

Comparative Physiology of Ecological Races in *Mimulus*

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Perhaps most important among the causes of the distribution patterns studied by ecologists are the underlying physiological mechanisms which lead the organisms to prefer the conditions they do. These ecological aspects of physiology are not easily investigated, because so many factors are usually interacting that straightforward separation into specific physiological questions is not usually possible. However in occasional rather rare situations only a small part of this complex needs to be considered and the ecological questions can be posed in more clearcut physiological terms. This happens when, for example, a pair of distinct but otherwise closely related kinds of organism have a mutually exclusive distribution coupled with a simple but definite environmental change. A case of this sort is found in the two species of *Mimulus*, *M. cardinalis* and *M. lewisii* of the western states of North America. Although very distinct in morphology and distribution these two are genetically close enough to be regarded from an evolutionary viewpoint as sister ecological races.

These two species of *Mimulus* are perennials, one adapted to lowland and the other to highland habitats. Although able to form vigorous and healthy hybrid offspring their marked differences in floral and vegetative morphology, in their preferred habitats, and in their geographic distribution (Fig. 1), together with an absence of natural backcrossing, allow them to be treated taxonomically as very distinct species. Their ability to form fully fertile offspring in crosses, apart from a very occasional F_1 , is limited to the experimental garden as they possess very different pollen vectors, neither of which is able to achieve pollination of the flower appropriate to the other. The high altitude *M. lewisii* has pale pink flowers pollinated mainly by solitary bees (Nobs,

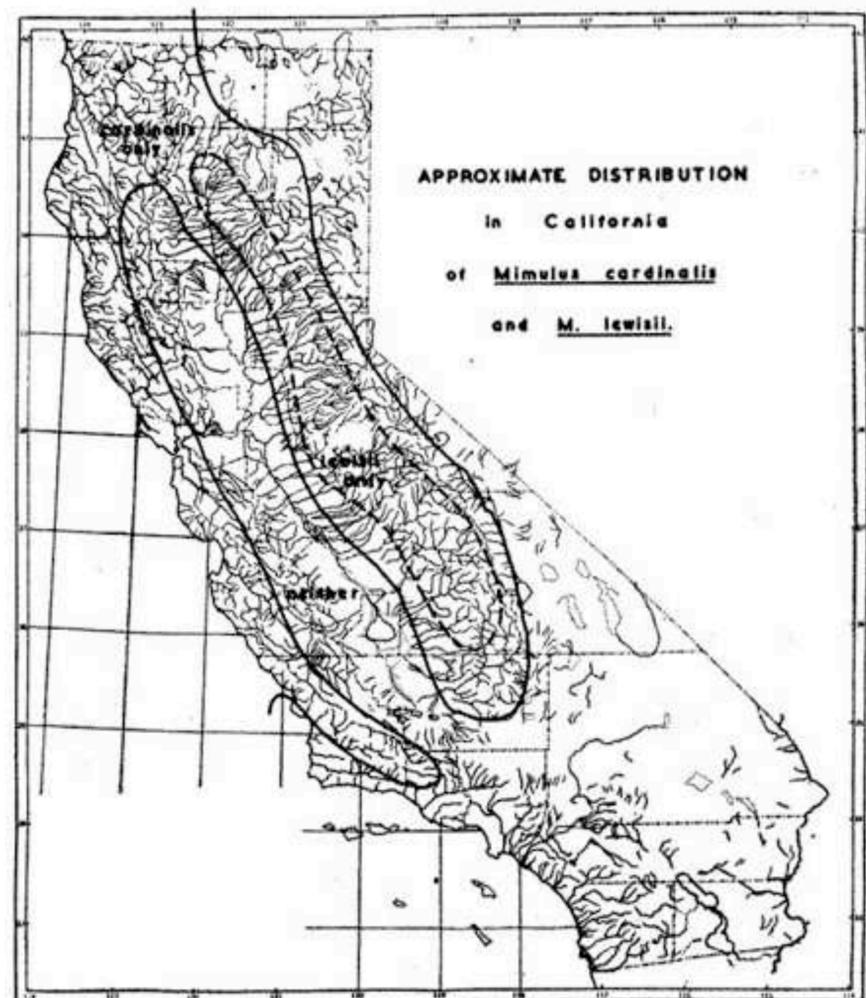


FIGURE 1.—Map showing approximate distribution of *M. cardinalis* and *M. lewisii* in California. Occasionally individuals of the alpine species are found downstream from their normal range and hybrids have occasionally been found.

unpublished) while the low altitude *M. cardinalis* has scarlet flowers usually pollinated by humming-birds. The colours, shapes and positions of the flowers are closely adapted to the appropriate pollinating agent (Fig. 2).

