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Heterophylly in *Eryngium vesiculosum* (Umbelliferae)

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Abstract *Eryngium vesiculosum* is a small rhizomatous, perennial umbellifer of coastal sands, lake margins, and riverbeds in New Zealand. The species is seasonally heterophyllous; summer leaves are laminoid and prickly, winter leaves are linear and fistular. This form of structural variation is classifiable as a conditional choice. Experiments using controlled conditions showed that daylength cues the change of leaf form which occurs in autumn and spring, and that total immersion in water affects leaf form to a lesser extent and prevents flowering. It is suggested that summer leaves are adapted to well-drained conditions, and winter leaves to inundation by water.

Keywords *Eryngium vesiculosum*; heterophylly; leaf form; daylength; aquatic plants; New Zealand

INTRODUCTION

Variation in plant structures may be classified into several more or less distinct classes. Conditional choices, one such class, occur when a cue from the external environment, or the plant's own status, triggers one of two or more distinct canalised pathways, depending on whether the cueing factor is above or below a critical threshold (Lloyd 1984). Examples include the production of cleistogamous and chasmogamous flowers when this is related to environmental factors (Lord 1981), sex change related to plant status (Policansky 1981), and seasonal heterophylly (Critchfield 1960; Green et al. 1979; Eckenwalder 1980; Westman 1981).

Multiple responses are those variation strategies which occur when a single class of individuals exists in a population and individuals simultaneously produce two or more distinct types of structure that perform the same general function (Lloyd 1984). Multiple responses include the production of two types of gametes by cosexual plants (Lloyd 1984),

and the production of specialised aquatic and aerial leaves by many aquatic plants (Sculthorpe 1967).

In a survey of variation strategies in the New Zealand flora Lloyd (1983) notes that there are very few examples of conditional choices for any function, although multiple responses are common. This paper describes a striking example of heterophylly in the native New Zealand *Eryngium vesiculosum* Labill. (Umbelliferae; Saniculoideae), relates this to the concepts of conditional choice and multiple response, and discusses the environmental control and adaptive significance of this leaf dimorphism.

Within New Zealand, *Eryngium vesiculosum* occurs in coastal sands and gravels in the North and South Islands, and grows further inland in some Canterbury riverbeds. It is native also to south-eastern Australia.

MATERIALS AND METHODS

Plants of two genotypes of *E. vesiculosum* were collected from gravel on the lakeshore of Lake Forsythe, coastal Canterbury, and grown on at Botany Division, Lincoln. The species is rhizomatous and once new rosettes had been produced these were potted on to give clonal material for experiments.

The response of plant leaf form to water was tested in the greenhouse under normal daylength at Lincoln. In the first treatment two plants of each clone were immersed in a water tank up to the level of the base of the rosette, and in the second treatment plants of each clone were completely immersed. Control pots were positioned embedded in charcoal ash next to the water tanks and were watered about three times weekly. All treatments were started in early summer when plants were producing spatulate prickly leaves and were continued until a change in leaf form was observed.

The effect of daylength was examined by putting four pots of each clone in growth chambers at the Department of Botany, University of Canterbury; two pots of each clone were subjected to 9-h days at 20°C and two to 16-h days at 20°C — both were given normal hand watering. Again control plants were observed under glasshouse conditions at Lincoln. All light treatments were started in early winter when plants were producing linear, entire leaves. After 10 weeks in these light treatments, one plant of each clone was transferred to the alternative light treatment for a further 7 weeks.

