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Diversity of polyisoprenoids in ten Okinawan mangroves

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Abstract: The distribution and occurrence of polyisoprenoids (dolichols and polyprenols) in the leaves and roots of nine true Okinawan mangroves and the leaves of one associate mangrove were analyzed using two-dimensional thin layer chromatography. In the leaves, the distribution of three types (I, II, and III) of polyprenols and dolichols were detected. (I) The predominance of dolichols over polyprenols (more than 90%) was observed in *Avicennia marina*, *Bruguiera gymnorrhiza*, *B. gymnorrhiza* (yellow leaves), and *Rhizophora stylosa*. (II) The occurrence of both polyprenols and dolichols is observed in *Excoecaria agallocha*, *Kandelia obovata*, *K. obovata* (yellow leaves), *Lumnitzera racemosa*, *Pemphis acidula*, and *Sonneratia alba*. (III) The predominance of polyprenols over dolichols (more than 90%) is observed in *Heritiera littoralis* and *Hibiscus tiliaceus*. However, in the roots, a type-I distribution was observed in *A. marina*, *B. gymnorrhiza*, *E. agallocha*, *H. littoralis* and *S. alba*. A type-II distribution was observed in *K. obovata*, *L. racemosa*, *P. acidula*, and *R. stylosa* with no type-III distribution. The chain-length distribution of dolichols in the leaves and roots was C₅₀–C₁₄₀ and C₆₀–C₁₂₀, respectively. A similar chain-length distribution of polyprenols of C₄₅–C₁₄₀ and C₆₅–C₈₅ was detected in the leaves and roots respectively. Taken together, sixteen out of twenty-one tissues indicated that dolichols are more abundant than polyprenols in both leaves and roots. The present study is the first to clarify the diversity of polyisoprenoids in both the leaves and roots of mangrove, suggesting the chemotaxonomic significance of polyisoprenoids in the mangrove tree species.

Keywords: Dolichol; leaf; Okinawan mangrove; polyprenol; root

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Introduction

Polyisoprenoid alcohols are secondary metabolites together with sterols, ubiquinones, and plant-specific isoprenoids, which form the largest class of natural compounds. Lipid and isoprenoid composition of Okinawan mangroves and North Sumatran mangroves have been previously reported (Oku et al., 2003; Basyuni et al., 2007, 2009, 2012, 2013). Polyisoprenoid alcohols are linear five-carbon unit polymers that are present in almost all living cells. Long-chain polyisoprenoids occur in various plant tissues (Swiezewska & Danikiewicz, 2005 and cited therein). There are two types polyisoprenoids with respect to the α -isoprene structure (Fig. 1). The first type is polyprenol (structure 1), allylic alcohols with a single double bond in each isoprenoid unit (α -unsaturated isoprenoid alcohols), which are characteristics of bacterial cells (Wolucka et al., 1994), plant photosynthetic tissues (Swiezewska & Chojnacki, 1991; Kurisaki et al., 1997; Tateyama et al., 1999; Skorupinska-Tudek et al., 2003), shoots (Kurisaki et al., 1997), seeds (Kurisaki et al., 1997; Tateyama et al., 1999; Skorupinska-Tudek et al., 2003), needles (Yu et al., 2012), flowers (Tateyama et al., 1999), and cultured cells (Skorupinska-Tudek et al., 2007). The second type is dolichol (structure 2) without a double bond in the OH-terminal isoprenoid unit (α -saturated isoprenoid alcohols). Dolichols occur mainly in animals (Sagami et al., 1992; Ishiguro et al., 2014), yeast cells (Grabinska & Palamarczyk, 2002), plant roots (Tateyama et al., 1999; Skorupinska-Tudek et al., 2003), and soybean seedlings (Ishinaga et al., 1992). It is noteworthy that the composition of polyprenols in

photosynthetic tissue is reproducible for certain botanical species and is considered a chemotaxonomic species-specific marker (Roslinska et al., 2002).

