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# Ecologically Based Differences in the Structure of Grass Stem

V. G. NIKOLAEVSKY and LIDIA D. NIKOLAEVSKAYA

Tsurupinsk Agrobiological Centre for Reed Research, Tsurupinsk, USSR

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**Abstract.** A quantitative anatomical study of the stem structure of grasses of various ecological groups: xerophytes, mespohytes, ephemers, hydrophytes and psammophytes (a total of 30 species) was carried out. The proportions of the various tissues in the stem were expressed as a percentage of the cross-sectional area of the stem. Stems of hydrophytes were found to have only small proportion of mechanical (4—8%) and conducting (2—5%) tissues but a large proportion of parenchyma (85—93% — primary cortex and basic parenchyma) and air system (38—40% — parenchyma channels or specialized aerenchyma). The stems of xerophytes possess a highly developed sclerenchyma (30—50%) and vessel bundles (6—13%) while the parenchyma is less developed (36—60%). The cells of the stems of hydrophytes are larger than those of xerophytes, but the cell membranes are thinner. The structure of mesophytes is intermediate between that of hydrophytes and xerophytes and the structure of ephemers is very similar to that of mesophytes. Psammophytes differ from xerophytes in having more mesomorphous features.

Differences in the structure of vegetative organs of grasses, which depend on various external conditions, have been studied by many authors. These studies were especially concerned with the ecological anatomy of plant leaves, because these were considered to be the most plastic organs of the plant (ALEXANDROV 1954). Grass stem has not been investigated so thoroughly.

The anatomical structure of the stem of *Poaceae* has been described by ROZHEVITS (1937), HAYWARD (1938), ESAU (1953), METCALFE (1960). SUTHERLAND and EASTWOOD (1916), SABNIS (1921), BLATTER, MC CANN, SABNIS (1929), PURER (1942), OGANESYAN (1947), KONSTANTINOVA (1950, 1960), BERTRAND (1960), VIKHIREVA-VASILKOVA (1964) and other workers have described the ecological anatomy of grass stem.

The above mentioned publications were mainly descriptive, without the use of quantitative anatomical methods or physiological observations. Hence it was not possible to form any sufficiently complete concept relating differences in the anatomy of grasses with their habitat, the effects of external conditions on the plant structure, and the main trend of the ecological evolution of *Poaceae.*

*Address*: Tsurupinsk 2, Kherson District, USSR.

The present work gives the results of a quantitative study of more than 30 species of both wild and cultivated grasses of the sub-family *Pooideae* (R. BR.) ASCH.

## Material and Methods

Representatives of the following ecological groups of grasses were investigated (see list of species in Table 1): xerophytes (5 species), psammophytes (5 species), ephemers (5 species), mesophytes (10 species), hydrophytes (5 species). The material used was collected in various parts of the Ukraine. The parts of the stem ( middle part of the second or third internodium above the soil) were taken from normally developed undamaged plants in the flowering phase or at the beginning of seed formation. The specimens were fixed in a mixture of formaldehyde and alcohol (98 parts of 96% alcohol, 2 parts of 10% formaldehyde). Sections were made by hand and were examined in glycerine. Investigations were carried out by means of the quantitative-anatomic method of ALEXANDROV (1954). In most cases, relative values were used because the absolute ones depend on the size of the organs studied (SINNOT 1964). All measurements were carried out by conventional methods (ROSKIN and LEVINSON 1957). The proportions of various tissues in the stems, determined by the gravimetric method based on precise images of the sections obtained by a microprojector (magnification 100—300×) were expressed as a percentage of the cross-sectional area of the stem. All data obtained were treated statistically (URBACH 1964).

## Results

On the basis of the data obtained, the following conclusions may be drawn:

1. Grass hydrophytes are characterized by a low percentage of mechanical and conducting tissues and by a high percentage of prarenchyma in the stem (Tables 1, 2). In the cross-sectional area of the stem, the proportion of sclerenchyma is 4—8%, of vessel bundles 2—5% and of parenchyma 85—93%. In some hydrophytes (*Oryza sativa* L.) the mechanical tissues occur below the epidermis in the form of a thin layer, whereas in others (*Zizania latifolia* TURZC., *Glyceria spectabilis* M. et K.) there are two rings of sclerenchyma below the epidermis and nearer to the centre of the stem. The chlorenchyma tissue (primary cortex) of hydrophytes is highly developed occupying 40—70% of the cross-sectional area and forming a layer of varying thickness between the two rings of mechanical tissue (*Glyceria spectabilis* M. et K., *Agrostis stolonizans* BESS.). In other species the basic parenchyma (up to 60—70%) occurs between the second sclerenchyma ring and the central cavity (*Zizania latifolia* TURZC., *Alopecurus aequalis* SOBOL).

