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MEETING OF THE SECTION FOR PLANT MORPHOLOGY, ANATOMY AND CYTOLOGY AND THE SECTION FOR FERTILIZATION RESEARCH IN PLANTS ON 27 SEPTEMBER 1996

Anther development in tomato: gibberellin regulated gene expression

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Gibberellins (GAs) are endogenous plant growth regulators that are involved in the regulation of many aspects of plant growth and development, including seed germination, extension growth and flowering. An approach to understand GA action is to isolate genes which are regulated by GAs and use these genes both as molecular markers for GA response and also to isolate the molecules which are involved in this regulation. GA-regulated genes are found in the aleurone layer of germinating cereal seeds, in vegetative shoot tissue and in flowers.

We have initiated a project to investigate the role of GA in the promotion of anther development in the gib-1 mutant of tomato, *Lycopersicon esculentum*. This mutant is deficient in GAs because its ability to convert geranylgeranyl pyrophosphate to copalyl pyrophosphate is reduced. The phenotype of this mutant, which includes dwarfism, failure to germinate and failure to flower normally, is reversed by exogenously applied GAs. The anthers become developmentally arrested when the flower bud is 2·5 mm in length and remains responsive to a single treatment with 50 ng gibberellic acid (GA3) per bud until a length of 3·7 mm. Developmentally arrested anthers contain pollen mother cells which are in the G1 phase of the premeiotic interphase, and outer and inner tapetum cells which are at the uninucleate and binucleate stages, respectively (Jacobsen & Olszewski, 1991, *Plant Physiol.* **97**: 409–414). The GA3 treatment of developmentally arrested flowers is known to cause specific changes in the gene expression of the gib-1 anthers (Jacobsen & Olszewski, 1994, *Planta* **192**: 372–378). A differential screening of a gib-1 anther cDNA library made 48 hours after GA treatment resulted in the isolation of several cDNAs. The mRNAs of the corresponding cDNAs could be placed in two classes with respect to the kinetics of their accumulation patterns in the gib-1 flowers. The first class consists of genes that increased in expression 8 hours after GA3 treatment and they were maximally abundant either 24 or 48 hours post-treatment, while the second class was not detected until 48 hours post-treatment. The genes of class I already showed a response when arrested buds were treated with 0·5 ng GA3/bud, while at least a single treatment of 5 ng GA3/bud was necessary for rescuing normal flower development. *In situ* hybridization experiments showed that 24 hours after a single treatment with 50 ng GA3/bud the localization of the gene expression was restored as in wild-type. Also the timing of the formation of interlocking hairs on the mutant anthers after treatment was comparable to that in wild-type, while these hairs were never found on anthers of untreated buds.

It has been shown that a single treatment restores normal flower and anther development in the mutant with respect to gene expression, timing and differentiation processes. The role of GA during anther development of tomato will be investigated further by using the molecular markers and performing a morphological study of the mutant.

Microtubule assembly and cell polarity in higher plants

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In higher plant cells devoided of centrosomes or defined microtubule-organizing centres, the nuclear surface has been found to function as a MTOC. *In vitro*, we have shown that isolated plant nuclei nucleate microtubule assembly at a tubulin concentration that is not efficient for spontaneous microtubule assembly (Stoppin *et al.*, 1994, *Plant Cell* **6**: 1099–1106). This does not exclude that other nucleation sites may be present at the membrane or the phragmoplast. Gamma tubulin, considered as a MTOC marker that is predominantly located at the centrosome(s) and the stem-body of animal cells, is found on the plant nuclear surface but surprisingly also within most plant microtubule arrays. The functional significance of such distribution remains enigmatic and could be linked to the singular redistribution of plant microtubules during spindle poles formation. How the mitotic polarity is achieved in higher plant cells remains obscure. Our observations suggest that microtubule interaction close to the nuclear surface, before nuclear envelope breakdown,

leads to the formation of multiple aster-like centres which progressively fuse into poles. Such mechanisms are under cell-cycle controls, including most probably the activity of minus-end directed motors and microtubule-associated proteins. Recent data indicate that higher plant microtubule-associated proteins affect both microtubule nucleation and growth at plant nuclei as well as at mammalian centrosomes (Stoppin *et al.*, 1996, *Eur. J. Cell. Biol.* **69:** 11–23). Redistribution of nucleation sites (protein complexes including gamma tubulin and microtubule-associated proteins) under cell-cycle controls (Lambert, 1993, *Curr. Opin. Cell Biol.* **5:** 116–122) combined with active minus-end directed interactions of microtubules may be therefore responsible for the establishment of mitotic polarity in higher plant cells devoided of centrosomal activity.

