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Genetic variability in *Plantago* species in relation to their ecology

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SUMMARY AND CONCLUSIONS

The investigations described in this thesis have been carried out as a part of a multi-disciplinary "grassland species research project". The aim of this project is the analysis of the mechanisms which determine how plant species maintain themselves in grasslands. This thesis is focused on the role of genetic variation in the maintenance of Plantago species. This analysis of genetic variation related with intra-specific ecological differences starts with the investigation of allozyme variation in the three species P. major, P. lanceolata and P. coronopus. Variability on this level is the highest in P. lanceolata, and the lowest in P. major. Compared with other species, which are similar with respect to breeding system and life history characteristics, the allozyme variability shows normal values in all three Plantago species.

In Chapter 1 the genetic analysis of the allozyme variation in P. major is presented. An association appears to exist between the presence of certain enzyme alleles and the number of seeds per capsule; some of these enzyme alleles are restricted to only one of the two subspecies (the main distinctive trait for these subspecies is seed number per capsule). In Chapter 2 it is made probable that not the enzymes themselves influence the ecological differences between the subspecies, but that this influence is due to chromosomally linked loci determining subspecies-specific characters like seed number per capsule, leaf morphology, inflorescence morphology and the time of first flowering. The genes coding for these characters appear to be clustered in linkage groups on some of the chromosomes.

Simultaneously with the analysis of the genetic basis and the linkage relationships of the allozyme variation in P. lanceolata, several factors affecting the breeding system are genetically analysed in Chapter 3. The self-incompatibility locus, preventing self-fertilization, has been placed in one of the linkage groups, and also several male-sterility loci have been localized.

In Chapter 4 a method is presented for the estimation of the three gene flow parameters: pollen dispersal, seed dispersal and selfing rate. The validity of this method has been checked by computer simulations of situations in nature. A new model of genetic neighbourhood and isolation by distance is developed, adapted to the characteristics of seed plants. The estimation method mentioned has been applied in Chapter 5, and indicates that P. major has the lowest level of gene flow, and is predominantly selfing. In the self-incompatible species P. lanceolata gene flow

is the highest of the three species; the population homozygosity is in this species, however, higher than expected. In P. coronopus, which is self-compatible, population homozygosity is not far from the value expected under random mating, making an independent measure of the selfing rate interesting. The differentiation between populations concerning allozyme variation appears to be low in all three species compared with most other species possessing similar breeding systems, and is probably due to special mechanisms for long-distance seed transport.

In P. coronopus no clear ecotypic differentiation could be noticed within The Netherlands until now. In P. lanceolata ecotypic differentiation certainly has been shown, though it occurs to a considerable extent within populations, which requires a small-scale description of environmental variability to be able to correlate environmental with genetic variation. In this thesis only a further analysis of the ecotypic differentiation within P. major is performed; in that species the differences mainly exist between populations. This finding and the high selfing rate favour such an analysis. In Chapter 6 the various ecotypes of both subspecies of P. major are compared as far as factors like juvenile growth, time of switch-over to the generative stage, allocation of seed biomass, etc., are concerned. Also their ability for growth and reproduction in several field situations and under experimental conditions has been studied. Differences in strategy between the ecotypes are split up into alternatives for resource allocation in various stages of the life cycle.

It can be concluded that in P. major, more than in the other two Plantago species studied, a broad array of genetically determined variation in strategy components, related with differences in resource allocation, forms the basis for a wide ecological amplitude. The subspecies pleiosperma is typically "r-selected", it reproduces early and tends to be annual. In the other subspecies, major, reproduction is delayed compared with ssp. pleiosperma. Maintenance of the individual plant is emphasized here at the cost of reproduction. This is realized by making more leaves, improving the ability for competition in an open but dense vegetation (in the lawn type of ssp. major), or by becoming trampling resistant (in the roadside type of ssp. major).

SAMENVATTING EN KONKLUSIE

Een bepaalde plantensoort in grote, soms in kleine aantallen bepalen zijn plaats groeien dienen minstens heden; ze moeten er uiteindelijk op meerdere plaatsen voor zoals verschillende grondgroeiing met andere konklusie mogelijk gemaakt worden. zijn zo plooibaar wat hun omstandigheden kunnen groeien erfelijk verschillen laatste geval houdt de oorspronkelijke variatie en de betekenis

De plantensoorten die geslacht weegbree (Plantago (Plantago major), de smalle weegbree (P. coronopus), (P. maritima). Alleen de onderzoek dat ze in dit onderzoek is al veel bekend voorkomen en over hoe hun Erfelijke verschillen bijvoorbeeld al waargenomen. Bij de groen twee ondersoorten bestaan uit soort major) en één met 1 ondersoort major is ook r "gazon type", dat tegen maai gaand type dat zeer goed

De uiterlijke kenmerken zaaddoos, bladvorm, aarvorm, verspreidingsmechanisme. Er zijn toch iets over de erfelijke verschillen met de erfelijke verschillen met betrekking tot genen verschillende vormen van een (een populatie) kunnen met forese, zichtbaar worden