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Source: Willdenowia, 49(1) : 43-52

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: https://doi.org/10.3372/wi.49.49106

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Willdenowia
Annals of the Botanic Garden and Botanical Museum Berlin

DETLEV DRENCKHAHN[1]

Panicle shoot, an overlooked stem type of several blackberries (*Rubus*, *Rosaceae*)

Version of record first published online on 29 March 2019 ahead of inclusion in April 2019 issue.

Abstract: Blackberries (*Rubus* subg. *Rubus*, *Rosaceae*) are perennial plants that form thickets of biennial spiny stems (canes), which grow in length in the first year and develop flowering laterals in the second year. In the present study, a hitherto overlooked separate type of stem is described, denoted as panicle shoot (PS, turio paniculatus) that occurs in several species of all three European blackberry sections. PSs are up to 2.5 m long, spring directly from the rootstock, terminate apically in a mostly large paniculate inflorescence (simple type) and may develop additional flowering branches (complex type). PSs can emerge from young (two-year old) and older rootstocks established sexually from seeds and vegetatively from tip-rooted canes, respectively. As a rule, they are biennially flowering shoots that develop flowering laterals in the second season. By virtue of their length, PSs tend to project with their panicles out of the surface of bushes and hence overcome the frequent fate of flowering laterals of low arching canes to become rapidly overgrown and overshadowed by surrounding vegetation.

Key words: anatomy, blackberry, flowering shoot, *Rosaceae*, *Rubus*, taxonomy

Article history: Received 13 September 2018; peer-review completed 18 January 2019; received in revised form 5 February 2019; accepted for publication 5 February 2019.

Citation: Drenckhahn D. 2019: Panicle shoot, an overlooked stem type of several blackberries (*Rubus*, *Rosaceae*). – Willdenowia 49: 43–52. doi: https://doi.org/10.3372/wi.49.49106

Introduction

Blackberries (*Rubus* L. subg. *Rubus*, *Rosaceae*), with European *R.* sect. *Rubus*, *R.* sect. *Corylifolii* Lindl. and *R.* sect. *Caesii* Lej. & Courtois, are semi-deciduous perennial plants that form thickets of long spiny stems (shoots, canes; for orientation see summarizing drawing Fig. 6A). Stems are woody with a biennial life cycle. Most species develop one type of stem, also termed cane. In their first year of growth, canes are commonly called primocanes (Bailey 1932). They grow throughout the summer to a final length of up to 10 m. Depending on the species, they may grow erect, arched, trailing or immediately prostrate. Primocanes are non-flowering stems supplied with alternating leaves. When the tips of primocanes contact the soil, they can develop nodal roots in the tip region (Fig. 1), which grow into the soil and pull the tip with its terminal bud underground (Rauh 1938; Weber 1995), a mechanism caused by swelling and shortening of proximal root portions (Wiesner 1883). Next spring, the apical hibernating bud continues growing to form the first primocane of the daughter plant, which is in a strict sense a continuation of the last-year primocane (Fig. 1). Tip rooting depends on the gene *Tr*, which also confers the ability to form roots from nodes (Jennings 1988). Primocanes may give off non-flowering branches during the first summer that may undergo tip rooting too. Leaves fall off in spring (*R.* subsect. *Hiemales* E. H. L. Krause) or in autumn (all other