Longitudinal profiles in growing maize roots

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To investigate the role of the cell wall in plant morphogenesis we studied cellulose microfibril orientation and variation in infrared absorbance in median longitudinal sections of maize roots growing at two different waterpotentials: well-watered (− 0·2 MPa) and water-stressed (− 1·6 MPa). Previous studies (Sharp *et al.*, 1988, *Plant Physiol.* **87:** 50–57) have shown that besides physiological differences there are marked morphological differences between primary roots growing under the two treatments: roots growing under well-watered conditions show a higher growth rate, reach a greater diameter and possess a longer growth zone than roots growing under water-stressed conditions.

We found that under both culture conditions the orientations of cellulose microfibrils and cortical microtubules in the root cortex at the tip of the root are transverse. In well-watered roots the orientation of the cortical microtubules shifts towards an S-helix at about 8 mm from the tip. The inner layer of microfibrils starts showing a parallel shift in orientation at 9 mm from the tip. In water-stressed roots the cortical microtubules show a shift towards an S-helix at about 4 mm from the tip. At this position the cellulose microfibrils, however, predominantly shift towards a Z-helix. This conflicts with the widely accepted mechanism of microtubular orientation of microfibril deposition (for review see Giddings & Staehelin, 1991 In: Lloyd C.W. (ed.): *The Cytoskeletal Basis of Plant Growth and Form*, pp. 85–99, Academic Press, London). At 10 mm from the tip in well-watered and at 8 mm from the tip in water-stressed roots the microtubules are longitudinal. The cellulose microfibrils show this orientation at 12 mm and at 5–6 mm, respectively.

The orientation profiles of the cellulose microfibrils offer no logical explanation for profiles of geometrical strain rates in the growing maize root, regardless of the growth conditions.

Preliminary studies with Fourier Transform Infrared Microspectroscopy (see McCann *et al.*, 1992, *Plant Physiol.* **100:** 1940–1947 for an introduction to this type of cell wall studies) of the sections revealed differences in the sections between positions and tissues. The intensities of 11 absorption maxima in the carbohydrate region of the absorption spectrum were coadded and the percentile contribution of each peak to the total absorption was calculated. Plotting these data as a function of position along the root resulted in highly reproducible longitudinal profiles that were slightly different for different tissue types. When these profiles were compared to geometrical strain rates, some interesting parallels were found that justify further examination.

Localization of the cytoskeletal proteins actin and myosin in lily pollen tubes

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The presence and localization of actin and myosin have been examined in pollen tubes of *Lilium longiflorum* utilizing four techniques: (1) immunocytochemistry, (2) immunofluorescence microscopy of actin and myosin following rapid freeze fixation, freeze substitution, and butyl methyl methacrylate embedment, (3) microinjection of fluorescein phalloidin into living pollen tubes and (4) immunogold labelling of actin in transmission electron microscopical sections. Pollen tube extracts analysed by immunocytochemistry and antibodies to actin, myosins IA and IB, myosin II and myosin V reveal the presence of these contractile proteins. Immunofluorescence microscopy reconfirmed that actin is localized longitudinally in the pollen tube. Myosin I was localized to the plasma membrane, the larger organelles, the surface of the generative cell and the vegetative nucleus. Myosin V was distributed in the vegetative cytoplasm in a punctate fashion representing smaller organelles, while Myosin II subfragment 1 and light meromyosin were also localized in a

punctate fashion but on the larger organelles. In addition, isolated generative cells and vegetative nuclei labelled only with the myosin I antibody. Competition studies indicated the specificity of the heterologous antibodies utilized in this study suggesting the presence of three classes of myosins in pollen, whereas injection of fluorescein phalloidin into a living, growing pollen tube indicates that the actin filament distribution is longitudinal along the length of the pollen tube but the actin microfilaments do not extend into the tip region. Immunogold electron micrographs of actin microfilaments labelled with pea anti-actin antibody indicate the same distribution.