The habitat of *M. lewisii* is between 6000 and 11,000 feet on wet debris or talus material near melting snow. Its growth is limited to the two months of the year when the ground is free of snow. *M. cardinalis* is generally confined to sheltered stream banks in forested areas below 5000 feet where

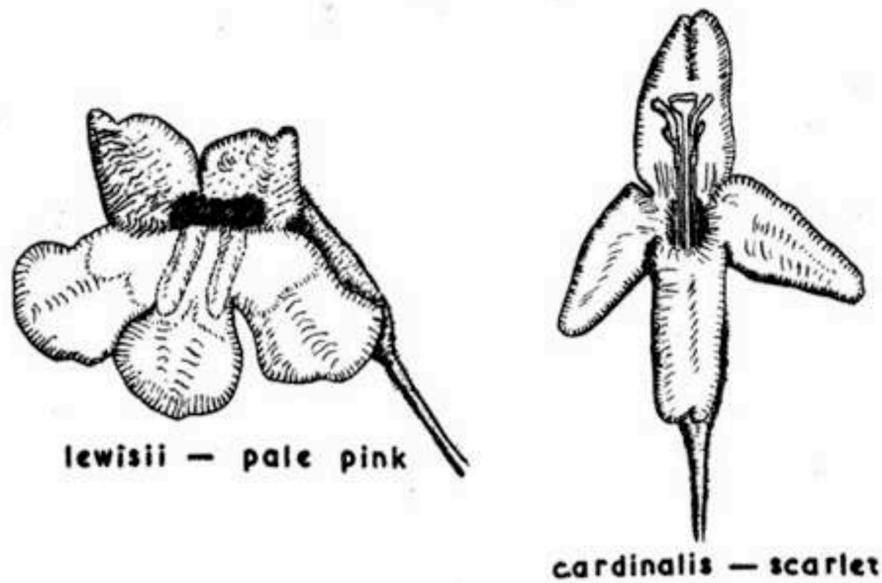


FIGURE 2.—Diagrams of the flowers of the two species showing their marked difference in shape and arrangement. The three lobes of the lower lip of *M. lewisii* form a kind of landing platform for the insect pollinators. The narrow tube of *M. cardinalis* cannot be entered by large insects but the nectar is easily reached by humming birds.

temperature extremes are much less common than in the exposed debris habitat of the highland species. Growth of *M. cardinalis* lasts throughout the year, the plants dying back to a small rosette during the winter. Dormancy of the alpine species has been found to be controlled by daylength, being induced by photoperiods of less than 15 hours. In *M. cardinalis* limited growth of the vegetative rosettes occurs until the daylength exceeds 13 hours when flowering buds are initiated (see Nobs, 1955).

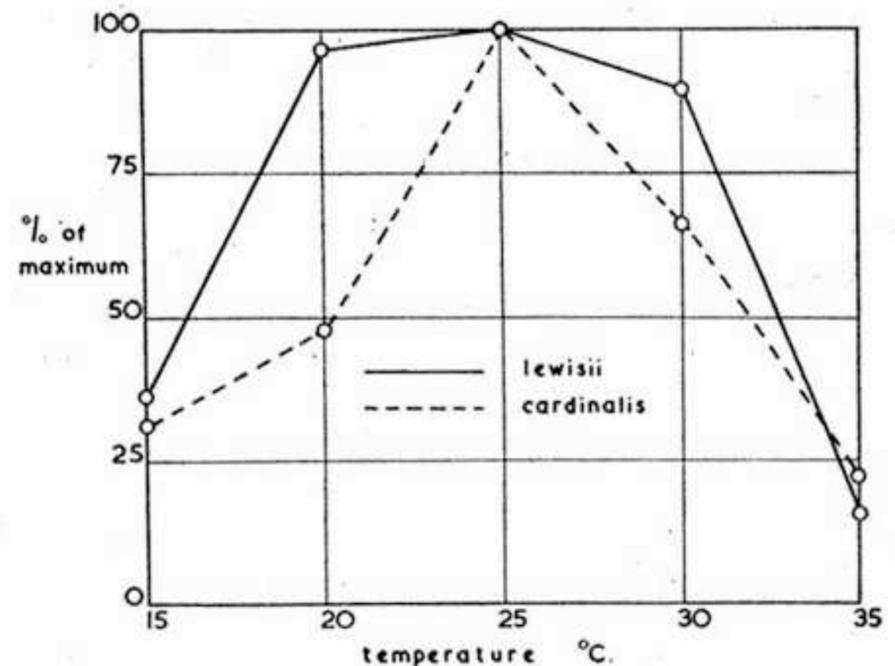
Preliminary experiments have been carried out to determine whether differences in growth rates and assimilation rates between the two species might help account for their distinct ecological preferences.

