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Phyllotaxis and morphology of proximal leaves on vegetative axillary shoots of *Salix* and their systematic implications

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Abstract

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This investigation concerns the proximal leaves on axillary shoots. Proximal leaves are defined as the first four leaf-like organs (1) to (4) of the middle shoot (not counting stipules and the organs of the lateral buds) inside the outer tubular bud scale. These may be scale-like or incompletely developed foliage leaves. The morphology of these proximal leaves, their angular positions with respect to the mother shoot, and the sense of rotation of the phyllotactic spiral were recorded in plants from 59 *Salix* taxa (species, subspecies, hybrids). The mean position ($\bar{\alpha}_1$) of the first proximal leaf = leaf (1) is defined as the divergence angle between this leaf and the median plane of the axillary bud. It ranges from -7° to $+91^\circ$. The phyllotaxis of the proximal leaves of the various *Salix* species corroborates to some degree the intrageneric classification by Skvortsov (1968).

In some species with the first proximal leaf close to 0° , this leaf had characteristics of a cataphyll, i.e. an additional bud scale. This is interpreted as a relictual characteristic from common ancestry with *Populus*.

In species with divergence angles $\bar{\alpha}_1$ between $+35^\circ$ and $+75^\circ$, homodromy (i.e. the same sense of rotation in succeeding shoot generations) occurred with a significantly higher frequency than the expected 50%.

Key words: Phyllotaxis, cataphyll, proximal leaves, homodromy, bud scales, *Salix*.

Introduction

The genus *Salix* includes 350–400 species, depending on the concept of species. Its natural distribution ranges from tropical regions (where only few species grow) to the high latitudes of the arctic. It has been suggested that the genus first evolved either in the warm temperate region or in the subtropics (Skvortsov, 1968; Dorn, 1976). This is supported by the softness of the wood, the usually single bud scale and the tendency to grow until late fall (Neumann, 1981). Some species also show an almost sylleptic growth pattern in that they may produce up to four shoot generations per year, with only short resting periods in between (Chmelař and Meusel, 1979).

Two basic phyllotactic patterns have been described for the distal part of mature shoots: spiral Fibonacci pattern with divergence angle close to 137.5° (= Fibonacci angle), by far the more common, and opposite decussate phyllotaxis. Within the latter, Chmelař and Neumann (1976) made a distinction between species with strictly opposite leaves, *S. amplexicaulis* Schneid., *S. integra*¹ (both sect. *Helix*), *S. subopposita* Miq. (sect. *Incubaceae*), and those with sometimes unsymmetrically oscillating internodes, *S. purpurea* (sect. *Helix*) and its hybrids and *S. salwinensis* Handel-Mazzetti (sect. *Psilotigmatae*, subgen. *Chamaetia*). In some species with spiral phyllotaxis, the spiral may not exactly follow the Fibonacci pattern, or its ascent may not easily be verifiable because the short shoots do not bear enough leaves. In some creeping high-elevation species, the spiral formed by the buds is difficult to recognize once the leaves have grown, since the leaves twist sharply sideways in their orientation to light.

In contrast to the phyllotaxis at the distal end of the shoots, little information about proximal phyllotactic patterns in *Salix* has been published. In a survey on dicotyledons, Furuya (1953) examined seven species within the *Salicaceae*, including four *Salix* species. He classified shoot types and suggested several possible phylogenetical relationships between them. Kimura and Sugaya (1965) made transections of axillary buds in the winter state of *S. bonplandiana* Kunth, *S. safsaf* Forsk. and *S. alba* L., and discussed details of bud scale formation and phyllotaxis of the proximal leaves.

Most *Salix* species have a single outer bud scale, formed by two prophylls in transversal positions and fused on both abaxial and adaxial sides (Kimura and Sugaya, 1965). In the section *Humboldtianae*, however, the two prophylls grow together only on the abaxial side. Leaf (1) is then situated on the adaxial side, thus covering the gap between the two non-fused lobes of the outer bud scale. In most species leaf (1) is green and has a similar type of venation as the following leaves. In the section *Glandulosae* (*S. chaenomeloides* Kimura, *S. mesnyi* Hance) a second bud scale is sometimes visible inside the first one. Skvortsov (1968) stated that "the bud in this section most closely resembles the bud of poplars" (p. 90). Two other species with a second or inner bud scale were reported from the section *Humboldtianae*. In *S. tetrasperma* Roxb., the first two proximal leaves take the function of supplementary inner bud scales and exhibit the typical parallel venation of cataphylls (Chmelař, 1978). Büchler (1991) described the same character for the first proximal leaf in *S. acmophylla* on an individual from northern Africa. This finding initiated a survey of bud characters and of phyllotaxis of proximal leaves within the genus. The purpose of the current investigation is to examine the taxonomic and phylogenetic relevance of these characters with regards to their use in the taxonomy of *Salix*.

Material and methods

The following definitions are used in this paper. The **sense of rotation (SOR)** of the phyllotactic spiral may be **clockwise (CW)** or **counter-clockwise (CCW)**. It is defined as seen in the direction of growth. The term **mother shoot (m-shoot)** is used for the parts of the branching system that grew the year prior to observation. The mother shoots carry the **daughter shoots (d-shoots)** that sprout during the year of observation. Mother shoot SOR and d-shoot SOR are called **homodromous** if they are turning in the same sense and **antidromous** if they are turning in opposite senses. The **outer bud scale** consists of two partially or completely fused prophylls. **Proximal leaves** are defined as the first four leaf-like organs (1) to (4) of the middle shoot (not counting stipules and the organs of the lateral

¹ The authors of species examined in the course of this investigation are given in Table 1.

buds) inside the outer tubular bud scale. These may be cataphylls of the **inner bud scale** type or incompletely developed foliage leaves. The proximal leaves are referred to as **leaf (1)** up to **leaf (4)**, counting from the base of the axis.

Most plant material was taken from the living collection of the author in Wetzikon near Zürich, Switzerland (altitude 550 m). This outdoor plant collection consisted of 212 individuals from 120 taxa (species, subspecies, varieties and hybrids), all identified and their origin documented. The subtropical species *S. humboldtiana* and *S. acmophylla* grew in pots within a greenhouse during winter while all the others grew outdoors, throughout the year. Additional plant material was taken directly from natural habitats.

Sprouting shoots from 70 plants of 51 taxa were examined in spring 1992. If available, at least one branch with a CW rotating and one with a CCW rotating phyllotactic spiral was chosen from each plant. The angular positions of the first four proximal leaves ($a_1 \dots a_4$) were recorded on a data sheet (for definitions see Fig. 1). A stereo microscope with a 22.5° polar grid integrated in its optical system was used. Also recorded were the successions of dormant buds, vegetative and flowering shoots, and the SOR of the m-shoot. Specimens of bud scales and the first four proximal leaves were collected.