These results suggest that Myosin I may move the generative cell and vegetative nucleus unidirectionally through the pollen tube to the tip, while myosin V moves the smaller organelles and myosins I and II move the larger organelles (bidirectionally) that are involved in growth. In addition, the distribution of actin microfilaments seen in living pollen tubes is contrary to the model describing an actin meshwork at the tips of all tip-growing systems.

Characterization of MAPs from carrot cytoskeletons

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The dynamics of microtubules (MTs) is regulated by a specific group of microtubule-associated proteins (MAPs). These so called 'structural' MAPs are well known from animal systems but virtually nothing is known about the MAPs that regulate MT dynamics in plant cells.

We recently reported on the isolation from carrot cytoskeletons of a MAP fraction which strongly stimulated MT assembly (Chan *et al.*, 1996, *Plant J.* **10:** 251–259) thus proving the presence of structural factors. Using affinity-purified antibodies against the individual proteins within this fraction we were able to show that some proteins codistributed with all MT arrays throughout the cell cycle, making them potential candidates for regulators of MT dynamics. Among the proteins identified as such was a group of three with MW between 60 and 68 kDa that was immunologically related to another group of proteins formerly described as the 65 kDa proteins (Jiang & Sonobe, 1993, *J. Cell Sci.* **105:** 891–901). One of these MAPs with a MW of 60 kDa (MAP60) has now been purified, allowing us to study the effects of a single plant MAP. MAP60 markedly stimulated the formation of brain MTs *in vitro*, an effect that could be inhibited by pre-incubating MAP60 with affinity-purified antibodies against the 65 kDa proteins. Further analysis demonstrated that MTs polymerized in the presence of MAP60 did not depolymerize upon dilution. MAP60 also greatly increased the cold stability of MTs. A nucleating activity, however, seemed absent. MAP60 shares the characteristics mentioned above with a small group of animal MAPs, including STOP protein and myelin basic protein, that specifically stabilize MTs. We are therefore convinced that MAP60 is a structural MAP, the first known from a plant source.

Localization and function of sucrose synthase and invertase during maize kernel development

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Sucrose synthase and invertase are the only two sucrose degrading enzymes in the plant. Their activity is an indicator for the sink strength of cells and organs, such as the maize kernel. For this study a method has been developed to show the activity of sucrose synthase on sections by precipitation of a blue formazan. This assay works on the production of UDP-glucose by the sucrose synthase in the tissue. A comparable assay is used to detect the activity of invertase, and responds to the production of glucose. Next to these enzymatical assays, light microscopical immunocytochemistry is used to localize the enzymes with anti-invertase or anti-sucrose synthase.

The assay and immunochemistry showed invertase being present and active in the basal endosperm, pedicel parenchyma and attached closing layer. However, the placento-chalazal tissue between endosperm and closing layer did not show any activity or presence of invertase. In the embryo invertase was localized in an excretion product around the primary roots.

In a kernel of 5 days after pollination no sucrose synthase was found by the immunocytochemical detection, while the enzyme assay did show activity. In older kernels migration of sucrose synthase activity was shown from the apical part of the endosperm towards the basal part, corresponding with the filling of endosperm with starch. This confirms the correlation of sucrose synthase activity with starch synthesis. In the aleurone layer sucrose synthase activity was found for a longer period than in the endosperm, but immunocytochemistry still showed presence of the enzyme after it had lost its activity. Possibly the enzyme is inactivated there. Sucrose synthase activity in the aleurone is probably associated with the abundant protein synthesis in these cells. In the embryo high activity of sucrose

synthase was found in the epithelium of the scutellum, but immunocytochemistry did not show labelling. The sucrose synthase might play a role in the digestion of the endosperm via the embryo scutellum during kernel development.

The results show that an enzyme histochemical assay is very useful next to immunocytochemistry. It provides more information about the actual activity of enzymes during the development of cells and organs.

