Responses of Barnyardgrass (*Echinochloa crus-galli* (L) Beauv. var. *crus-galli*) to Water Drained, Saturated and Flooded Soils in Root Aerenchyma Formation*

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Abstract: Responses of barnyardgrass (*Echinochloa crus-galli* var. *crus-galli*) to water drained, saturated, or flooded soils were assessed in relation to the aerenchyma formation in crown roots. Plant height, fresh weight of shoots, the number of crown roots, and the fresh weight of roots of 4-week-old barnyardgrass increased in the following order: saturated>drained>flooded. By contrast, aerenchyma was radially well developed in the cortex of crown roots when flooded, but no extensive aerenchyma formation was observed when the soil was drained. Both root porosity and the total area of aerenchyma increased in the following order: flooded>saturated>drained; however, these values varied with the portion and/or ages of crown roots tested. In relation to the diameter of the crown roots, barnyardgrass showed different responses from those of root aerenchyma, i.e., the root diameter increased significantly when the soil was saturated but decreased as the root aged. These results suggest that the response to flooding in barnyardgrass is related to the formation of root aerenchyma which developed in a polar direc-

tion from the basal parts to the apical parts as the roots aged.

Key words: barnyardgrass (*Echinochloa crus-galli* (L.) Beauv. var. *crus-galli*), root aerenchyma, root porosity

Introduction

Under anaerobic conditions most flood-tolerant plant species develop cortical aerenchyma in their roots^{5,6)}. This development can be attributed to the fact that when flooded, aerenchyma plays an important role in enhancing oxygen diffusion from leaves to roots³⁾. Thus, root aerenchyma seems to be closely related to an acclimatic response of flood-tolerant plant species to oxygen deficiency. However, previous studies concerning root aerenchyma have concentrated on cultivated plants. Even in barnyardgrass (*Echinochloa crus-galli* var. *crus-galli*) which is a noxious weed found worldwide in several crop productions, its wide habitat ranging from paddy to upland has rarely been investigated as regards the root anatomy. The objective of the present study was to investigate the response of barnyardgrass to water drained, saturated, and flooded soils as it affects root aerenchyma. Shoot and root growth were also considered in the present study.

Materials and Methods

Plant culture: Seeds of barnyardgrass

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(*Echinochloa crus-galli* var. *crus-galli*) were collected in the fall of 1997 in paddy fields of Utsunomiya University Agronomy Research Farm at Mooka City, Tochigi, and stored at 5°C in the dark until use. Ten seeds of the weed were planted in plastic pots (16 cm diam by 30 cm tall) filled with 5 liters of Utsunomiya clay loam soil and 5 g of granular fertilizer (N-P-K, 10%-10%-10%). The seeds were grown under water drained, saturated, or flooded conditions. To achieve the drained conditions, the pots were watered twice a week so that the soil water content was kept between 33 to 39% (w/w). In saturated and flooded treatments, water levels of pots were adjusted to 100% soil water content and 3 cm deep. At the first leaf stage, seedlings were thinned to five seedlings per pot. Shoot length, the fresh weight of shoots, the fresh weight of roots, and the number of crown roots were measured 4 weeks after seeding; the crown roots were then subjected to anatomical studies. All experiments were conducted in a green-house under natural daylight at 23~35°C and were replicated three times.

Observation of root aerenchyma: The soil was carefully washed away from the root systems and the crown roots were divided into three groups on the basis of growth stage: matured (ca 20 cm long), extending (ca 10 cm long), and young roots (ca 5 cm long). Thereafter, 10 mm-long fresh segments were cut with a razor from apical (5 mm from apex), central, and basal parts (5 mm from the basal part of the stem) of each crown root. The segments were fixed and preserved in formalin-acetic-alcohol for 2 days at 5°C. After washing the segments with tap water, they were dehydrated in a graded series of ethanol (from 50 to 100%) and were then embedded in paraffin wax. Fifteen μm -thick transverse cross sections were cut and

were stained with Mayor acid-haemalaum. The specimens were observed and photographed with a light microscope. At least 20 transverse cross sections per replicate were examined before representative photographs were taken.