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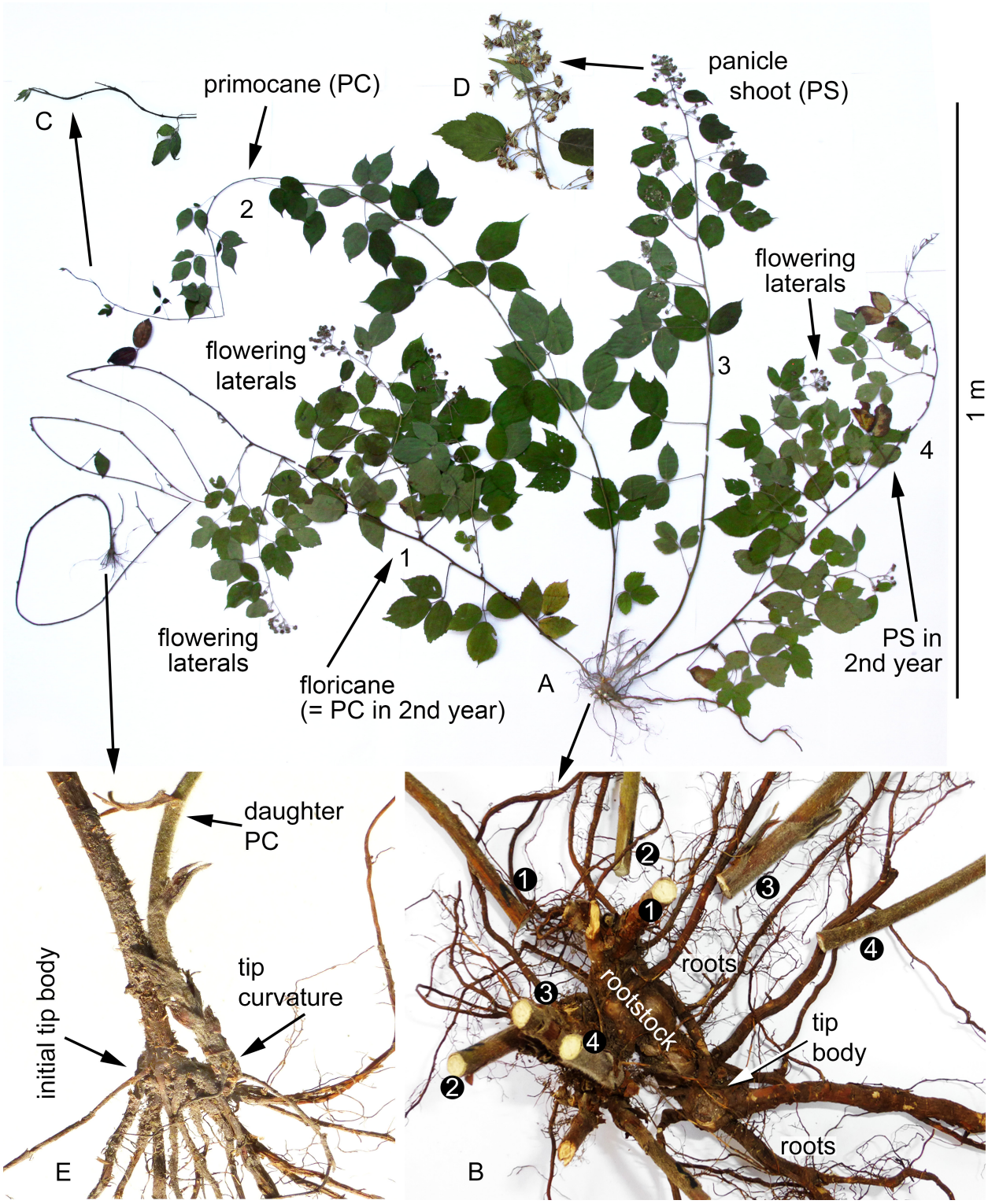

Fig. 1. *Rubus pedemontanus* – A: whole bush; B: detail of root system; numbering of stems in first and second year (in A) corresponds to numbering of their stumps at rootstock; C: detail of tip of primocane; D: tip of panicle shoot; E: detail of root system of young daughter plant resulting from tip-rooted primocane. – Herbarium specimen: Germany, Rheinland-Pfalz, NW of Wissembourg, 49.051156°N, 7.887293°E, 2 Jul 2017, *Drenckhahn 020717-5(1–12)* (B).

sections / subsections). Most erect-growing blackberries do not undergo tip rooting. Canes in their second year are termed floricanes (Bailey 1932). They lack leaves on the main stem and its last-year branches. Instead, flowering laterals are formed from the axillary buds of the stem including its (last-year) branches.