One of the most characteristic features in hydrophytes is the formation of air channels and cavities inside the stem occupying from 5—8% (*Oryza sativa* L., *Agrostis stolonizans* BESS.) up to 38—40% (*Glyceria spectabilis* M. et K., *Zizania latifolia* TURZC.) of the cross-sectional area. Some plants have these channels in the form of schizolysigenous channels either in the basic parenchyma (*Oryza sativa* L.) or in the chlorenchyma (*Alopecurus aequalis* SOBOL). Other plants (*Glyceria spectabilis* M. et K., *Zizania latifolia* TURZC.) have a specialized aerenchyma with large number of air extracellular compartments which occupy up to 50% of the tissue area. The aerenchyma is most frequently derived from the primary cortex.

2. Grass xerophytes growing in dry soils are characterized by a high proportion of mechanical and conducting tissues and by a low proportion of parenchyma in the stem (Tables 1 and 2). Mechanical tissues occupying 30—50% of the stem area produce a thick layer of sclerenchyma on the periphery below the epidermis, the vessel bundles occupying 6—13% and parenchyma 36—60% of the area. Most xerophytes (*Stipa capillata* L., *Festuca sulcata* HACK., *Aneurolepidium ramosum* (TRIN.) NEVSKI.) have a low proportion of chlorenchyma (2%) which forms small strips in the sclerenchyma on the periphery of the stem. These minute strips of chlorenchyma are obviously the remnants of the primary cortex which occupies

Table 1

Proportions of various tissues in the stem of grasses of different ecological groups (in % of the cross-sectional area of the stem)

| Ecological groups and sorts of grasses | Epidermis | Mechanical tissues | Vessel bundles | Parenchyma tissues | | |
|---|---|---|---|---|---|---|
| | | | | Whole content | Chlorenchyma | Basic parenchyma |
| Hydrophytes | | | | | | |
| *Oryza sativa* L. | 2·02 | 8·00 | 4·84 | 85·24 | 0·00 | 85.24 |
| *Zizania latifolia* TURZC. | 1·70 | 6·00 | 2·05 | 90·30 | 20·30 | 70·00 |
| *Glyceria spectabilis* M. et K. | 0·80 | 4·14 | 2·01 | 92·91 | 76·50 | 16·41 |
| *Alopecurus aequalis* SOBOL. | 4·78 | 5·94 | 4·64 | 84·71 | 21·31 | 63·40 |
| *Agrostis stolonizans* BESS. | 5·47 | 4·19 | 3·75 | 86·73 | 42·15 | 44·58 |
| Perennial mesophytes | | | | | | |
| *Alopecurus pratensis* L. | 2.34 | 18·45 | 5·06 | 74·25 | 13·50 | 60·75 |
| *Festuca pratensis* HUDS. | 2·98 | 24·61 | 5·12 | 67·25 | 10·00 | 57·25 |
| *Bromus inernis* Leyss. | 2·20 | 17·78 | 7·65 | 72·52 | 6·12 | 66·40 |
| *Arrhenaterum elatius* (L.) J. et K. PRESS. | 3·21 | 19·75 | 6·37 | 70·77 | 4·97 | 65·80 |
| *Lolium perenne* L. | 2·48 | 23·61 | 5·96 | 67·94 | 4·54 | 63·40 |
| Annual mesophytes | | | | | | |
| *Triticum durum* DEST. | 2·24 | 15·05 | 6·44 | 75·65 | 1·76 | 73·89 |
| *Secale cereale* L. | 2·69 | 22·80 | 6·88 | 67·72 | 2·27 | 65·45 |
| *Bromus mollis* L. | 2·88 | 18·50 | 4·73 | 74·27 | 2·87 | 71·40 |
| *Avena sativa* L. | 2·21 | 12·91 | 4·86 | 80·10 | 1·86 | 78·24 |
| *Lolium multiflorum* LAM. | 2·67 | 15·27 | 4·89 | 77·42 | 2·82 | 74·60 |

