

MEETINGS OF THE ROYAL BOTANICAL SOCIETY OF THE NETHERLANDS

MEETING OF THE SECTION FOR PLANT TAXONOMY AND PHYTOGEOGRAPHY ON NOVEMBER 28, 1980

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Apomixis: diversity and adaptive significance

Apomixis is often considered to be synonymous with asexual reproduction as opposed to sexual reproduction which is then called amphimixis. It occurs in two forms, *viz.*, as vegetative reproduction (by means of rhizomes, stolones, bulb clusters, etc.), and as agamospermy, *i.e.*, the production of seed by means of an asexual process. Agamospermy has a strong influence on the evolution, taxonomy and ecology of certain taxa.

Life cycles of agamosperous taxa belong principally to one of the following categories:

(1) Diplospory, *i.e.*, a normal meiosis I sets in but is not completed and univalents are formed which come together in one so-called restitution nucleus which is diploid; the second meiotic division takes place normally, after that a seemingly normal embryo sac (e.s.) with 8 nuclei is formed, but its nuclei are diploid. The egg cell develops parthenogenetically into an embryo and the tetraploid secondary e.s. nucleus produces the endosperm (*Hieracium* subgen. *Euhieracium*, *Taraxacum*, *Calamagrostis*). (2) Apospory, *i.e.*, the meiotic divisions are usually normal, but subsequently a vegetative cell of the nucellus develops into an aposporic embryo sac cell (e.s.c.) which is diploid and ousts the legitimate e.s.c. which degenerates. In the aposporic e.s.c. 8 diploid nuclei are formed, one of which (a "diploid egg cell") forms the embryo parthenogenetically, and the secondary e.s. the tetraploid endosperm (*Hieracium* subgen. *Pilosella*, *Crepis*).

Diplospory and apospory may be combined with pseudogamy, *i.e.*, a pollination is required for the fertilisation of the polar nucleus (or nuclei) but not of the "egg cell". The combination of apospory and pseudogamy is known to occur in *Rubus*, *Potentilla* and *Poa*; diplospory with pseudogamy in, for instance, *Allium* and *Rudbeckia*.

A special case is nucellar embryony: the embryo is formed directly out of one or several somatic cells of the nucellus and no embryo sac is formed (*Ci.rus*).

In the anthers also a degeneration of the meiosis may occur. In pseudogamous species the microsporogenesis is normal, but in the non-pseudogamous apomicts it is often much disturbed so that sometimes no pollen is produced (*Taraxacum*).

Apart from the obligatory agamospermy as discussed above there is also a facultative one. In the latter case in one individual, or even in the same inflorescence, normal and disturbed megagametogenesis are found, which has far-reaching biological consequences. It has been established that agamospermy is controlled by a set of different genes but environmental factors influence the rate of agamospermy.

Adaptive significance:

(1) A characteristic feature of obligatory agamospermy is the absence of genetic recombination, which is advantageous in habitats where a rapid build-up of populations consisting of best adapted individuals is required. Obligatory agamospermy is advantageous as long as the environment remains constant and extreme, but as soon as changes occur genetic recombination is necessary to create well-adapted genotypes. Such a recombination is achieved by means of facultative agamospermy as found in nearly all agamosperous species aggregates.

(2) Agamospermy is almost invariably concomitant with polyploidy and hybridisation. Several agamospermous taxa form so-called agamous aggregates in which, on the basis of original, diploid species, by hybridisation and polyploidisation an overlying complex of agamospermous polyploids originated. Since both polyploidy and hybridisation have an adaptive significance, their association with agamospermy yields unique biological situations.

Agamospermy perpetuates successful, hybridogenous allele combinations; when agamospermy is combined with polyploidy individuals with uneven sets of chromosomes can reproduce almost indefinitely.

(3) In sexually reproducing populations a minimum density is required for successful maintenance of the populations. In agamospermous populations this is not a prerequisite because each individual is capable of producing a progeny, which is a great advantage when new sites with a scarcity of (animal) pollen vectors are being colonised.