In spring 1993 and 1994 many of these plants were again examined, but with more shoots per plant and with an improved instrumentation that allowed a higher precision. Both years, observations were made between late March and mid May on shoots sprouting from winter buds (some species of more tropical origin may show sylleptic branching with more than one bud generation per year).

To summarize data, the shoots with CCW rotation were mirrored at the median plane and added to the CW data (Fig. 2). From the results of 1993/94 data the circular mean value \bar{a} and the circular standard deviation s' of leaf positions per plant were calculated. The results from low sample sizes (1992) are marked with **q** (qualitative data) and given as the approximate range of angles. The classification of Skvortsov (1968) is followed in this paper.

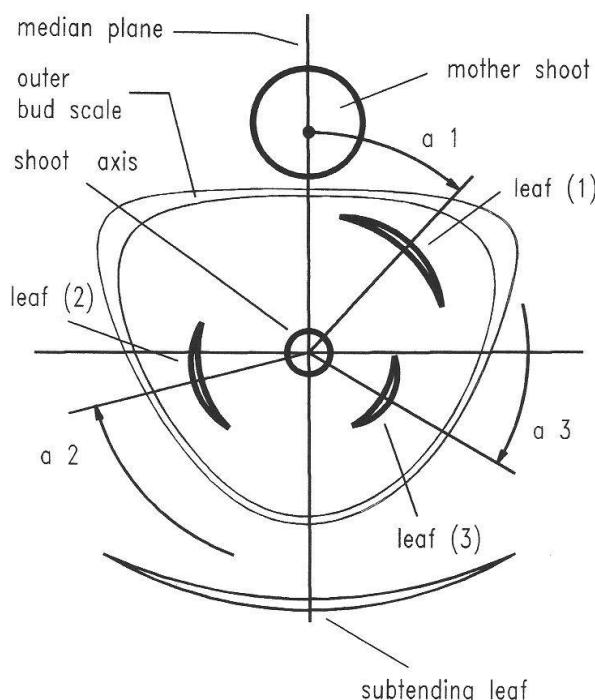


Fig. 1. Definitions and positions of first 3 leaves shown on a CW rotating daughter shoot. View from the distal end of the shoot towards the shoot base. a_1 = divergence angle between leaf (1) and the median plane.

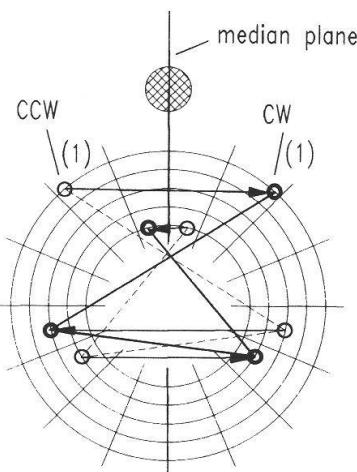


Fig. 2. Relationship between leaf positions of CW-rotating and CCW-rotating shoots.

Results

Phyllotaxis of proximal leaves

Seventy-seven plants out of 58 taxa have been examined. The results show a large diversity of leaf arrangements. The positions of leaf (1) (Tab. 1 and Fig. 4, mean angles \bar{a}_1 per plant) range from -7° to $+91^\circ$. The circular standard deviation s' varies between $\pm 5^\circ$ and $\pm 27^\circ$. Between plants of the same species \bar{a}_1 differs usually less than 20° . In some sections the angle \bar{a}_1 varies only a few degrees; in others up to 50° (Fig. 4).

The large variety of phyllotactic patterns may be presented in a linear fashion with the angular position of leaf (1) as a variable (Fig. 4). In plants with \bar{a}_1 close to 0° , CW and CCW rotating shoots have their first leaves in the same cluster (e.g. *S. acmophylla*, Fig. 3 a). The SOR may then only be determined by looking also at leaves (2) and (3). The ultimate phyllotaxis on the distal part of the shoot in this group is of the Fibonacci spiral type.

As leaf (1) moves to a higher angle (e.g. *S. hegetschweileri*, Fig. 3 b) the clusters for CW and CCW rotating shoots separate. The SOR may now be determined from the position of leaf (1). The phyllotaxis of the shoot changes without transition from the decussate pattern of the prophylls (=outer bud scale) to the Fibonacci spiral arrangement. The angles between the first four successive leaves oscillate in most plants around 137.5° , the angle of Fibonacci systems. Up to an angle \bar{a}_1 of about 75° , leaf (1) is always distinctly smaller than leaf (2) and is positioned closer to the shoot base.

As the angle \bar{a}_1 approaches $+90^\circ$, leaf (2) moves toward -90° (opposite-decussate pattern, e.g. *S. integra*, Fig. 3 c). Leaves (1) and (2), forming an opposite pair, now have a similar size and are almost at the same distance from the shoot base. Leaves (3) and (4) are positioned at a 90° angle compared to leaves (1) and (2), forming at least a short opposite decussate arrangement. The phyllotaxis on the distal part of the shoot may turn into a Fibonacci system somewhere between leaves (5) and (10) or remain opposite decussate (*S. integra*).

Morphology of the outer bud scale

The outer bud scale is tubular in most of the species studied, due to a total fusion of the two opposite prophylls (except for *S. humboldtiana* and *S. acmophylla*). The outer bud

Tab. 1. List of all plants examined (classification according to Skvortsov, 1968; species not treated in Skvortsov were added according to other authors). Leaf positions of CCW rotating shoots were mirrored at the median plane and added to the CW-data.