Occasionally, flowering laterals arise from hypogeal parts of the floricane base (Focke 1877; Beijerinck 1956;

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Fig. 2. *Rubus rhombicus* – A: panicle shoot with portion of rootstock (1) and stump of broken last-year panicle shoot (2); B: portion of primocane of same plant; C: portion of floricane of same plant. – Herbarium specimen: Germany, Bayern, Leinach, 49.866455°N, 9.817968°E, 23 Jun 2017, *Drenckhahn 230617-2(1–6)* (B).

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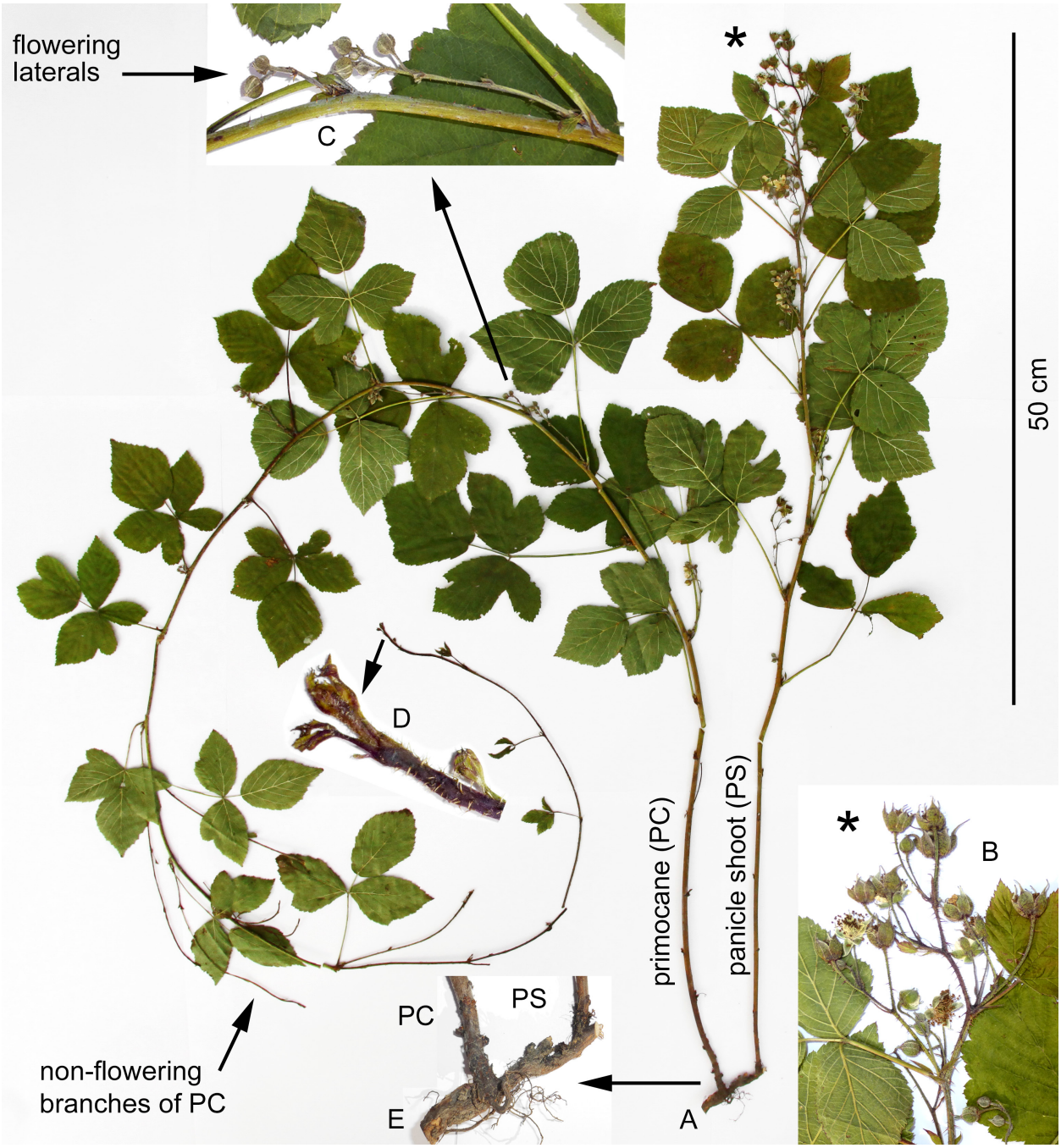

