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SOME CONCLUSIONS OF ECOLOGICAL INVESTIGATIONS ON GRASS SPECIES OF PALUDAL AND OF FIELD ORIGIN I.

Comparative studies on the ecology and production biology of reed canarygrass /Phalaroides arundinacea /L./ RAUSCH.*/

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Introduction

The reed canarygrass having circumpolar area, is commonly native in the Northern Hemisphere. It starts to be ubiquitous in the whole World have been introduced into S-America, Australia and New-Zeeland, and Africa as a forage crop or an ornamental plant /ANDERSON 1961/.
The reed canarygrass is a very common species in the spontaneous flora of Hungary, nevertheless its frequency does change from a phytogeographical district to another /Figure 1/.

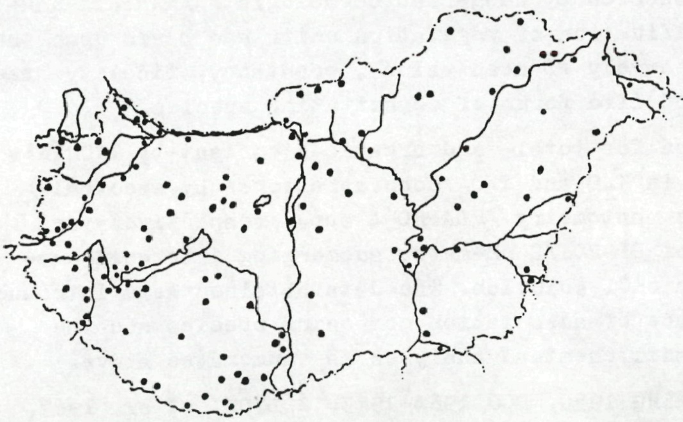

Figure 1. The occurence of reed canarygrass in Hungary

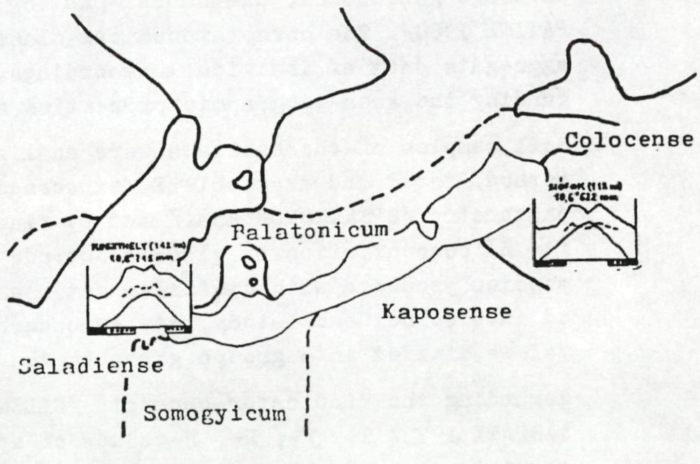

Figure 2. The floristical districts of the Balaton-region with climatodiagramm of Keszthely and Siófok

The investigations on reed canarygrass have been accumulated with an accelerating tendency since the 20s of this century in Europe, regardless the earlier studies of practical nature /e.g. Sweden 1749, England 1824, Germany 1850, N-America 1898 - HEATH-HUGHES 1969/.
Certain revaluation has been going on for years in the cenotaxonomy and -systematics characterized by an intuition of the point of view of synecological role of reed canary-

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*Phalaris arundinacea - about the synonymity of the species see: SZABÓ, I. 1980. Botanikai Közlem. 67. 49-57.

grass /KOCH 1926, LIBBERT 1932, UJVÁROSI 1947, HUNDT 1958, KOPECKY-HEJNY 1965, JEAN-PLONG 1968, MIYAWAKI-OKUDA 1972, SOÓ 1966-73, KÁRPÁTI 1973, BALÁTOVÁ-TULÁCKOVÁ - HÜBL 1974/.

The reed canarygrass and stands of its content proved to be useful in the water management by their practical application in biological embankment /KOPECKY 1965, KÁRPÁTI 1974, SZABÓ 1980/. However these results have been surpassed by the successes in field forage growing of its pure stands of high productivity /HEATH-HUGHES 1969, ECKER 1977 - but there are critical remarks on it too, e.g. SHAEFFER-HOVIN-RABAS 1981 in favour of mixtures of grasses of high productivity/.

Some results of phytosociological studies and such basic issues of the production biology of reed canarygrass are reported in this paper as the questions of adaptability of this species of wetland origin to field conditions with an apparent drought resistance and as the expressibility of the course of developmental events of phytomass production /see at BARNARD 1964, BOOYSEN-NELSON 1975, BROWN-BLASER 1965, EVANS 1962, GABORCIK 1982, HUNT 1978, MILTHORPE-IVINS 1966, PRÉCSÉNYI 1969, RALPH-BEIDLEMAN 1969, SESTÁK-ČATSKY-JARVIS 1971/.

Materials and methods

Our studies have covered a decade since 1974. The phytosociological records, following out of the spirit of the Code of Phytosociology /BARKMAN et al. 1976/, were carried out by BRAUN-BLANQUET's method modified for the simultaneous estimation of frequency and of coverage /abundance, dominance - AD/ of species by Hungarian coenologists /KÁRPÁTI-KÁRPÁTINÉ 1968/. The coenotaxonomical classification of vegetation units was based upon the aggregate data of individual recordings, namely AD mean values, constancy, fidelity, regarding the area-geographic properties and life forms of constituting species.

Soil samples of the habitats were analized for total- and organic-N content by TJURIN's method, for K and available P /expressed in K_2O and P_2O_5 concentrations/ by spectral-photometry /SPEKTROMOM app./ and by flame-photometry /FLAPHO-4 app./ respectively and for H^+ concentration by glass-electrode of OP-201/2 pH-meter submerging into soil suspension produced with distilled water and nKCL solution. The data obtained were introduced into coincidence study between occurence of association composing species and the values divided into groups given by the soil chemical analyses as enumerated above.

Regarding the "indicator-concept" /ELLENBERG 1950, SOÓ 1964-1973, ZÓLYOMI et al. 1967, KÁRPÁTI 1973/ T-, W-, R-, N-values of species of communities were used to designe a complete diagramm of spots in the cause of illustrating certain relations between vegetation units and their environment /see Figure 4/.

The crop of the pastures was evalueted by the "hay-value" scale of BALÁZS /1949, 1960/: $Q = \frac{kt}{T}$; where t = AD·m = the relative crop of species /the product of the AD and the mean height of species; T = t; k = quality value of species, regarding their usefulness, palatability or - in other hand - their unpreferable properties, expressed by numbers ranging from +7 to -3; kt = the relative agricultural value of species. $Q > 4$ means green or hay of high quality, Q = 3-4 means crop of good quality, Q = 2-3 means that of weak quality, $Q < 2$ for crop of poor quality /low rate/.

The greater part of reed canarygrass /'K-52' line/ studies was carried out on the fields of the state farm of Agricultural University at Keszthely and on wetlands near Balaton /spontaneous stands of unbreaded reed canarygrass/ in comparison with other geophyte /Bromus inermis/ and hemikryptophytes /Dactylis glomerata, Festuca arundinacea/.

The main features of developmental processes /root- and rhizom establishment, leaf appearance and growth, shooting, initiation and organogenesis of flowering, summer depression of growth and winter dormancy/ were recorded permanently together with the productivity measurements going on as follows.

The growth characteristics /RADFORD 1967, HUNT 1978/ were calculated on the basis of dry weight and that of the total surface /area/ of assimilating organs /not only the leaf area, but the cumulated area of the culm covered by leaf sheats, leaf blades, assimilating tissue containing parts of panicle e.g. axes, palea and gluma were taken into account/. Consequently in addition to RGR, CGR, instead of RLGR and LAR the Relative Assimilating Surface Growth Rate /RAGR/ and Assimilating Surface Area Ratio /ASAR/ was calculated and introduced into NAR. This particular work has not been in want of approximations by plant geometry /SZABÓ 1983/.

The dry weight and assimilating surface increment of reproductive tillers were described by the logistic equation of growth functions /RICHARDS 1959, SVÁB et al. 1968, HUNT 1978, VENUS-CAUSTON 1979/. The computed weight and area data were substituted into formulae of growth characteristics above listed, to obtain smoothed growth curves in addition to those of the actual weight and area data.