Table I (continued)

| | | | | | | |
|---|---|---|---|---|---|---|
| Ephemers | | | | | | |
| *Secale silvestre* HOST. | 2·44 | 21·84 | 5·05 | 70·63 | 1·38 | 69·25 |
| *Hordeum murinum* L. | 2·29 | 13·60 | 4·50 | 79·48 | 1·18 | 78·30 |
| *Bromus squarrosus* L. | 2·67 | 18·31 | 4·93 | 73·99 | 1·64 | 72·35 |
| *Bromus tectorum* L. | 2·13 | 16·30 | 4·76 | 76·75 | 1·10 | 75·65 |
| *Aegilops cylindrica* HOST. | 3·16 | 14·78 | 4·52 | 78·70 | 1·35 | 76·35 |
| Xerophytes | | | | | | |
| *Stipa capillata* L. | 1·99 | 52·18 | 9·41 | 36·60 | 1·15 | 35·45 |
| *Festuca sulcata* HACK. | 4·13 | 42·12 | 8·20 | 45·88 | 1·18 | 44·70 |
| *Agropyron pectiniforme* ROEM. et SCH. | 3·78 | 36·88 | 8·40 | 51·03 | 4·72 | 46·31 |
| *Koeleria gracilis* PERS. | 2·87 | 29·84 | 6·36 | 60·94 | 3·34 | 57·60 |
| *Aneurolepidium ramosum* (Trin.) NEVSKI. | 3·70 | 36·23 | 12·68 | 47·38 | 1·18 | 46·20 |
| Psammophytes | | | | | | |
| *Stipa borysthenica* KLOK. | 2·15 | 28·30 | 8·85 | 60·88 | 1·08 | 59·80 |
| *Festuca Beckeri* HACK. | 4.03 | 30·42 | 7·98 | 57·63 | 1·93 | 55·70 |
| *Agropyron dazyanthum* Led. | 2·83 | 26·65 | 7·05 | 63·23 | 3·52 | 59·70 |
| *Koeleria sabuletorum* CZERN. | 2·65 | 23·65 | 6·34 | 67·36 | 3·16 | 64·20 |
| *Elymus sabulosus* M. B. | 1·74 | 22·45 | 5·10 | 70·64 | 3·64 | 67·00 |

considerable area in the stem of hydrophytes and some mesophytes. There are no air channels in the stem of xerophytes.

3. Grass hydrophytes have much larger stem cells than xerophytes (Table 3.). The thickness of sclerenchyma fibres of hydrophytes is 15—20 $\mu$m as compared with 11—12 $\mu$m in xerophytes, the thickness of the whole parenchyma cells being 55—56 $\mu$m as compared with 33—34 $\mu$m. On the other hand, the corresponding thickness of the membranes of sclerenchyma cells of xerophytes is double that of hydrophytes and 1·2—1·3 times higher than in mesophytes. This is also valid for the thickness of the epidermis and the extension of its outer wall (Table 3).

4. Mesophytes have an anatomical structure intermediate between that of hydrophytes and xerophytes (Tables 1, 2, 3). The mechanical tissues of these plants occupy 13—24% of the cross-sectional area of the stem, the conducting ones 4—6% and the parenchyma 67—80%. The chlorenchyma occupies relatively large area (up to 13%) and produces strands or strips of varying thickness in the sclerenchyma on the periphery of the stem (below the epidermis or hypodermis). There are some structural differences between annual and perennial mesophytes mainly in the different degree of development of chlorenchyma. The chlorenchyma of perennial mesophytes occupies 5—13%, in the annual ones 1·8—2·9% of the stem area, the latter proportion being similar to the ephemers.

5. The anatomical structure of ephemers is very similar to mesophytes (Tables 1, 2, 3).

6. Psammophytes exhibit a higher structural mesomorphy than the grasses growing in steppes. Psammophytes differ from xerophytes by a lower

proportion of sclerenchyma and conducting tissues and by a higher proportion of parenchyma and chlorenchyma (Tables 1, 2). The stem cells of psammophytes are larger than those of xerophytes but their membranes are thinner.

