Root Anatomical Responses to Waterlogging at Seedling Stage of Three Cordage Fiber Crops

Tepwadee Changdee1,2, Shigenori Morita1, Jun Abe3, Kaori Ito1, Ryosuke Tajima1 and Anan Polthanee2

1Field Production Science Center, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Midori-cho 1-1-1 Nishitokyo, Tokyo 188-0002, Japan; 2Department of Plant Science and Agricultural Resources, Faculty of Agriculture, Khon Kaen University, Khon Kaen 40002, Thailand; 3AE-Bio, Graduate School of Agricultural and Life Sciences, The University of Tokyo, Bunkyo-ku, Tokyo 113-8657, Japan

Abstract: Waterlogging tolerance of tropical cordage fiber crops is an important agricultural subject in northeast Thailand, because they are often grown in dry-wet transition period as pre-rice crops. Since root anatomical characteristics are often considered to be important traits determining waterlogging tolerance of plants, we examined root anatomy of three fiber crops that are different in waterlogging tolerance one another. Seedlings of three cordage fiber crops, Hibiscus cannabinus (kenaf, cv. KhonKaen60), Hibiscus sabdariffa (roselle, Thai kenaf, cv. NonSoong2) and Corchorus olitorius (jute, cv. KhonKan1), were grown in tall beakers of 1000 ml vermiculite with 40% v/v (control) and 80% v/v (waterlogging) water contents. It is known that the H. cannabinus cultivar is tolerant to waterlogging while other two species (C. olitorius, H. sabdariffa) cultivars are sensitive to waterlogging from soil-grown pot experiments in northeast Thailand. Ten days after sowing, freehand cross-sections of taproot (i.e., primary root) were made with 1 cm increments from the root tip along root axis followed by staining by toluidine blue O (0.01%) for light and fluorescence microscopy. Only H. cannabinus formed aerenchyma in cortex of the taproot under waterlogging condition. The aerenchyma of waterlogged H. cannabinus first appeared at 3 cm from the root tip and developed up to the base of taproot. The formation of aerenchyma in H. cannabinus roots may contribute to the waterlogging tolerance. Casparian bands were found in both endodermis and exodermis of taproot in all the three species. However, formation of exodermal Casparian bands was not stable, and they were restricted to the basal part of taproot in H. sabdariffa and C. olitorius. Waterlogging treatment suppressed formation of Casparian bands, particularly in exodermis.

Key words: Aerenchyma, Casparian band, Jute, Kenaf, Root endodermis, Root exodermis, Roselle, Seedling.

Tropical cordage fiber crop, including Hibiscus sabdariffa (roselle), Hibiscus cannabinus (kenaf) and Corchorus olitorius (jute), is one of major crop categories in northeast Thailand, which is used as materials to make string and bags (Kobayashi, 2001a; Kobayashi, 2001b). Among the three species, H. sabdariffa, so-called “Thai kenaf”, had been the most popular and many cultivars were bred in northeast Thailand. As these fiber crops are often grown in dry-wet transition period as pre-rice crops, waterlogging and excessive soil moisture often damage these plants. KK60 (meaning “Khon Kaen 60”) is a new Thai cultivar of H. cannabinus (kenaf, so-called “Cuba kenaf”) cultivar. H. cannabinus produces larger biomass and provides better fiber quality than H. sabdariffa, while H. sabdariffa has advantage in tolerance for drought and nematode (Kobayashi, 2001a). The other advantage of this cultivar KK60 is the waterlogging tolerance. It showed better growth than H. sabdariffa and C. olitorius cultivars in a soil-grown pot experiment under waterlogging condition (Changdee et al., 2007). In that experiment, the shoot growth of the three species was suppressed by waterlogging treatments with severer growth inhibition by longer period of the treatment (45-105 days). H. cannabinus (KK60) produced the highest shoot dry weight (e.g., 97% of control after 45 days treatment and 53% of control after 105 days treatment) than those of the other two species (e.g., 83% after 45 days and 35% after 105 days treatments in H. sabdariffa, and 83% after 45 days and 32% after 105 days treatments in C. olitorius, respectively).