(4) Agamospermy is reproduction by means of seeds (fruits), which has appreciable advantages in respect of vegetative reproduction, such as the large numbers of individuals in the offspring, the extended period of germination (dormancy), and the potentially far horizontal displacement of the dispersed seeds (fruits).

(5) *a.* Weedy and colonising species are often agamospermous (or autogamous).

b. Recombination-reducing mechanisms, such as low numbers of somatic chromosomes and low chiasmata frequencies, are more commonly found in species of areas with a temperate climate.

c. Agamospermy and autogamy are of rare occurrence in the tropics.

These generalisations agree with corresponding ones in the animal kingdom. Tropical biocenoses are very rich in species including many predators, competitors, parasites and pathogens. The continuous interaction between such groups necessitates a constant re-adaptation to new situations, which is achieved by genetic recombination, *i.e.*, by sexual reproduction. VAN VALEN 1973 has formulated this as follows: the environment of a given species does not change primarily as the result of abiotic factors but because of the evolution of other, (sympatric) species in the ecosystem. Sexuality and genetic recombination are in particular necessary adaptations in biologically complex ecosystems, and to a lesser extent in open and relatively simple ones in which abiotic factors prevail. *Relative frequency of agamospermy and parthenogenesis:* The number of recorded animal taxa with some form of parthenogenesis lies between 1,000 and 10,000, *i.e.*, at about 1 pro mille of the known species. Among the seed plants agamospermy has so far been found in about 75 genera, *i.e.*, in about 0.5 per cent. of all recognised ones. These figures permit the conclusion that agamospermy and parthenogenesis are not of paramount importance. Conceivably their adaptive significance is appreciable in short-term evolution, but in the long run they may form a barrier to further evolutionary progression.

GRANT, V. (1971): *Plant speciation*. London. pp. 435.

MAYNARD SMITH, J. (1978): *The Evolution of Sex*. Cambridge. pp. 213.

RUTISHAUSER, A. (1967): *Fortpflanzungsmodus und Meiose apomiktischer Blütenpflanzen*. Wien. pp. 245.

VALEN, L. VAN (1973): A new evolutionary law. *Evol. Theory* 1: 1-30.

WHITE, M. J. D. (1978): *Modes of Speciation*. San Francisco. pp. 455.

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Taxonomic problems in European brambles

When approaching the taxonomy of *Rubus* along conventional systematic lines one encounters an appreciable number of stumbling blocks, some of which are of such a nature that the formal taxonomic rules are not consequently applicable. Not all European species of *Rubus* are obligatory apomicts: the incidence of apomixis varies from 0% to 100%. Hybrids formed are often not strictly sterile; in the next generation apomixis usually becomes re-established, which may give rise to new forms (GUSTAFSSON 1943). Also those forms which originated in other ways, *e.g.*, by genome and/or chromosome multiplication or bud mutation, may maintain themselves apomictically and extend their range of distribution. Such phenomena result in a wealth of forms which often have but a limited

area of distribution. In hilly and mountainous regions every valley may have its own set of species – sometimes scores of them – and if one would decide formally to describe them all, one would arrive at a total of thousands of species. Such a procedure would hardly serve a useful scientific purpose.

On the other hand one cannot incorporate such forms of limited distribution in other species simply because they (1) are either so clearly distinguishable from species with a much wider range of occurrence – sometimes more clearly so than the latter among themselves – that there is no other motive than the limited area of distribution to refer them to a species of the wide-range group, or (2) occur so far outside of the range of the most approximate species that a close genetical relationship is highly improbable. Besides, apart from the morphological discontinuity, there is a genetical barrier between the various microspecies. It is on account of this fact in particular that one usually has not hesitated to regard two taxa with a large area of distribution, even if morphologically differing only slightly (but consistently), as two different species. This holds already for taxa with largely coinciding distributional ranges, but the more so when they occur allopatrically.