Measurements of root porosity: In this study root porosity (%) was defined as percentage of the total area of aerenchyma in the cortex. Five representative photographs were rendered as digitized images at a resolution of 100 dpi. Thereafter, the total area of the aerenchyma and cortex were measured and then the root porosity and the root diameter were calculated. A series of image analyses were made in the manner described previously⁴⁾. The data were subjected to an analysis of variance. For all treatments, means were compared using Fisher's Protected LSD test at the 0.05 probability level.

Results and Discussion

Prior to the investigation of root aerenchyma, 4-week-old barnyardgrass shoot and root growth were measured. When the plants were grown under drained, saturated, or flooded conditions, the values of plant height, the fresh weight of shoots, the number of crown roots, and the fresh weight of roots increased in the following order: saturated > drained > flooded. This tendency was especially marked in the case of the fresh weight of roots; the values of saturated roots were more than 5 times greater than those of flooded roots (Table 1). These results suggest that flooding is unfavorable for barnyardgrass, especially for root growth. In contrast to the growth of shoots and roots, aerenchyma fully developed at the central and basal parts of crown roots when flooded. A similar result on aerenchyma formation was reported for *E. crus-galli* (L.) Beauv. var. *praticola*¹⁾. Both root porosity and the total

area of root aerenchyma of barnyardgrass increased in the following order: flooded>saturated>drained. Although there were exception to this order, barnyardgrass seems to gain its great adaptability to the flooded conditions by increasing intercellular gas space in the crown roots. The response of

root aerenchyma varied with the portion and/or aging of the crown roots that were tested in the following order: basal parts>central parts, and matured roots>extending roots>young roots (Tables 2 and 3). Thus, barnyardgrass seems to develop the aerenchyma in a polar direction from the basal

Table 1. Shoot and root growth of *Echinochloa crus-galli* var. *crus-galli* grown under drained, saturated, or flooded conditions.

Growth condition	Plant length (cm)	Fresh weight of shoots (g)	Number of crown roots/plants	Fresh weight of root (g)
Drained	42.7 ^a	2.9 ^b	15.7 ^b	1.8 ^b
Saturated	46.0 ^a	6.8 ^a	23.7 ^a	3.8 ^a
Flooded (3 cm deep)	34.9 ^a	1.5 ^c	10.0 ^c	0.7 ^c

Means within each column followed by the same letter are not significantly different according to Fisher's Protected LSD test at P=0.05.

Table 2. Root porosity in crown roots of *Echinochloa crus-galli* var. *crus-galli* grown under drained, saturated, or flooded conditions.

Growth condition	Root porosity (%)								
	Young root*			Extending root*			Mature root*		
	Apical part	Central part	Basal part	Apical part	Central part	Basal part	Apical part	Central part	Basal part
Drained	0	1.9 ^a	10.0 ^b	0	26.9 ^a	27.5 ^a	0	29.2 ^c	25.9 ^b
Saturated	0	2.3 ^a	14.1 ^b	0	18.6 ^b	28.8 ^a	0	35.5 ^b	40.4 ^{ab}
Flooded (3 cm deep)	0	3.0 ^a	33.2 ^a	0	27.9 ^a	27.9 ^a	0	46.1 ^a	44.7 ^a

Means within each column followed by the same letter are not significantly different according to Fisher's Protected LSD test at P=0.05

*: See text.

Table 3. Total area of aerenchyma in crown roots *Echinochloa crus-galli* var. *crus-galli* grown under drained, saturated, or flooded conditions.

Growth condition	Area of aerenchyma (mm ²)								
	Young root*			Extending root*			Mature root*		
	Apical part	Central part	Basal part	Apical part	Central part	Basal part	Apical part	Central part	Basal part
Drained	0	0.012 ^a	0.077 ^c	0	0.235 ^b	0.126 ^b	0	0.123 ^c	0.144 ^b
Saturated	0	0.047 ^a	0.266 ^b	0	0.222 ^b	0.367 ^a	0	0.427 ^b	0.531 ^a
Flooded (3 cm deep)	0	0.039 ^a	0.448 ^a	0	0.322 ^a	0.283 ^a	0	0.523 ^a	0.559 ^a

Means within each column followed by the same letter are not significantly different according to Fisher's Protected LSD test at P=0.05

*: See text.

parts to the apical parts as the roots age.