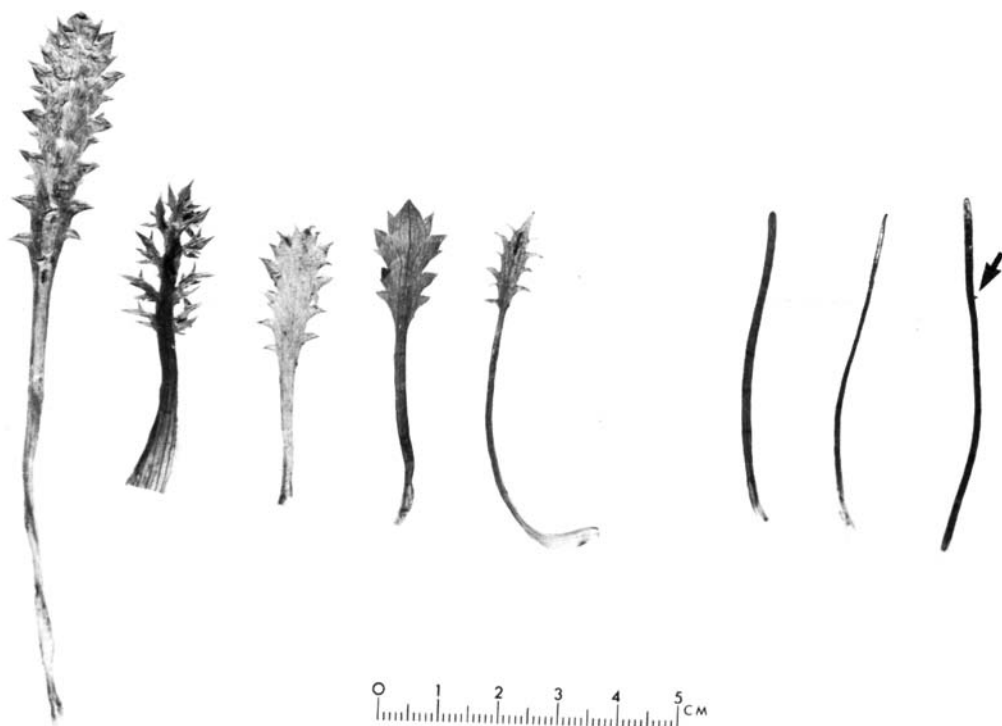


Fig. 1 Leaf form in *Eryngium vesiculosum*. Left: five summer leaves showing variation in leaf form. Right: three winter leaves; small tooth at septum arrowed. (Photo: J. Miles).

RESULTS

Leaf form

Eryngium vesiculosum produces two distinct types of leaves. During the summer and while the plant is flowering, all leaves are tough, laminoid, spathulate, petiolate, and with distinctly prickly margins or are even pinnatisect (Fig. 1). These are termed *summer leaves*; their petioles are flattened but hollow, and the lower part of the leaf blade may be hollow within the midrib. During the winter, prickly leaves are absent, and soft, fistular, linear, septate leaves are produced; these leaves have no clearly distinguishable petiole, and no prickles, but occasionally have one or two small projections on the septa at the margins (Fig. 1). These *winter leaves* are cylindrical or slightly flattened and are hollow throughout their length. The small projections at the septa indicate that the winter leaves are derived from reduction of the whole leaf. The difference between the two leaf forms also involves a change in leaf area. The adaxial surface area, excluding the petiolar sheath but including the petiole, is about three times greater in the summer leaves (summer leaves, $113.0 \pm 10.1 \text{ mm}^2$, $n = 10$; winter leaves, $33.6 \pm 3.1 \text{ mm}^2$, $n = 10$). Transition between the

two leaf forms occurs in early spring and early autumn, when intermediate forms of leaf are produced, often with narrow flattened blades with a few prickles at the margin.

Seedling leaves are of the linear, winter form.

Response to water

Plants which were immersed in water tanks in early summer to the base of the rosette continued to produce summer leaves similar to those of control plants. A change in leaf form did not occur until autumn; at this time both the immersed plants and the control plants began to produce intermediate leaves and eventually the typical winter leaves were produced by all plants. The change to winter leaves occurred somewhat more rapidly in the immersed plants, probably because of their generally more vigorous growth and greater rate of leaf production.

Plants completely immersed in water to more than 3 cm above the leaf tips initially continued to produce prickly leaves. However, after 7 weeks immersed plants of both clones produced intermediate, almost-linear leaves with a few marginal prickles, while control plants continued to produce



Fig. 2 Experimental plants of *Eryngium vesiculosum* photographed against white card around base of plant and covering pots. Left: plant from 9-h day with two prickly leaves from previous summer but otherwise continuing to produce winter leaves. Right: plant of same genotype after 8 weeks in 16-h day showing production of summer leaves. Scale as for Fig. 1. (Photo: J. Miles).

summer leaves. When the water level dropped to just above the leaf tips the immersed plants again produced summer leaves but with a reduced area of leaf blade. When the water level was again raised to 3 cm above the leaf tips, leaves of intermediate form were produced with short narrow blades fringed with incurved prickles.

