ON COMPETITION BETWEEN *GALIUM SAXATILE* L. (*G. HERCYNICUM* WEIG.) AND *GALIUM SYLVESTRE* POLL. (*G. ASPERUM* SCHREB.) ON DIFFERENT TYPES OF SOIL

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The publication, so long ago as 1865, of Nägeli's paper on the conditions of occurrence of species and varieties within their areas of distribution[1] brought into prominence an ecological problem of considerable interest and importance, namely the relation of competition between species, particularly closely related species, to their soil preferences.

The striking case of *Achillea moschata* and *A. atrata*, particularly their distribution in the Heuthal, a high alpine valley in the Bernina region of the Upper Engadine, at once suggests the investigation of this relation, but definite attempts to elucidate the problem appear to have been lacking.

Achillea moschata is a widely distributed species of siliceous soils in the Alps and is reputed calcifuge: *A. atrata*, on the other hand, is calcicole; and each, on its own soil, is said to suppress the other. But where either of the two is absent altogether from a region the other grows on calcareous and non-calcareous soils alike, though *A. atrata* is said to colonise non-calcareous soils with less difficulty than that experienced by its congener in colonising calcareous soils. In the Heuthal Nägeli found a large block of limestone, barely covered with a thin layer of soil, which had fallen on to an area of non-calcareous schist. On this block a colony of *A. moschata* had established itself, competition with the other species being excluded.

A number of pairs of closely allied species or varieties, both in the Alps and in other parts of Europe, show similar strongly contrasted soil preferences, and the relation described by Nägeli, each form being "bodenstet" where both occur and "bodenvag" where its congener is absent, appears to be common[2].

In order to elucidate this interesting phenomenon it is evidently first necessary to grow the two species of such a pair in competition on different types of soil and to see exactly what happens. Of a number of pairs of closely allied

[1] **Nägeli,** "Ueber die Bedingungen des Vorkommens von Arten und Varietäten innerhalb ihres Verbreitungsbezirkes." *Sitzungsber. d. königl. bayrischen Akademie*, 1865, p. 367.

[2] Cf. **Schimper,** *Pflanzengeographie auf physiologischer Grundlage*, 1898, pp. 115–118. See also **Drude,** *Die Ökologie der Pflanzen*, 1913, pp. 247–258.

species native to this country and naturally inhabiting strongly contrasted soil types, *Galium saxatile* and *G. sylvestre* proved by far the most suitable for experiment. The former is ubiquitous on light siliceous soils, the latter, absent from western Scotland, Wales and eastern England, appears to be confined to limestone hills and pastures. Where both types of soil occur within the area of distribution of *G. sylvestre*, each of the two species is very strictly confined, so far as the present writer's observation goes, to its own type of soil. For instance on the Mountain Limestone plateaux of Derbyshire the ground is often covered with a thick layer of non-calcareous chert through which the limestone crops out here and there, and in such situations the two species may be found growing within a few inches of one another, each sharply limited to its own soil. So far as observation and available records go, *Galium saxatile* does not however occur, like *Achillea moschata*, on limestone soil in the regions where its calcicole congener is absent, though it has been observed on the surface layer of non-calcareous soil which often covers the chalk to some little depth.

The experiments of which an account is given below were begun in the Botanic Garden at Cambridge by Miss E. M. Hume in the autumn of 1911 at the writer's suggestion, and continued until she left Cambridge in the autumn of 1913. They were then carried on by the late Captain A. S. Marsh until he joined the army in the autumn of 1914. Subsequent observations on Miss Hume's and Captain Marsh's cultures have been made at intervals by the writer up to the autumn of the present year, 1917.

The original method employed by Miss Hume was to sow the seeds of the two species together in deep boxes containing markedly different types of soil. The soils originally chosen were (1) a calcareous garden soil of medium texture (the ordinary Botanic Garden soil), (2) a non-calcareous and rather clayey reddish yellow garden "loam," and (3) a strongly acid peat, such as is used by gardeners for growing heaths and other strongly "calcifuge" plants. Later on (4) a natural sandy loam from an open woodland of heathy type on which *G. saxatile* is abundant was also used. Controls of pure sowings were also made on the various soils. The idea was to trace the course of competition between the two species on soils which each "prefers" in nature, and also on a soil which neither naturally inhabits.