The situation becomes problematical, however, when the morphological differences are so slight that on account of the morphological characters alone a separation of the taxa is no longer warranted, whereas the allopatrism is of such a kind that the species concerned are presumably of different genetical origin.

As regards the supraspecific taxa, a good classification of the species is only possible in a multidimensional system. Some species can readily be combined to form a series or section, but among them there are often several species which show links with three or even more such series, and some species do not link up satisfactorily with any such assembly.

In order to counter all these difficulties, the following suggestions are made:

1. one should only refer those individuals to a species if they meet with the following conditions:
 - (a) the area covered by the species must have a diameter of at least 40 km;
 - (b) its morphological features clearly separate it from related taxa, and
 - (c) its morphological features are reasonably constant;
2. one should refer only those species to a series or section which are clearly eligible and maintain all other ones as individual species.

Admittedly such a procedure is at variance with the Code of Nomenclature, but here one must accept that nature passes nurture.

GUSTAFSSON, Å. (1943): *The genesis of the European blackberry flora.*

G. E. VAN DIJK (*Stichting Instituut voor Plantenveredeling, Droevendaalsesteeg 1, 6708 PB Wageningen*)

Apomixis in plant breeding

Apomictic plant species yield a uniform progeny, so that a single individual suffices for obtaining a homogeneous cultivar. Such cultivars are easy to describe. As long as a sufficient rate of variation is present, the gathering and testing of material (ecotypes, aberrant phenotypes, etc.) enables the breeder to obtain satisfactory results. However, recombination by crossing is much more difficult than in amphimictic crops. In facultatively apomictic forms apo- and amphimixis may occur in the same individual and crossing is possible, but the varying degrees of sexuality in the offspring render the breeding schemes rather vague. A hybridization programme for obligatory apomicts is only possible if sexual and apomictic types occur within the species or in related and compatible species. The advantage is the clear-cut distinction between apo- and amphimictic specimens. *Poa pratensis* L. ($2n = 28$ to 147) is a facultative apomict with which intra- and interspecific crosses can be made. By means of interspecific hybridization certain useful characteristics of other species can be introduced into *Poa pratensis*. *Cenchrus ciliaris* L. ($2n = 36-54$) is a well-known example of the breeding with obligatory apomicts.

Mutagenic radiation is also applied to improve apomictic forms. For future work the search for methods to regulate the ratio between apomictic and sexual reproduction in facultative apomicts will become very important. The introduction of apomixis into such amphimictic crops as beetroot and maize or even wheat may offer good opportunities.

T. W. J. GADELLA (*Vakgroep Populatie- en Evolutiebiologie, Padualaan 8, 3584 CH Utrecht*)
Cytology and reproduction of *Hieracium pilosella* L. and some related diploid species

Species of the subgenus *Pilosella* of the genus *Hieracium* are characterized by various modes of reproduction: vegetative reproduction by stolons, agamospermy (of the aposporic type) and cross-fertilization (self-incompatibility).

The section *Pilosellina* (of which three species were studied: *H. pilosella*, *H. peleterianum* and *H. hoppeanum*) is also highly variable cytologically: $2n=18, 27, 36, 45, 54, 63$ (and up to $2n=108$ in artificial hybrids). In floras, many hybrids are distinguished, usually using morphological criteria only; experimental proof is often lacking. The enormous morphological and cytological differentiation and the frequency of hybridization are unexpected phenomena in view of the occurrence of apospory. This brief report deals with the results of studies on the cytology and mode of reproduction of 1800 plants, collected in 598 European populations, and of 750 inter- and intra-specific artificial hybrids. An analysis of the mode of reproduction in various cytotypes:

- diploids ($2n=18$): *H. peleterianum* and *H. hoppeanum*. All plants allogamous and strictly self-incompatible.
- triploids ($2n=27$): interspecific hybrids between *H. pilosella* and *H. hoppeanum* or *H. peleterianum*. All plants turned out to be completely sterile.
- tetraploids ($2n=36$): *H. pilosella*. Most populations allogamous and strictly selfincompatible. In some cases (3 populations and 4 intraspecific hybrids) the reproduction is apomictic (of the aposporic type). Apomictic tetraploids in natural populations grow in close proximity to *H. peleterianum* and may represent hybrids; however, these putative hybrids could not be obtained by crossing triploids with *H. peleterianum*.
- pentaploids ($2n=45$): *H. pilosella*. Reproduction usually apomictic, or the plants are sterile (especially intraspecific hybrids).
- hexaploids ($2n=54$): *H. pilosella*. Reproduction in many areas of Europe apomictic, but in the Alps (Graubünden and French Alps) also amphimictic (strictly self-incompatible).
- heptaploids ($2n=63$): *H. pilosella*. Sometimes sterile, but reproduction usually apomictic.
- dekaploids ($2n=90$): *H. pilosella*. Hybrids originating from fertilization of unreduced egg-cells of heptaploids ($2n=63$) and pollen with the reduced chromosome number of apomictic hexaploids ($2n=54$). The reproduction of these plants is always apomictic.

Diploids and tetraploids form many good achenes, of which at least 85% germinated. Pentaploids, apomictic hexaploids and heptaploids, on the other hand, form many achenes that are not able to germinate (4–25% germination).

On the Dutch Wadden Island of Vlieland tetraploids are less numerous than pentaploids. Each capitulum of a tetraploid plant produces three or four times as many seedlings as a capitulum of a pentaploid plant. Pentaploids produce many apparently sterile achenes. Often the tetraploid populations are smaller, producing fewer flowerheads than pentaploid clones. In order to produce about the same number of seedlings, each pentaploid clone should be at least twice as large as a tetraploid clone.

The distribution of the cytotypes in Europe is as follows: the tetraploids are widespread in lowland areas and do not occur in the North, whereas the polyploids (penta- en especially hexaploids) occur at higher elevations (Alps) and in Scandinavia and Scotland. Hybridization in nature is only possible if the taxa and cytotypes are sympatric. Since *H. peleterianum* and *H. hoppeanum* are largely allopatric, natural hybrids are unknown. However, some experimental hybrids could be produced.

The results of crossing experiments permitted the following conclusions:

- a. Amphimictic plants of *H. pilosella* (tetraploids and hexaploids) can be crossed with the amphimictic diploid species *H. peleterianum* and *H. hoppeanum*. The triploid hybrids are sterile, the mode of reproduction of the tetraploid hybrid has not been tested so far. The hybrids resemble the *H. pilosella* parent (which contributed two or four genomes) in most respects and are not intermediate in morphology.
- b. Pollination of *H. peleterianum* and *H. hoppeanum* with pollen-grains of apomictic strains of *H.*

pilosella does not result in the formation of hybrids.

c. The pollen-grains of apomicts (penta- and heptaploids) are functional and are able to fertilize amphimicts. The progeny of the cross amphimict (♀) × apomict (♂) shows various modes of reproduction: apomictic, amphimictic or the plants are sterile. Apomixis can be transferred by pollen-grains, this means that amphimictic plants can produce apomictic offspring. The reverse has not been observed to occur. Most plants of *H. pilosella* reproduce either sexually or apomictically. Apo-amphimictic plants are not found in pure populations. In mixed populations, where tetraploids and pentaploids grow close together or intermingled, both apomictic and sexual offspring may be produced by sexual tetraploid plants.

d. A cross between a tetraploid and hexaploid plant always results in the production of pentaploids, which are sterile if the reproduction of both parents is amphimictic and apomictic or sterile if the reproduction of the pollenparent is apomictic.

