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Senecio lautus complex in Australia IV. The biology of the complex¹)

By

Syed Irtifaq ALI²)

Botany School, University of Melbourne, Australia With 1 Figure

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1. Introduction

Senecio lautus complex is widely distributed in Australia and New Zealand, growing in extremely varied ecological regions from alpine,

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²⁾ Present address: Dr. Syed Irtifaq ALI, Department of Botany, University of Karachi, University Road, Karachi-32, Pakistan.

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moist gullies, mallee, sand dune and extreme maritime habitats along the coast to severe desert conditions in Central Australia. It has been shown earlier that six genoecodemes (five Australian and one New Zealand) may be recognised in this complex (ALI 1964 b) and that taxonomically it seems best to accommodate them under the same species (ALI 1964 a). The genetic system operative in this complex has been discussed subsequently with a view to explain the variation pattern (ALI 1966). In order to have a better understanding of the adaptive mechanism operative in this complex, in addition to the genetic system, an understanding of the biology of the complex, is imperative. It is with this view that the data available about various aspects of the problem is being presented here. Some of the aspects discussed earlier (ALI 1964 b; 1966) seem relevant here as well. However, in this paper, only additional evidence not presented earlier is put forward, though in discussion, effort is made to present a coordinated view of the whole problem.

2. Material and methods

Representative populations of various Australian genoecodemes of Senecio lautus were grown under glass house conditions, the environment of which has been previously documented (ALI 1964 b).

The germination studies were carried out under controlled conditions, so that the information regarding the percentage of germination may not be applicable under different environmental conditions. Samples of 60 seeds, representing three different gatherings, from each of the genoecodemes (except the montane, desert and New Zealand genoecodemes, where material from fewer sources was available) were germinated in moist vermiculite, which was supplied at weekly intervals with one-tenth the original strength of modified Hogland's solution. The growth room conditions may be summarized as follows: Temperature $70-80^{\circ}$ F.; humidity 70-80 per cent; illumination provided by a combination of warm white flourescent tubes and incandescent strip lamps, giving a light intensity of c. 1000 f. c. at the level of the seedlings. The experiment was repeated twice, first with 8 hours and then with 16 hours light regimes. The results obtained in both cases were not very different. The experiment was continued for about seven weeks.

3. Observations and results 3.1. Duration of life

It is interesting to note that the montane and the moist gully genoecodemes are definitely perennial; most of the coastal and coastal sand-dune forms also seem to fall in this category, although a few are probably unable to survive the severity of the environment. The mallee and the inland desert forms behave as annuals in nature. However, under glass-house conditions, an appreciable number of plants representing mallee genoecodeme were able to over-summer, though the inland desert forms behaved strictly as annuals. In nature, because of the intense heat during the summer, only a few mallee plants can live through the summer. The situation has been summarized in Table 1.

Table 1

Average Reproductive Capacity, duration of life and Vegetative Propagation

Genoecodeme	Average Reproductive Capacity	Duration of life	Vegetation Propagation
Desert	103.09	Annual	Nil
Mallee	813.01	Mostly Annual	Nil
Coastal	2851.96	Mostly perennial	Uncommon
Moist Gully	405.92	Perennial	Common
Montane	552.50	Perennial	Common

3.2. Vegetative propagation

The genoecodemes of (I) mountains, (II) moist gullies and (III) coastal regions were observed to reproduce vegetatively by rooting at the nodes, though this tendency seems more pronounced in the first two cases. In the montane genoecodeme where the branches form a prostrate cushion-like structure and the erect branches are only produced at the time of flowering, the rooting at the nodes is a common feature, and by the disappearance (by death, etc.) of the intervening portions of the plant between two such points, independent plants may come into existance. In the moist gully genoecodeme, generally a number of robust branches are produced near the base of the main stem; most of these branches remain erect, but in most cases one (or more) of the branches becomes decumbent, thus touching the ground. The roots are formed, not only at the nodes, but also all along the internodes, and even from those portions which are not in direct contact with the soil. A fair amount of moisture, however, is necessary for this purpose, which, under natural conditions, is plentiful.

Among the plants of the coastal genoecodeme vegetative propagation is uncommon in nature. This is probably because of the lack of moisture in the surface layer. Under glasshouse conditions, however, rooting at nodes, particularly when in contact with the moist sawdust or soil, was frequently observed. This indicates at least the potentiality of the plant to resort to vegetative propagation under similar conditions.

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3.3. Fruit weight

The mean weight of the fruit in different genoecodemes is presented in Table 2. The desert and New Zealand genoecodemes bear the heaviest fruits, while fruits from the moist gully genoecodeme are comparatively the lightest.