The seeds were sown either with a seed of one species surrounded, at a distance of half-an-inch or one inch, with six seeds of the other species, or in several straight parallel rows, seeds of the two species being placed alternately in each row, so that each seed was at the distance of half-an-inch or an inch from a seed of the other species both in its own row and in the adjacent rows. The percentage germination of the seeds of both species on all the soils turned out however to be too low for this method to give the intended result. But in nearly all the experimental boxes some seeds of each species germinated, and the rapid growth of the seedlings after they became established brought the two into competition at latest during the second growing season.

The following table shows the germination percentages of the two species on soils (1) and (3).

	(1) Calcareous soil (4 boxes)		(3) Acid peat (3 boxes)	
	Range	Mean	Range	Mean
Galium saxatile	5 to 17	10	5 to 20	13
Galium sylvestre	9 to 37	22	7 to 24	15

In the fourth box of peat no germinations of either species occurred and the same thing happened in the single box of soil (2), the garden "loam."

It will be seen from these figures that while the germination of *G. saxatile* is somewhat better on peat than on calcareous soil, and that of *G. sylvestre* is better on calcareous soil than on peat, the percentage germination of *G. sylvestre* is better than that of *G. saxatile* on both these soils. In view of the small number of trials however no great reliance can be placed on this last result, especially as in one of the control cultures of *G. saxatile* on soil (4), the natural sandy loam, 38 per cent. of the seeds ultimately germinated, a percentage germination which is practically the same as the maximum recorded for *G. sylvestre* on calcareous soil.

The normal course of development is the same whether the seed is sown in the autumn, immediately after ripening, or in the following spring. Germination occurs in April and the seedlings of *G. sylvestre* come into flower on the calcareous soil in July, and fruit in August and September. Sometimes a small second crop of flowers is produced in the autumn. *G. saxatile* did not flower in any of the experimental boxes during the first year, but both species flower in June of the second year. Whether growing singly or in competition the plants cover the soil (except on peat) during the first summer and form a dense mat during the second. When the plants are allowed to flower and set seed fresh seedlings spring up where there is room between the original plants. The mats have now maintained themselves for six years from the original sowings.

BEHAVIOUR OF THE PLANTS ON THE DIFFERENT SOILS.

On the calcareous soil (1) the seedlings of *G. sylvestre* grow quite normally, but those of *G. saxatile* show marked chlorosis[1] very shortly after germination, and growth is very slow for many weeks. A considerable proportion of the seedlings succumb. Those which survive usually become normal from the third to the fifth month after germination, and when growing in competition maintain themselves for a considerable time in the midst of the continuous mat of *G. sylvestre*. Towards the end of the first growing season or at latest during the second summer the surviving plants of *G. saxatile* were overgrown by shoots of *G. sylvestre* and died, nothing being seen of them in the ensuing

[1] The terms "chlorosis" and "chlorotic" are used to designate the yellow or yellowish brown colouring of the leaves of the seedling. It appears to be the same phenomenon as is often observed in the leaves of plants other than calcicoles growing on highly calcareous soils.

spring. In one case however a plant of *G. saxatile* grew up on to the edge of the box and maintained itself there, leafing and flowering freely, well into the fourth summer. Its root was well established in the highly calcareous soil and it had a long bare stem, covered with shoots of *G. sylvestre,* terminating in the luxuriant flowering shoot system on the edge of the box. In the fourth summer during a long drought this plant died.

On the peat (3) the behaviour of the two species was very different from their behaviour on the calcareous soil. Germination of both species was slow and the plants remained small and did not flower during the first year. During the second year growth was considerably more vigorous and some plants of both species flowered. *G. saxatile* spread rapidly during the third summer (1914), forming a continuous mat over considerable areas of the soil, in which isolated shoots of *G. sylvestre* maintained themselves quite vigorously. The growth of *G. saxatile* in the peat boxes was not however so rapid and luxuriant as that of *G. sylvestre* in the boxes containing calcareous soil, and even in 1915 the peat was by no means completely covered. In the autumn of 1917 all three of the peat boxes were completely covered (except for some patches occupied by *Molinia*[1]) with *G. saxatile,* among which a few quite healthy plants of *G. sylvestre* were still maintaining themselves.