This proves that polyploidy *per se* does not favour or facilitate apomixis.

e. Increase of chromosome number is possible by crossing higher apomictic polyploids. Usually only matroclinous offspring results from such crosses, but occasionally unreduced egg-cells may be fertilized (leading to so-called addition-hybrids).

f. Many crosses were performed between tetraploid amphimictic plants (♀) and higher polyploids (♂; penta-, hexa- and heptaploids). From these crosses it became clear that uneven polyploids (penta- and heptaploids) are able to produce two different kinds of pollen-grains, with different chromosome number. Both kinds of gametes may be functional, but usually not in the same cross.

g. Artificial pentaploid hybrids produce smaller numbers of viable achenes than pentaploids from natural habitats.

From these studies it became clear that the three species, *H. peleterianum*, *H. pilosella* and *H. hoppeanum* belong to one polyploid complex. To this complex belong at least 10 other species of the subgenus *Pilosella*. Hybridization plays an important part in producing new variability, which is maintained by vegetative reproduction, by agamospermy, or by both. The pollen-grains of the apomictic forms are still capable of fertilization and contribute substantially to the variation pattern of the complex.

MEETING OF THE SECTION FOR VEGETATION RESEARCH ON MARCH 20, 1981

H. J. DROST and J. VISSER (*Rijksdienst voor de IJsselmeerpolders, Lelystad*)

Water-tables as structuring factors for natural vegetation on embanked sand-flats

Several hundreds of ha desalinated embanked sand-flats (clay content less than 1½%) occur in the nature reserves of the Lake IJssel Polder Development Authority.

Hydrological and pedological research revealed that the ground water as a rule can supply at least part of the water demand of the vegetation. It appears that these sand-flats represent in a hydrological sense a habitat for the "mesoseris" (LONDO 1971). It is proposed to make a division within this "mesoseris" habitat between a hydrologically steady type and a hydrologically dynamic type.

In the steady type water-tables are, both in winter and in summer, more or less equal to the level of the surrounding open water. During dry periods even superficially rooting vegetations experience hardly any water deficit.

In the dynamic type the water-table undergoes strong seasonal fluctuations. During winter it is at the soil surface. In summer it falls rapidly, often to levels far below that of the surrounding open water. In many summers, though not in all, superficially rooting vegetations suffer serious drought during one or more periods.

The vegetations in the areas studied resemble young dune-slack vegetations, with *Nanocyperion flavescens* species and *Caricion davallianae* species. In the steady type many species of both syntaxa are present. In the dynamic type only the pioneer *Nanocyperion* species occur.

Apparently the – mostly ephemeral – *Nanocyperion* species are able to stand up against the

uncertain moisture conditions of this habitat, whereas the *Caricion davallianae* species – mostly perennial – require more steady conditions.

LONDO, G. (1971): Patroon en proces in duinvalleivegetaties langs een gegraven meer in de Kennemerduinen. *Verhandelingen R.I.N., Leersum, The Netherlands*, nr. 2.

G. J. C. BUTH and A. M. GROENENDIJK (*Delta Instituut voor Hydrobiologisch Onderzoek, Vierstraat 28, 4401 EA Yerseke*)

Comparative investigations of vegetation and soil of former mud- and sand-flats in relation to the time of embankment

Investigations into vegetation development on intertidal soils after embankment have been carried out in the S-W Netherlands by Dr. W. G. Beefink and collaborators for more than fifteen years. For this purpose permanent sampling plots were established in the mud soon after a barrage was built and followed year after year (NOORDWIJK-PUIJK et al. 1979). In relation to these investigations an attempt was made in 1975 to detect temporal sequence in a spatial pattern of vegetational and environmental structure of creek-bank areas of different ages of embankment, using the side-by-side method (MUELLER-DOMBOIS & ELLENBERG (1974). Differences in management were excluded as much as possible; all areas were mowed or extensively grazed by sheep. The age of embankment varied from five to about three hundred years. The soil texture ranged from sandy silt to clay; silt in the upper 20 cm varied from 4 to 20 %.