Despite the ubiquitous distribution of polyisoprenoids in the plant kingdom, studies on the polyisoprenoids from mangrove trees are scarce. Long-chain rubber-like polyisoprenoids occur in the leaves of the mangrove tree species *Lumnitzera racemosa* (Skoczylas et al., 1994). Furthermore, the contents of polyprenols and dolichols increased in a tissue or organ with senescence and upon abiotic and biotic stress (Zhang et al., 2008; Bajda et al., 2009; Baczewska et al., 2014). Despite the physiological importance of polyisoprenoids, no information on polyisoprenoid distribution in mangroves trees is available. We report here for the first time the occurrence and tissue distribution of polyprenols and dolichols together with solanesol and bombiprenone (Fig. 1, structure 3 and 4, respectively) in ten Okinawan mangroves.

Materials and methods

Chemicals

Dolichol from pig liver was obtained from Sigma-Aldrich Co. (St. Louis, Missouri, USA). A mixture of dolichol (C_{90} – C_{105}) standard compounds was isolated from horse testicles along with a mixture of polyprenol (C_{90} – C_{100}) from *Malus sp.* (Swiezewska & Danikiewicz, 2005). The dolichols (C_{95} – C_{110}) standards were derived from skipjack tuna livers (Ishiguro et al., 2014). The dolichol and polyprenol standards were generously provided by Dr. Ewa Swiezewska, and used to identify the polyisoprenoids that were detected in this study. The identification of the family corresponding to polyprenols or dolichols was performed in at least three experiments. Bombiprenone (C_{43}) as described by Toyoda et al. (1968) and Irvine et al. (1972) was purified by the silica-gel chromatography of non-saponifiable lipids of the $CHCl_3/CH_3OH$ (2:1) extract of dry perilla leaves and its identity was confirmed by HPLC/MS to have an m/z value $[M + Na]^+$ of 625.53183 corresponding to $C_{43}H_{70}O$ (bombiprenone). Solanesol (C_{45}) standard was prepared as described previously (Kurisaki et al., 1997). Silica gel 60 TLC plates and reversed-phase silica RP-18 HPTLC plates were purchased from Merck (Darmstadt, Germany). All of the other chemicals and solvents were of reagent grade (Sigma-Aldrich Co.).

Plant materials

The leaves and roots of nine true mangrove tree species on Iriomote Island, Okinawa Japan were collected 2–3 replicates in February: *Avicennia marina*

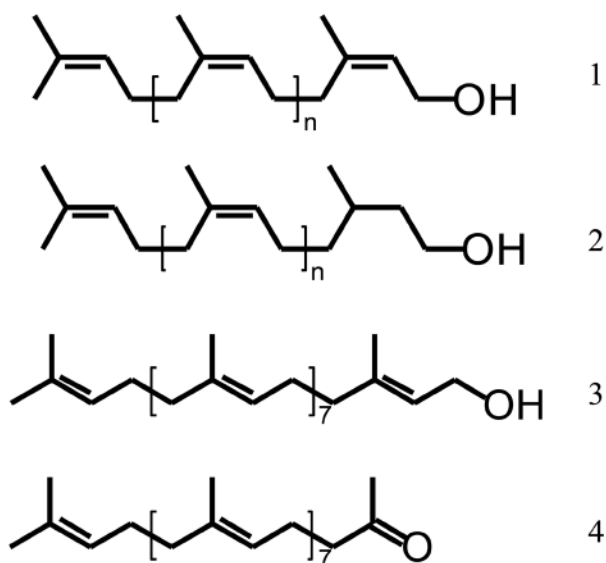


Fig. 1. Structure of polyprenol (1), dolichol (2), solanesol (3), and bombiprenone (4). n shows the number of internal isoprene residues

(Forsk.) Vieh (Acanthaceae), *Bruguiera gymnorrhiza* (L.) Lamk. (Rhizophoraceae), *Excoecaria agallocha* L. (Euphorbiaceae), *Heritiera littoralis* Dryand. (Sterculiaceae), *Kandelia obovata* (S., L.) Yong (Rhizophoraceae), *Lumnitzera racemosa* Wild. (Combretaceae), *Pemphis acidula* Forst. (Lythraceae), *Rhizophora stylosa* Griff. (Rhizophoraceae), and *Sonneratia alba* J. Smith (Sonneratiaceae). The leaves of one mangrove associate, *Hibiscus tiliaceus* L. (Malvaceae), were also obtained from the same island in November. The age of green leaves was estimated approximately as 2–5 months whereas yellow leaves was roughly as 6–8 months. Yellow leaves still attached to branches and ready to abscise were collected randomly. Mangrove plants grew naturally with exposure to natural sun light. The average of temperature in the month of collection was 18 °C and average humidity was 73%. All of the fresh samples were kept at –80 °C until used.