Allometry and entropy /for the latter SHANNON's diversity by PIELOU 1969/ were also counted for the description of growth and developmental processes on the level of individual organisms.

The sampling frequency in the case of measurements above listed took four days during the growing season with 10s of reproductive tillers regularily. The above- and below-ground living and died phytomass was collected from spots of 0.25 m^2 of field experiments and from soil monolites in 0.4 m depth belonging to the spots, every week in the reproductive growth phase, otherwise every two weeks and monthly in winter.

The comparative studies of water saturation deficites /actual - AWSD, critical or sub-lethal - SLWSD/ and the loading of water balance of grasses were recorded in their foliage leaf segments by STOCKER 1929, ČATSKY 1963, in the case of reed canarygrass in field stands and on wetland habitats /SZABÓ 1984/.

The water soluble carbohydrate content /WSC/ - as an easily mobilizable nutrient fund for growth and developmental demands of grasses - was leached out from the ground and sieved material of several plant organs with a method proposed by DERIAZ /1961/, BALASKO-SMITH /1973/, CHATTERTON et al./1974/ and JAKUBOWSKI-STUCZYŃSKA /1982/. The concentration of reducing sugars was determined by HAGEDORN-JENSEN's iodometric titration after a protein praecipitation by BRUGOWITZKY /1956/.

Results and discussion

Synecological studies

There is a lot of virtual or - in absence of adequate scientific knowledge - unsolved contradictions revealed by the studies of phytosociological characters and ecological relationships of reed canarygrass and its communities /UJVÁROSI 1947, KOPECKY 1961, 1967, SOÓ 1966-73, KOPECKY-HEJNY 1965, JEANPLONG 1968, KÁRPÁTI 1973, SZABÓ 1977, 1980/.

The postulation of KOPECKY /1967/ is advisable to be taken into consideration entirely or partly, namely that along the river system of middle reach of Elbe and Odera the associations of Phalaridion arundinaceae have developed; along the upper and middle river system of Vistula, and along some rivers runing from the Carpathians into the Danube the Agropyro-Rumicion crispi NORDH. 40 /later Rumici-Phalaridion KOP. /61/ 68/ has developed; now at last there are diminishing structural and ecological differences, supposed by the author cited, among the communities belonging to Phalaridion KOP. /60/ 61, Phragmition KOCH 26 and Caricion gracilis NEUHäUSL /57/ 59 on the N-German, N-Polish and Pannonian-plain. - The theory of "diminishing ecological differences" can not be accepted by us, but the foregoing problem as a whole can be solved for Hungarian conditions by our studies.

It seems to be reasonable to range the reedy and meadow associations of reed canary-grass among Phragmition, Magnocaricion and Agrostion groups in Hungary. /Table 1./

Table 1. A comprehensive summary of reed canarygrass communities in Hungary

coenotaxa	locality of community	"hay-value"
Phragmition communis KOCH 26 em. SOÓ 47		
Scirpo-Phragmitetum KOCH 26 medioeuropaeum TX 41 p.p.em. SOÓ 71 phalaroidetosum SOÓ 57	Sárrét, Tiszazug, Balaton-region	2.6-2.75
Magnocaricion elatae KOCH 26		
Caricion rostratae /BAL.-TUL.63/ OB.67		
Caricetum elatae KOCH 26 phalaroidetosum	middle region of Tisza; Ipoly, Rába, Balaton	0.95
Caricion gracilis /NEUH.59, BAL.-TUL. 63/ OBERD. 67, SOÓ 68		
Caricetum gracilis ALMQ.29, GRäBN.f.et HUECK 31, TX 37 typicum subass. phalaroidosum	South-Alföld, Sárrét, Gaja-riv. Balaton	0.72
Carici-Phalaroidetum SOÓ 71	Balaton, Kisbalaton, Zala-river, Hévìz-basin	1.33-2.25
Caricetum acutiformis-ripariae SOÓ /27/,30, 69 phalaroidetosum	Somogy: Kiskoppány Ipoly	2.25 1.75
Agrostion stoloniferae SOÓ 71 nom.corr.		
Deschampsion caespitosae /HORV. 30 s. str./ SOÓ 71		
Agrostio-Deschampsietum UJV. 47 phalaroidetosum	Sárrét	2.73
Agrostio-Phalaroidetosum SOÓ 71	Zala, Rába, Dráva, Kiskoppány, Ipoly, Taktaköz	2.58-2.68
Agrostio-Phalaroidetum SOÓ 71 phalaroidetosum	Dráva, Somogy, Taktaköz	2.78
Alopecurion pratensis PSRG. 46 p.fed. SOÓ 71		
Carici-Alopecuretum pratensis SOÓ 71 phalaroidetosum	North- and South-Tisza-region, Danube, Balaton-Zala, Ipoly, Dráva	2.61
Salicion triandrae MÜLL.et GÖRS. 58		
Salicetum purpureae /SOÓ nom.nud./WENDBG.-ZEL. 52, KÁRP. 70 phalaroidetosum	Rába, Duna, Dráva	
Salicetum triandrae MALC.29, KÁRP.70 phalaroidetosum	Rába, Duna, Dráva, Sajó	
Salicion albae /SOÓ nom.nud.40 p.p./ MÜLL. et GÖRS.58		
Salicetum albae-fragilis ISSL.26 phalaroidetosum	Rába, Duna, Dráva, Tisza	
Alno-Padion KNAPP 42 em. MEDV.-KORNAS 57		
Ulmion OBERD. 53		
Fraxino pannonicae - Ulmetum SOÓ 60 s.str. populetosum /subass.cult./ phalaroidosum	Duna: Szigetköz	

The adaptation of Phalaridion arundinaceae KOP. 61 and of Rumici-Phalaridion arundinaceae KOP./61/ 68 groups to home taxonomy of associations is questionable. These taxa were in one respect supervised and modified by the author himself /KOPECKY 1968/. In our oppinion the associations containing reed canarygrass and Rumex species have relations with Agropyro-Rumicion crispi NORDH. 40 group along the river Danube in Hungary.

The subassociation Scirpo-Phragmitetum phalaroidetosum SOÓ 73 is very frequent in Hungary, in spite of anthropogenic degradation of its habitats and greater number of component species as usual, especially in the Balaton region.

A distinction must be drawn in Magnocaricion group between communities of Caricion rostratae and Caricion gracilis subgroups as follows: Caricetum elatae phalaroidetosum and Caricetum gracilis typicum subass. phalaroidosum fac., Carici-Phalaroidetum, Caricetum acutiformis-ripariae phalaroidetosum according to Table 1 respectively.

The reed canarygrass communities belonging to Agrostion group differ from those of the above mentioned groups in species composition and in environmental features. Transdanubian basophylous reed canarygrass meadows represent a lately introduced coenotaxon: Agrostio-Deschampsietum UJV. 47 phalaroidetosum. The Agrostio-Phalaroidetum SOÓ 71 phalaroidetosum is proposed by us for the typical reed canarygrass meadows in Hungary. The Carici-Alopecuretum SOÓ 71 phalaroidetosum occupies an intermediate position between Magnocaricion and meadow-foxtail /Alopecurion pratensis/ stands. The reed canarygrass communities are synthetized in Table 2. The great number of phytosociologicaly indifferent species is remarkable, showing with several others the anthropogenic degradation of vegetation.

The occurance of Phalaroides arundinacea in the Balatonicum floristical district is constant, usually sporadical, but its stands of greater extent exist near Tihany-Balatonfüred /Scirpo-Phragmitetum phalaroidetosum/. It occurs in the Somogyicum sporadically too, but it is driven back because of the expansion of resort. On the Northern shore of Balaton at Keszthely-Balatongyörök Scirpo-Phragmitetum phalaroidetosum and Caricetum elatae phalaroidetosum stands of great extent were banked up a few years ago. In the peat and marshland district of Saladiense, mainly in the place of ancient bays of Balaton, large areas are covered by several sedge- and grassland communities of reed canarygrass: in the Héviz-basin and in Kisbalaton Caricetum acutiformis ripariae phalaroidetosum, in the lower valley of Zala-river and in Kisbalaton Caricetum gracilis phalaroidetosum, Agrostio-Deschampsietum phalaroidetosum, Agrostio-Phalaroidetum phalaroidetosum, Carici-Alopecuretum pratensis phalaroidetosum. The majority of these stands will be flooded by the storage lakes of Kisbalaton environmental protection system.