In each area a series of compound sampling plots placed along a gradient from low to high soil surface was established. At each sampling station the vegetation was analysed by relevés; soil samples were taken for analysis of pH, clay, moisture, carbonate, humus, chloride, and phosphate. Vegetation and soil data were processed with cluster analysis using BIOPAT, and diversity estimates were calculated (HOGEWEG 1976).

Near the edge of the water the vegetation was poor in species and the soil parameters showed extreme and partly highly fluctuating values. Beyond the direct influence of the adjacent stagnant water-body the number of species increased strongly and the soil showed a remarkable decrease in its extreme and dynamic character (salinity, humidity, and nutrient supply). In most areas the gradient character of the soil was apparent from parameters running from wet to dry, from saline to fresh, and/or from relatively rich to poor in nutrients. Most gradients showed high species richness and diversity in the middle of the gradient assuming a maximum in spatial environmental diversity and/or a minimum in temporal fluctuations. In the older areas, beyond this zone, the vegetation was formed by communities which are rich in species and characteristic for hayfields. Species in these communities were characteristic for environments with lower dynamics.

Framing these areas in a temporal sequence it appeared that large changes took place in the vegetation in the first fourteen to twenty years after embankment. Different stages followed each other with high frequency. These changes seemed to be caused chiefly by maturation processes in the soil. After this period the floristic and structural differences appeared to be caused mainly by the local situation and above all by management. Soil-moisture content and its fluctuations seemed to be an important factor determining the direction of the succession into relatively dry or wet series, i.e. *Arrhenatherion elatorius* or *Calthion palustris*. Bryophytes had an important role in the development of the vegetation during the first fourteen years. After twenty years they played a smaller part because of the increasing density of the herb layer.

HOGEWEG, P (1976): *Topics in biological pattern analyses*. Thesis, Utrecht.

MUELLER-DOMBOIS, D. & H. ELLENBERG (1974): *Aims and methods of vegetation ecology*, pp. 379–380. Wiley & Sons, New York.

NOORDWIJK-PUIJK, K. VAN, W. G. BEEFTINK & P. HOGEWEG (1979): Vegetation development on salt marsh flats after disappearance of the tidal factor. *Vegetatio* 39: 1–13.

T. J. DE KOGEL (*Deltadienst, hoofdafd. Milieu en Inrichting, postbus 439, 4330 AK Middelburg*)
Vegetation development on recently exposed mud-flats in the southwestern part of The Netherlands

The enclosure of a number of sea-arms in the southwestern parts of The Netherlands resulted in

exposed mud-flats. The progressive development of vegetation on this new land is described on the basis of three habitat types:

1. *Rapidly desalinated clay-rich salt marshes.* Within a few years the original halophytic vegetation disappeared to a large extent and was replaced by nitrogen rich weedland vegetation of principally *Cirium arvense* and *Epilobium* spp. After some years a number of coarse grass species appeared in this vegetation (e.g. *Elytrigia pungens* and *Calamagrostis epigejos*). Especially in the dead vegetation of *Spartina anglica* an immediate establishment of woody species like *Sambucus nigra* and *Salix* spp. occurred.

2. *Rapidly desalinated sandy mud-flats and sand-flats.* Before the tidal influence disappeared these mud- and sand-flats were bare grounds. After the enclosure a short stage of development of halophytes was soon followed by pioneer vegetations of *Nanocyperion flavescens*, characteristic of young wet dune slacks with e.g. *Centaureum* spp., *Sagina nodosa* and *Gnaphalium luteo-album*. After this more grassy vegetations developed from *Caricion davallianae* with e.g. *Parnassia palustris*, *Epipactis palustris* and of the woody species especially *Salix* spp. On the drier parts a closed moss vegetation developed with a thin layer of herbaceous plants in which eventually species appeared from dry dune grasslands and in some places many lichens; of the woody species especially *Hippophaë rhamnoides* was able to establish itself.