Isolation of polyisoprenoid alcohols

The procedure for the isolation of polyisoprenoids was performed as previously described (Sagami et al., 1992; Kurisaki et al., 1997). The green and yellow leaves and roots were dried at 60–75 °C for 1–2 days. The dried tissue (5 g each) was crushed into fine powder and immersed in 30 ml of chloroform/methanol (2/1, v/v) solvent for 48 h. The lipid extract of the leaves and roots was saponified at 65 °C for 24 h in 86% ethanol containing 2 M KOH. The non-saponifiable lipids of each tissue were extracted with hexane, and the organic solvent was evaporated and re-dissolved in hexane. The leaf (20–50 mg) and root (50–100 mg) extracts were applied to each TLC plate.

Analysis by two-dimensional thin layer chromatography

First-dimension TLC was carried out for 60 min on a silica gel glass plate (20 × 3 cm) with a solvent system of toluene-ethyl acetate (9:1) as previously described (Sagami et al., 1992). The polyprenol family moved slightly faster than did the corresponding dolichol family. The longitudinal edge of the first-dimension TLC plate 1 cm in width and the concentration zone of a reversed-phase C-18 TLC were clamped using two magnetic bars (4.0 × 1.1 × 0.8 cm) facing each gel phase. The bound TLC plate was then developed perpendicularly to the first dimension to transfer polyprenol and dolichol to the concentration zone of the reversed-phase TLC plate. The second-dimension reversed-phase C-18 silica gel TLC was performed with acetone for approximately 30 min. The position of the separated polyisoprenoid

alcohols being developed by two-dimension silica gel TLC were identified by visualization of polyisoprenoid spots on TLC chromatograms with iodine vapor prior scanning. To determine whether the family corresponds to dolichols or polyprenols, in the case of the one family that observed on two-dimensional TLC, dolichol or polyprenol reference was added to the sample line of the first-dimension TLC and developed with a solvent system as previously described. The developed chromatographic images were obtained and digitally scanned with Canon MG6100 series printer. The polyisoprenoid family was identified by the comparison of mobility on TLC with that of authentic standards of dolichol and polyprenol that were applied in the second-dimensional development.

Quantification of polyisoprenoid was done by making a standard solution using dolichol or polyprenol standard sample as internal standard for the second-dimension TLC development. A standard curve relation between dolichol or polyprenol and tentative iodine-color estimation using dolichol standard on the reverse-phase C-18 was drawn. Relative ratio of the iodine colors between dolichol analyzed on two-dimensional TLC and mangrove dolichol or polyprenol. The standard curve was then used to estimate the concentration of dolichol or polyprenol from mangrove samples. The polyprenols and dolichols that were detected on HPTLC RP-18 plates were quantified using ImageJ 1.46r (Schneider et al., 2012) with dolichol and polyprenol standards as references. The rubber-like compounds remaining on the top solvent front area of the first silica-gel plate without being transferred to the RP-18 plate with acetone were detected by iodine vapor.

Results

The search for long-chain polyisoprenoids from ten Okinawan mangroves was performed by two-dimensional TLC (Sagami et al., 1992) to separate polyisoprenoids into polyprenol and dolichol families with different chain lengths. Tables 1 and 2 summarize the analytical results of the occurrence and distribution of polyprenols and/or dolichols and the carbon-chain lengths of each family, respectively.