On the natural sandy loam (4) the two species were sown broadcast, both together and separately. Both germinated and grew well, *G. saxatile* somewhat more vigorously than *G. sylvestre*[2]. The former became dominant, but the latter maintained itself as isolated plants among the mat of *G. saxatile* so long as the cultures were kept (three years).

On the garden loam (2), which is not a type of soil on which either species ordinarily occurs in nature, the original experiment failed owing to lack of germinations. In the autumn of 1912 *G. saxatile* was sown, and established itself during the next season (1913). In June, 1914, a healthy tuft of *G. sylvestre* grown on the same type of soil was planted in the middle of the mat and established itself during the summer. In July, 1915, this plant was holding its own quite successfully in the midst of the mat of *G. saxatile* which had in the meantime spread over the whole box. During 1916 however the *G. sylvestre* steadily spread, overshadowing the *G. saxatile,* whose growth became less vigorous. In 1917 this process continued and by September *G. saxatile* had completely disappeared and the box was almost entirely occupied by a mat of *G. sylvestre* derived from the tuft planted in 1914. This curious reversal of dominance on garden loam in the course of the experiment requires further investigation.

[1] The large alien weeds likely to interfere with the growth of the Galia were consistently removed.

[2] In the later experiment (see p. 177) however *G. saxatile* was less vigorous than *G. sylvestre* on this soil. This curious result remains unexplained.

EXPERIMENTS TO DETERMINE WHETHER THE COMPETITION BETWEEN THE TWO SPECIES OCCURS THROUGH THE SHOOTS OR THROUGH THE ROOTS.

In 1914 Captain Marsh devised a method intended to separate the effects of root competition from those of shoot competition. Wooden boxes were constructed 12 inches long by 5 inches broad by 10 inches deep, and in the middle of each box a sheet of glass the length of the box was inserted in the soil. In two of the boxes (*S*), intended to allow of shoot competition but to exclude competition between the roots of the two species, the glass reached from the bottom of the box to the surface of the soil, completely separating the soil of the two halves. In two other boxes (*R*), the glass only just entered the soil and projected several inches above it, so that it would completely separate the shoots of plants growing on the two sides, but would leave the roots free to penetrate below the glass to the other side of the box. One *S* box and one *R* box were filled with soil (4) and the two others (one *S* and one *R*) with a mixture of equal parts of soil (4) and a highly calcareous soil. In February, 1914, ten seeds of *Galium sylvestre* were sown on one side of each of the four boxes and ten seeds of *G. saxatile* on the other sides. Controls of pure sowings were also started on the two soils. Unfortunately none of the *saxatile* seeds germinated, and all efforts to start competition by subsequent plantings failed. Accordingly in March, 1915, the writer started the experiment afresh on the same lines but with broadcast sowings. By May a full crop of *G. sylvestre* seedlings was obtained in all four boxes, and also a fair crop of *G. saxatile* seedlings. Markedly fewer of these last however appeared in the calcareous than in the non-calcareous soil. On the calcareous soil the seedlings of *G. saxatile* decreased in numbers in the two boxes rapidly and progressively during the summer.

Decrease in numbers of G. saxatile *seedlings on calcareous soil.*

	Root competition box	Shoot competition box
1915		
May 22	26, all chlorotic	22, all chlorotic
June 18	20, ,,	14, ,, but some recovering
July 11	8 ,, and feeble	7, recovering but less than half inch high
Aug. 15	2, very small, one chlorotic	1, quite recovered and with long shoots
1916		
April 24	none	1, weak

Thus the direct unfavourable effect of the calcareous soil on the germination, and especially on the seedlings, of *G. saxatile*, already noted in the original competition experiments, was even more marked in this experiment in which the soil was differently made up, and led to the death of practically all the seedlings within a year.

On the non-calcareous soil *G. saxatile* made fair and quite healthy growth during the summer, but in no case were the plants so luxuriant as those of *G. sylvestre*, which in July averaged two inches in height in all the boxes. As

usual *G. saxatile* did not flower during the first season. Some plants of *G. sylvestre* flowered in every box.