Fig. 3. *Rubus caesius* – A: simple type of panicle shoot and first-year flowering primocane growing from separate portions of rootstock; B: detail of tip of panicle shoot; C: detail of portion of primocane; D: detail of tip of primocane; E: rootstock. – Herbarium specimen: Germany, Schleswig-Holstein, Langholz, 54.518473°N, 9.990795°E, 17 Jul 2017, *Drenckhahn 170717-1(1–3)* (B).

see also Fig. 6). New primocanes develop from adventitious buds (replacement buds) at the basal hypogeal portion of last-year primocanes or directly from buds of the rootstock. Some erect-growing blackberries can propagate vegetatively by suckers arising from adventitious buds of the root (Weber 1995; Jennings 1988; Strik & Finn 2012). This mechanism of proliferation from roots is also typical of raspberries (*R.* subg. *Idaeobatus* Focke).

There are two exceptions from this general scheme of growth, i.e. (1) occasional formation of flowering laterals from primocanes, commonly seen in *Rubus caesius* L. and in some other European and American species (Fig. 3, 6B; Bailey 1932; Beijerinck 1956; Weber 1995) and (2) formation of non-flowering (vegetative) branches from floricanes emerging from the stem or even from flowering laterals (Fig. 6B) that eventually undergo successful tip rooting as mentioned first by Salter (1845) for *R. ulmifolius* Schott and confirmed and extended in this study for *R. geniculatus* Kaltenb., *R. ulmifolius* and *R. vestitus* Weihe.

In the present study, evidence is provided for a hitherto overlooked different type of flowering stem, for which

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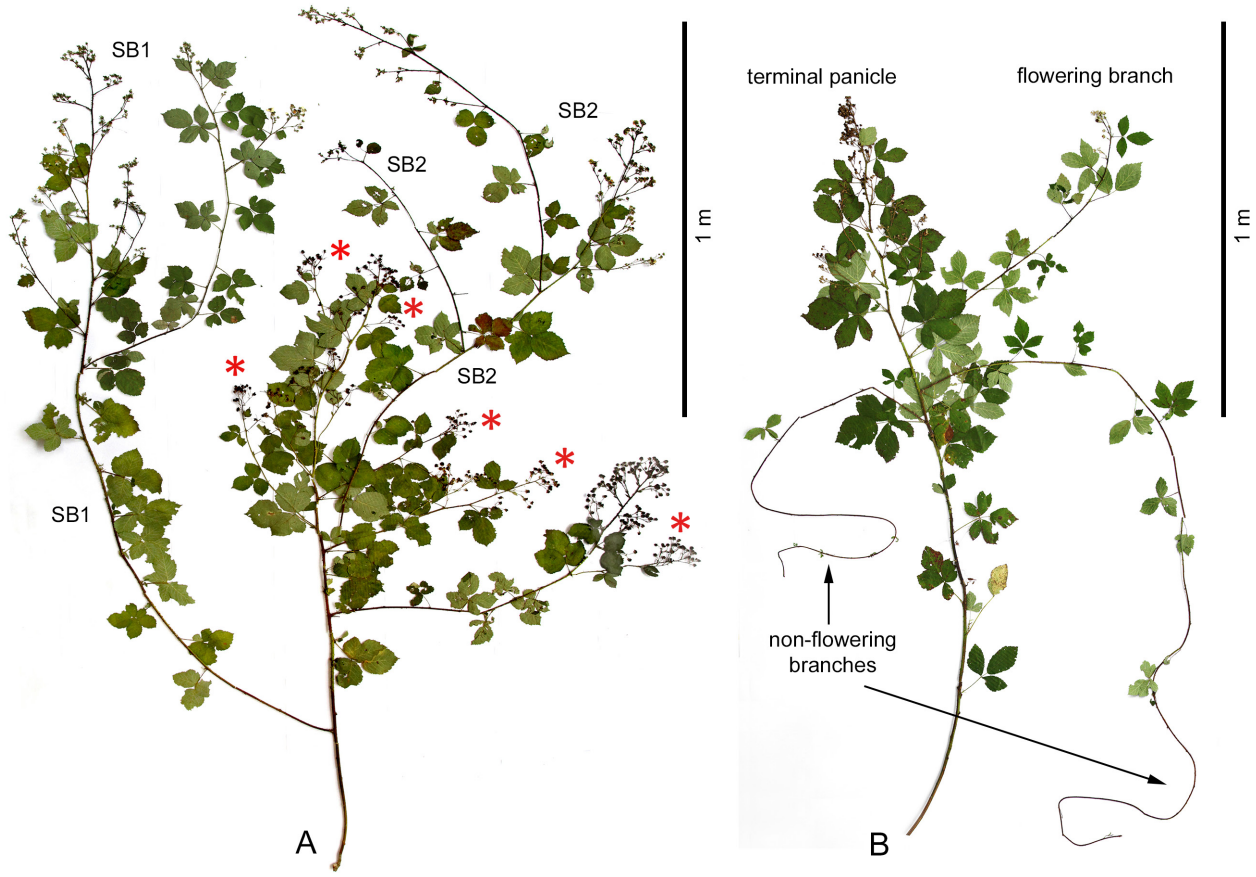