3. *Slowly desalinated sandy mud- and sand-flats.* During the progressive desalination halophytic vegetations developed consisting of a succession of vegetations of *Salicornia europaea*/*Suaeda maritima*, *Puccinellia* spp./*Aster tripolium*, *Sagina maritima*/*Agrostis stolonifera*/mosses.

Future and management. The managerial measure: doing nothing in the desalinated areas along a salt lake, will result in the development of various wood and shrub vegetations. Grazing and mowing on wet nutrient-poor sandy soils will probably result in the development of vegetations of *Caricion davallianae* and *Calthion palustris*. On the drier, nutrient-poor sandy soils vegetations of *Galio-Koelerion* will be able to establish themselves and on the clay rich salt marsh soils vegetations of *Arrhenatheretum elatioris* and *Lolio-Cynosuretum*. Along the shore various types of halophytic vegetations will become established.

W. JOENJE (*Vakgroep Plantenecologie, Biologisch Centrum, Postbus 14, 9750 AA Haren (Gn)*)
Arrival and fate of early colonists

On the former tidal flats in the 1969 embanked Lauwerszee-polder colonization by vascular plants was studied. The predominant anemochorous and hydrochorous dispersal is demonstrated by the species lists of the mussel banks; the species numbers of these quickly desalinated "islands" are related to their surface area. Special emphasis is given to immigration, ecesis, aggregation, and emerging monocultures, and to population dynamical quantification of the early colonizing halophytes *Salicornia europaea* (two ssp.), *Atriplex hastata* and *Suaeda maritima*.

After three years of exponential increase in number of ever smaller plants the steady state was reached and in the fourth year visible (density dependent) mortality rose up to 70%, indicating the end of plasticity and the onset of a severe biotic selection. Some data confirm the model of YODA et al. ($W = cp^{-3/2}$).

Studies of species interactions in aggregates together with experimental addition of nutrients (N, P and/or K) support the conclusion that root competition for mineral N is the main cause for the annual halophytes to give way to deeper rooting, mostly perennial species such as *Puccinellia* spp., *Spergularia* spp. and eventually *Agrostis stolonifera*. Apparently the influx of these and other new species is not hampered by the presence of the annual vegetation, but governed by migration and/or salt tolerance.

See also:

W. JOENJE (1978): *Plant colonization and succession on embanked sandflats.*
Thesis, Groningen.

A. G. F. VAN DIJK (*Laboratorium voor Plantenoecologie, Biologisch Centrum, Postbus 14, 9750 Haren (Gn)*)

Sheep grazing in a new polder: aspects influencing structure and development of the vegetation

Vast communities of halophytes dominated the saline sand-flats of the Lauwerszeepolder (The Netherlands) in the first years after embankment in 1969. Changes in the environment, especially desalination of the soil, lead to a decrease of the area occupied by halophytes and a rapid invasion by grasses. A new niche for big ungulates developed and thus 75 ewes with their lambs were introduced in a 330 ha area on the northern, sandy part of the polder in 1977. The influence of the introduction of sheep on the vegetation was studied in 1979, from August till November.

Trampling caused a variation in soil compaction and locally resulted in an abundance of trampling-resistant plants such as *Plantago coronopus* (moderate) and *Plantago major* (heavy trampling). Selectivity in grazing may stimulate certain plant species and reduce others. Assessment of selectivity by grazing sheep indicated a strong preference for *Aster tripolium*, *Juncus articulatus* and *Puccinellia maritima*, whereas the abundantly occurring *Agrostis stolonifera* was hardly eaten. In the grazed part *Aster tripolium* was kept at a low rank compared to ungrazed vegetation. *Puccinellia maritima* is known to be stimulated by grazing. *Phragmites australis* and *Salix* spp. were readily eaten, which suggests a positive influence of grazing on the open character of the landscape. Vegetation succession is to a large extent dependent on the development of an organic buffer in the system which prevents leaching of nutrients. Formation of this organic layer results from the accumulation of litter within the vegetation. Estimates of the maximum standing crop and consumption of plant materials by sheep within various communities indicated a strong negative relationship between maximum standing crop and consumption by the sheep. Sheep grazing seemed to enhance the existing difference in productivity between plant communities. The season of grazing differed between the vegetation types. Young tufts of *Puccinellia maritima* were grazed and showed little senescence, whereas a light grazing in *Agrostis* dominated vegetation only occurred when much of the foliage was already dead and accumulating in thick mats. Finally, there exists an input of sheep dung and urine on the limited area of the sleeping grounds which indicates a redistribution of nutrients.