Plant identification			Results		
Subgenus/Section/Species	Abrev. of individuals studied/sex	Original (natural) place of growth	Number of shoots examined	Position of leaf (1) $\bar{a}_1 (\pm s')$	Morphology of leaf (1)
Subgenus <i>Salix</i>					
Sect. <i>Humboldtianae</i>					
<i>S. humboldtiana</i> Willd.	humb 1/f	Buenos Aires, Argentina	27	+9° (24°)	foliage
<i>S. acmophylla</i> Boiss.	acmo 1/f	Bot. Garden Kairo, Egypt	15	+2° (± 5°)	scale
Sect. <i>Amygdalinae</i>					
<i>S. triandra</i> L. ssp. <i>concolor</i> Koch	tria 1/f	Pontarlier, Jura, France	25	+12° (± 25°)	foliage
<i>S. triandra</i> L. ssp. <i>discolor</i> Koch	tria 2/m	Wattwil, Toggenburg, Switzerl.	q	[-20° ... +20°]	foliage
Sect. <i>Pentandrae</i> (<i>Salicaster</i>)					
<i>S. pentandra</i> L.	pent 2/f	Frambourg, Jura, France	13	+4° (± 9°)	scale
<i>S. pentandra</i> L.	pent 1/m	Frambourg, Jura, France	9	+11° (± 17°)	scale
<i>S. lucida</i> Mühlb. ¹	nature/m	Boise, Idaho, USA	q	[-12° ... +12°]	intermed.
<i>S. lucida</i> Mühlb. ¹	nature/f	Boise, Idaho, USA	q	[-12° ... +12°]	intermed.
Sect. <i>Salix</i>					
<i>S. alba</i> L. <i>sensu stricto</i>	nature/?	Wetzikon, Switzerland (from natural habitat)	26	+49° (± 14°)	foliage
<i>S. alba</i> L. "Chermesina"	alb 2/m	nursery	q	[-15° ... +15°]	foliage
<i>S. alba</i> L. var. <i>vitellina</i> L. Stokes	nature/m	Boendlerried, Wetzikon, Switzerl.	q	[0° ... +30°]	foliage
<i>S. fragilis</i> L.	frag 1/m	Wattwil, Switzerland	5	-4 (± 5°)	scale
<i>S. alba</i> × <i>fragilis</i>	alba × frag 1/m	Schwerzenbach, Switzerland	q	[-15° ... +15°]	intermed.
Sect. <i>Longifoliae</i> ¹					
<i>S. exigua</i> Nutt. ¹	nature/f	Boise, Idaho, USA	q	[+85° ... +95°]	foliage
<i>S. exigua</i> Nutt. ¹	nature/m	Boise, Idaho, USA	q	[+85° ... +95°]	foliage
<i>S. interior</i> Mühlb. ¹	inte 1/f	Moreau river, S-Dakota, USA	q	[+82° ... +95°]	foliage
Sect. <i>Magnifica</i> ²					
<i>S. magnifica</i> Hemsl. ²	magn 1/m	nursery, Setchuan, China	q	[-10° ... +10°]	scale
<i>S. moupinensis</i> Franch. ²	moup 1/f	nursery, W-Setchuan, China	12	-5° (± 16°)	foliage
Subgenus <i>Chamaetia</i>					
Sect. <i>Myrtilloides</i>					
<i>S. myrtilloides</i> L.	myrt 2/m	Gamperfin, Toggenburg, Switzerland	6	+52° (± 7°)	foliage
Sect. <i>Glaucae</i>					
<i>S. glaucosericea</i> Floderus	gls 1/m	Fluelapass, Engadin, Switzerl.	11	+2° (± 15°)	foliage
Sect. <i>Myrtosalix</i>					
<i>S. breviserrata</i> Floderus	brev 1/m	San Bernardino Pass, Switzerl.	q	[+65° ... +95°]	foliage
Sect. <i>Lindleyanae</i> ²					
<i>S. serpyllum</i> Anderss. ²	serp 1/?	Nepal, Langtang-Himalaya	5	+18° (± 13°)	scale
Subgenus <i>Vetrix</i>					
Sect. <i>Hastatae</i> (<i>Cordatae</i>)					
<i>S. hastata</i> L.	hast 5/f	Kronberg, Appenzell, Switzerl.	11	+52° (± 27°)	foliage
<i>S. hastata</i> L.	hast 4/f	Gletschboden, Wallis, Switzerl.	q	[+70° ... +95°]	foliage
<i>S. americana</i> hort. ^{1, 5}	cord 1/m	Schwerzenbach, Switzerland	11	+66° (± 11°)	foliage

Tab. 1. (continued).