Formation of new adventitious roots is one of major adaptive responses of crops under waterlogging conditions (Bacanamwo and Purcell, 1999; Mano and Omori, 2007). Moreover, aerenchyma is developed in cortex of new and existing roots of some plant species, which is also thought to contribute to waterlogging tolerance (Arikado and Adachi, 1955; Armstrong et al., 1991). The typical crop species is rice that develops aerenchyma well and adopt flooded conditions. Several upland crops also form aerenchyma in roots, in particular under anoxia conditions, and

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the aerenchyma development may contribute to waterlogging tolerance. In addition to aerenchyma, attentions have been paid to other specific structures in cortex, namely Casparian bands in root exodermis and endodermis, in recent studies on plant responses to anaerobic and waterlogging stresses (Enstone and Peterson, 2005). Casparian bands is a specified structure of cell walls modified with the deposition of hydrophobic materials such as suberin and lignin (Perumala and Peterson, 1986; Enstone and Peterson, 1997; Lux et al., 2004). Although the eco-physiological function of Casparian bands is still unknown, the suppression of apoplastic flow and translocation of water and nutrients by Casparian bands suggests a role to prevent the entrance of toxic components formed by soil reduction in anaerobic condition (Enstone et al., 2003). It is reported that the onset of Casparian bands formation is enhanced or suppressed by environmental stresses, which is estimated by the distance from the root tip (Enstone et al., 2003; Karahara et al., 2004; Lux et al., 2004). However, the information of Casparian band formation including the responses to environmental stresses has been reported in limited plant species, and still unknown for the cordage fiber crops.

In this study, differences in root anatomical characteristics (especially aerenchyma and Casparian bands in exodermis and endodermis) and their response to waterlogging were compared in the three Thai fiber crops that differ in waterlogging tolerance.

**Materials and Methods**

Seedlings of three tropical fiber crops, *Hibiscus cannabinus* (kenaf, cv. KhonKaen60; KK60), *H. sabdariffa* (roselle, Thai kenaf, cv. NonSoong2; NS2) and *Corchorus olitorius* (jute, cv. KhonKaen1; KK1), were used in this study. Certified seeds of *H. cannabinus*, *H. sabdariffa* and *C. olitorius* were obtained from the KhonKaen Agronomy Research Station, KhonKaen province, Thailand. Seeds were germinated on wet filter paper in Petri dishes at 25°C for 24 hours in the dark. Thereafter, six germinated seeds were sown in each tall beaker (ca. 10 cm in diameter and 19.5 cm tall) that contains ca. 1000 ml of vermiculite with 40% v/v (control) and 80% v/v (waterlogging) water contents (Niki and Gladish, 2001). The beakers were covered with aluminum foil and sterilized by autoclave at 120°C for 90 min. The plants were grown at 27°C with 14 h daylight of 45 μmol m⁻² s⁻¹ (PPFD). Ten days after sowing, the plants were taken with washing out the taproot (i.e., primary root) with laterals from vermiculite, and three plants that showed standard growth in the individual
treatments were selected for anatomical observation of roots.

Freehand cross-sections of taproot with 1 cm increments from the root tip along the root axis followed with staining by toluidine blue O (0.01%) for light and fluorescence microscopy (BX-51, Olympus) equipped with a CCD digital camera (VB7000, Keyence). The Casparian bands were identified by the autofluorescence under ultraviolet illumination of fluorescence microscopy (U-MWU2: excitation filter, BP330-385; barrier filter, BA-420; dichroic mirror, DM-400).

**Results**

Ten days after sowing, the three tropical fiber crops subjected to waterlogging gave significant higher shoot length (data not shown) and higher shoot dry weight than those of the control (Fig. 1). The mean shoot dry weight increased in waterlogged condition by 38.7%, 36.4% and 38.9% over control for *H. cannabinus*, *H. sabdariffa* and *C. olitorius*, respectively.

Fig. 2 shows typical light microscopic images of taproot cross section at 5 cm from the root tip. There were many small intercellular spaces in the cortex, but aerenchyma was not found in any species in the control (Fig. 2A-B; Table 1). Although a large aerenchyma-like intercellular space was found in root cortex of *H. cannabinus*, it did not connected to the basal part of the root (Table 1). In waterlogging condition, only *H. cannabinus* formed aerenchyma in the cortex of taproot (Fig. 2C-D). The aerenchyma-like structure of *H. cannabinus* first appeared at 3 cm from tip and continued to the basal part of taproot in waterlogging treatment (Table 1). Although many small intercellular spaces were detected, aerenchyma-like structure was not found in other two species (Fig. 2E-G; Table 1) even in waterlogging treatment. No clear aerenchyma was found in the lateral roots of *H. cannabinus*, but the intercellular spaces in cortex were enlarged in the waterlogging treatment (Fig. 2H).