The total lipid content of mangrove leaves (Table 1) ranged from 34–264 mg g⁻¹ dry weight with an average of 112 mg g⁻¹ dry weight and the lowest and the highest in *P. acidula*, and *K. obovata*, respectively. In contrast, the total lipid content of mangrove roots ranged from 2–212 mg g⁻¹ dry weight, with an average of 44 mg g⁻¹ dry weight and, the lowest in *H. littoralis* and the highest in *A. marina*, respectively. The quantity of polyisoprenoids was the highest in *H. tiliaceus* leaves (13.9 mg g⁻¹ dry weight). The low-

Table 1. Occurrence and distribution of polyprenols and dolichols in ten Okinawan mangroves

Species	Tissue	Total lipids (mg/g dw)	Polyisoprenoids (mg/g dw)	Polyprenols (mg/g)	Dolichols (mg/g)	% in total lipid			% in polyisoprenoid	
						Polyiso- prenoid	Poly- prenol	Doli- chol	Poly- prenol	Doli- chol
<i>A. marina</i>	leaves	108±8.4	3,3	0,1	3,2	3,1	0,1	3,0	4,2	95,8
<i>B. gymnorrhiza</i>	leaves	154±15.5	3,7	nd	3,7	2,4	nd	2,4	nd	100,0
	yellow leaves	116±9.2	4,0	0,4	3,6	3,4	0,3	3,1	9,1	90,9
<i>E. agallocha</i>	leaves	72±9.5	2,4	1,5	0,9	3,4	2,1	1,3	62,3	37,7
<i>H. littoralis</i>	leaves	86±6.0	9,2	9,2	nd	10,7	10,7	nd	100,0	nd
<i>H. tiliaceus</i>	leaves	100±5.7	13,9	13,9	nd	13,9	13,9	nd	100,0	nd
<i>K. obovata</i>	leaves	264±18.0	5,9	1,4	4,5	2,2	0,5	1,7	23,7	76,3
	yellow leaves	92±2.8	12,9	7,4	5,5	14,0	8,0	6,0	57,1	42,9
<i>L. racemosa</i>	leaves	120±12.1	6,7	3,0	3,7	5,6	2,5	3,1	44,8	55,2
<i>P. acidula</i>	leaves	34±7.1	1,5	0,7	0,8	4,4	2,2	2,2	49,3	50,7
<i>R. stylosa</i>	leaves	136±7.8	6,1	0,4	5,7	4,5	0,3	4,2	6,3	93,7
<i>S. alba</i>	leaves	60±17.0	8,6	5,0	3,6	14,4	8,3	6,1	57,8	42,2
<i>A. marina</i>	roots	212±12.7	2,3	nd	2,3	1,1	nd	1,1	nd	100,0
<i>B. gymnorrhiza</i>	roots	14±2.1	0,8	0,1	0,7	5,5	0,4	5,1	6,6	93,4
<i>E. agallocha</i>	roots	14±1.4	0,8	nd	0,8	5,6	nd	5,6	nd	100,0
<i>H. littoralis</i>	roots	2±1.4	0,7	nd	0,7	34,0	nd	34,0	nd	100,0
<i>K. obovata</i>	roots	54±4.9	1,2	0,3	0,9	2,2	0,6	1,6	25,4	74,6
<i>L. racemosa</i>	roots	6±2.1	0,8	0,2	0,6	13,3	3,3	10,0	25,0	75,0
<i>P. acidula</i>	roots	26±2.8	0,9	0,1	0,8	3,5	0,5	3,0	15,2	84,8
<i>R. stylosa</i>	roots	32±1.0	1,0	0,4	0,6	3,1	1,2	1,9	38,8	61,2
<i>S. alba</i>	roots	36±1.4	1,0	nd	1,0	2,7	nd	2,7	nd	100,0

nd = not detected. Total lipids are represented as the mean ± SD (n = 2-3).