MEETING OF THE SECTION FOR VEGETATION RESEARCH ON 16 OCTOBER 1996

Effects of fertilizer misplacement and herbicide drift on arable field boundary vegetation

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The decline in species richness of arable field boundaries in recent decades may have been caused by the increased use and subsequent drift of fertilizer to the vegetation outside the field. Two experiments, similar in design, were established in spring 1993, lasting until spring 1996, to determine the effects of fertilizer misplacement and herbicide drift on the vegetation of (i) a low-productive meadow and (ii) a high-productive old field sown with a mixture of grassland forbs. To simulate the effects of drift, low doses (0, 5, 10 and 50% of standard agricultural dose) of the herbicide *fluroxypyr* and artificial fertilizer (NPK, 0, 25, 50%) were supplied to the vegetation in each of these sites.

In the meadow, fertilizer application resulted in a decreased species richness, but herbicide treatment did not affect species richness significantly. Two individual species, however, were affected negatively by the herbicide treatments. The effects in the old field were larger and both herbicide and fertilizer treatments reduced species richness significantly. The effects of both factors appeared to be additive, but the fertilizer affect was stronger and more constant. A considerable number of species was significantly decreased in abundance, either by the herbicide or by the fertilizer treatment. Differences in effects between the two experiments may be explained by a reduced efficacy of herbicides in low-productive vegetation.

In conclusion, drift of herbicides and fertilizer may seriously decrease species richness in arable field boundaries.

The impact of tourism on the vegetation of Antarctica; a trampling experiment

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As a member of the international Project Antarctic Conservation, I studied tourist activities and their impact on the vegetation, in the Antarctic summer 1992/1993, to prepare long-term research on this subject. Tourism increases rapidly and takes place in the short austral summer on a few snow-free areas on the coast. The vegetation is scarce and wildlife is breeding in this period in the same areas. Besides guided ecotourists on cruise ships, more and more adventurers and holiday-makers are coming and stay for a longer time, which is a bigger threat. On Cuverville Island (64°41'S, 62°38'W) the vegetation was mapped and described; see C.C. de Leeuw *et al.* (1997: Nova Hedwegia, in press). Both Antarctic spermatophytes, 19 species of bryophytes, 29 species of lichens and one species of macro-algae were found, sampled and kept in herbaria. The trampling experiment was carried out on a *Polytrichum alpestre* vegetation, which was the most common, accessible and vulnerable vegetation on the island. Simulated trampling by a group of 50 people damaged the vegetation within a week, to such an extent that no recovery was possible during the same growing season. Follow-up research has to provide the answer to the question which vegetations are potentially threatened by trampling and what is the power of recovery of damaged vegetations, thus revealing information for the regulation of tourism.

Methods to compare vegetation maps using GIS

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Two major problems often arise when comparing vegetation maps. (1) The legends of maps contain different legend units (vegetation types). As the classification of a set of vegetation samples is almost never exactly identical, the resulting vegetation types on a map differ thematically. Also the interpretation of aerial photos into polygons is, mainly, not identical. As a result vegetation types often also differ geometrically. When ignoring this problem and treating the most resembling vegetation types as being identical, the overall accuracy can drop dramatically. In a study in the Millingerwaard near Nijmegen, The Netherlands, two maps of the same area in the same

period had an overlap of only 52%. (2) The amount of information is, especially when comparing several sequential maps at the same time, rather large and complex. One can define a change as a transition of an area from one vegetation type into another. When comparing two maps with each X types there are X*X possible transitions. The number of possible transitions increases exponentially with the number of maps that are compared.

The first problem can be solved by establishing which vegetation types have a thematical overlap. The change of a vegetation type into a thematically overlapping type should be treated as non-significant.

The second problem can be solved by using a structured approach in analysing the data. Structure can be attained by dividing the methods of analysis in a geometric and a thematic approach. A geometric approach means the comparison of the geometrical description of legend units through the years. A thematical approach means the comparison of the thematical description of map elements through the years. The resulting changes in vegetation type can be interpreted in terms of ecological processes, by using numerical vegetation-analysis methods, or with the aid of the Basic Botanical Register. A second way of attaining a structured analysis is to divide the subject of analysis into three different levels, i.e. species, vegetation and landscape/vegetation complex.