Fig. 4. Examples of complex types of panicle shoots. – A: *Rubus scabrosus*; asterisks (*) indicate axial portion with panicles that flowered end of June to mid-July and fruited in July–August; SB1 & SB2 indicate large side branches that began to grow in July and flowered end of August to mid-October. – Herbarium specimen: Germany, Bayern, Thüngersheim, 49.891730°N, 9.839030°E, 29 Aug 2017, *Drenckhahn 290817-1(1–11)* (B). – B: *Rubus rhombicus*; this panicle shoot developed additional non-flowering vegetative branches, one of which underwent tip rooting. – Herbarium specimen: Germany, Bayern, Retzstadt, 49.905289°N, 9.852753°E, 28 Sep 2017, *Drenckhahn 280917-1(1–7)* (B).

the name panicle shoot (PS) is proposed, in Latin turio paniculatus (from turio: shoot, sprout; and paniculatus: having a cluster of flowers).

Material and methods

Analysis of growth characteristics of blackberries required excavation of entire plants with their root system. Removed stems or excavated whole plants were spread on a plain background such as nearby roads, bed sheets or white wallpaper and were then analysed and photographed. A total of 52 excavated plants and 66 PSs cut from the rootstock were studied. Many PSs and some excavated entire plants including their root system were saved as herbarium specimens. For this purpose, stems, branches and inflorescences were cut in 20–40 cm long segments, which were numbered according to their position and origin in the root system, and were then pressed and dried as described by Weber (1977). For photographic documentation, pressed plant segments were assembled in a positional correct arrangement on a white background (e.g. chipboard covered with white paper). An example of a pressed whole plant of *Rubus pedemontanus* Pinkw. with its root system is shown in Fig. 1. Studies were also performed in the winter months, when leaf covering is absent or scarce and stems can be better traced down to the ground. Quantitative data are expressed as arithmetic mean ± standard error and, in brackets, range and number (*n*) of samples.

Results

Anatomy of PSs — PSs resemble superficially large flowering laterals of floricanes with a terminal panicle, which is continuous with the axis of the stem. But PSs spring directly from the rootstock and not from canes and are generally several fold longer with much larger inflorescences than flowering laterals of the same plant (Fig. 1, 2, 5A). The average length of PSs determined in *Rubus caesius* was 83.4 ± 3.5 (43–128, *n* = 36) cm (example: Fig. 3), in *R. elegans* P. J. Müller 112 ± 7.6 (54–138, *n* = 19) cm (example: Fig. 5), in *R. exarmatus* H. E. Weber & W. Jansen 83.3 ± 5.2 (52–112; *n* = 13) cm and in *R. scabrosus* P. J. Müller 184.9 ± 9.6 (88–265,