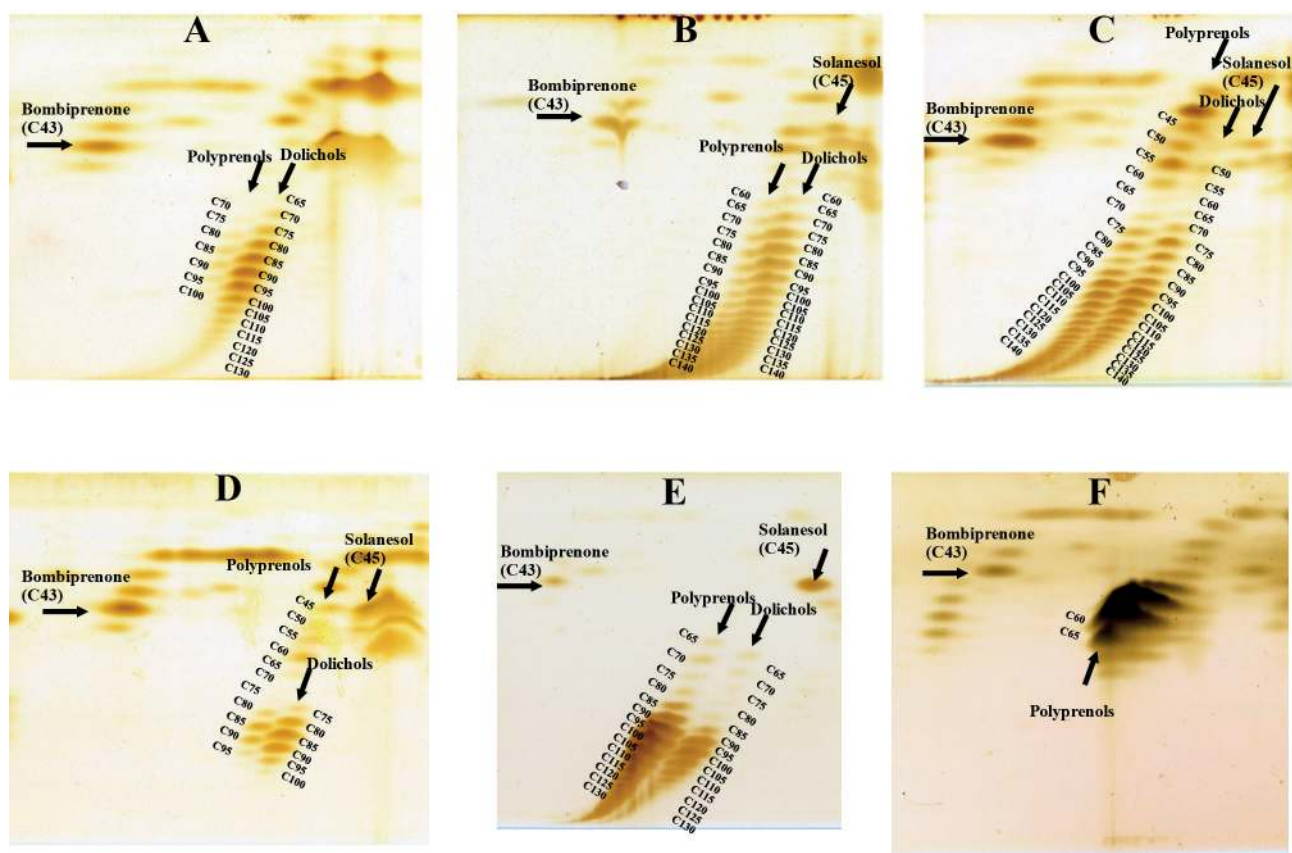


Fig. 2. Two-plate TLC of polyisoprenoids from *A. marina* leaves (A), *L. racemosa* leaves (B), *P. acidula* leaves (C), yellow leaves of *K. obovata* (D), *S. alba* leaves (E), and *H. tiliaceus* leaves (F). The carbon number refers to the carbon-chain length of polyisoprenoid alcohols

Table 2. Carbon-chain lengths of polyprenols and dolichols occurring in ten Okinawan mangroves*