Table 2

Fruit weight in different genoecodemes

Genoecodemes	No. of samples	No. of fruits	Mean weight of fruits in gms.
Desert	2	300	0.000686
Mallee	3	250	0.000273
Coastal	3	300	0.000295
Moist gully	3	265	0.000234
Montane	2	160	0.000395
New Zealand	2	200	0.000639

3.4. Fruit dispersal

In S. lautus, dispersal of fruits by wind is most common, as in the case of other Composites, because of the presence of plumed fruits. To a limited extent dispersal by birds and other animals probably also takes place, because the fruits, particularly when wet, are capable of adhering to various parts of the animal. In the present case the pappus is very easily detached from the fruit, so that, when the fruit comes up against a branch or other obstruction in the course of flight, it becomes detached from the pappus and falls on the ground. Thus, as expected, the plants of this species are present in open countries, on edges of thickets and bases of hedges etc. because they are less likely to reach dense forests. This agrees with the generalisations made by RIDLEY 1930 that "plants with plumed fruits are characteristic of open countries..."

3.5. Seed germination

The results of seed germination studies are presented graphically in Fig. 1. It is observed that germination in five out of six genoecodemes starts on the fifth day after sowing; however, the rate as well as the percentage of germination is strikingly different in different cases. On the seventh day, when the desert genoecodeme has just started germination, 78.33 per cent of the seeds have already germinated in the cases of montane and New Zealand genoecodemes. After 38 days the New Zealand genoecodeme shows the highest percentage of germination and the desert genoecodeme the lowest (22.5 per cent).

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3.6. Reproductive capacity

In the case of *S. lautus* the number of seeds per plant per year depends upon (a) the number of capitula per plant per year (in the case of perennials the values will have to be obtained at different stages of reproductive maturity), and (b) the number of cypsela per capitulum formed under natural conditions. These values are then multiplied by the average percentage of germination to obtain the value of "Average Reproductive Capacity." However, in view of the various limitations, it has not been possible to obtain information about various aspects of this problem under natural conditions, although the information obtained from the representatives of various genoecodemes, when grown under similar conditions, is discussed here.

The information about the number of capitula per plant per year is presented in Table 3. The number of fruits per capitulum formed under open system of pollination is presented in an earlier paper (ALI

Genoecodeme	No. of plants	No. of capitula per plant Minimum, mean and maxim				
Desert	5	3-(6.4)- 11				
Mallee	5	26-(35.6)- 53				
Coastal	7	5-(83.4)-251				
Moist Gully	5	9-(35.4)- 72				
Montane	13	4-(19.4)- 55				

T	a	bl	e	3	

Number of capitula per plant per year

1966) and the information regarding germination percentage has already been discussed. The values of "Average Reproductive Capacity" have been calculated for various genoecodemes and are presented in Table 1.

3.7. Insect and fungal pests

The reproductive capacity of the plant, as well as its performance in other respects, is expected to be considerably affected by various insect and fungal pests, and, therefore, consideration of this aspect seems desirable.

3.7.1. Insect pests

Information concerning the insects that cause damage to *S. lautus* is extremely scanty, but the information that is available is presented here.

1. Homoeosoma farinaria TURNER (Phycitidae) — Larvae seen feeding on the roots and the bark at the base of the stem. (ANONYMOUS 1957).

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2. Aphids, particularly from the mallee areas (personal observation).

3.7.2. Fungal pests

1. Puccinia erechtitis MCALPINE, reported from New Zealand (CUNNINGHAM 1931), New South Wales (ANONYMOUS 1958).

2. Puccinia distincta McAlpine (Langdon 1957).

3. Albugo tragopogonis (DC.) S. F. GRAY — New South Wales (ANONYMOUS 1958).

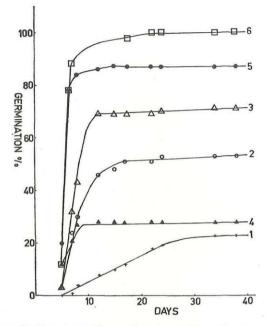
4. Sphaerotheca fuliginea (SCHLECHT.) POLLACCI (PARBERY — unpublished).

4. Discussion

It is well known that a delicate balance exists between the genotypic composition of a taxon and its environment, the later acting as sieve to eliminate the unfavourable genetic combinations. Thus only those combinations can survive which are especially adapted for the particular circumstances. (CLAUSEN, KECK & HIESEY 1940; 1948; TURESSON 1922 a; 1922 b; STEBBINS 1950; GRANT 1963; ALI 1964 b).

The adaptive mechanism operative in different taxa involves a flexible compensatory system of adaptation where a relative lack of fitness in one character may be compensated by special suitability in another character (CLAUSEN, KECK & HIESEY 1948; STEBBINS 1950). Thus the dynamic process of adaptive mechanism operative in a taxon may be quite complicated and is generally effective at numerous stages involving many compromises (CLAUSEN, KECK & HIESEY 1948; STEBBINS 1950; GRANT 1963). Further, it is expected to vary slightly from individual to individual in minute details. Only the salient features of such adaptations can possibly be taken into account, the minute details more often remain obscure.