The successional pecularities of littoral vegetation zones of Balaton were described by KÁRPÁTI-KÁRPÁTI 1968, KÁRPÁTI 1973, KÁRPÁTI-VARGA 1975. The line diagramm of Table 3 illustrates the role of reed canarygrass in the communities around the Balaton according to the authors pre-cited.

The reed canarygrass and its communities usually occure on slightly acidic, neutral or slightly alkalic soils of organic or of mineral origin at a rich water and nutrient suply /Figure 3 and 4/. Certain groups of associations containing reed canarygrass are vertically arranged in the systems of lacustrian and fluvial inundation areas /Figure 5/.

The variability of the water level seasonally or by geomorphological stages has influences over the total and available nutrient content of the soil. A persisting sommer flooding seems to be more dangerous for the reed canarygrass populations from the point of view of their survival, than a long dry periode. It is such an interesting phenomenon being worthy of further investigations as the salinity tolerance of reed canarygrass observed on sodic soils of the Great Hungarian Plain. -

Table 2: The species composition of reed canarygrass communities

	Sci-Phr-pha		Car ela pha		Car gra pha		Car acu pha		Agr-Pha		Agr-Des pha		Agr-Pha pha		Car-Alo pha	
	AD	K	AD	K	AD	K	AD	K	AD	K	AD	K	AD	K	AD	K
<u>Phragmitetea-Phragmition</u>																
Epi. hirsut.	+-1	I														
Ali.pla.aqu.	+	I														
Aco.calamus	+	I														
Cal.canesc.	+	I									+	I				
Phr. austr.	+-4	IV	+	I							+-1	II				
Stach.pal.	+	III			+	IV	+	I			+	I	+-1	II		
Iris pseu.	+-1	III	+	IV	+	III	+	III	+	III	+	II	+	I	+	II
Lycop. eur.	+	II			+	IV										
Myos.palust.					+-1	IV			+	II	+	I				
Mentha aqu.	+-1	III			+-1	II	+	II			+	II			+	I
Schoen.taber.	1-2	II									+	I				
Sium latif.	+-2	II	+-1	I			+	II	+	I	+	I				
Glycer.maxima	++2	II	+-1	III	+-1	III	+-1	II	+	I	+-2	II	+-2	II		
Typha latif.	+-2	II			+-2	I										
<u>Glycerio-Sparganion</u>																
Scroph.umbr.													+	I		
<u>Magnocaricion</u>																
Galium pal.	+-1	III	1	III	1	I	+	IV	+	I	+	III	+-1	II	+	IV
Carex vulp.	+-1	II	+-1	III			+	IV					+	I	+-2	IV
Carex elata			1-3	III												
Carex grac.					2-3	V									+	II
Carex acutif.							+-5	V							+-2	II
Scutel.galer.							+	I								
<u>Molinio-Arrhenatheretea</u>																
Lathyr.prat.			+	II							+	I				
Cardam.prat.							+	I								
Poa trivial.											+-1	I	+-1	I	+-1	II
Alopec.prat.													+-2	IV	1-3	V
Lych.flos.c.															+	I
Vicia crac.	+	I					+	IV	+	I					+	I
Centaur.jac.													+	I		
<u>Molinio-Juncetea</u>																
Poa palust.					+-1	I			+-1	IV						
Equis.palust.					+-1	II	+-1	I			+	II	+-1	III		
Cirsium pal.											+	II			+	I
Allium ang.											+-1	II			+	I
Juncus subn.															+	I
<u>Molinietalia</u>																
Desch.caesp.											+-1	V				
Festuca aru.											+	I				
Sanguis off.											+	I				
Thalict.luc.							+	I								
<u>Agrostion</u>																
Symphyt.off.	+-1	III			+	I			+	II	+	III	+-1	VI	+	III
Phalar. aru.	1-5	V	2-4	V	1-3	V	1-5	V	2-5	V	2-5	V	2-5	V	+-4	V
Agrost.stol.	+-1	II					+-1	I	+-3	V	1-3	III			+-1	IV
Gratiol.off.							+	II	+	I	+	I			+-3	II
<u>Chenopodio-Scleranthea</u>																
Tanacet.vulg.									+	I	+	II				
<u>Calystegion</u>																
Calyst.sep.	+	I	1	IV	+	II	+	II			+	II	+	IV	+	I
Solidago gig.									+	I	+-2	II	1-3	II	+	I
Echinoc. lob.			+-1						+	I	+	II	+	II		
<u>Bidention</u>																
Bidens trip.									+	II	+-2	II				
Polygon.min.									+	I						
Galega off.											+	II				
Pulic. vulg.											+	I				
<u>Agropyro-Rumicion crispi</u>																
Rumex hydr.	+	I	+	I	+	II										
Rumex congl.							+	I								
Rumex crisp.									+	II	+-1	III	+	II		
Agrop. rep.									1	I	1	I	+	I		
Rorippa aus.											+	I				
Pol.amph.f.terr.	+	I					+	II			+-1	II	+-1	II	+	II
<u>Salicetea</u>																
Rubus caes.									+-1	II						
<u>Salicion albae</u>																
Humulus lup.													+	I		
Myosoton aqu.											+	II				
<u>Phytosoc. indifferent and miscellaneous</u>																
Ranunc. rep.	+-1	II			+-1	IV			+-1	II	+	III	+	I	+	III
Rorippa amph.					+	I									+	III
Lysimach.num.					+	II	+-1	II	+-1	II			+-1	I	+	II
Potent. rept.	+-1	II			+-1	I	+-1	II	+-1	III	+	II	+-2	IV	+	II
Urtica dio.	+	I			+	I	+	I			+	I	+	I	+	I
Rorippa silv.									+-1	III					+	I
Lythrum sal.	+	III	+-1	I			+-1	III			+	III	+-1	III	+	I
Polygon.pers.															+-1	I
Potent.anser.					+	I					+-1	II			+-1	I
Lysim. vulg.					+-1	III	+	II					+-1	I		
Eupat. cann.							+-1	II					+	I	+	I
Caltha pal.													+-1	I		
Eleoch. pal.			+-1	I			+-1	II								
Carex hirta													+	I		

