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ECOLOGICAL RESPONSE CURVES OF RHINANTHUS SEROTINUS: A SYNECOLOGICAL STUDY

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SUMMARY

Relationships between the hemiparasite *Rhinanthus serotinus* (Schönh.) Oborny and some environmental variables have been compared to those of some other species.

The ecological response curves show that *Rh. serotinus* is not strongly influenced by spatial variation of macro-nutrients (nitrogen, phosphate and potassium). The species is absent on relatively wet spots, possibly due to effects of inundation. The wide amplitudes with respect to nutrients and the relatively low sensitivity to drought are probably the result of its hemiparasitic behaviour and the large number of potential hosts.

A multivariate analysis of vegetation records demonstrated *Rh. serotinus* to be indicative for a stage in a secondary succession series of hayfield vegetation after termination of agricultural management.

The structure of vegetation appears to be related to the quantity of *Rh. serotinus* within a community.

1. INTRODUCTION

Rhinanthus serotinus (Schönh.) Oborny is an annual hemiparasitic plant, occurring in open vegetation types, e.g. hayfields. Its ecology and biology were studied by several authors (Ter Borg 1972, Karlsson 1974, Mizianty 1978, Kwak 1979). Some descriptions of plant communities, related to presence of *Rh. serotinus* are available.

The position of the species in connection with factors controlling species composition, however, is unclear, especially with respect to small scale patterns within lots. Still knowledge of these relations is a necessary step on the road to understanding the mutual connections between hemiparasites and host communities.

The determination of controlling environmental variables is in general carried out by means of multivariate analyses, such as ordination and clustering. If the problem to be solved concerns one vegetation variable, such as a single species, different processing techniques can be applied. The ecological response curve (amplitude) represents relations of one species to one environmental variable. The connexion of one dependent to more independent variables can be described by means of a multiple regression equation. In this study both approaches have been used. An attempt has been made to combine the results.

2. VEGETATION AND ENVIRONMENT

BOERWINKEL and SCHENKENBERG VAN MIEROP (1976) studied the vegetation along some height gradients in hayfields containing *Rh. serotinus*. For this study 44 of their vegetation records were used. The Londo-decimal scale (a modification of the Braun-Blanquet combined estimation scale) was applied. The vegetation was analyzed along transects in three lots: "Smalbroek" (10 records), "Hoogholtje" (17 records) and "de Strengen" (17 records). All three transects contained a maximum density of *Rh. serotinus* somewhere in the middle and lower densities at both ends. The terrains are situated in the valley of the small river Drentse A. They are managed by the State Forestry Service (Staatsbosbeheer). Originally they were fertilized pastures and hayfields, carrying a rather uniform and species-poor vegetation. Management aims at a nutrient-poor substrate which is achieved by means of haymaking (BAKKER 1976).

Making allowance for initial situations such as intensity of the former agricultural management, a series of decreasing amounts and availability of nutrients might be distinguished: Smalbroek-Hoogholtje-de Strengen. This can be illustrated by the average pH-values in the dryest class of records in the three lots: 5.83 - 5.21 - 4.74. "Smalbroek" as a whole is dryer, more sandy and with a smaller amount of iron in the upper soil layer compared to the other two lots. Besides it has more relief which means that hydrological and climatological conditions may be slightly different.

A number of chemical and physical soil factors were analyzed. Depth of ground water (cm in May), in total nitrogen (Kjeldahl-Lauro analysis), phosphate (extracted in ammonium lactate) and potassium (atomic absorption spectrophotometer) have been used in this study.

Nine species were selected to have their spatial distribution compared to that of *Rh. serotinus*: three grasses – *Anthoxanthum odoratum, Holcus lanatus* and *Poa trivialis*; six herbs – *Cirsium palustre, Filipendula ulmaria, Plantago lanceolata, Ranunculus repens, Trifolium pratense* and *T. repens*. The remaining species were left out of consideration, except for the sum of all percentages cover per record, varying from 55% to 120%, being a measure of vegetation structure and possibly microclimate.

Response curves were fitted to one out of three distributions: normal (symmetric), log-normal (skewed to the right) or a reflected (with regard to x = optimum) log-normal distribution (skewed to the left).