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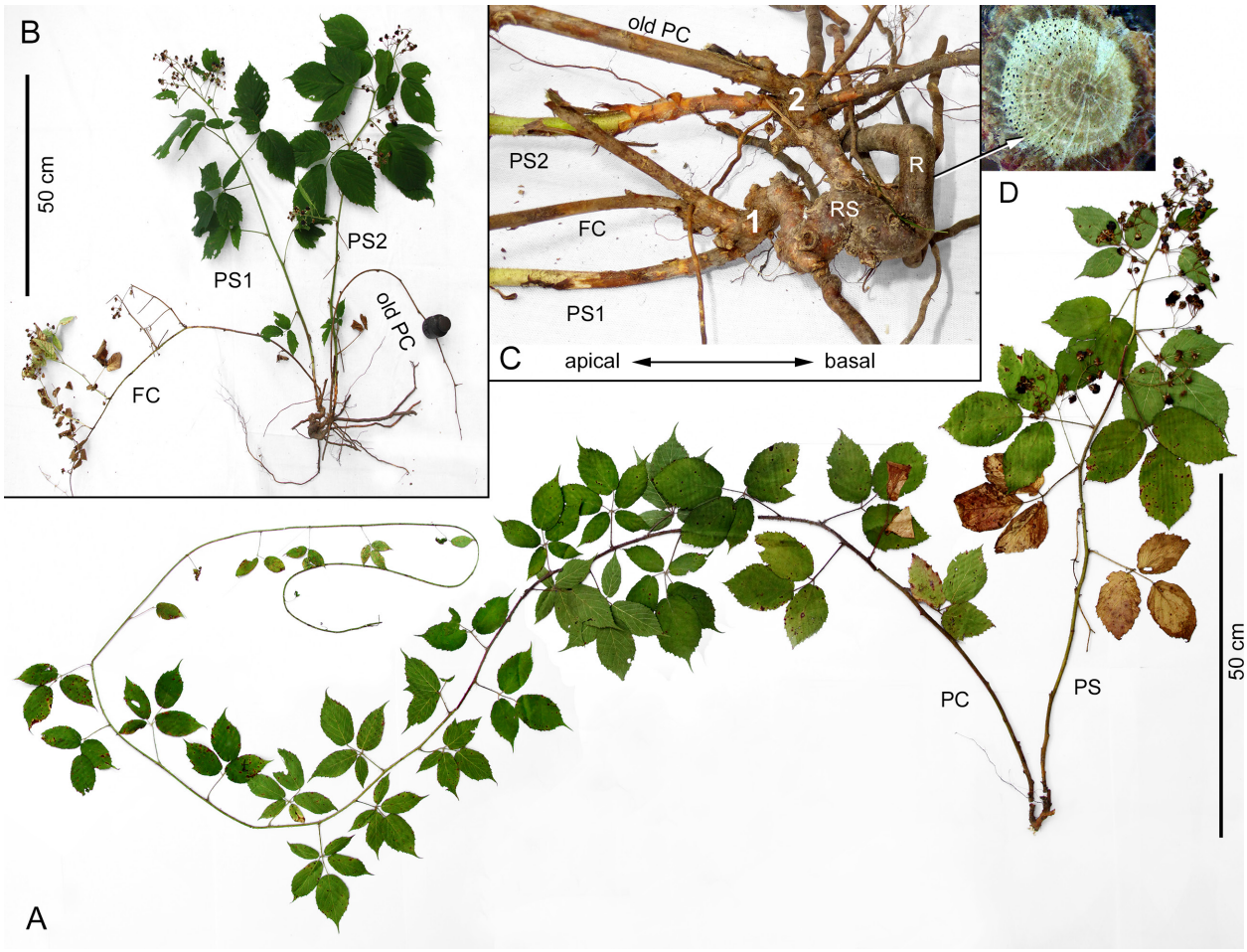

