanks.

R. adoneus (Fig. 3-f) occurs in the central Rocky mountains in Wyoming, southwards into Utah and central Colorado. It is found in open, exposed sites, receiving direct sunlight, and always occurs very close to patches of melting snow at high altitudes



FIGURE 4. Distribution map of the hexaploid, *R. eschscholtzii* in western North America (continuous line). The diploid and tetraploid species are confined to the cross-hatched area. With the exception of *R. oxynotus* populations in southern California, the diploids and tetraploids occur within the geographical range of *R. eschscholtzii*.

(above 3,500 m), where air and soil temperatures are low. Its leaves are even more finely dissected than those of *R. suksdorfii* subspecies *caespitosus*.

Occurring the full length of the Rocky Mountains in Montana and extending slightly into northern Wyoming, is *R. eximius* (Fig. 3-g). While frequently found in exposed sites, it occurs also within the forest margin, in some places alongside *R. eschscholtzii*.

The most widely distributed member of this group is *R. eschscholtzii* (Fig. 3-h), its range extending from the Aleutian Islands of Alaska to southern California and New Mexico (Fig. 4). In the southern part of its range it is found beside streams within the forest in quite deep shade. North of the Canadian border it often occurs in more exposed situations.

The distinct geographical and ecological distribution patterns of these *Ranunculus* species suggested that the group would be ideal for physiological investigation. Plants of these six species which were collected in the field were grown under controlled environmental conditions. Their photosynthetic response to various light and temperature regimes was measured using an infra-red gas analyser in a closed system, with a temperature controlled leaf chamber. There appeared to be a relationship between geographical origin and habitat, and the observed photosynthetic response.

All six species had a wide temperature tolerance within the 10°C to 30°C range, an advantage for alpine species in a habitat characterised by sudden and wide fluctuations in temperature.

The species which occur in open alpine herb-fields (*R. adoneus*, *R. suksdorfii* subspecies *caespitosus* and subspecies *trisectus*) required light intensities above 6000 foot-candles (ft-c) for light saturation of photosynthesis at 20°C. These species have more narrowly lobed leaves and a greater degree of leaf dissection than the other species. Boundary layer resistance is lower in dissected leaves than in entire leaves, so the more dissected or smaller the leaf, the lower is its resistance to heat transfer, carbon dioxide uptake or water loss (Lewis, 1972). It is possible to speculate that the lower resistance to carbon dioxide uptake may help these species to maintain high rates of photosynthesis at the high light intensities in the exposed habitats, while the lower resistance of their dissected leaves to heat

transfer would keep leaf temperature and hence respiration rate low. As these plants are always found close to melting snow, the lower resistance to water loss would not be disadvantageous. Since the growing season at high altitudes is very short, these plants must be able to make full use of high light intensities whenever possible.

Light saturation of photosynthesis occurred at 2000 to 4000 ft-c for species which are found in both open herb-fields and forest margins, or in open herb-fields in cloudy regions (*R. oxynotus*, *R. macauleyi*, *R. suksdorfii* subspecies *suksdorfii*, and *R. eximius*). These species have more entire leaves than those from the more exposed sites.

R. eschscholtzii had the lowest light requirement, with light saturation occurring at 1500 ft-c and with higher photosynthetic rates at the low light intensities than the other species. *R. eschscholtzii* has adapted to the forest margin habitat which is more continuously available throughout the western mountains than the high light, cool conditions beside snowbanks in open herb-fields. This remarkable range extension may have occurred with the change to the hexaploid level, as *R. eschscholtzii* has migrated rapidly far beyond the limits of the other species. The boundary for the northernmost extent of the diploid and tetraploid species seems to be the southern-most extent of the maximum Pleistocene glaciation, suggesting perhaps that either they have not had time to migrate north or that they are restricted by the unavailability of the specific habitat to which they are adapted.

ACKNOWLEDGMENTS

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