Plant identification			Results		
Subgenus/Section/Species	Abrev. of individuals studied/sex	Original (natural) place of growth	Number of shoots examined	Position of leaf (1) $\bar{a}_1 (\pm s')$	Morphology of leaf (1)
Sect. <i>Breweriana</i>¹					
<i>S. lasiolepis</i> Benth. ¹	lasi 1/?	Lake Cachuma, Calif. U.S.A.	12	+9° (±19°)	foliage
<i>S. irrorata</i> Andersson ¹	irro 1/m	SW-USA	7	+44° (±7°)	foliage
Sect. <i>Glabrella</i>					
<i>S. crataegifolia</i> Bertoloni	crat 2/m	Orto di Donna, Apuan. Alps, Italy	9	+5° (±17°)	foliage
<i>S. crataegifolia</i> Bertoloni	crat 1/f	Orto di Donna, Apuan. Alps, Italy	q	[-15° ... +15°]	foliage
<i>S. glabra</i> Scop.	glab 1/f	Val Colla, Ticino, Switzerland	q	[+20° ... +65°]	foliage
<i>S. glabra</i> Scop.	glab 3/?	Val Colla, Ticino, Switzerland	10	+25° (±15°)	foliage
<i>S. reinii</i> Fr. et Sav.	rein 1/f	Honshu (N-Hondo), Japan	13	+13° (±10°)	foliage
Sect. <i>Nigricantes</i>					
<i>S. nigricans</i> Smith	nigr 2/f	St. Antönien, Prättigau, Switzerl.	9	+46° (±12°)	foliage
<i>S. nigricans</i> Smith	nigr 1/m	Scheftenu, Wattwil, Switzerl.	10	+42° (±9°)	foliage
<i>S. mielichhoferi</i> Sauter	miel 2/f	Tauern, Steiermark, Austria	13	+54° (±11°)	foliage
<i>S. cantabrica</i> Rech. ²	cant 1/f	Sia-Pass, Kantabria, Spain	20	+33° (±12°)	foliage
Sect. <i>Vetrix</i>					
<i>S. laggeri</i> Wimm.	lagg 4/?	Juifenau, Tirol, Austria	12	+36° (±14°)	foliage
<i>S. appendiculata</i> Vill.	appe 2/f	Wattwil, Switzerland	10	+13° (±21°)	foliage
<i>S. caprea</i> L.	capr 1/f	Wetzikon, Switzerland	7	+5° (±20°)	foliage
<i>S. caprea</i> × <i>viminalis</i> ³	capr × vimi 1/m	Niederuster, Switzerland	15	+42° (±20°)	foliage
<i>S. cinerea</i> L.	cine 1/m	Wetzikon, Switzerland	14	+43° (±9°)	foliage
<i>S. atrocinerea</i> Brotero	atro 1/m	Rohrspitz, Bodensee, Switzerl.	q	[+45° ... +85°]	foliage
<i>S. aurita</i> L.	auri 1/f	Neuenalp, Kau, Appenz., Switzerland	17	+57° (±13°)	foliage
<i>S. starkeana</i> Willd.	star 1/f	Irrendorfer Hardt, S.-Germany	10	+42° (±16°)	foliage
<i>S. wallichiana</i> Andersson ²	wall 1/m	Langtang, Nepal	q	not recorded	scale
Sect. <i>Arbuscella</i>					
<i>S. phyllicifolia</i> L.	phyl 1/m	Oppdal, Lake Gjevil, Norway	q	[+17° ... +65°]	foliage
<i>S. phyllicifolia</i> L.	phyl 3/f	Longmuir Moss, Scotland	19	+63° (±9°)	foliage
<i>S. hibernica</i> Rech. fil.	hibe 1/f	Benbulben, Ireland	q	[+65° ... +95°]	foliage
<i>S. hegetschweileri</i> Heer	hege 3/f	Urserental, Switzerland	22	+49° (±4°)	foliage
<i>S. hegetschweileri</i> Heer	hege 6/f	Paznaunertal, Tirol, Austria	35	+44° (±10°)	foliage
<i>S. hegetschweileri</i> Heer	hege 5/m	Paznaunertal, Tirol, Austria	16	+51° (±12°)	foliage
<i>S. hegetschweileri</i> Heer	hege 8/f	Urserental, Switzerland	20	+42° (±9°)	foliage
<i>S. hegetschweileri</i> Heer	hege 9/f	Urserental, Switzerland	q	[+50° ... +90°]	foliage
<i>S. bicolor</i> Willdenow	bico 2/f	Brocken, Harz, Germany	q	[+35° ... +70°]	foliage
<i>S. bicolor</i> Willdenow	bico 1/f	Puy de Sancy, Mass. Centr. France	q	[+38° ... +76°]	foliage
<i>S. foetida</i> Schleich.	foet 2/f	Silsersee, Engadin, Switzerland	6	+46° (±9°)	foliage
<i>S. waldsteiniana</i> Willd.	wald 2/f	Kronberg, Appenzell, Switzerl.	q	[+60° ... +95°]	foliage
<i>S. waldsteiniana</i> Willd.	wald 1/m	Kronberg, Appenzell, Switzerl.	11	+27° (±18°)	foliage
Sect. <i>Vimen</i>					
<i>S. viminalis</i> L.	vimi 1/m	Mosnang, Toggenburg, Switzerl.	18	+87° (±6°)	foliage
<i>S. viminalis</i> L.	vimi 2/f	Wattwil, Toggenburg, Switzerl.	q	[+80° ... +100°]	foliage
<i>S. dasyclados</i> Wimm.	dasy 5/f	Hamburg, Germany	17	+36° (±24°)	foliage
<i>S. dasyclados</i> Wimm.	dasy 3/f	Hamburg, Germany	q	[+25° ... +80°]	foliage
<i>S. sachalinensis</i> F. Schmidt ²	sach 3/f	Hokkaido, Japan	14	+77° (±8°)	foliage
<i>S. sachalinensis</i> F. Schmidt ²	sach 2/m	Honshu (N-Hondo), Japan	15	+47° (±14°)	foliage
<i>S. sachalinensis</i> F. Schmidt „Sekka“ ²	sach 1/m	nursery, orig. Asia	q	[+70° ... +90°]	foliage
Sect. <i>Subviminale</i>					
<i>S. gracilistyla</i> Miq.	crac 1/m	nursery, orig. Asia	16	+56° (±6°)	foliage
<i>S. obscura</i> Anderss. ²	obsc 1/f	Langtang, Nepal-Himalaya, Asia	7	+13° (±34°)	foliage

Tab. 1. (continued).

Plant identification			Results		
Subgenus/Section/Species	Abrev. of individuals studied/sex	Original (natural) place of growth	Number of shoots examined	Position of leaf (1) $\bar{a}_1 (\pm s')$	Morphology of leaf (1)
Sect. <i>Canae</i>					
<i>S. elaeagnos</i> Scop.	elae 2/f	Wattwil, Toggenburg, Switzerl.	6	$-7^\circ (\pm 14^\circ)$	foliage
<i>S. elaeagnos</i> Scop.	elae 1/m	Wattwil, Toggenburg, Switzerl.	q	$[-15^\circ \dots +15^\circ]$	foliage
<i>S. elaeagnos</i> Scop. ssp. <i>angustifolia</i>	elae 3/m	nursery	q	$[-10^\circ \dots +10^\circ]$	foliage
Sect. <i>Villosae</i>					
<i>S. helvetica</i> Vill.	helv 2/?	Fluelapass, Engadin, Switzerland	q	approx. $+90^\circ$	foliage
Sect. <i>Daphnella</i>					
<i>S. daphnoides</i> Vill.	nature/m	Schwerzenbach, Switzerland	q	$[+70^\circ \dots +95^\circ]$	foliage
Sect. <i>Incubaceae</i>					
<i>S. repens</i> L.	repe 5/f	Schwantenau, Kt. Schwyz, Switzerland	q	$[+70^\circ \dots +100^\circ]$	foliage
Sect. <i>Helix</i>					
<i>S. caesia</i> Vill.	caes 1/f	not known	26	$+91^\circ (\pm 27^\circ)$	foliage
<i>S. purpurea</i> L. spp.					
<i>lambertiana</i> ⁶	purp 1/f	Volketswil, Kt. Zürich, Switzerl.	10	$+87^\circ (\pm 5^\circ)$	foliage
<i>S. × peloritana</i> Presl ⁴	pelo 1/m	Monti Peloritani, Sizily, Italy	11	$+61^\circ (\pm 6^\circ)$	foliage
<i>S. integra</i> Thunb. ⁶	integ 1/f	Honshu (N-Hondo), Japan	10	$+90^\circ (\pm 6^\circ)$	foliage

m/f: male/female

q: qualitative examination; data not fully recorded

foliage: foliage leaf (Fig. 9c)

scale: scale-like leaf (see results, morphology of leaf (1), Fig. 9a)

intermed.: intermediate form between a scale-like leaf and a foliage leaf (see results, morphology of leaf (1), Fig. 9b)

¹: taxonomy according to Dorn, 1976²: taxonomy according to G. Argus, pers. communication³: intersectional hybrid (Sec. *Vetrix* × Sec. *Vimen*)⁴: *S. pedicellata* × *S. purpurea* (?), (Neumann, 1981)⁵: syn. *S. cordata* Mühlb. (Neumann, 1981)⁶: these species retain the opposite decussate phyllotaxis to the end of the shoot.

scales were all more or less cutinized and did not grow after the elongation of the shoot. However, the outer scales of summer buds of *S. humboldtiana* showed a light yellow-green colour and grew to about three times their former length after sprouting of the shoot (as an exception included in the observations, not shown in Tab. 1). Chmelař and Neumann (1976) reported a similar pattern for winter buds of the creeping high-elevation species *S. reticulata* L., *S. herbacea* L., and *S. retusa* L.