Growth rates of the species were determined between 15 and 35°C. in steps of 5°. Sterilised seeds (H_2O_2 and bleaching solution) were germinated on Heller's medium (Heller 1953), nutrient agar, in 200 ml. flasks under approximately 1000 f.c. from white fluorescent tubes. Dry weights were determined at the end of two months (Fig. 3). The seedlings of *M. cardinalis* (Los Trancos population) grew most rapidly at 25°C. with the rate falling off steeply at high or lower temperatures. The seedlings of *M. lewisii* (White Wolf population) produced a fairly

flat response between 20° and 30°C.

In order to provide a physiological basis for these differences in temperature tolerance shown in the growth experiments, the rates of CO_2 uptake and output were determined over a similar range of temperatures. In this preliminary experiment only a small number of plants were used and though a satisfactory level of precision (3 ppm.) was available in the apparatus used, the initial results must be regarded as provisional owing to variability between the plants. A Liston-Becker infra-red gas-analyser was used for measuring CO_2 exchange, the plants being kept at a constant temperature in a water bath which also helped reduce the heating effects of the lamps (Fig. 4). The response curves for the two species (Fig. 5) correspond to those for the growth rate experiments. The peak in the curve for *M. cardinalis* was again found to be at 25°C. while that for *M. lewisii* was found to be at 27°C. Again, a broad temperature tolerance is shown in the curve for *M. lewisii* and a narrow one for *M. cardinalis*.

It should be asked how far these responses help provide a physiological explanation of the observed distribution patterns. The alpine talus habitat is characterised by sudden and marked fluctuations in temperature and



GROWTH. 64 days agar, 1000 f.c. 16 hr. day

FIGURE 3.—Response curves for growth rates measured as dry weights after two months at each of five temperatures. Compare with curves for assimilation rates in Fig. 5. Twenty seedlings were grown at each temperature.

hence a broad tolerance might be expected to be advantageous to the alpine species, particularly as the growing season is so short. The narrow response of the lowland species may be seen to correspond to the relatively uniform temperatures and long growing season of the lowland forest-margin habitat.

However, important questions are left unanswered. The difference in temperature tolerance range does not explain the absence of the broadly tolerant species in the lower altitude environment, where presumably slightly higher temperatures should be quite suitable. A possible explanation is that the daylength effect on dormancy in the alpine species might place it at a disadvantage at low altitudes. It was found by Nobs (1955) that the highland species loses all its leaves irrespective of the temperature during the ten months when normally dormant while the daylength is less than 15 hours. Under warm conditions at lower altitudes than normal, it is possible that all reserves in the storage organs are consumed by accelerated respiration before summer growth is resumed under appropriate daylengths. If this is the explanation then perhaps a threshold line exists along the lower distribution limit of the species where just sufficient reserves remain for the plants to survive the dor-