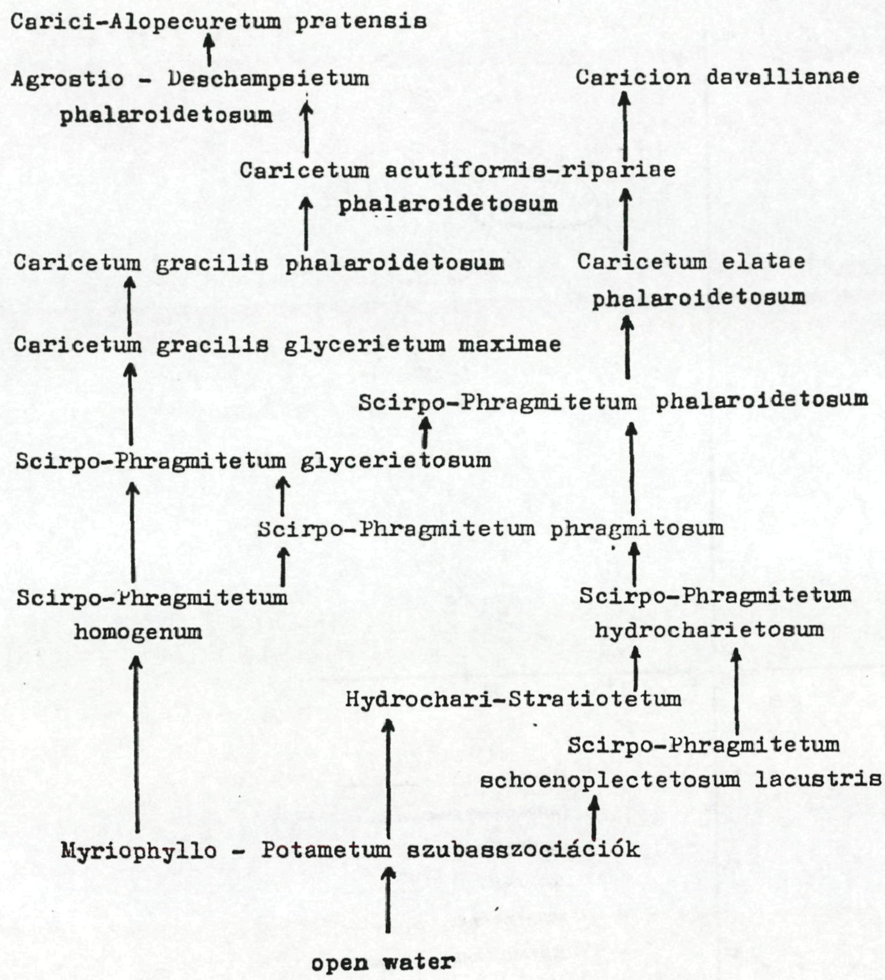
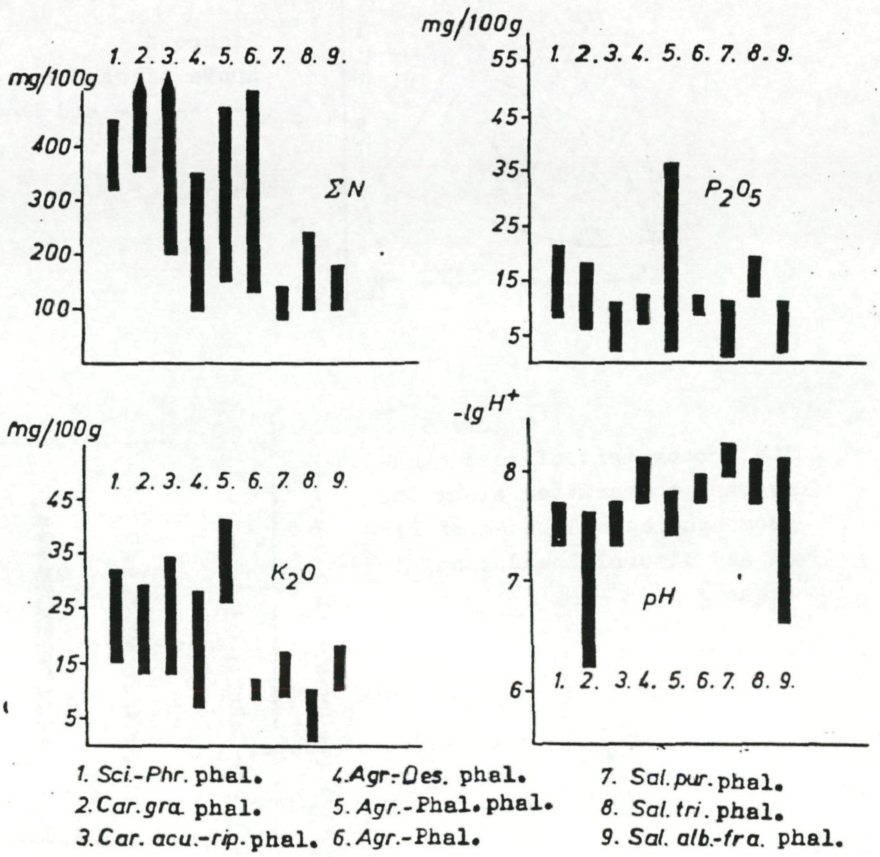


Table 3
Communities of reed canarygrass taking part in the succession of vegetation of the Kisbalaton and Lower-Zala-valley.

Figure 3
Results of soil chemical analyses from the habitats of reed canary-grass communities.



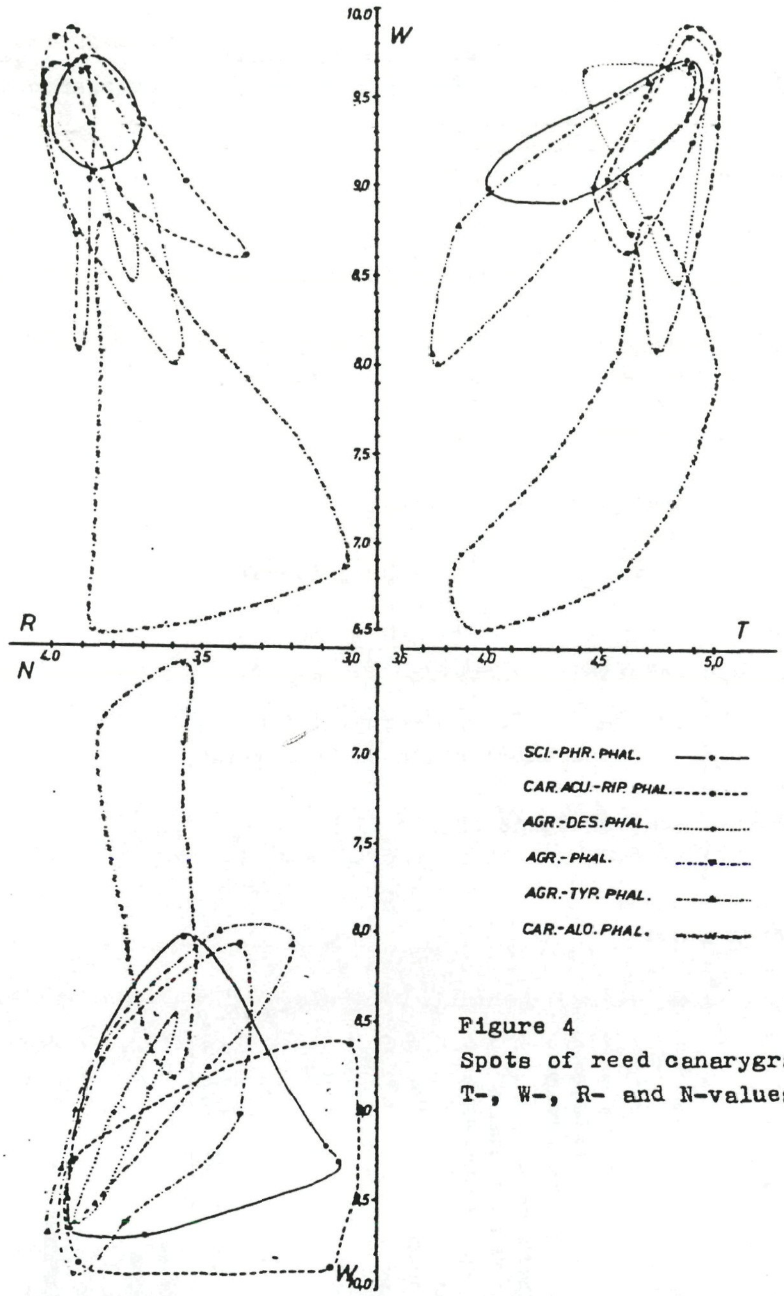
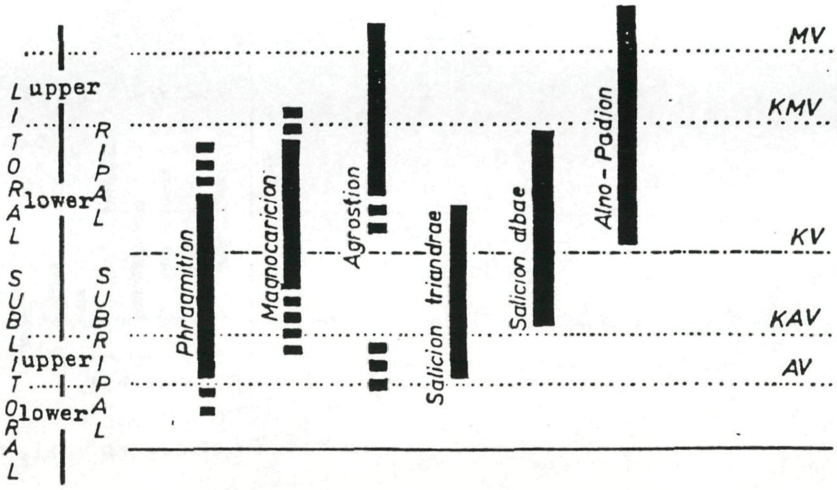


Figure 4

Spots of reed canarygrass communities based upon T-, W-, R- and N-values of composing species

Figure 5

The arrengement of reed canarygrass communities along the geomorphological zones of ripal and litoral inundation areas



Notes to the Tables 1-3 and Figures 3-5.
For the nomenclature of names of vegetation units discussed Phalaroides arundinacea /L./ RAUSCH. scientific name is used regardless the synonyms used originally by the authors cited!
Table 2:
Plant names are abbreviated arbitrarily but expressively as far as possible in the frames of the table failing an official code for abbreviations useful for e.g. computing.
The coenological characterization for grouping the species by SOÓ SYNOPSIS III. 1968.