Species	Tissue	Sub-ber-like	C43	C45	Polyprenol	Dolichol
<i>A. marina</i>	leaves	o	o		70 75 80 85 90 95 100	65 70 75 80 85 90 95 100 105 110 115 120 125 130
<i>B. gymnorhiza</i>	leaves					75 80 85
	yellow leaves				90 95 100	75 80 85 90
<i>E. agallocha</i>	leaves	o	o	50 55 60 65		70 75 80
<i>H. littoralis</i>	leaves	o		60 65		
<i>H. tiliaceus</i>	leaves	o	o	60 65		
<i>K. obovata</i>	leaves	o	o	o	75 80 85 90 95 100	70 75 80 85 90 95 100
	yellow leaves		o	45 50 55 60 65 70 75 80 85 90 95		75 80 85 90 95 100
<i>L. racemosa</i>	leaves	o	o	o	60 65 70 75 80 85 90 95 100 105 110 115 120 125 130 135 140 and more	60 65 70 75 80 85 90 95 100 105 110 115 120 125 130 135 140
<i>P. acidula</i>	leaves	o	o	o	45 50 55 60 65 70 75 80 85 90 95 100 105 110 115 120 125 130 135 140 and more	50 55 60 65 70 75 80 85 90 95 100 105 110 115 120 125 130 135 140
<i>R. stylosa</i>	leaves		o	o	85 90 95	75 80 85 90 95
<i>S. alba</i>	leaves		o	o	65 70 75 80 85 90 95 100 105 110 115 120 125 130 and more	65 70 75 80 85 90 95 100 105 110 115 120 125 130
<i>A. marina</i>	roots	o				60 65 70 75 80 85 90 95
<i>B. gymnorhiza</i>	roots				75 80 85	70 75 80 85 90
<i>E. agallocha</i>	roots	o				70 75 80
<i>He. littoralis</i>	roots	o				75 80 85
<i>K. obovata</i>	roots				85 90 95	80 85 90 95 100 105
<i>L. racemosa</i>	roots	o	o	o	80 85 90 95 100 105	80 85 90 95 100 105 110 115 120 125 130 135 140
<i>P. acidula</i>	roots	o	o	o	85 90 95 100 105	85 90 95 100 105 110 115 120 125 130 135 140
<i>R. stylosa</i>	roots				75 80 85 90	75 80 85 90 95
<i>S. alba</i>	roots		o			75 80 85 90 95 100 105

*The numbers refer to the carbon-chain length of polyisoprenoid alcohols. The chain length of the main polyisoprenoid alcohols in each tissue are indicated in bold. o = detected.

est content of polyisoprenoids was in the roots (0.7 mg g^{-1} dry weight) of *H. littoralis*.

The distribution of polyisoprenoids in the leaf's polyisoprenoids can be classified into three types (I, II, and III). In type -I, the predominance of dolichols over polyprenols (more than 90%) was observed in *A. marina*, *B. gymnorrhiza*, *B. gymnorrhiza* (yellow leaves), and *R. stylosa*. In *A. marina* and *R. stylosa*, a trace amount of polyprenols with chain lengths similar to those of dolichols was detected as shown in Fig. 2A and Supplementary Fig. 1F, respectively, but in *B. gymnorrhiza* leaves and yellow leaves (Supplementary Fig. 1A and 1B, respectively), polyprenols with chain lengths similar to those of dolichols were not detected, although polyprenols that were much longer than dolichols were detected in *B. gymnorrhiza* (Supplementary Fig. 1B and Table 2). In type -II, the occurrence of both polyprenols and dolichols was observed in *E. agallocha*, *K. obovata*, *K. obovata* (yellow leaves), *L. racemosa*, *P. acidula*, and *S. alba* (Table 1). In *E. agallocha*, the chain lengths differed between polyprenols and dolichols, as shown in Supplementary Fig. 1C and Table 2. In both *K. obovata* and *K. obovata* (yellow leaves), polyprenols with a chain length similar to that of dolichols were detected, as shown in Supplementary Fig. 1E and Fig. 2D, respectively, and another polyprenol family was also detected especially in yellow leaves. In *L. race-*

mosa, *P. acidula*, and *S. alba*, polyprenols much longer than dolichols in chain length were also detected, as shown in Fig. 2B, Fig. 2C, and Fig. 2E, respectively (See Table 2). In type -III, the predominance of polyprenols over dolichols (more than 90%) was observed in *H. littoralis* and *H. tiliaceus* (mangrove associate). In these cases, the chain length of the detected polyprenols were C_{60} and C_{65} , as shown in Supplementary Fig. 1D and Fig. 2F, respectively, and in Table 2. Similar shorter-chain polyprenols were also detected in *E. agallocha* leaves, *P. acidula* leaves and yellow leaves of *K. obovata* (Supplementary Fig. 1C, Fig. 2C, and Fig. 2D, respectively and Table 2).