Representative photographs taken of the central parts of young roots are shown in Fig. 1. Root aerenchyma developed radially in the cortex when flooded. Although a cubic configuration of the cells occurred throughout the cortex, no extensive aerenchyma was formed when drained. Justin and Armstrong²⁾ divided 91 plant species into 4 main types on the basis of root anatomy: gramineous, cyperaceous, *Alium* and *Rumex*. In the first two types, root aerenchyma arose radially due to the separation and destruction of cells. The other two types of species featured cell sepa-

ration without collapse. Webb and Jackson⁶⁾ reported that rice plants develop aerenchyma in the cortex even in the absence of environmental stimuli such as flooding and anoxia. Therefore, barnyardgrass might belong to the gramineous or cyperaceous group with regards root anatomy, and aerenchyma formation in barnyardgrass seems to be lysigenous and constitutive as true of rice plants. On the other hand, the root diameter of barnyardgrass increased in the following order: saturated>flooded>drained (Table 4). These findings suggest that the root diameter can be regarded as a morphological

Fig. 1. Micrographs of transverse sections of crown roots in *Echinochloa crus-galli* var. *crus-galli* *E. crus-galli* var. *crus-galli* was grown in drained, saturated, or flooded soils for 4 weeks and then 20 mm segments from the basal part of the stem in mature roots were observed under a light microscope. Abbreviations of tissue names are as follows: ae, aerenchyma; ep, epidermis; ex, exodermis; co, cortex; pe, pericycle; st, stele.

Table 4. Diameter of crown roots in *Echinochloa crus-galli* var. *crus-galli* grown under drained saturated, or flooded conditions.

Growth condition	Diameter of crown root (mm)								
	Young root*			Extending root*			Mature root*		
	Apical part	Central part	Basal part	Apical part	Central part	Basal part	Apical part	Central part	Basal part
Drained	0.878 ^b	0.993 ^b	1.056 ^b	0.675 ^b	1.063 ^b	0.689 ^b	0.961 ^b	0.785 ^b	0.908 ^b
Saturated	1.251 ^a	1.474 ^a	1.623 ^a	1.176 ^a	1.263 ^a	1.335 ^a	1.166 ^a	1.269 ^a	1.334 ^a
Flooded (3 cm deep)	1.021 ^{ab}	1.313 ^{ab}	1.353 ^{ab}	0.972 ^{ab}	1.240 ^a	1.180 ^a	1.008 ^b	1.237 ^a	1.306 ^a

Means within each column followed by the same letter are not significantly different according to Fisher's Protected LSD test at P=0.05
*: See text.

factor reflecting saturated conditions (favorable for the weed) but not for flooded conditions. Thus, the response to flooding in barnyardgrass seems to be closely related to the formation of root aerenchyma rather than root diameter. However, in a related study of root morphology, Justin and Armstrong²⁾ demonstrated that: rooting depth is also an important factor for the evaluation of acclimatic responses of plants, aerenchyma is not exclusive to hygrophytes and mesophytes, and shallow rooting is the only obvious survival strategy for hygrophytes. Therefore, to achieve a deeper understanding of the ecological characteristics of this weed, further investigation concerning root distribution in soil and inter- or intraspecific variation in root anatomy is needed.

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畑、飽水および湛水条件下におけるイヌビエの根通気組織

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摘 要

イヌビエ (*Echinochloa crus-galli* (L.) Beauv. var. *crus-galli*) の環境適応性を明らかにすることを目的に、異なる水ストレス下で4週間育成したイヌビエ幼苗の茎葉と根の成長、および根の通気組織を調べた。

イヌビエの草丈、茎葉新鮮重、冠根数、根重およ

び根の直径は、畑区>飽水区>湛水(3 cm)区の順で大きな値を示した (Tables 1 and 4)。しかし、冠根における通気組織の発達程度を表わす間隙率は、湛水区>飽水区>畑区の順で高かった。また、通気組織はいずれの処理区においても冠根の先端部には形成されず、基部に近い部分あるいは成熟した冠根において顕著に観察された通気組織は皮層内の細胞崩壊によるものであった (Fig. 1, Tables 2 and 3)。したがって、イヌビエ冠根における通気組織は破生的に形成されるものであり、しかも低酸素条件 (湛水) に適応するための根の形態反応のひとつであると考えられた。

キーワード：イヌビエ、根通気組織、根間隙率

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