3. RESULTS AND CONCLUSIONS

Response curves with respect to ground water, total nitrogen and phosphate are shown in *figs. 1, 2 and 3*. The overall image of response curves with respect to potassium is rather similar to those of phosphate and they were therefore omitted. *Rh. serotinus* turns out to have a relatively wide (nitrogen) or very wide (phosphate) amplitude regarding nutrients. This fits in with conclusions from physiological investigations. GOVIER et al. (1967) conclude an annual hemiparasite to be

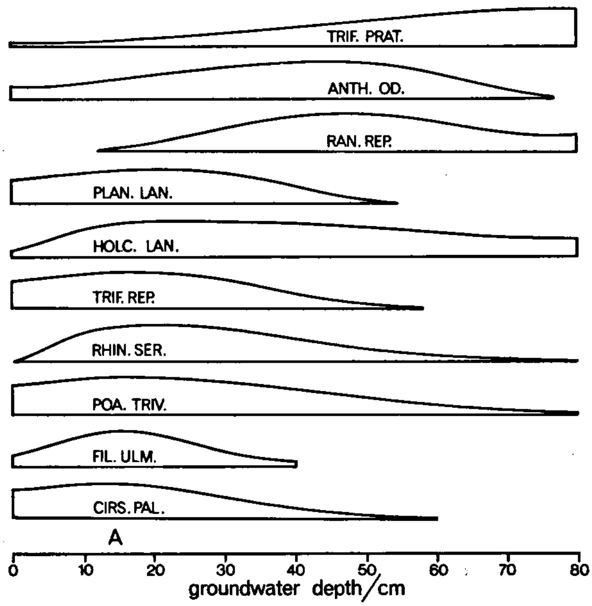

Fig. 1. Response curves with respect to water-table. From *Trifolium pratense* (dry) to *Cirsium palustre* (wet).

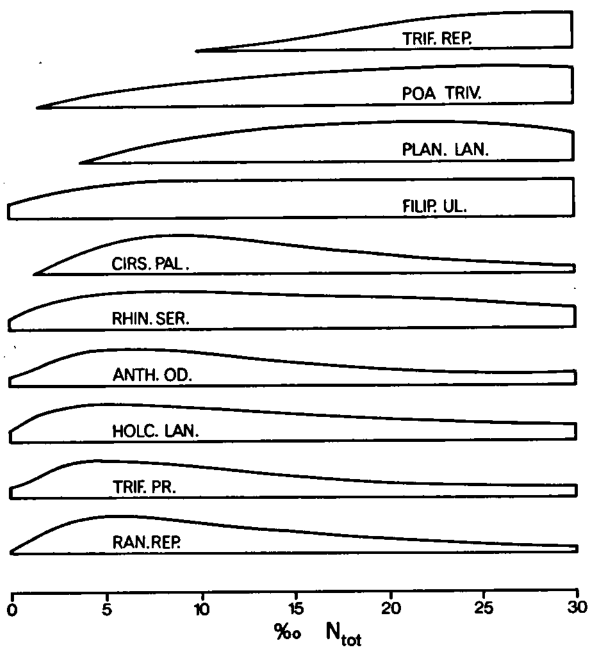

Fig. 2. Response curves with respect to total nitrogen. The sequence is determined by the place of the local optimum. From *Trifolium repens* (rich) to *Ranunculus repens* (poor).

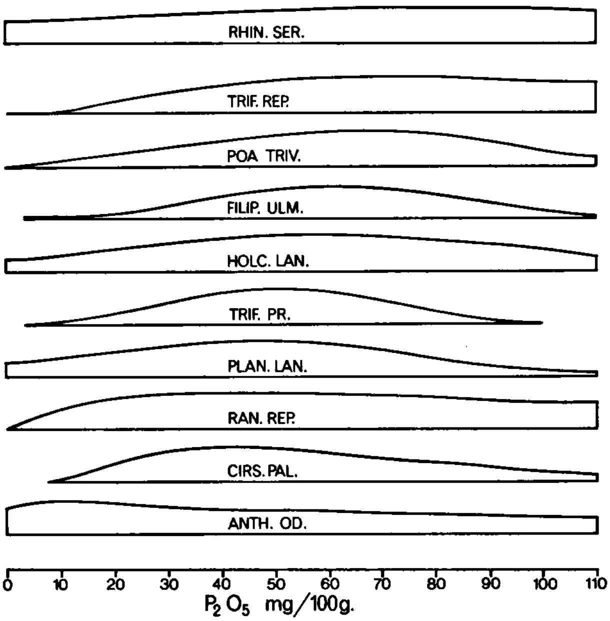

Fig. 3. Response curves with respect to phosphate. From *Rhinanthus serotinus* (rich, but indifferent) to *Anthoxanthun odoratum* (poor).

(partly) dependent on the host for water and minerals. This was confirmed by KLAREN (1975) for *Rh. serotinus*. This implies that the hemiparasite takes advantage of the host's adapted mechanism for the uptake of nutrients. Besides a large number of species is able to act as a host for *Rh. serotinus* (TER BORG 1972). Hence variation in chemical environment must be buffered for a wide-spectrum hemiparasite. The response curve with respect to ground water is skewed to the right (the dry side). On relatively dry spots low densities/coverages of *Rh. serotinus* can be observed, whereas the highest density/coverage is in general close to the lower (wet) border of the population. This is most likely due to the fact that the parasitic behaviour of the species buffers its sensitivity with respect to water on relatively dry spots. On lower places, however, there is a direct ecological relation to water conditions. Observations of TER BORG (1972) showed that inundations in spring can prevent successfull germination of seeds and were found to have a lethal effect on seedlings and juvenile plants.