Fig. 5. *Rubus elegans* – A: plant with one primocane (PC) and one panicle shoot (PS); B: plant with two panicle shoots (PS1 & PS2), last year having developed two primocanes as indicated by floricane (FC), with fruiting laterals perishing, and dead primocane (old PC); C: root system of plant shown in B, consisting of 6- to 7-year-old rootstock (RS) with a major (tap) root (R); rootstock containing two active vertical processes (stem domains; 1 & 2), each of which gave rise to one panicle shoot in current year; D: cross-section of major root R shown in C, with 6 or 7 annual rings. – Pressed (A) and living (B–D) plants: Germany, Hessen, Bad Orb, 50.214547°N, 9.341942°E, 25 Aug 2018, *Drenckhahn* (not saved as herbarium specimens).

n = 36) cm (example: Fig. 4A); whereas the length of flowering laterals of floricanes of the same individuals were in *R. caesius* 22.4 ± 1.9 (8–42, *n* = 25) cm, in *R. elegans* 38.7 ± 3.3 (27–71, *n* = 22) cm, in *R. exarmatus* 35.2 ± 3.3 (25–76, *n* = 17) and in *R. scabrosus* 41.1 ± 1.3 (27–60, *n* = 25) cm. Hence, in these species, PSs are on average about four times (up to about ten times) longer than flowering laterals of the corresponding floricanes. PSs may contribute more to the biomass of individual plants than primocanes. Fig. 4A shows a 2.5 m long, richly ramified PS with several flowering branches. The total length of this PS including its branches and panicles is 11.4 m, whereas the tip-rooted primocane of the same plant (with one branch) was 7.6 m long (not shown). Fig. 5 shows two examples of *R. elegans*, one consisting of one PS and one primocane (Fig. 5B) and the other developed two PSs and no primocane in the year of excavation. PSs occur in two varieties: (1) simple type and (2) complex type. The simple types of PSs bear a terminal panicle only (Fig. 1–3, 5) that can be up to 85 cm long with the lower rami of the panicle up to 40 cm long. In addition, separate small axillary panicles may develop along large parts of the stem (Fig. 3, 5). The complex types of PSs possess in addition to the terminal panicle one to four separate flowering side branches. These flowering branches are sometimes even longer than the entire long axis of the PS (up to about 2 m) and often further ramify to give off additional flowering side branches (Fig. 4). Simple and complex types may occur in the vicinity of the same plant and may originate from the same portion of the rootstock.

Simple types of PSs can develop to complex types by later growth of new flowering branches. These often grow out later in the season, thereby contributing to constant flowering of bushes from June throughout the entire summer and autumn. The complex PS depicted in Fig. 4A was monitored in one to two week intervals from end of June to beginning of September and was then harvested. It shows two large ramified flowering side branches that began to grow by the end of July. Most of the panicles of these branches were not yet in flower, whereas the terminal panicle of the stem and its early side branches had