The abbreviations of coenotaxa are derivated from their scientific names used the first three letters of them.

The reed canarygrass can not be regarded as a native circumpolar species in the Hungarian flora only, but as a species showing great adaptability to the changing /=becoming degradated/ environment. For this reason there are vegetation units of great importance for further studying within the scope of investigations of secondary succession as follows:
- disturbed vegetation units being very rich in Artemisetea elements on dry shores and on dams of channelized water-courses,
- shallows, poorly grown over grasses and annual herbs on the lower stages of river beds,
- in the sedge belt or woody zone of forest lakelets,
- depressions, subsidiarily getting moisten, without an outlet by road and railway buildings,
- floating plants of sodds of initial successional stage in storage lakes.

Productivity studies

The reed canarygrass gives a harvest of great mass and of good quality itself, but because of the species of lower palatability and other poisonous ones, the green and hay production of communities above studied is only of second-rate quality /Table 1/; finaly there are hardnesses of harvesting owing to the physiognomy of wetland habitats.

The meadow hay production of Rorippo-Phalaridetum /MÁTHÉ 1956, JEANPLONG 1968/ near rivers Ipoly and Rába are 360 g/m² and 220-260 g/m² respectively, by MOLNÁR's /1975/ estimations. The two years average crop of pure stands of reed canarygrass 'K-52' line introduced from marshlands into field conditions is 1652 g/m² /SZABÓ 1983/. The difference may be due to the advances of pure and fertilized stands against mixed or spontaneous ones, and to the result of yield-growing selective breeding work; but it is important to study the environmental factors and developmental features of great productivity of this grass.

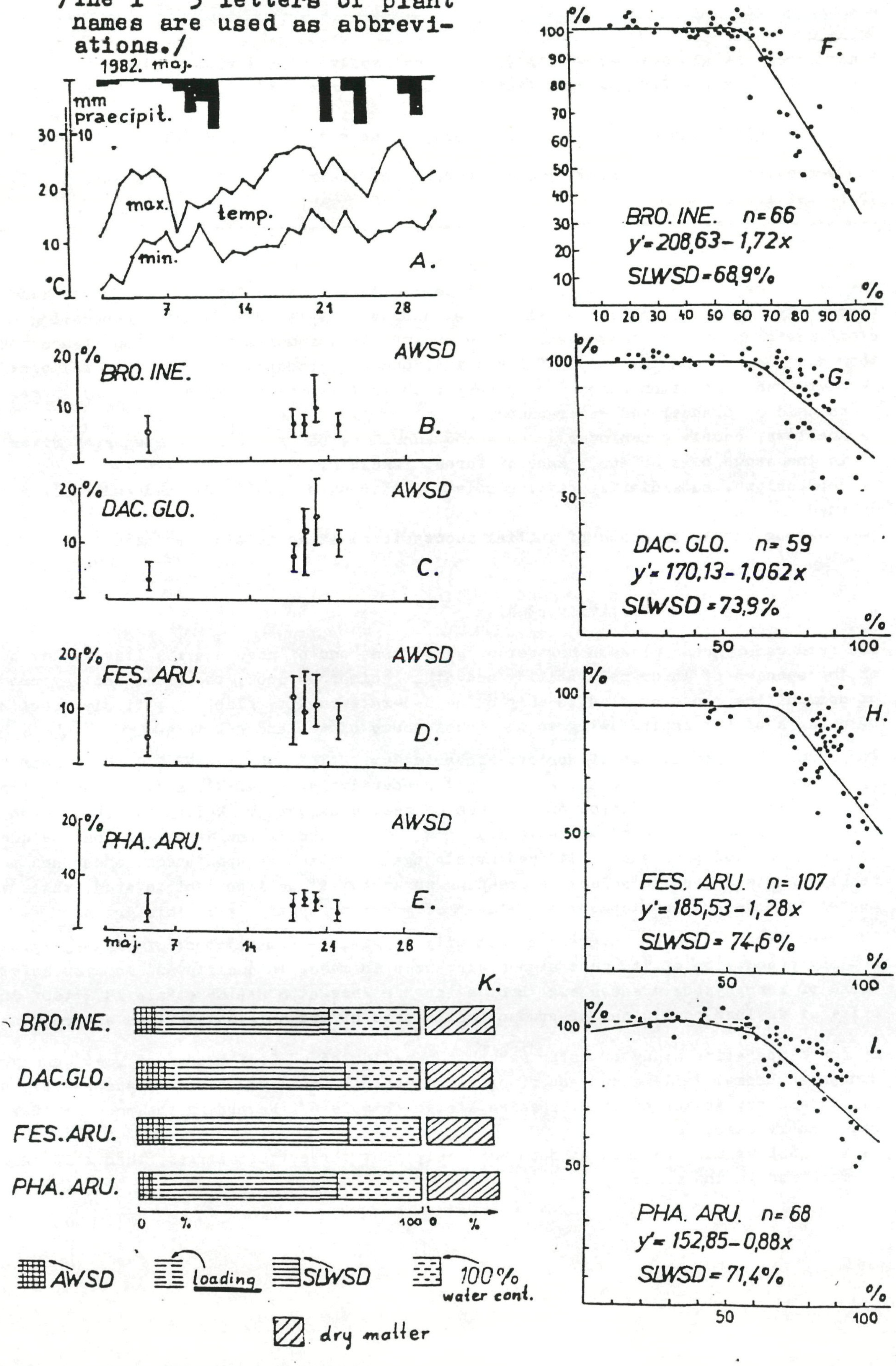
The reed canarygrass has a great oppurtinity in grassland management of Hungary: green and hay production of its pure stands surpasses in mass, in quality and in crop safety those of xerophytous grasses e.g. Bromus inermis /see at SCHALLER et al. 1972 too/ in spite of dryland conditions of production instead of the original wetland environment.

By our comparative study of water saturation deficites of leaf blades of reed canarygrass, Hungaryan brome, tall fescue and of orchardgrass, the AWSD values has a succesively upright tendency in the order of species listed /Figure 6/. Regarding the pecularities for reed canarygrass:
- the AWSD values measured at noon were only just three times larger, than AWSD values measured in the morning,

Figure 6

The graphical interpretation of AWSD /B–E/, SLWSD /F–I/ and of loading /K/.

/The 1st 3 letters of plant names are used as abbreviations./



- the SLWSD values were 15 time larger than AWSD values /in the case of papilionaceae 2-5, in the case of grasses 3-7 ratios were reported by RAHLMANYINA-AHMEDOV 1976/,
- the loading /mean AWSD divided by SLWSD and the ratio is expressed in percentage/ of the water balance of leaf blades was only the half of the largest value measured for the orchardgrass among the grasses studied,
- the ability of water resaturation in leaf blades maintained up to high AWSD values,
- there were no significant differences between the results of WSD studies either in wetland habitats /lake shore/ or in dryland field conditions.

These pecularities of water balance make a considerable contribution to the establishing drought resistance of reed canarygrass. After all, there is an open question: does the water retention illustrated above restrain the ceeling of productivity, and if it does, to what extent?