Morphology of leaf (1)

In most species, leaf (1) is yellowish-green to green in colour and may therefore be regarded as the first foliage leaf. However, in some species with leaf (1) close to 0° , this leaf shows distinctly different characters:

- The broadest part is at the base or close to it; it surrounds the shoot with an insertion angle of 180° or more.
- The venation consists of three or more parallel veins which branch irregularly.

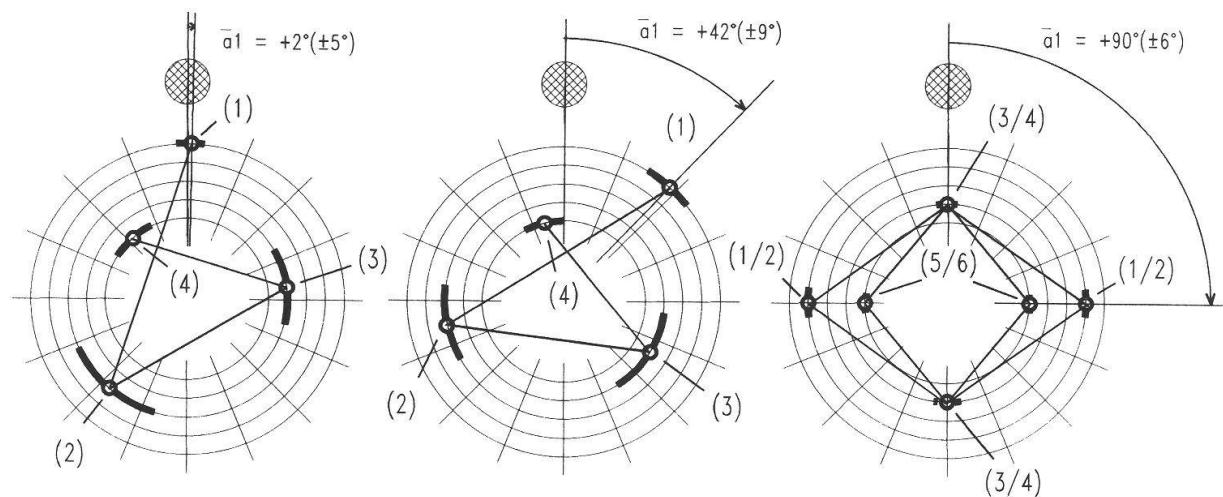


Fig. 3a. *S. acmophylla* (acmo 1) Fig. 3b *S. hegetschweileri* (hege 8) Fig. 3c *S. integra* (integ 1)
 Examples of phyllotactic patterns. The diagrams show the positions (circular mean angle and circular standard deviation) of leaves (1), (2), (3) etc. over the samples from one plant. The plant number (e.g. acmo 1) indicates the plant individual. The outer bud scale (tubular) is not shown in the diagrams.

Subgenus Section

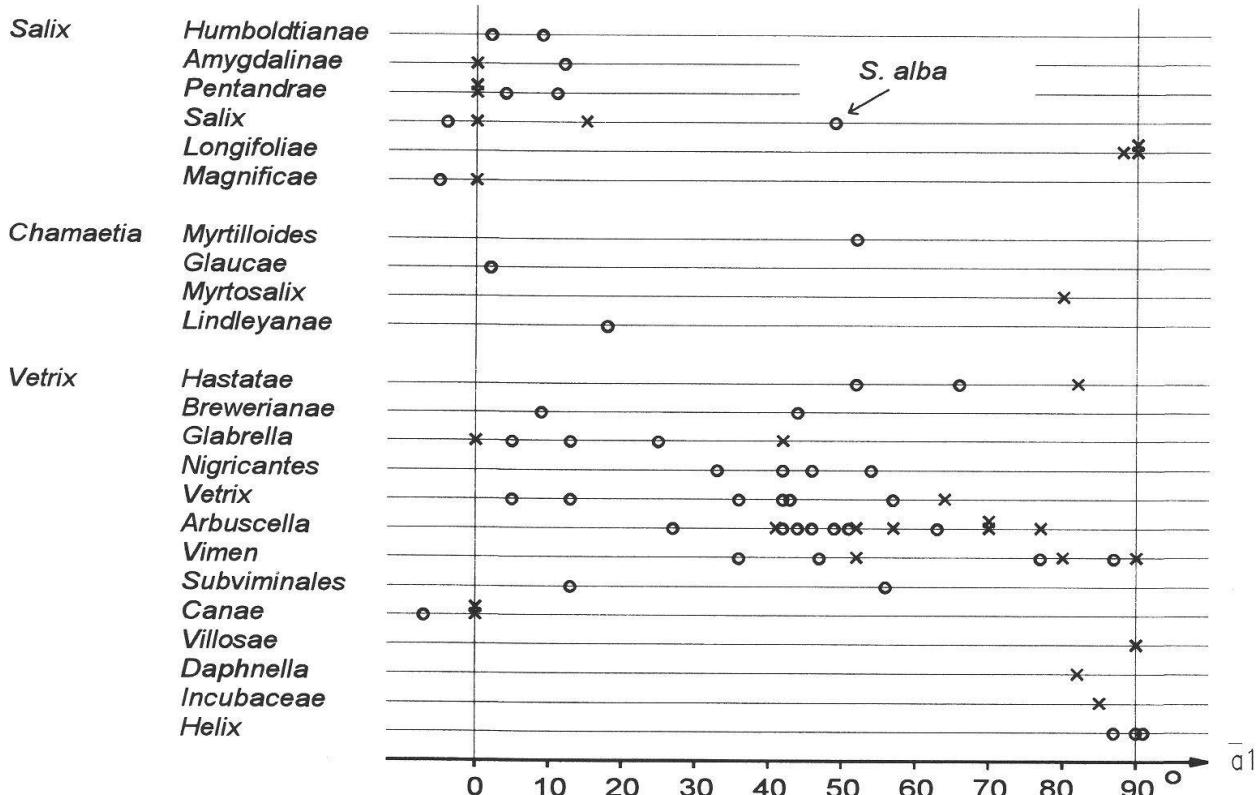


Fig. 4. Summary of Table 1: Distribution of angular positions of leaf (1) ($=\bar{a}_1$) in axillary buds of subgenera and sections of *Salix*. Each symbol equals one plant. Hybrids between sections have been omitted in the diagram. \times qualitative result (mean between range limits); \circ mean value.