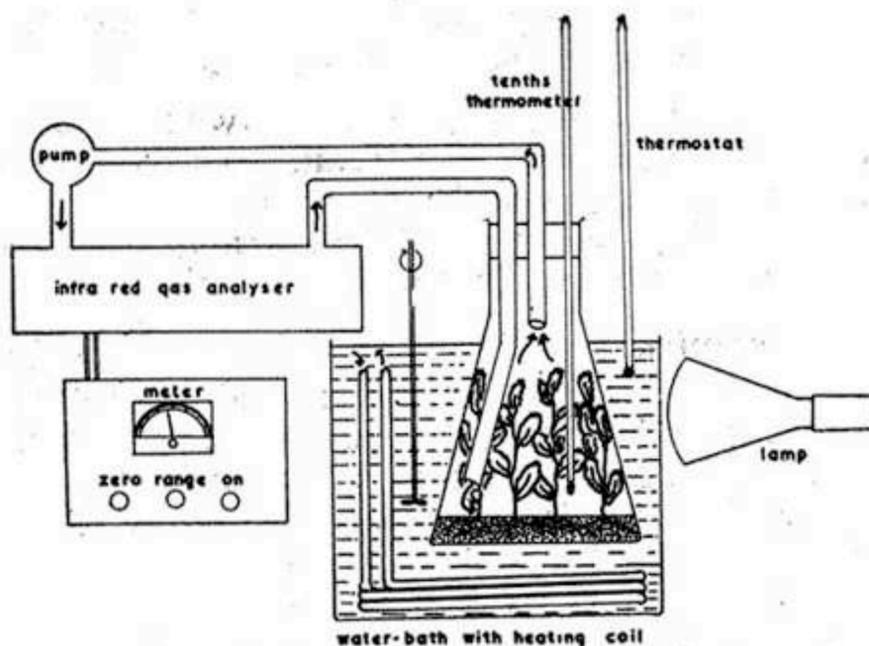
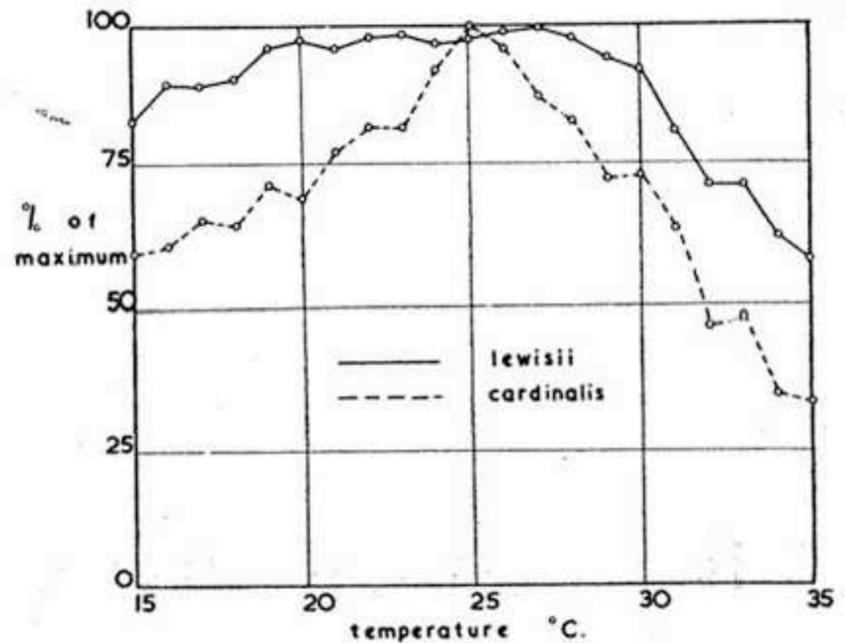


FIGURE 4.—Schematic diagram of apparatus used for measuring CO₂ exchange in *Mimulus*. Temperatures were kept constant by the circulation of hot or cold water through the heating coil, the pump being controlled by a capacitor-thermostat utilising the water bath thermometer.



CO₂ UPTAKE. 52-day seedlings. aqar. 1000 f.c. 300ppm.

FIGURE 5.—Response curves for CO₂ uptake as measured by the infra-red gas analyser. Each point represents the mean of five determinations, each flask containing between 5 and 30 seedlings.

mant season. Nobs (ibid) also found that the lowland species succumbs to frosts in the higher habitat, so again perhaps the lowland species is prevented from migrating to higher situations at a certain threshold beyond which frost damage prevents recovery.

In conversation, Dr. J. A. Rattenbury has suggested that the boundary required for limiting the intermigration of the two species might be the winter snowline which in some parts of western North America is extremely consistent from year to year.

Postscript

Since these studies were carried out at the Stanford laboratory of the Carnegie Institution of Washington more intensive work has been initiated. Preliminary reports (see Milner et al. 1958) indicate a high variation in temperature responses even between individuals of the same population as well as significant differences between samples from different races.

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