There is a whole developmental range of individual tillers of different turnover time and turnover rate moving on succesively or parallely through the life of reed canarygrass stands as follows:

	turnover time	turnover rate
a/ tillers appearing after harvesting, later beeing overwintered, give the next year crop	1.08	0.92
b/ tillers of the same appearence as under a/, but will be winterkilled	0.5-0.75	2-1.3
c/ tillers of winter and late winter origin, thermoinduced for generative developmental phase	0.75-0.5	1.3-2
d/ tillers of the same appearence as under c/, but unsuccesfully competing amoung other tillers in spring	0.5-0.3	2-3
e/ tillers of short /1-2 months/ life span.	0.08-0.23	4-12

The number of tillers per area, establishing the crop of the stand, decreases in the reproductive phase of growth with a degree of 32.5 % in the case of reed canarygrass, because of the competition between vernalized and unvernalized tiller individuals /Figure 9/. The expected loss of biomass production however, was not only compensated by increased growth of the remaining tillers, but the individual gain in weight of them was the main determinant of the final crop to be harvested. Comparatively, in the case of tall fescue, the main factor of phytomass production was the number of tillers per ground area. The appearance of new aerial shoots during the reproductive phase of growth is an other question: that of the next regrowth, because of their beeing deeper as the level of cutting used to be practised.

Certain tendencies of concentration changes of water soluble carbohydrates /WSC/ in different organs of reed canarygrass are connected with its growth and development /Figure 7/. The WSC concentration in the vegetative organs decreases untill the time of flowering, increases simultaneously in the generative parts /panicle/, and decreases after a ceeling in these latter because of the establisment of oligo- and polysaccharides. Probably, the construction of reproductive organs is based not only on the carbohydrate /and other nutrient/ reserves of storage organs, but - in addition to opinion of SINGH et al. 1980 - also on the current photosynthetic activity of assimilating organs /including panicle too/, regarding the demands for reserves of appearing new tillers.

The gain in weight of reproductive tillers is time dependent process of events, which enjoys a proper complexity by their growth expressed by dry weight increment of culms, leaves and of reproductive organs /Figure 8/.

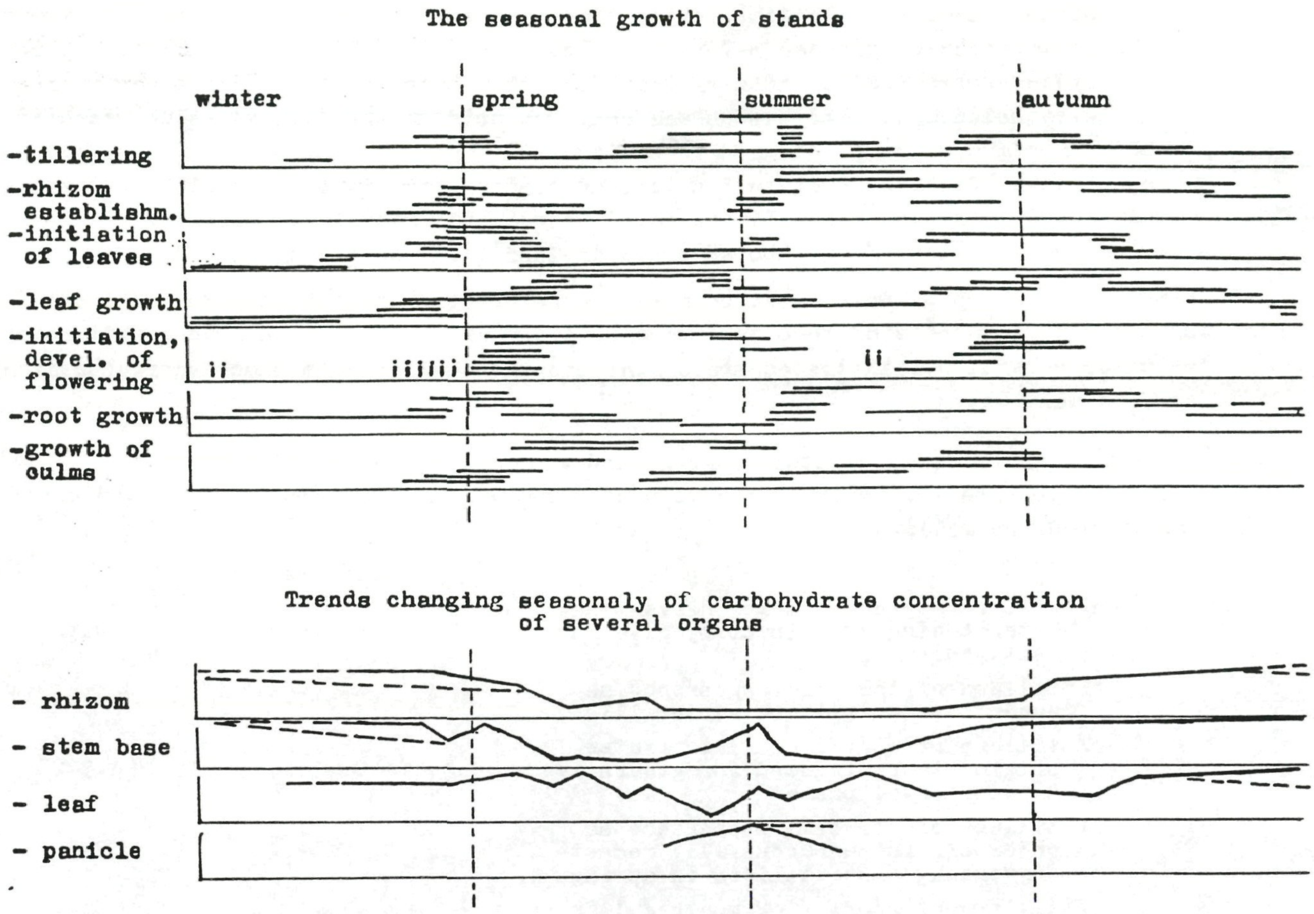


Figure 7
The seasonal growth and developmental processes of reed canarygrass stands with the seasonal changes of water soluble carbohydrate concentrations

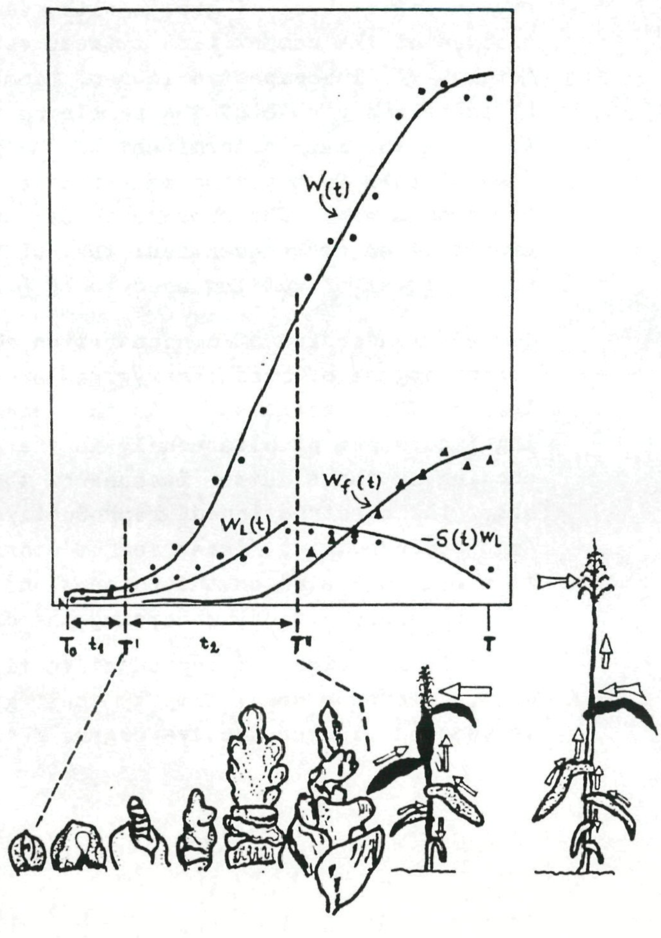


Figure 8
Growth processes of a reproductive tiller.
For W/t/ a logistic growth function, for leaf growth W_L/t/ an exponential one used to be used.
W_f/t/ means the growth of flowering and -S/t/W_L a function for senescence of leaves; W/t/ for total dry wight.
Below:
the development of panicle.