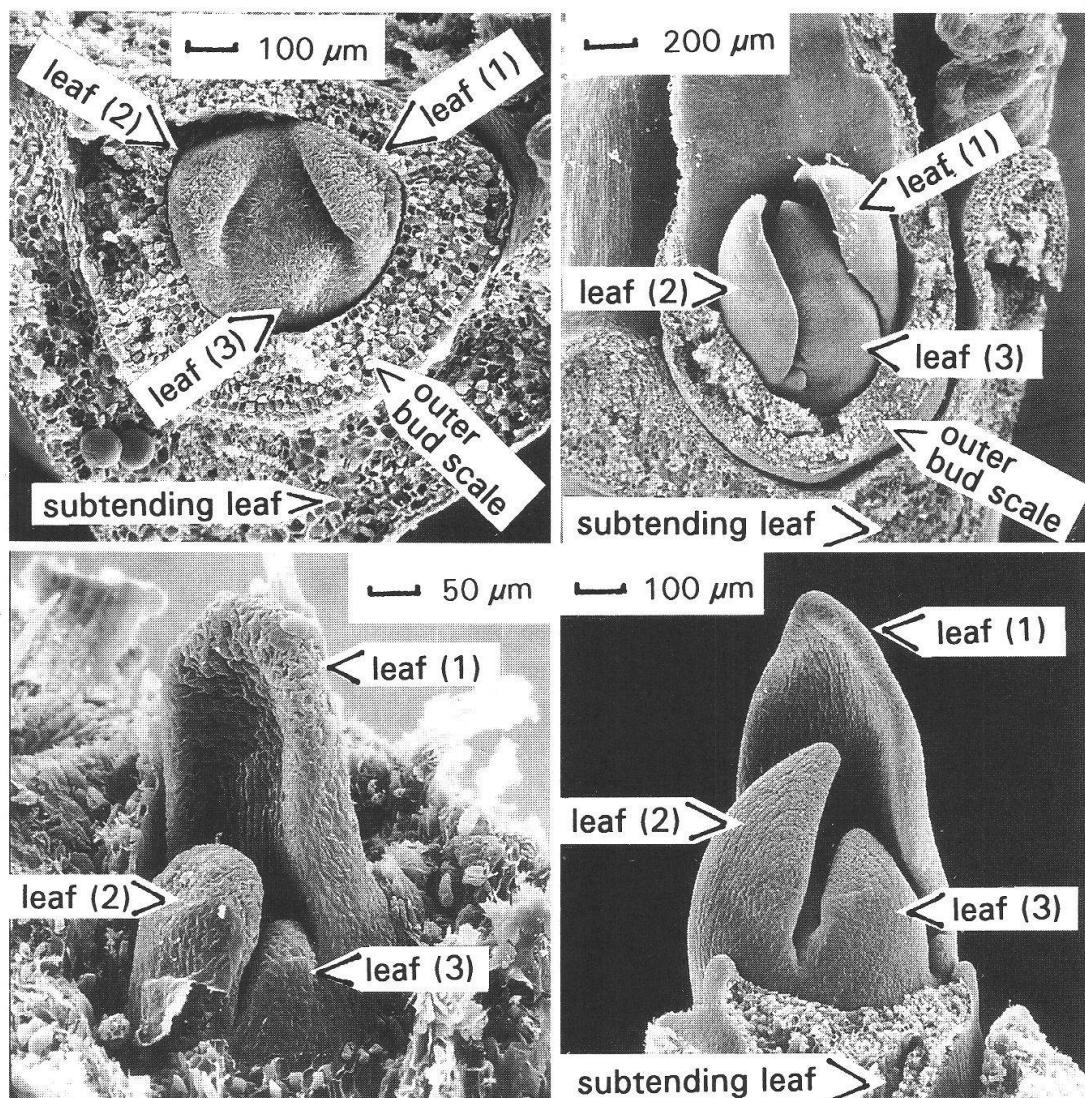


Fig. 5 (upper left) Leaf primordia in axillary bud of *S. hegetschweileri* (hege 3, May 1, 1994), CW.
 Fig. 6 (upper right) Slightly later stage of bud development than in Fig. 5 (hege 3, CW).

Fig. 7 (lower left) Leaf primordia in axillary bud of *S. elaeagnos* (elae 2, May 1, 1994). Leaf (1) in adaxial position, i.e. with \bar{a}_1 close to 0° (see Table 1). Subtending leaf and outer bud scale removed.

Fig. 8 (lower right) Another axillary bud of *S. elaeagnos* (elae 2, May 1, 1994). Slightly later stage than in Fig. 7.

- The leaf is cutinized and its colour is yellowish-brown to brown.
- The leaf (or its scar) remains at the base during elongation of the shoot.
- The leaf dries out and abscises soon after sprouting of the shoot.

Leaves of this type have been found in *S. acmophylla*, *S. fragilis* (Fig. 9a), *S. pentandra*, *S. serpyllum*, *S. magnifica* and *S. wallichiana* (Tab. 1). Intermediate forms between the type described above and a typical first foliage leaf differ in the following characters:

- The base is distinctly narrower than the broadest part (no petiole).
- The venation consists of a main vein and two or more smaller parallel veins. The main vein branches almost like a typical first foliage leaf.
- The colour is greenish-brown to yellowish-brown, depending on its developmental stage.

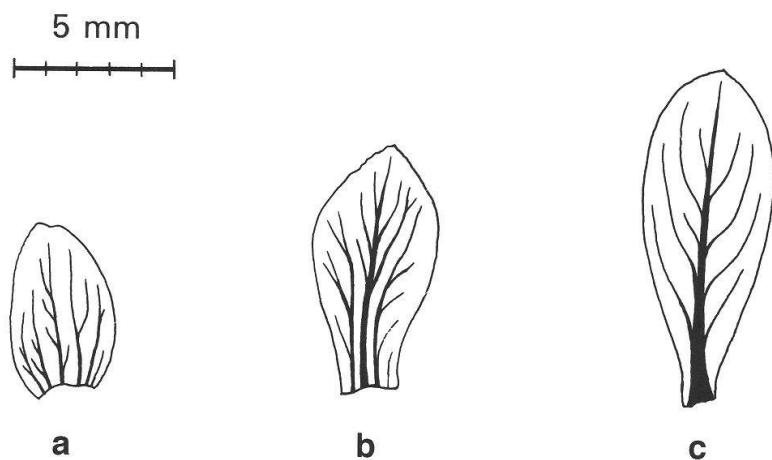


Fig. 9. Morphology of first leaf (1) inside tubular outer bud scale of *Salix* ssp.:
a: *S. fragilis*, inner bud scale = scale-like leaf (1).

b: *S. alba* \times *fragilis*, intermediate form between bud scale and foliage leaf.

c: *S. alba*, leaf (I) resembling foliage leaf.