During the late summer all control plants flowered, plants submerged to the base of the rosette also flowered, although less vigorously, while none of the completely submerged plants flowered.

Response to daylength

Plants producing winter leaves continued to do so when subjected to a 9-h day at 20°C, whereas a gradual transition to summer leaves was evident in plants in a 16-h day at 20°C — intermediate leaves were produced after 5 weeks with full summer leaves being produced after 8 weeks (Fig. 2).

When one plant of each clone was then transferred to the alternative daylength, reversal of leaf form occurred in both instances in less than 7 weeks.

Control plants at Lincoln continued to produce only winter leaves throughout the period of these daylength treatments.

Both genotypes reacted similarly in all experiments.

DISCUSSION

Although the leaf dimorphism described here for *Eryngium vesiculosum* is striking, it was not recorded in the original description of the species (Labillardière 1805), and only summer leaves are described in New Zealand and Australian floras (e.g., Hooker 1864; Bentham 1867; Allan 1961; Curtis 1963). Heterophylly is not discussed in more general ecological references to the species either (e.g., Cockayne 1910; Moore & Adams 1963). However, a similar form of heterophylly has been described for a group of about 12 Californian species of *Eryngium* (Hooker 1847; Jepson 1925; Sheikh, unpublished Ph. D. dissertation, 1978). These species produce linear leaves when submerged in vernal pools in winter, and produce prickly leaves and flower once these pools dry out.

The experiments reported here show that a change in leaf form for *E. vesiculosum* is cued by daylength and is affected to a lesser extent by water level. For Californian species of *Eryngium*, Jepson (1925) described the linear leaves as an aquatic leaf form, and Sheikh (unpublished data) has shown that plants which are kept completely submerged continue to produce linear leaves and do not flower. Sheikh concluded that change in leaf form is controlled by water level and temperature but that there is considerable flexibility closely related to ecolog-

ical conditions. Californian plants are perennial if provided with a continuous water supply but are functionally annual in the field. Water level affects flowering and leaf form in rhizomatous perennial *E. vesiculosum* but it is not possible to judge the relative effects of daylength and water level on Californian and New Zealand species because the effect of daylength was not investigated for Californian plants. As California has more marked wet and dry seasons than does New Zealand, water level may be a more reliable cue for change in leaf form there.

Both forms of leaf may be found simultaneously on plants of *E. vesiculosum* especially when new rosettes with only winter leaves are produced on rhizomes in autumn. However, with the exception of a short period when transitional leaves are formed, only one type of leaf is actually produced by the plant at any time, and therefore the heterophylly found in this species is classifiable as a conditional choice, following the definitions of structural variations outlined by Lloyd (1984). This, therefore, represents one of the few examples of a conditional choice known for the New Zealand flora.

Seasonal heterophylly is known in several species and the different leaf forms are usually assumed to be adapted to the conditions prevailing when they function (Green et al. 1979; Westman 1981), although other authors stress the pattern of leaf ontogeny as a cause of leaf form (Critchfield 1960). It seems likely that in *E. vesiculosum* the leaf forms are adapted to different seasonal growing conditions, including water levels, light conditions, and temperature in spite of the fact that the change in leaf form is cued by daylength. Linear leaves are known in many aquatic plants (Sculthorpe 1967; P. N. Johnson, pers. comm.) and in fact the winter leaves of *E. vesiculosum* closely resemble those of the aquatic genus *Lilaeopsis* (Umbelliferae; Apioidae). *Cotula maniototo* similarly produces pinnatifid leaves in summer and simple linear leaves in winter (Lloyd 1972), but daylength is not an effective cue in this species (Lloyd, unpublished data). The hard prickly summer leaves of *E. vesiculosum* probably reduce the loss of water through transpiration — divided leaves are frequent in seasonally dry habitats (Givnish 1979). Although the production of prickles is sometimes interpreted as a defence against mammalian herbivores (Givnish 1979), in *E. vesiculosum* it is more likely to be a response to dry summer conditions. The prickly summer leaves are typical of those found in the genus as a whole.

The seasonal heterophylly described here for *E. vesiculosum* fits the species well to its known habitats — coastal areas, lake shores, and riverbeds — which are likely to be inundated by water in winter but well-drained and dry in summer.

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