Advantageous water- and nutrient supply is very important through the time t_2 /Figure 7/ in this particular case, in favour of the development of generative organs, which is characterized by relatively slow gain in weight but by rapid morphogenetic changes. The intensive growth of inflorescence in mass moves on at decreasing area and weight of leaves.

The main characteristics for production of reed canarygrass were in the average of experimental years /1981-83/:

- the W_{max} of reproductive tillers /above-ground/ = 4.1 g /at ripening/,
- the W_{max} of culms covered by leaf sheats = 2.95 g,
- the W_{max} of leaf blades = 0.79 g /from shooting till flowering/,
- the W_{max} of panicle = 0.75 g /all of them in dry weight/;
- the A_{max} of vegetative organs = 214.1 cm^2,
- the estimated A_{max} of panicle = 181.0 cm^2 /1/;
- the rate of yearly main W and of W_{max} = 0.69 /in the case of tall fescue 0.63 and of orchardgrass 0.49/,
- W_{max} = 4153.8 g per 1 m^2 ground area and 0.4 m^2 soil monolite alltogether,
- the 80.1 % of the below-ground phytomass was congregated in the upper soil layer of 10 cms, and the maxima of below -ground phytomass were measured in March and in October. /Although these amounts were regarded as the indicators of the richness of the soil monolite in plant parts, not as the absolute amount of below-ground phytomass - see also SIMON-BATANOUNY 1971/.

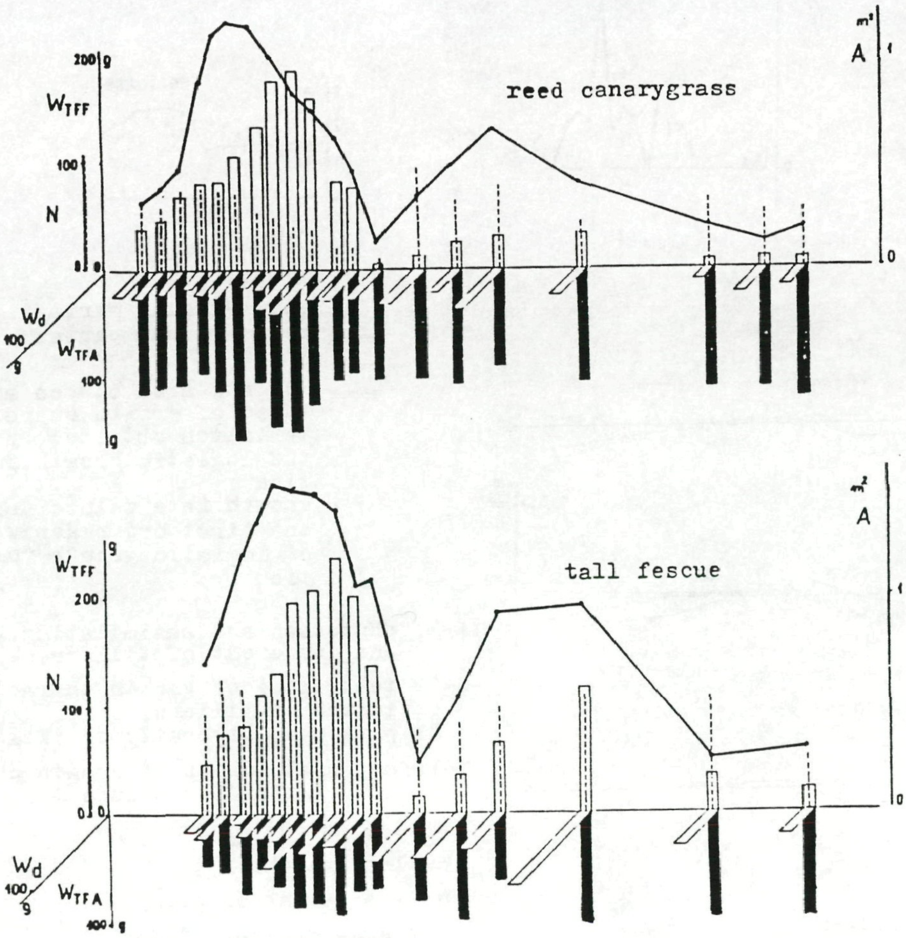


Figure 9

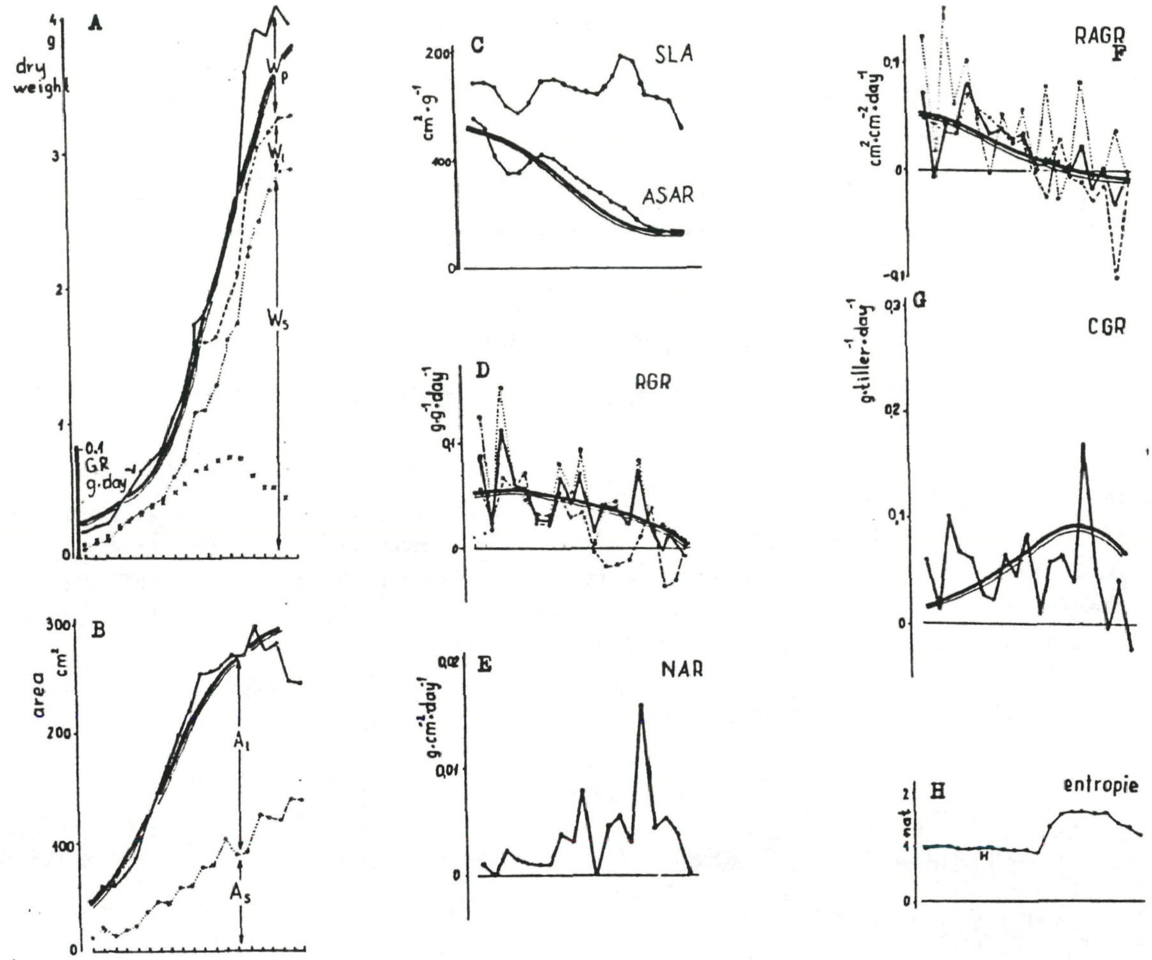
Comparative studies of production in reed canarygrass and tall fescue field stands /1982/