Leaves of this type have been found in *S. lucida* ($\bar{\alpha}_1 \approx 0^\circ$), *S. alba* \times *fragilis* ($\bar{\alpha}_1 \approx 0^\circ$, Fig. 9 b), *S. alba* "Chermesina" ($\bar{\alpha}_1 \approx 0^\circ$), *S. alba* var. *vitellina* ($\bar{\alpha}_1 \approx +15^\circ$) and *S. alba* \times *pentandra* (examined on herbarium specimens, not included in Tab. 1). In *S. alba* sensu stricto ($\bar{\alpha}_1 = +49^\circ$) leaf (1) resembles the distal foliage leaves in venation type, colour and shape (Fig. 9 c).

In the angular range near 0° the transition from the intermediate form to the foliage leaf is gradual. The foliage-like leaves have a distinct petiole, but the lowest secondary vein on each side may run separately through the petiole instead of joining the midvein.

Sense of rotation: homodromy versus antidromy

All data concerning the relationship between m-shoot SOR and d-shoot SOR were sorted into groups for plants with similar positions of leaf (1). The H_0 hypothesis that CW and CCW rotating d-shoots occur independently of m-shoot SOR was then tested using chi-squared test (Tab. 2).

Tab. 2. Number of homodromous and antidromous shoots depending on the angular position of leaf (1); all data from Tab. 1 included.

Angular range of leaf (1) = $\bar{\alpha}_1$	d-shoot SOR homodromous to m-shoot SOR	d-shoot SOR antidromous to m-shoot SOR	chi-squared	P
$-7^\circ \dots +15^\circ$	302	273	1.5	$0.10 < P < 0.25$
$+15^\circ \dots +35^\circ$	49	42	0.5	$0.25 < P < 0.50$
$+35^\circ \dots +55^\circ$	301	199	20.8	$P < 0.001$
$+55^\circ \dots +75^\circ$	96	60	8.3	$0.001 < P < 0.005$
$+75^\circ \dots +95^\circ$	114	101	0.8	$0.25 < P < 0.50$
all plants	862	675	20.5	$P < 0.001$

Tab. 3. Numbers of homodromous and antidromous shoots summarized over 4 plants of *S. hegetschweileri*.

Species	d-shoot SOR homodromous to m-shoot SOR	d-shoot SOR antidromous to m-shoot SOR	chi-squared	P
<i>S. hegetschweileri</i>	65	29	13.8	$P < 0.001$

Homodromy occurs with a significantly higher frequency than 50% in the angular range of $+35^\circ \dots +75^\circ$. The chi-squared test was also performed for each plant. The highest degree of homodromy within a species was found for *S. hegetschweileri* which has its first leaf in the range of $+42^\circ \dots +51^\circ$ (Tab. 3).

Mother shoots of *S. hegetschweileri* and *S. elaeagnos* were collected on May 1, 1994, when the buds were formed in the axils of subtending leaves. The proximal leaf primordia were examined with a Scanning Electron Microscope. Figure 5 shows early stages of leaves (1), (2) and (3) in *S. hegetschweileri* (hege 3, the plant with the highest degree of homodromy, $\bar{a}_1 = +49^\circ$). Leaves from the same plant at a later stage remain similar in the proportion of their sizes (Fig. 6). In *S. elaeagnos* (elae 2, the plant with the lowest degree of homodromy, $\bar{a}_1 = -7^\circ$), the three leaves differ much more in their developmental stage (Figs. 7 and 8).

Discussion

Analysis of data significance

Because the majority of the plants used in this study were cultivated in an arboretum, it is not known to what extent the present data correspond to plants growing in their natural habitats. It was possible to compare wild growing individuals of *S. caprea*, *S. purpurea*, *S. nigricans* and *S. exigua*, at least qualitatively, to plants from the arboretum. No significant difference was observed. Plants of 10 more species were compared to plants growing in the arboretum of H. Oberli in Wattwil, Switzerland (altitude 670 m). Here too, no significant differences were found.

A change of phyllotactic pattern may be expected when the growth rate of a plant is strongly affected by an environmental factor. When a thick branch of a mature *S. integra* broke off, the replacing lateral shoot showed a spiral phyllotaxis instead of an opposite decussate one. Mechanically disturbed plants, as well as plants which obviously grow under unfavourable conditions, should therefore not be used for phyllotactic observations. Even under this precaution, variability of $\pm 10^\circ \dots \pm 20^\circ$ may be found for \bar{a}_1 within a species due to environmental and genetic influences.

Comparing \bar{a}_1 data between plants of the same species gives an estimate about how relevant the angular position of the first leaf is as a taxonomic character. For 16 species, data from two or more plants are available (Tab. 1). For 11 of these species the mean difference between all \bar{a}_1 values is smaller than the mean of all standard deviations. In *S. hegetschweileri*, where five plants were examined, the \bar{a}_1 of four plants lay between $+42^\circ \dots +51^\circ$. In five species the mean difference between \bar{a}_1 values is higher than the mean of the standard deviations (Tab. 1, *S. hastata*, *S. glabra*, *S. phylicifolia*, *S. wald-*

steiniana and *S. sachalinensis*). In *S. hastata*, *S. phylicifolia* and *S. waldsteiniana* other characters are also known to be especially variable.

Possible systematic implications

There is a general correlation between the phyllotaxis of proximal leaves and Skvortsov's (1968) taxonomic classification (Tab. 1 and Fig. 4). Looking at the range of the angular position of leaf (1), the lower end ($\bar{\alpha}_1 \approx 0^\circ$) is mainly occupied by some sections of the subgenus *Salix*, that is regarded as the most primitive subgenus by Skvortsov (1968). In its sections *Humboldtiae*, *Pentandrae* and *Salix* most of the species with a scale-like leaf in position (1) are found. This feature, together with its angular position near 0° (at 90° from the two fused outer prophylls), likely provides effective bud protection. In this respect this group of species within subgenus *Salix* is more similar to the poplars than the other subgenera and sections (Skvortsov, 1968, p. 162, Furuya, 1953, Pizzolato and Larson, 1977, Fig. 1A). The main functions of bud scales are protection against desiccation, insect larvae attacking from the adaxial side and possibly fungi. Considering that bud scales can not effectively protect against cold, it is not surprising to see the described features also in *Salix* species growing in tropical and subtropical climates.

The section *Longifoliae*, another group in the subgenus *Salix*, is found at the other end of the range ($\bar{\alpha}_1 \approx +90^\circ$). Its representatives have retained the primitive flower structure, a hypodermis below the upper as well as the lower leaf epidermis, and the capability for the formation of root suckers, characteristics shared with *Populus* (Skvortsov, 1968, p. 162). *Salix exigua* and *S. interior* (both species show an opposite decussate phyllotaxis in the proximal range) seem to be misplaced in the subgenus *Salix*. Schneider (1919), Skvortsov (1968) and Dorn (1976) regarded the section *Longifoliae* as morphologically extremely isolated from all other sections of the genus. The proximal phyllotactic patterns therefore confirm this interpretation.