Table 2

Correlation analysis of the data concerning the proportions of various tissues in the stem of grasses of various ecological groups (in % of the cross — sectional area)

| | Ecological groups of grasses | Mean values ($\bar{x}$) | True correlation dispersion (F) | Minimum statistically significant difference at P = 0·95 |
|---|---|---|---|---|
| Sclerenchyma (% of the area) | Hydrophytes | 5·64 | | |
| | Perennial mesophytes | 20·86 | | |
| | Annual mesophytes | 16·92 | 35·20 | 5·64 |
| | Ephemers | 16·96 | | |
| | Xerophytes | 39·44 | | |
| | Psammophytes | 26·32 | | |
| Vessel bundles (% of the area) | Hydrophytes | 3·46 | | |
| | Perennial mesophytes | 6·04 | | |
| | Annual mesophytes | 5·54 | 8·57 | 1·93 |
| | Ephemers | 5·78 | | |
| | Xerophytes | 9·02 | | |
| | Psammophytes | 7·06 | | |
| Parenchyma (% of the area) | Hydropkytes | 87·98 | | |
| | Perennial mesophytes | 70·54 | | |
| | Annual mesophytes | 75·04 | 26·24 | 7·55 |
| | Ephemers | 75·90 | | |
| | Xerophytes | 48·46 | | |
| | Psammophytes | 63·94 | | |

Critical value of F is 4·10 at $f_A = 5$, $f_Z = 20$ and P = 0·99

## Discussion

The results presented indicate that there are remarkable differences in the anatomical structure of stems of grasses of various ecological groups (xerophytes, mesophytes and hydrophytes). These differences are obviously due to the differences in the ecological evolution of grasses belonging to the same family (Bews 1929).

The structural differences of grasses growing under various conditions also apparently depend on the differences in their physiology. As reported

Table 3
The size of cells, thickness of epidermis. and the extension of the cell walls in stem of grasses of various ecological groups

| | Ecological groups of grasses | Mean values (x) | True correlation dispersion (F) | Minimumy statisticall significant difference at P = 0·95 |
|---|---|---|---|---|
| Thickness of the sclerenchyma fibre in the cross-section (μ) | Hydrophytes<br>Mesophytes<br>Ephemers<br>Xerophytes | 20·95<br>15·24<br>13·12<br>11·69 | 7·88 | 4·45 |
| Diameter of the cells of basic parenchyma (μ) | Hydrophytes<br>Mesophytes<br>Ephemers<br>Xerophytes | 55·83<br>51·43<br>53·30<br>33·10 | 7·00 | 11·64 |
| Thickness of the epidermis (μ) | Hydrophytes<br>Mesophytes<br>Ephemers<br>Xerophytes | 15·18<br>15·21<br>10·46<br>8·50 | 7·77 | 3·75 |
| Extension of the epidermis cell walls (% of the epidermis thickness) | Hydrophytes<br>Mesophytes<br>Ephemers<br>Xerophytes | 22·32<br>31·05<br>36·60<br>46·55 | 13·78 | 7·96 |

Critical value of F is 5·40 at $f_A = 3$, $f_Z = 15$ and P = 0·99

by many authors (ZNAMENSKY 1948, SHIELDS 1950, KOLPIKOV 1957, BEYDEMAN 1960, SVESHNIKOVA 1963, LAVRENKO and SVESHNIKOVA 1965), grasses of various ecological types differ considerably in physiological features.

The main functions of the stem of xerophytes are the transport of water and plastic substances and mechanical supoprt; the mechanical and conducting tissues are therefore especially well developed. In hydrophytes stems, on the other hand, these tissues are poorly developed and this is obviously due to the lower transpiration rate and to the presence of sufficient amount of external water; the elasticity of plant tissues may in these conditions be maintained by means of turgor. The normal function of the root system of hydrophytes is mantained even in soil saturated with water owing to special system of air channels in the stem.

Under conditions of water defficiency the tissues of xerophytes consist of relatively small cells. Owing to the special metabolism of xerophytes, most sugars produced by photosynthesis are used in the formation of cell membranes, causing the significant thickening of the membranes. In order to prevent excessive evaporation, the outer membranes of xerophytes epidermis also become considerably thickened (MAXIMOV 1952, VASILEVSKA 1954, SHIELDS 1950). This is confirmed by our results.