![Fig. 2](image-url)

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Table 1. Formation of aerenchyma-like large intercellular spaces in the taproots of *Hibiscus cannabinus* seedlings.

| Distance from root apex (cm) | Aerenchyma-like structure |
|-----------------------------|--------------------------|
|                             | Control              | Waterlogging       |
| 1                           | +                     | ++                 |
| 2                           | +                     | ++                 |
| 3                           | +                     | +++                |
| 4                           | +                     | +++                |
| 5                           | ++                    | +++                |
| 6                           | +++                   | +++                |
| 7                           | +++                   | +++                |
| 8                           | +++                   | +++                |
| 9                           | +++                   | +++                |
| 10                          | +++                   | +++                |
| 11                          | +++                   | +++                |
| 12                          | +++                   | +++                |
| 13                          | +++                   | +++                |
| 14                          | +++                   | +++                |
| 15                          | +++                   | +++                |
| 16                          | +++                   | +++                |
| 17                          | +++                   | +++                |
| 18                          | +++                   | +++                |
| 19                          | +++                   | +++                |
| 20                          | +++                   | +++                |

The numbers of plus (+) indicate the number of seedlings that formed aerenchyma or aerenchyma-like large intercellular spaces among the three seedlings examined. The broken lines indicate the position of the base of the roots.

No aerenchyma-like large intercellular space was observed in the taproots of *H. sabdariffa* or *C. olitorius*.
bands formation; it appeared only at the basal part in *H. cannabinus*’s taproot and not appeared in other two species (Fig. 3F).

**Discussion**

Waterlogging is a major problem restricting the plant growth by leading to oxygen deficiency around roots and rhizomes, and consequently it can be fatal because aerobic respiration ceases and levels of energy-rich adenylates drop rapidly resulting in a dramatic decrease in ion uptake and transport (Huang et al., 2003; Vartapetian et al., 2003). When soil is saturated with water, gas diffusion is reduced. Consequently one of the main effects of flooding is a lower pool of available O₂ in submerged plant parts. This decline in O₂ is heightened by aerobic processes taking place in the root zone of plants. Accordingly anoxic conditions develop, leading to a reduction in ATP production and consequent decrease in root metabolism. The decline in available energy can subsequently reduce other active cellular processes such as nutrient uptake, osmotic adjustment or regulation of cytoplasmic pH (Probert and Keating, 2000). In this study, however, the seedlings of *H. cannabinus*, *H. sabdariffa* and *C. olitorius* rather increased shoot biomass in waterlogged conditions. The short period from germination in this study may have resulted in sufficient supply of nutrients from seeds to the shoot even in waterlogged condition. In addition, not only O₂ deficiency but also generation of toxic compounds caused by soil reduction can be a major stress to these fiber crops in real soil culture.

This is the first report of anatomical structure of roots for these tropical fiber crops as long as we know. Despite the unclear damage and small interspecific difference in the shoot response to waterlogging, remarkable difference was found in the root aerenchyma formation. Root aerenchyma-like structure was formed in only KK60, the waterlogging tolerant cultivar of *H. cannabinus*, as a response to waterlogging. Because this structure was connected from basal to subapical part of the taproot, it is expected to work as aerenchyma. This suggests that aerenchyma formation can be a cause for the tolerance of this species to waterlogging. Relationship of aerenchyma formation in roots and/or hypocotyl with waterlogging tolerance between close species has been reported, for example, between maize (*Zea mays* L.) and teosinte (*Z. nicaraguensis*, *Z. luxurians*) (Ray et al., 1999; Mano et al., 2006), soybean (*Glycine max* Merr.) and wild soybean (tsurumame, *G. soja* Sieb. et Zucc.) (Arikado, 1954; Shimamura and Mochizuki, 2005). In these studies, aerenchyma formation is considered to be an important reason of relatively high tolerance to waterlogging of teosinte and wild soybean, although further studies are required to clarify the degree of contribution by aerenchyma to maintain the