Restoration of the vegetation of dune lakes

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The number of oligotrophic dune lakes in the Dutch coastal dunes had sharply declined as a consequence of dune fixation, drainage, eutrophication and atmospheric nitrogen deposition since the beginning of this century. In particular, vegetations of the early stages of dune lakes have become rare. As part of a Dutch restoration programme against acidification and eutrophication, a number of eutrophied, well buffered (alkalinity 1-2 meq l^{-1}) dune-lakes in calcareous dunes (Oostvoorne) and in non-calcareous dunes (Terschelling) have been restored. All living and dead organic matter from the lake sediment and water layer and its immediate surroundings, excluding some remnants of the vegetation of the early stages of dune lakes, have been removed in wintertime. The effects of this measure upon water and sediment chemistry of these waterbodies and the development of the macrophyte vegetation have been followed during *c.* 5 years after restoration. The abiotic characteristics of an early-stage dune lake returned. The water became again oligotrophic ($o\text{-}PO_4$: <0·2 µmol l^{-1}, NO_3 and NH_4: <10 µmol l^{-1}), above mineral sediments in an open dune landscape. A quick recolonization by characteristic plants of early stage dune-lakes occurred after restoration. Especially Littorelletea and Charetea communities with several endangered plant species returned. Apart from atmospheric deposition, two possible causes for renewed eutrophication were found: excess input of excrements of large grazers and waterfowl and litter from nearby trees. Because of the rather high buffer capacity, acidification is a rare phenomenon in Dutch dune lakes. It is, until now, only observed in a few non-calcareous dune slacks. It is therefore concluded that restoration of dune lakes is relatively simple and in most cases very successful. It can serve as an alternative in areas of the dune landscape, where spontaneous, large-scale formation of dunes and lakes is restricted.

Effects of cessation of fertilizer application and different management regimes on composition, structure and erosion susceptibility of seadike grassland

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In grassland on Dutch seadikes the influence of cessation of fertilizer application in combination with different management regimes on factors affecting water erosion was experimentally investigated. From 1991 to 1994 botanical composition, vegetation cover and root density were studied, and erosion susceptibility was tested in a laboratory device for water erosion by centrifugation. Non-fertilized, species-rich grasslands were also investigated as a reference. The aboveground biomass production of these grasslands was about 5 tonnes dry matter $ha^{-1}.yr^{-1}$, which is half the amount of fertilized grasslands. The root density in $m.dm^{-3}$ as well as the erosion resistance (time needed for the loss of % weight) was twice as high compared to the fertilized grasslands, at a depth of 3 cm and below.

Cessation of fertilizer application, together with hay-making on formerly sheep-grazed dike grassland, led to a decrease in the aboveground biomass production from 10–11 tonnes $ha^{-1}.yr^{-1}$ to 6·5–7·5 tonnes $ha^{-1}.yr^{-1}$. There was an increase in root density and erosion resistance at a depth of 5–10 cm, and a change in the dominance of species of nutrient-poor soils. This proves the positive effects of a more extensive management of dike grasslands for improving resistance against erosion. Less obvious results,

however, were observed in experiments with sheep-grazing and cessation of fertilizer. Continuation of the experiments is necessary in order to investigate the long term effects of hay-making as well as sheep-grazing without the use of fertilizer on root density and sod quality.

Native trees and shrubs, a neglected side of the wild flora

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In floristic and vegetational science, ligneous plants are a neglected taxonomical group. For centuries, many kinds of trees and shrubs have been planted, cultivated and traded. With regard to biodiversity and gene-conservation, an understanding of the original native flora of ligneous plants is very important. In The Netherlands in 1992, the Department of Agriculture, Nature-Conservation and Fishery started the Genetic Quality project. The intention of this project is to create comprehension of indigenous material of trees and shrubs still present, their decline, protection and possible harvest and use.

Determining the original, native quality of a tree or ligneous plant is not an easy task. As definition of indigenous plants we follow H.M. Heybroek (Behoud en ontwikkeling van het genetisch potentieel van onze bomen en struiken. Wageningen, 1992): 'Indigenous is plant material which since its spontaneous settlement after the last ice-age has always reproduced itself locally, or has been rejuvenated artificially using strictly local material.'