Ephemers grow during a relatively short but sufficiently moist and cold season; their structure is therefore more like the structure of mesophytes growing under conditions of high external humidity than xerophytes which have the same growing season. Many authors (UBAYDULLAYEV 1959, VASILEVSKA 1941) noted this feature which is also characteristic for other species. Similarly, grasses growing in sandy soils (psammophytes) differ from those growing in the steppes by a variation of significant features of mesophytes. This is perhaps due to the fact that the conditions of soil humidity are more suitable in sandy soils than in sandy soils with clay or even clay soils with sand (LAVRENKO 1953, STARR 1912).

These results show that, contrary to general opinion, representatives of *Poaceae* vary widely in their anatomical structure according to the differences in their ecological evolution.

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V. NIKOLAJEVSKIJ, LIDIA NIKOLAJEVSKAJA, Curupinská vědecko-výzkumná agrobiologická stanice pro studium třtiny: **Kvantitativní anatomické studium struktury stébla u travin ve spojitosti se zvláštnostmi jejich ekologie.** — Biol. Plant. **9** : 321—329, 1967.

Bylo provedeno kvantitativní anatomické studium struktury stébla u travin různých ekologických typů — xerofytů, mesofytů, efemerů, hydrofytů a psammofytů (celkem 30 druhů). Poměr mezi tkáněmi stébla se vyjadřoval % plochy příčného řezu stěny stébla. Bylo zjištěno, že stéblo hydrofytů se vyznačuje slabým vývojem mechanických (4—8 %) a vodivých (2—5 %) tkání, avšak silným vývojem parenchymu (85—93 %, v to počítaje primární kůru a základní parenchym) a také ventilačního systému (38—40 %, v tom lakuny v parenchymu nebo specialisovaný aerenchym). U xerofytů je ve stéblech silně vyvinut sklerenchym (30—50 %) a vodivé svazky (6—13 %). Parenchym je méně zastoupen (36—60 %). U hydrofytů se ve stéblech vytvářejí větší buňky než u xerofytů, tloušťka stěny je však v obráceném poměru. Střední polohu mezi hydrofyty a xerofyty podle stavby zaujímají mesofyty. Struktura stébla u efemerů je velmi podobná struktuře stébla mesofytů. Psammofyty se od xerofytů liší silnějším vývojem mesomorfních znaků. Podle názoru autorů jsou rozdíly ve struktuře stébla travin různých ekologických skupin spojeny s ekologicko-fysiologickými zvláštnostmi představitelů těchto skupin a odráží charakter a směr jejich ekologické ovulace.

В. Г. Николаевский, Лидия Д. Николаевская, Цюрупинская научно-исследовательская агробиологическая станция по изучению тростника: **Количественно-анатомическое изучение структуры стебля у злаков в связи с особенностями их экологии.** — Biol. Plant. 9 : 321—329, 1967.

Было проведено количественно-анатомическое изучение структуры стебля у злаков различных экологических типов — ксерофитов, мезофитов, эфемеров, гидрофитов и псаммофитов (всего 30 видов). Соотношение между тканями в стебле выражалось в % от площади поперечного среза стенки соломины. Установлено, что стебли гидрофитов отличаются слабым развитием механических (4—8%) и проводящих (2—5%) тканей, но сильным развитием паренхимы (85—93%, в том числе первичная кора и основная паренхима), а также вентиляционной системы (38—40%, в том числе лакуны в паренхиме или специализированная аэренхима). У ксерофитов в стеблях мощного развития достигают склеренхима (35—50%) и проводящие пучки (6—13%), а паренхима развита значительно меньше (36—60%). У гидрофитов в стеблях формируются более крупные клетки, чем у ксерофитов, однако относительное утолщение клеточных оболочек у последних больше, чем у первых. Промежуточное положение между гидрофитами и ксерофитами по своему строению занимают мезофиты. Структура стебля эфемеров очень близка к таковой у мезофитов, а псаммофиты отличаются от ксерофитов более мезоморфными признаками. По мнению авторов своеобразие структуры стеблей злаков различных экологических групп связано с эколого-физиологическими особенностями представителей этих групп и отражает характер и направление их экологической эволюции.