It is concluded that extensive grazing by big ungulates affects the vegetation structure and differentiation positively and should be considered a relatively cheap and useful management tool in young polders.

MEETING OF THE SECTION FOR PLANT MORPHOLOGY AND -ANATOMY AND OF THE SECTION FOR PLANT TAXONOMY AND PHYTOGEOGRAPHY ON APRIL 10, 1981

W. A. VAN HEEL (*Rijksherbarium, Postbus 9514, 2300 RA Leiden*)
A S.E.M.-investigation on the development of free carpels

The early development (ontogeny) of the carpels of 20 species belonging to 8 apocarpous families was investigated with the scanning electron microscope. The results indicate that on the floral apex a meristem with a circular outline or a convex meristem, by unequal growth of its periphery, develops from a bowl-shaped phase into an obliquely ascidiate primordium which, by further unequal growth, develops into a young carpel. The terminal mouth of a cup becomes the lateral cleft of a carpel. The different forms of the young carpels in different species are defined by the varying degree of development of the adaxial region of the initial meristem and/or its margin on the side of the floral apex. This hypothesis is theoretically evaluated against some current morphological and phylogenetical carpel theories.

To be published in *Blumea* (1981) 27.2.

A. KLOOS (*Instituut voor Systematische Plantkunde, Postbus 80.102, 3508 TC Utrecht*)
Multidisciplinary systematic research in Moreae (Moraceae) – leaf anatomy of the
Maclura-groep.

The “*Maclura*-group”, comprising 8 provisionally defined genera, *Maclura*, *Cudrania* (2 sections), *Plecosperrum*, *Cardiogyne*, *Chlorophora*, *Bagassa*, *Broussonetia* (2 sections) and *Batocarpus*, belongs to the tribe Moreae of the family of the Moraceae.

An analysis of leaf anatomical characters of the 24 species in the *Maclura*-group confirms the (provisional) delimitations of the genera and their subdivisions. Besides, in *Chlorophora* there appears to be a sharp distinction between *C. tinctoria* on the one hand and *C. excelsa* and *C. regia* on the other hand. The following leaf anatomical characters, being constant for the genera and sub-generic divisions, are used to compare the taxonomic units: cuticular ornamentation, vein prominence, presence of lithocysts or cystolith-hairs, indument, multiple epidermis, vascularisation patterns in midrib and petiole and the presence of special features such as a different type of glandular hairs, foliar sclereids, dimorphous spongy parenchyma and the occurrence of idioblasts.

Based upon the presumed derived character states of each of these characters, an effort is made to clarify the possible phylogenetic relationships between the members of the *Maclura*-group. Thus, it was concluded that *Maclura*, *Cudrania*, *Plecosperrum*, and *Cardiogyne* have many common derived characters and likely constitute a natural group. *Chlorophora tinctoria* has few derived character states in common with *C. excelsa* and *C. regia*. The latter two species combine very well with *Bagassa*; *C. tinctoria* seems to be related to the genera *Maclura*, *Cudrania*, *Plecosperrum* and *Cardiogyne*. The position of *Broussonetia* can not be established by using the presumed derived character states alone. *Batocarpus* occupies a rather isolated position among the other genera and seems to be related to the genus *Artocarpus*, another member of the Moreae.

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Morphology of the Moreae (Moraceae)

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