The used working procedure assumes several criteria which can be used both for the plant itself and for its growing location. The procedure is used to assign the probability of indigenous quality. A first test is a topographic map (scale 1:50·000 or 1:25·000), dating from 1850 or earlier. Landscape features existing on both the old map and on a recent map are possible locations of indigenous material. Usually, these features date back much further than the map itself. It is important to establish whether the landscape feature truly is old. In this respect, herbs and ligneous plants characteristic of old woods are useful indicators, as well as the local history of the wood, found in old archives. Examples are coppice woods and coppice standards.

Between 1992 and 1996 stocktaking has been done for several regions in The Netherlands. This research revealed the repression to which native ligneous plants are exposed. Nearly half of the approximately 100 native ligneous plants (blackberries excluded) are endangered, rare or extinct.

Flowering phenology and bumblebee-mediated pollen flow in *Phyteuma spicatum* ssp. *nigrum* (Campanulaceae)

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Pollen dispersal varies substantially during the flowering period. When can we expect the largest distances of pollen flow or the best period for outcrossing? Several aspects determining pollen flow were measured during the flowering season of the rare plant species *Phyteuma spicatum* ssp. *nigrum* in 1994 and 1995. This self-incompatible species flowers during 3 weeks in May and June and is mainly pollinated by bumblebees, queens and workers. Visitation rate decreased from early flowering till the end of flowering. Distances of pollen flow are estimated from pollinator foraging distances, measured as inter-inflorescence distance and as the overall distance between the first and eleventh inflorescence visited. Special attention was paid to the amount of large distances, the tail of the dispersal graph and to the amount of intra-plant movements. Flown distances followed the mean inter-inflorescence distances. However, maximum distances of inter-inflorescence movements and of overall distances were larger during early flowering than during peak flowering. During late flowering distances were even smaller than during peak flowering. Observations on individually marked bumblebees appeared to be useful in the explanation of these differences. We must realize that the flower visitors, e.g. bumblebees, make the decision what plant species to visit and to what extent. The choice of the bumblebee is influenced by the presence and number of flowering plant species which, of course, vary during the season. The best period for outcrossing in *P. spicatum* ssp. *nigrum* in 1994 and 1995 was early in the flowering season.

SYNDIAT, SYNtaxon DIAgnostics Tool, a computer program based on the deductive method of community identification

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Identification of plant communities usually refers to descriptive syntaxonomical classification with character species, according to the Braun-Blanquet approach or similar. In many cases adequate identification can only be done with experience in syntaxonomy and thorough knowledge of the classification referred to.

Recent trials with computer programs for identification are based mainly on some similarity index with the frequency data of all species found in the relevés that were used for the description of the syntaxa. However, not frequency itself but difference of frequency data between syntaxa is a good diagnostic measure. Character species reflect these differences and should be used therefore. Hierarchical classification, reflecting ecological amplitude, is also well described by character species and can thus also be involved in the analyses.

K. Kopecký *et al.* (1995, *Vegetatio*, **117**: 95–112) published an algorithm that completely links up with these ideas. This algorithm was adopted as the basis for the computer program. It was extended with a measure for saturation of the community, characteristic cover of species, typical layer for the character species and analyses of groups of similar relevés. For all syntaxa in the classification, regardless of their hierarchical position, a value is calculated based on the existence of their character species in the relevé under analysis. These values are added to the values of the syntaxa of a higher order under certain conditions. Identification takes place by searching top-down through the hierarchy for the highest values. All values, saturation data and character species involved are listed.

An example was shown of a management experiment in which Arrhenatheretum elatioris slowly decreased in weight in 4 succeeding years, while Artemisietea vulgaris aspects increased. Another example was derived from a discussion in J.H.J. Schaminee *et al.* (1995, *De Vegetatie van Nederland*, Opulus Press, I, p 126) on the syntaxonomical status of some relevés belonging to either Eleocharitetum multicaulis or Scirpetum fluitantis (both Littorelletea). SYNDIAT proved to be a useful tool for fast and adequate syntaxonomical identification of relevés.