During the summer of 1916 shoots of *Galium sylvestre* spread over on to the other side of the *S* boxes, overshadowing *G. saxatile* which now showed less vigorous growth. Unfortunately nearly all the plants in the boxes on non-calcareous soil died during the late summer, probably as a result of overheating of the boxes and soil owing to undue exposure to hot sun.

This experiment is clearly not decisive as between root and shoot competition, because supposing the former to be effective, it had not sufficient time to come into play. From the records of the earlier experiments however shoot competition, supervening on the differential effect of the soil on the two species, appears adequate to account for the observed results, and this conclusion is reinforced by the later experiment. It must be noted that the samples of soil used in the later experiment, calcareous and non-calcareous alike, were evidently more favourable to *G. sylvestre* and less favourable to *G. saxatile*, than those used in the earlier experiments, and the meaning of this difference remains unexplained.

Summary of Results.

1. *Galium sylvestre* germinates on calcareous soil, sandy loam and acid peat, most freely on calcareous soil and least freely on acid peat. It also establishes itself on all the soils employed, even on acid peat, though there reduced to a subordinate position. Some plants maintain themselves on peat in competition with the dominant *Galium saxatile* for at least six years.

2. *Galium saxatile* germinates on all the soils employed, but the percentage germination is on the whole lower than is the case with *G. sylvestre*. The germination rate is lowest on calcareous soils, and of the seedlings produced all become chlorotic and many die. Those which survive and become normally green do not survive competition with *G. sylvestre*.

3 On acid peat the growth of the seedlings of both species is slow. When more vigorous growth begins that of *G. saxatile* distinctly surpasses that of *G. sylvestre*.

4. On sandy loam from a heathy woodland both species germinate freely. In the first set of experiments *G. saxatile* grew more vigorously than *G. sylvestre*, when the two were mixed, and became dominant. The relations of the two species resemble those obtaining on peat, but the growth of both species is stronger during the first year.

5. On calcareous soil the growth of *G. sylvestre* is normal and vigorous from the first, while that of *G. saxatile* is very slow. All seedlings of the latter species become "chlorotic" and many die. Those which survive recover and establish themselves, but do not survive prolonged competition with *G. sylvestre*.

6. Competition appears to work through the direct suppression of the shoots of one species by those of the other as a result of the more vigorous

growth of the species which is growing on its "preferred" soil. Shoot competition acting in this way appears to be adequate as the cause of the suppression of one species by the other.

7. No evidence of root competition was found, but the experiments are not decisive against it, though the case of the plant of *G. saxatile* which flourished on the corner of the box of calcareous soil, where its shoot escaped the competition of the shoots of the dominant *G. sylvestre*, is *pro tanto* evidence against the effectiveness of root as opposed to shoot competition.

CONCLUSION.

In the case investigated, the calcifuge species (*Galium saxatile*) is heavily handicapped, especially in the seedling stage, as a direct effect of growing on calcareous soil, and is thus unable to compete effectively with its calcicole congener, *Galium sylvestre*. The calcicole species is handicapped as a result of growing on acid peat and is therefore reduced to a subordinate position in competition with its calcifuge rival, which is less handicapped. Both species can establish and maintain themselves—at least for some years—on either soil. If these results are of general application they would explain the observed distribution in the case of other similar pairs of species, viz. that they are "bodenstet" where both members of the pair occur and "bodenvag" where only one occurs. Where however the handicapping is very severe, as in the case of *G. saxatile* on calcareous soils, it is unlikely that seedlings germinating on such soils would survive the general competition of the other vegetation even in the absence of plants of the congeneric competitor, and this would explain the absence of *G. saxatile* on calcareous soils in this country outside the area of distribution of *G. sylvestre*. The cause of the absence of *G. sylvestre* on the chalk of southern and eastern England is not at all obvious. Attempts to establish this species on the chalk in the neighbourhood of Cambridge by sowing seeds on bare chalk soil and in turf were without success.

No attempt was made to analyse the causes of the effect of calcareous soil on the seedlings of *Galium saxatile*, or of the effects of acid peat on the two species. Such an attempt would form the subject of an interesting investigation in physiological ecology.