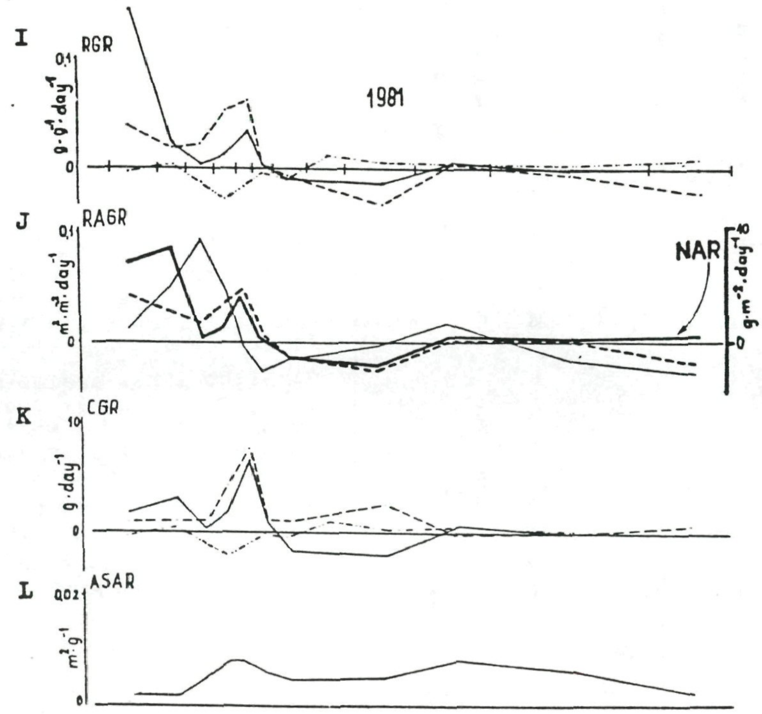
Straight line: assimilating area, dotted line: the number of tillers/N/, white column: weight of above-ground parts /W_{TFF}/, slanting white column: weight of the litter /W_d/ per m^2; black column: weight of below-ground parts /W_{TFA}/ per 0.4 m^2

Figure 10

Quantitative description of the growth of reproductive tillers /A-H/, and that of stands /I-L/ of reed canarygrass

. 1981





-·-·- above-ground parts
– – – below-ground parts
—— total
═══ weight, area curves and those of growth characteristics obtained by the logistic growth function
×××× growth rate values from the first order derivate of logistic growth function

A-B: phytomass and assimilating surface increment of tillers,

C-G: tendencies of growth characteristics of tillers,

H: phytomass diversity of tillers,

I-L: seasonal curves of growth characteristics for stands

W_p=the weight of panicle

W_l=leaf weight

W_s=the weight of culm

A_l= area of leaf blades

A_s= area of culms covered by leaf sheats

The smoothed curves, obtained by the replacement of calculated data using logistic growth function into formulae of growth characteristics, describe general courses of growth processes /FIGURE 10. C-G/. Positive correlation exists between RGR and RAGR values /that of average strength/, between RGR and ASAR values /close correlation/, negative one does between RGR and CGR values; there was no correlation between NAR and CGR values.

Diagrammes of growth characteristics computed from the actual W and A values show special pecularities of certain stages of development. The decreasing tendency of ASAR shows biomass accumulation of higher rate than expansion rate of assimilating surface. Continuous biomass accumulation against decreasing assimilating area can be observed at the late phase of growth /negative RAGR values/. Initial great amplitudes of RGR and RAGR are caused by spring frost-killing of leaf blades and by entering of new ones. The NAR_{max} is preceeded by RGR_{max} and $RAGR_{max}$; and CGR_{max} is preceeded by NAR_{max} in time.

We did not make an effort to record optimal /critical/ LAI on the next considerations. The determination of LAI_{opt} is very complicated because of the hardnesses in collecting entire-plant increment data. The LAI_{opt} is a model based upon the light as a limiting factor alone, regardless the additive and non-additive effects of other environmental factors. There is a possibility of reaching a plateau for several species, instead of a peak, on which those persist their maximal productivity /see at LEOPOLD-KRIEDEMAN 1981/. A certain value of A appeared really - in spite of the possible errors of our experiments - close to the inflexion point of the curve fitted to area values, and this point means the beginning of the slope in area increment. The step of LAI over an "optimal" value coincides with the decrease of NAR at that very moment, as it was demonstrated by several authors. However, the beginning of leaf area decrement /negative RAGR values/ is not too fare from the maxima of CGR and NAR in our studies.

The measurement of leaf area /LA/ only, seems not to be sufficient in the growth studies of Gramineae. The surface of culms and of assimilating tissue containing parts of panicle must be taken into consideration. E.g. see the area of panicle two pages earlier and the ratios between area of stem and leaf blades are as follows

species	$\frac{A_{Smax}}{A_{Lmax}}$
Hungarian brome	0.6
orchardgrass	0.9
tall fescue	1.0
reed canarygrass	0.45 .

The gain in weight refered only to leaf/blade/ area /LWR/ does not reveal the essential features of grass production. On the other hand collecting total area data is a Sisyphean task unless one has methods of the closest approximations... After all, SLA is such an important component of ASAR as it is that of LAR /Figure 10. C/.

The parameters of $Y = M/1+be/^{-kt}$ logistic growth function for weight and area growth in experimental years are as follows:

		dry weight	assimilating surface
1981	A	4.500	350.000
	b	20.81464	9.35029
	k	0.06577	0.04754
	R^2	0.96504	0.94850
1982	A	4.250	250.000
	b	33.41615	6.35544
	k	0.07788	0.06018
	R^2	0.98883	0.88261

/cont. next page/

/cont. from the page 35/

1983	A	7.000	250.000
	b	28.19986	6.33621
	k	0.05329	0.04988
	R^2	0.97023	0.95737

The high M value in 1983 is remarkable, being established within meteorological extremities of the year to a certain extent. On the other hand, M was chosen from a set of its values heuristically tested one by one to the closest fitting of growth curves to basic data. For this reason M was regarded as a tool much rather than as extremity of growth since it did more or less surpass the $area_{max}$ and $weight_{max}$ of tillers developing under the pressure of limiting environmental factors. The symbol k used to be named instantaneous rate of growth, and can be defined by first order derivation of growth function under this discussion /Figure 10. A/.

The changes of weight proportions between culms and leaf blades are not interpreted by the entropie from shooting till heading, but these changes mean alteration in phytomass diversity of reproductive tillers /Figure 10. H/. The diversity increases at heading and returns slowly during flowering and ripening to the beginning level.

The early spring frost-killing of leaves mentioned above, is shown by the allometric growth of culms and leaves of reed canarygrass /Figure 11. G: negative relationship/. An other negative relationship occures in the case of tall fescue at heading /Figure 11. H/, because of the successive death of foliage leaves acropetaly by the culm. An abruptly opposite tendency appears at ripening caused by the losses in weight of culms and leaves of tall fescue. The weights of organs studied of reed canarygrass maintain in the reproductive phase.

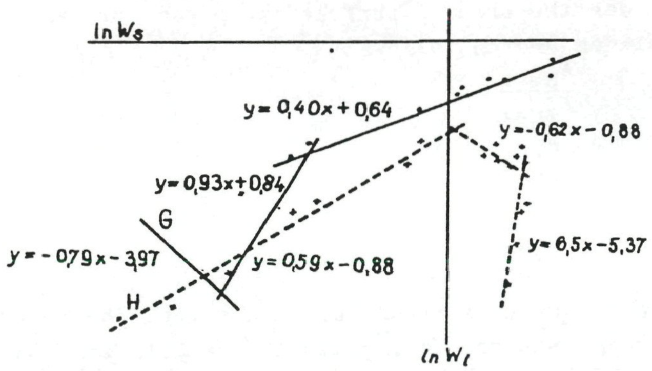


Figure 11.
The allometric growth of culms /W_s/ and leaves /W_l/ of reed canarygrass /G/ and of tall fescue /H/.

The growth characteristics were studied in stands too, with a special care for below-ground parts /Figure 10. I-L/. The comparision of growth characteristics of above- and below-ground parts illustrates the functional connections between assimilating and non-assimilating organs of grasses, e.g. CGR_{max} is preceeded by $RAGR_{max}$. Trends of stand growth characteristics have pecularities differing from those of reproductive tillers, because of coexistence of tillers composing of different turnover values. The growth analyses of stands and those of reproductive tillers are complementary to each other.

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*Detailed bibliographical data of papers and books referred to in this study but being not enumerated here, are obtainable from the author.