Comparison of ecological amplitudes of species seems to be a suitable way to obtain insight in ecological habitat differences within a community complex. Of course this method does not supply information on effectiveness of environmental factors. Therefore it should in general be used in combination with multivariate analysis.

A clear relation exists between the coverage of *Rh. serotinus* and vegetation structure. *Fig. 4* shows that the maximum coverage of *Rh. serotinus* occurs in relatively open vegetation types. In a dense vegetation hardly any *Rh. serotinus* is present. This holds along the entire wet-dry gradient. It is obvious that further understanding of the distribution of *Rhinanthus* can only be obtained by means of microclimatological studies.

A Q-type Wisconsin comparative ordination (COTTAM et al. 1973) demonstrates the spatial relationship between species composition and environmental factors (*fig. 5*). Firstly the coordinates of records were calculated with respect to three axes. Secondly the average position of attributes (species and factors) was computed in the space so obtained. Thirdly the average position of the lots in this space was determined. The first axis was obviously controlled by differences between the three sites. The second axis was found to be determined by phosphate and potassium, the third by water-table and nitrogen. (Spearman

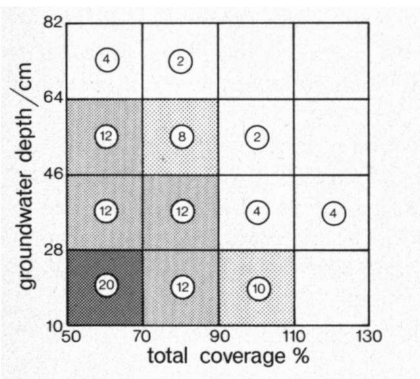

Fig. 4. Maximum coverage of *Rh. serotinus* observed in classes of vegetation records determined by watertable and the sum of coverages of all the species in the record.

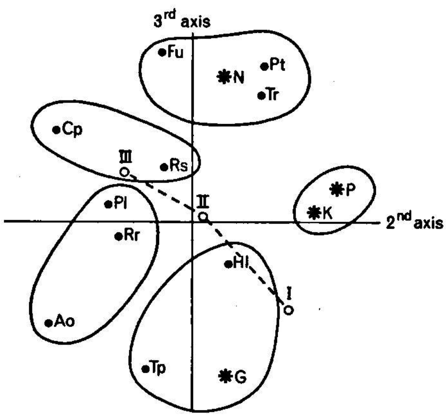

Fig. 5. Two axes of a Q-type Wisconsin Comparative Ordination. Average positions of 10 species, 4 environmental variables (N = total nitrogen, P = phosphate, K = potassium and G = groundwater) and 3 sites (I = "Smalbroek", II = "Hoogholtje", III = "de Strengen"). Groups of attributes, resulting from a simple agglomerative clustering are indicated.

rank correlation coefficients: GW/N + .58, GW/P + .37, GW/K − .03, N/P + .28, N/K − .17, P/K + .62.) *Rh. serotinus* has a central position which implies an indifferent (P, K) or average (GW, N) relation to the controlling variables. A clustering of attributes matches *Rh. serotinus* to *Cirsium palustre*, which is caused by the high frequency of both species in "de Strengen". *Rh. serotinus* shares its indifferent/average position with regard to the environmental factors with *Holcus lanatus*, *Ranunculus repens* and *Plantago lanceolata*. This corresponds to the response curves. The centres of gravity of the lots in the graph show that lot I ("Smalbroek") is the richest and the dryest, lot III ("de Strengen") is the poorest and the wettest. As noted before lot I may represent the youngest stage in the series from modern agricultural management to "old-fashioned" unfertilized hayfields and lot III the oldest. These data support the hypothesis that the three sites exemplify a succession series: from type A (*Holcus lanatus* and *Trifolium pratense*), via type B (*Plantago lanceolata*, *Ranunculus repens* and *Rhinanthus serotinus*) to type C (*Cirsium palustre* and *Rhinanthus serotinus*).

Though it is obvious that caution is necessary in drawing conclusions on succession from vegetation data which are collected from sites that may represent different ecological conditions, this study may contribute to a next step in the research on the ecology of *Rh. serotinus*. The hypotheses resulting from a comparison of the species with the remaining species within the plant communities are to be tested by means of experiments. These conclusions are:

1. *Rh. serotinus* is indifferent with respect to spatial variation of macro-nutrients.
2. The species is sensitive with respect to inundation.
3. In hayfields, withdrawn from modern agricultural management, it appears after a number of years, directly succeeding the decline of typical agricultural species.
4. The density of a population of *Rh. serotinus* is correlated to the structure of vegetation. It is not clear whether the structure affects the hemiparasite (micro-climate) or the opposite or both.

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