However, regarding the root's polyisoprenoids, the predominance of dolichols over polyprenols was observed in *A. marina*, *B. gymnorrhiza*, *E. agallocha*, *H. littoralis*, and *S. alba*, similar to that found in the type-I leaves. In *A. marina*, *E. agallocha*, *H. littoralis*, and *S. alba*, dolichols with no polyprenols were observed as shown in Supplementary Figs. 2A, 2C, 2D, and 3C, respectively, although a trace amount of polyprenols was detected in *B. gymnorrhiza* (Supplementary Fig. 2B). A significant amount of polyprenols together with dolichols were observed in the roots of *K. obovata*, *L. racemosa*, *P. acidula*, and *R. stylosa*, similar to type-II leaves. Both polyprenols and dolichols were detected in *K. obovata* (Supplementary Fig. 2E) and in *R. stylosa* (Fig. 3C). In *L. racemosa* (Fig. 3A) and *P.*

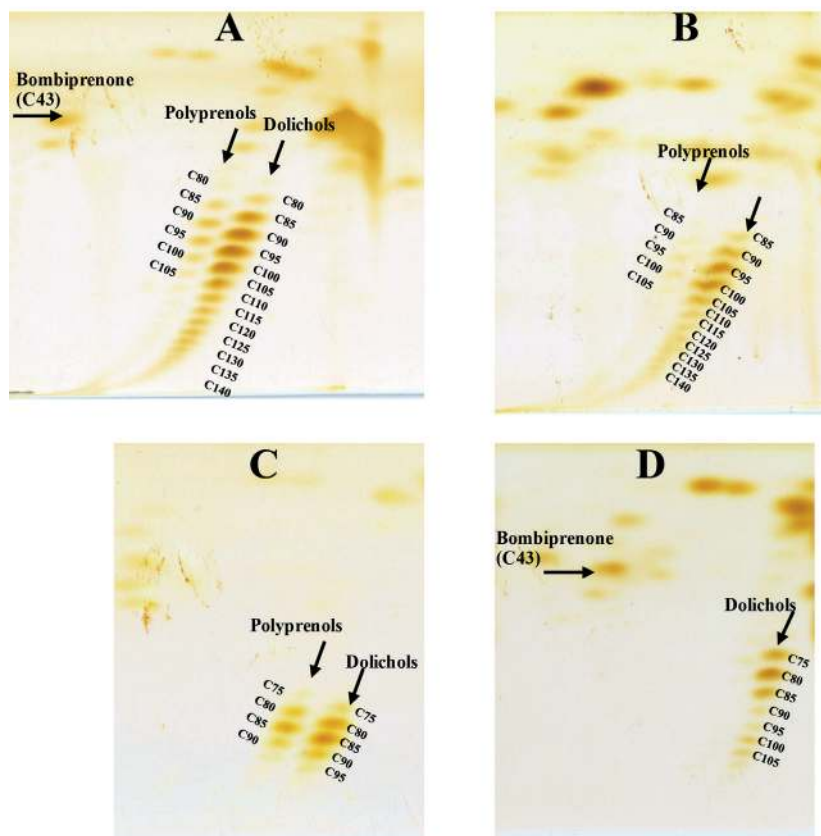


Fig. 3. Two-plate TLC of polyisoprenoids from *L. racemosa* roots (A), *P. acidula* roots (B), *R. stylosa* roots (C), and *S. alba* roots (D). The carbon number refers to the carbon-chain length of polyisoprenoid alcohols

acidula (Fig. 3B), longer dolichols were also detected, similar to those in their leaves. The distribution of the predominance of polyprenols over dolichols, similar to type-III leaves, was not observed in any roots, though analytical studies were not performed for *H. tiliaceus* roots.

Discussion

Analysis of polyisoprenoid in leaves of mangrove plants the major polyisoprenoid alcohols are not polyprenols but dolichols. As shown in Table 1, dolichols were found in all tissues except for the leaves of *H. littoralis* and *H. tiliaceus*. It has been suggested by Tateyama et al. (1999) that the chain length of dolichols varied from tissue to tissue, even in the same species and appeared to form distinct families with dominating molecule species. Polyprenols also occurred as one or two polyprenols families, depending on the plants and tissues. Two polyprenols families were detected in yellow leaves of *K. obovata* (Fig. 2D) and the leaves of *L. racemosa* and *P. acidula* (Fig. 2B and 2C, respectively). The major molecules in each family varied with mangrove species: C₆₀ and C₈₅ for *K. obovata*; C₅₅ and C₉₅–C₁₀₀ for *P. acidula*; and C₈₀–C₉₀ and C₁₂₀ for *L. racemosa* (Table 2). The longer chain polyprenol family was also found in *L. racemosa* leaves (Fig. 2B), *P. acidula* leaves (Fig. 2C), and *S. alba* leaves (Fig. 2E). In contrast to this observation, dolichols occurred as one dolichol family with a dominating length of C₈₀–C₉₅ in *L. racemosa* leaves, C₇₅–C₈₀ and C₉₀–C₁₀₀ in *P. acidula* leaves and C₉₅–C₁₀₅ in *S. alba* leaves depending on the mangrove species and tissue (Table 2). These results therefore indicate that the biosynthetic pathway from polyprenols to dolichols may be regulated by polyprenol reductase with strict substrate specificity to chain-length in mangrove plants.