All species with $\bar{\alpha}_1 \approx 90^\circ$ (Fig. 4 and Table 1) show an opposite decussate phyllotaxis at least within the first four leaves: all species studied of sect. *Longifoliae*, 3 species studied of sect. *Helix*, *S. viminalis* and *S. helvetica*.

Salicx alba (sect. *Salix*) differs in the position of its leaf (1) ($\bar{\alpha}_1 = +49^\circ$) from the other studied members of the subgenus *Salix*. This is unexpected at least with regards to *S. fragilis* and *S. pentandra* (see Table 1). The three species are all tetraploid and hybridize easily. The hybrids are often fertile. Some cultivars of *S. alba* (*S. alba* "Chermesina" and *S. alba* var. *vitellina*, $\bar{\alpha}_1 \approx 0^\circ \dots +15^\circ$) have a different pattern than the main form ($\bar{\alpha}_1 = +49^\circ$). Although this could be explained by a gene introgression from *S. fragilis* ($\bar{\alpha}_1 = -4^\circ$) (which is also suggested by other affinities with this species), more individuals of *S. alba* sensu stricto should be examined to understand the whole plasticity within the species. Kimura and Sugaya (1965) show a transection through an axillary bud in the winter stage of *S. alba* in which the first leaf is placed at an angle of about 75° . Although this angle may not directly be compared to the leaf angle after sprouting, it confirms that in *S. alba* the first leaf is not near 0° .

The middle range of $\bar{\alpha}_1$ ($10^\circ - 80^\circ$) is dominated by species of the large subgenus *Vetrix* that is regarded as phylogenetically young by Skvortsov (1968). These species have the highest degree of homodromy of all *Salix* species studied.

In the subgenus *Vetrix*, *S. elaeagnos* (monotypic member of section *Canae*, $\bar{\alpha}_1 \approx 0^\circ$) and *S. caesia*, *S. purpurea* and *S. integra* of section *Helix* ($\bar{\alpha}_1 \approx +90^\circ$) take extreme positions. Here again the phyllotactic patterns may reflect the relatively isolated taxonomic position of these groups (e.g. Skvortsov, 1968).

Salix crataegifolia of section *Glabrella* (subgen. *Vetrix*) is a morphologically striking species. Its phyllotactic pattern fits as well into the section *Magnifica* as into *Glabrella* (Tab. 1 and Fig. 4). Although being endemic to a very small area in the Apuane Apennines, it has close affinities in leaf and floral characters to *S. ernestii* Schneid., *S. fragesii* Burkitt (both subgen. *Vetrix*, sect. *Psilotigmatae*) and *S. moupinensis* (subgenus *Salix* sect. *Magnifica*) (Skvortsov, 1968, and Chmelař, 1981) from South-Western China. Chmelař (1981) therefore regarded *S. crataegifolia* as a tertiary relict.

Hybrids between species with different angles \bar{a}_1 show intermediate patterns. For example, *S. caprea* \times *viminalis* ($\bar{a}_1 = +42^\circ$) is between *S. caprea* ($\bar{a}_1 = +5^\circ$) and *S. viminalis* ($\bar{a}_1 = +87^\circ$).

Morphology of leaf (1)

It has already been suggested that species with inner bud scales, i.e. leaf (1) being scale-like instead of a foliage leaf, are more frequent in the probably phylogenetically old subgenus *Salix*, especially sections like *Humboldtiae*, *Pentandrae*, *Salix* and *Magnifica* (Skvortsov, 1968). Inner bud scales were also observed in this study in *S. wallichiana* (subgenus *Vetrix*) and *S. serpyllum* (subgenus *Chamaetia*). The few species with scale-like leaf (1)=inner bud scale (Tab. 1) are scattered over the whole world and include high growing trees like *S. fragilis* as well as prostrate high mountain species like *S. serpyllum*. This suggests that an inner bud scale is either a convergent feature or a primitive character pointing to an ancestry with the genus *Populus*. The second hypothesis was already proposed by Skvortsov (1968, p. 143) who stated that wide lower cataphylls with parallel venation seem to be more primitive than narrow lower cataphylls with a venation like the leaves.

Salix alba and *S. fragilis* differ not only in the angle of the first leaf, but also in its morphology. In *S. alba*, leaf (1) is resembling a foliage leaf while in *S. fragilis* it has the pattern of a typical inner bud scale. The hybrid between the two species shows the intermediate form (Fig. 9a–c). Lautenschlager (1993, and personal communication) found this character more convenient to distinguish between the hybrid and its parent species than classical characters like the indumentum of the leaves.

All scale-like leaves (1)=inner bud scales, or the intermediate form, are positioned at angles \bar{a}_1 close to 0° (the largest deviation was observed in *S. serpyllum* with $\bar{a}_1 = 18^\circ$). There is a weak correlation between the scale-like morphology of leaf (1) and the position of the leaf at $\bar{a}_1 \approx 0^\circ$.

Sense of rotation: homodromy versus antidromy

Species with $\bar{a}_1 = +35^\circ \dots +75^\circ$ preferentially show homodromy, i.e., they produce the same SOR as the m-shoot on which they grow (Tab. 2). This raises the question, by which mechanism m-shoot SOR information may be transferred into the d-shoot. Furuya (1953) noticed a correlation between an asymmetrical position of the subtending leaf scar (relative to the median plane) and the SOR of the d-shoot in some dicotyledons. Although no distinct asymmetries of any kind have been noticed in the present study, the idea of a mechanical determinant seems reasonable. A slight geometrical asymmetry of the subtending leaf base (caused by m-shoot SOR) might offer a preferred (asymmetrically situated) space in one of the two adaxial corners of the triangular space between the subtending leaf and the m-shoot axis (Fig. 5). Quickly after leaf (1) is initiated, leaf (2) arises at the remotest place from leaf (1) which is in the second adaxial corner. At this time the d-shoot SOR is set. Species with \bar{a}_1 closer to 0° have no preference for homo-

dromy (or nearly so) as compared to those with \bar{a}_1 in the middle range. This seems to be correlated with a more pronounced developmental difference between the leaves (1) and (2) when \bar{a}_1 is close to 0° (Figs. 7–8).

Homodromy may be an indirect result of an adaptation to a shorter vegetation time. Especially for high mountain and northern species with relatively short shoots, it may be advantageous that already the first leaves are arranged in a Fibonacci pattern and that a succession of leaves is ready for rapid sprouting in spring. Both features are best accomplished by the triangular arrangement described above and by short plastochrons.

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