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**Fig. 3.** Fluorescent microscopic images of cross-sections at basal part of the taproot at ten day after sowing. *Hibiscus cannabinus* at 18 cm from the root apex (A) in control, and *H. cannabinus* at 16 cm from the root apex (B). *H. sabdariffa* at 13 cm from the root apex (C) and *Corchorus olitorius* at 8 cm from the root apex (D) in waterlogging. Endodermal casparian bands (E) and exodermal casparian bands (F) at 16 cm from the root apex of *H. cannabinus* in waterlogging. The white arrowheads indicate the presence of Casparian bands in either endodermal or exodermal cell walls. Bar = 100 μm in A-D and 50 μm in E-F. en, endodermis; ex, exodermis; p, phloem pole; x, xylem pole.
physiological function of roots under anaerobic soil conditions. A question is the intra-specific variation of *H. cannabinus* in the development of aerenchyma under waterlogging. However, there may be varietal difference in the degree of aerenchyma development in *H. cannabinus*, which may cause intra-specific difference of tolerance to waterlogging. In addition, introduction of genes controlling aerenchyma formation from *H. cannabinus* by inter-specific breeding hybridization may be a method to improve the waterlogging tolerance of *H. sabdariffa*.

Casparian bands can be detected by staining with fluorescent dyes (Brundrett et al., 1988; Lux et al., 2005), and, in some plant species, by autofluorescence under UV microscopy (Morita et al., 1996) because of the deposition of hydrophobic materials (e.g., suberin and lignin) on the cell wall. In this study, the Casparian bands in the taproots of the three fiber crops were clearly detected by autofluorescence. The waterlogging-tolerant species, *H. cannabinus*, developed Casparian bands better than other two species, in particular in exodermis. In general, it is expected that Casparian bands and suberized cell walls may be a barrier against toxic materials and prevent against oxygen loss from aerenchyma (Enstone et al., 2003.). Such roles of Casparian bands under waterlogging is obscure, because Casparian bands formation is rather suppressed in some species under anaerobic conditions. In maize roots, anaerobic stress enhanced suberin lamella development in exodermal Casparian bands but delayed suberin lamella formation in endodermis (Enstone and Peterson, 2005). In this study, the formation of Casparian bands was delayed and/or suppressed by waterlogging in both exodermis and endodermis of the taproot, except endodermal Casparian bands of *H. sabdariffa*. However, the formation of exodermal Casparian bands in early stage (i.e., close to root apex) in field-grown *H. cannabinus* under normal condition (i.e., before waterlogging) may enhances the tolerance of the root to a later flooding and the following soil reduction.

This study clarified anatomical features of three tropical fiber crops with reference to tolerance against waterlogging, especially focusing on aerenchyma development in cortex as well as development of Casprain bands in both endodermis and exodermis.

### Table 2. Formation of endodermal and exodermal Casparian bands in the taproot of three fiber-crop seedlings in control (C) and waterlogging (W) conditions.

| Distance from root apex (cm) | *Hibiscus cannabinus* | *Hibiscus sabdariffa* | *Corchorus olitorius* | *Hibiscus cannabinus* | *Hibiscus sabdariffa* | *Corchorus olitorius* |
|-----------------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|
|                             | C         | W         | C         | W         | C         | W         | C         | W         | C         | W         | C         | W         |
| 1                           | +         |           |           |           |           |           |           |           |           |           |           |           |
| 2                           | ++        | +         |           |           |           |           |           |           |           |           |           |           |
| 3                           | ++ ++     | ++        | ++        | ++        | ++        | ++        | ++        | ++        | ++        | ++        | ++        | ++        |
| 4                           | +++ ++    | +++ ++    | ++        | +++ ++    | ++        | +++ ++    | ++        | +++ ++    | ++        | +++ ++    | ++        | +++ ++    |
| 5                           | +++ ++    | + ++      | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 6                           | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 7                           | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 8                           | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 9                           | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 10                          | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 11                          | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 12                          | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 13                          | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 14                          | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 15                          | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 16                          | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 17                          | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 18                          | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 19                          | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |
| 20                          | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    | +++ ++    |

The numbers of plus (+) indicate the number of seedlings that formed Casparian bands among the three seedlings examined. The broken lines indicate the position of the base of the roots.
Although further study with grown-up and soil cultured plants is necessary, it is suggested that the anatomical structures of roots could contribute to waterlogging tolerance in the fiber crop species.

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