The accumulation of polyprenols with age was noted with yellow leaves of *K. obovata* with a 5-fold increase (Table 1). Polyprenols and dolichols in yellow leaves of *K. obovata* similarly increased with age, while yellow leaves of *B. gymnorrhiza* were opposite in that dolichols slightly decreased with age. The increase in polyprenols with age has been reported in old ginkgo leaves (Tateyama et al., 1999), old rubber leaves (Tateyama et al., 1999) and senescing leaves (Swiezewska et al., 1994). The pattern of polyprenyl esters was more complex in old *L. racemosa* leaves, with polyprenyl esters in the range of prenol-20 to prenol-80 forming 2–3 subgroups (Skoczylas et al., 1994). However the results of the previous analysis (Skoczylas et al., 1994) is slightly different, namely dolichols have not detected in leaf extract. This discrepancy with our present study might it result from the differences in the age of the leaves or environmental conditions. These observations suggest that

the biosynthetic pathways of shorter polyprenols, medium polyprenols, longer polyprenols and dolichols are differently regulated in the plant kingdom, including mangrove plants.

The occurrence of longer dolichols in the roots of *L. racemosa* and *P. acidula* (Fig. 3A and 3B, respectively) appeared to be at least partly correlated with a cross-section of the main roots of seven Okinawan mangroves, divided into two types of main roots (Oku et al., 2003). One structure is well-developed aerenchyma in the cortex (Tomlinson, 1986), as exemplified by *A. marina*, *B. gymnorrhiza*, *K. obovata*, *R. stylosa*, and *S. alba*. These species were comprised of shorter to medium dolichols (C₆₀–C₁₀₅), including *E. agallocha* and *H. littoralis* in this study. Another type showing a broad lacunose cortex, no trichosclereids and containing longer dolichols (C₈₀–C₁₄₀) developed (Tomlinson, 1986) in *L. racemosa* and *P. acidula* (Oku et al., 2003).

Dolichols were predominated in sixteen out of twenty-one mangrove tissues, including the leaves and roots (Table 1 and 2). Therefore, the occurrence of larger amounts of dolichols even in the leaves of mangrove plants, implies that polyprenols play no important role in several mangrove leaves, although the function of polyprenols in the plant world remains unclear. Finally, the present study importantly revealed that much longer chain dolichols (C₁₃₀–C₁₄₀) occur in *L. racemosa* and *P. acidula* leaves and roots. In the future, it will be very important to understand whether those longer dolichols are able to function as sugar-carrier lipids in the biosynthesis of *N*-glycoproteins, together with the understanding of whether polyprenol reductases in *L. racemosa* and *P. acidula*, which catalyze the conversion of polyprenol to dolichol corresponding to the SRD5A-3 protein in animals (Cantagrel et al., 2010), differ from those of other mangrove plants in reduction activity.

Conclusions

In the plant world (especially in leaves), polyprenols rather than dolichols are usually abundantly detected (Swiezewska et al., 1994; Tateyama et al., 1999; Swiezewska & Danikiewicz, 2005). In addition, in the animal world (livers), dolichols were predominant, and few polyprenols occurred (Chojnacki & Dallner, 1988; Daniels & Hemming, 1990; Sagami et al., 1992). The distribution of dolichols and polyprenols found in mangrove plants varies depending on each tissue. Further experiments are necessary to clarify the physiological significance of polyisoprenoid alcohols under environmental stresses such as salinity and shading as well as the molecular cloning of the polyisoprenoid biosynthesis gene in mangrove plants.

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