The variation pattern of *Senecio lautus* complex has been explained by the author in the light of the breeding systems met with in various genoecodemes (ALI 1966). In this connection the duration of the life of the plant is also very important. As shown in Table 1, different genoecodemes are quite variable in this respect also. The moist gully and montane genoecodemes behave as perennials, the coastal genoecodeme consists of mostly perennial members, the mallee genoecodeme has mostly annual plants and the desert genoecodeme consists of only annual representatives. STEBBINS 1950; 1958 has already pointed out the correlation between the perennial habit and capacity for vegetative propagation in flowering plants in general. In the case of *Senecio lautus* we find that there is direct correlation between the duration of life of the plant and the capacity for vegetative propagation in closely related genoecodemes of a species (Table 1). The low percentage of germination of desert and moist gully genoecodemes (Figure 1) may reflect specialised environmental conditions



F i g. 1. Germination percentage of seeds. 1, Desert genoecodeme; 2, Mallee genoecodeme; 3, Coastal genoecodeme; 4, Moist Gulley genoecodeme; 5, Alpine genoecodeme; 6, New Zealand genoecodeme.

which may be essential for germination of seeds in either case. On the other hand the presence of dormancy may be looked upon as an advantageous feature. In the case of desert plants it is indeed advantageous that all the seeds do not germinate after the first shower, for, unless the seedlings have proper environmental conditions, they may not be able to survive, and the lack of dormancy may result in the complete disappearance of a particular species, as in the case of *Clarkia* (LEWIS 1962). CROCKER 1948 has stated that delayed and distributed germination is very common in wild plants, and BARTON & CROCKER 1948 have emphasized that, from the point of view of continuance of species, delay in germination is of great value to the plant.

In the case of moist gully genoecodeme, enough moisture is available all the year round and therefore immediate germination may be possible. But as already pointed out by ALI 1964 b competition from other plants is one of the important factors affecting the establishment and survival of moist gully plants. It is not unlikely that in such situations also, where competition is active and the suitable habitat is not imme-

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diately available because most of the ground is covered by other plants, seed dormancy is found to have adaptive significance.

It may be assumed that in fruits having similar metabolites, fruit weight is a rough approximation of the amount of the food supply available for the seedling. Therefore it affords some indication of the length of time the seedling can persist under conditions below the "compensation point" (SALISBURY 1942). Thus, under adverse conditions, seedlings obtained from heavier fruits in the desert genoecodeme might have been evolved to cope with the unfavourable environmental conditions, by conferring upon the seedlings better survival value by virtue of the greater amount of stored food in the fruits.

The presence of comparatively heavy fruits in the New Zealand genoecodeme, which is the inbreeding member of the complex, is thoughtprovoking. As yet no attempt has been made to correlate the fruit or seed weight and breeding systems of closely related taxa; however, it is tempting to suggest that this aspect of the problem is likely to yield interesting results. An inbreeding genoecodeme will be in a comparatively disadvantageous position, lacking potentially advantageous combinations conferred by heterozygocity, particularly in a new or modified environment. In order to survive in such a situation, therefore, the plant must have some other advantageous features. One of these may indeed be the presence of comparatively heavier fruits to enable the seedling to establish itself in the early stages.

In the present case, the values of the Reproductive Capacities, could not be calculated under natural conditions, which would have been most desirable for understanding its evolutionary significance (CROSBY 1966). It must be pointed out, therefore, that these values may be very different from the values which are operative under natural conditions. The data is useful in emphasizing the strikingly different behaviour of different genoecodemes as expressed in terms of "Average Reproductive Capacity" under similar environmental conditions.

However, if these values could be accepted to give some indication of the values of average Reproductive Capacity operative under natural conditions, some pattern seems to emerge when the data is analysed in conjunction with the duration of life and the capacity for vegetative propagation. The low values of Average Reproductive Capacities of moist gully and montane genoecodemes seem to be balanced by the vegetative propagation and the perennial habit. The highest value of Average Reproductive Capacity has been observed in the case of Coastal Genoecodeme, which consists of mostly perennial plants and where vegetative propagation in rather uncommon. The value of average Reproductive Capacity of the desert genoecodeme obtained in the present case may not be correct because it was calculated by observing the percentage of germination of seeds over a period of about seven weeks. This time may be too short to indicate the correct percentage of germination operative in the desert genoecodeme in view of the prevalent dormancy. On the other hand, the low value of the reproductive capacity of the desert genoecodeme may be an expression of overall genetic superiority of its members in view of limited duration of their life, because they do not have to suffer with the 'evolutionary lag' with which the perennials have to suffer (ARBER 1928) resulting in comparatively less suitable genetic combinations, within a specified time.

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6. Summary

The biology of the *Senecio lautus* complex is discussed with a view to have a better understanding of the adaptive mechanism operative in this complex. Evidences obtained from duration of life, vegetative propagation, fruit weight, fruit dispersal, seed germination and reproductive capacity are discussed in this connection.

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