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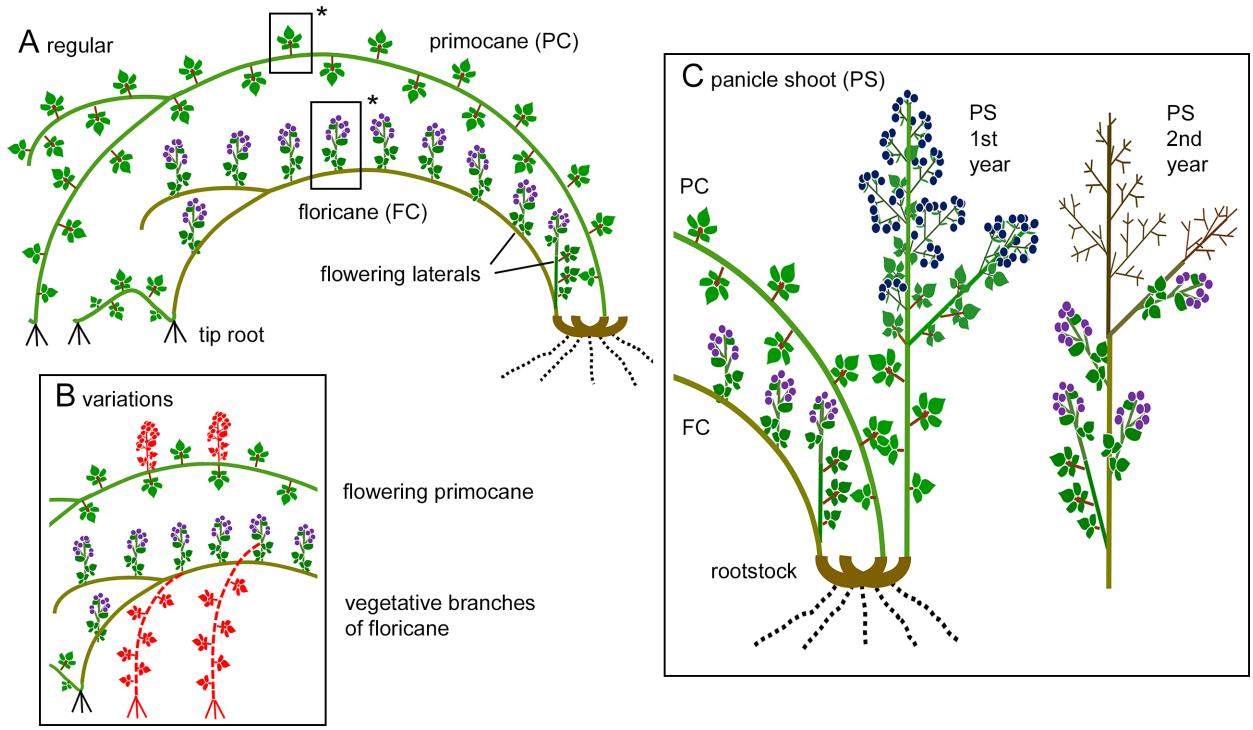

Fig. 6. Summarizing drawing of biennial growth characteristics of trailing blackberries. – A: regular growth pattern; boxes with asterisks (*) indicate taxonomically relevant parts for herbarium specimens; B: variations of regular growth pattern; C: development of panicle shoots in addition to canes. Horizontal rootstock contains vertical stem domains. Note flowering lateral that grows from base of floricane and could be mistaken for a panicle shoot.

finished flowering by the end of July. Both simple and complex types of PSs can develop additional non-flowering (vegetative) side branches that emerge from the stem (Fig. 4B) or even from flowering branches and are able to undergo tip-rooting if they touch the ground.

Occurrence of PSs in Rubus *subg.* Rubus — Species so far found to regularly develop PSs are *Rubus caesius*, *R. elegans*, *R. exarmatus*, *R. hirtus* Waldst. & Kit. sensu lato, *R. lividus* G. Braun, *R. pedemontanus*, *R. rhombicus*, *R. scabrosus*, *R. viridilucidus* Drenckh., *R. visurgianus* H. E. Weber and some unnamed species of *R.* sect. *Corylifolii* and *R.* sect. *Rubus* ser. *Glandulosi* (Wimm. & Grab.) Focke. Müller (1860) mentioned for *R. flaccidifolius* P. J. Müller (*R.* ser. *Glandulosi*) flowering panicles originating from the ends of special root sprouts: "Rispe häufig das Ende von besonderen Wurzeltrieben einnehmend und dann beträchtlich verlängert". And Focke (1877) observed flowering branches springing from underground parts of the stem: "Bei schwächeren Arten gehen nicht selten blühende Zweige unmittelbar aus den unterirdischen Stengeltheilen hervor". This indicates that the flowering entities he had seen were at least in part flowering laterals originating from the base of floricanes. PSs may also occur in some North American *Rubus* sections (though not mentioned by Bailey 1932), as indicated by the development of PSs in erect "primocane-fruiting" cultivars (which fruit on PSs, see below) that go back to crossings with the diploid cultivar 'Hillquist' which was selected in the wild in 1949 from an unnamed *Rubus* species in Virginia, U.S.A. (Clark & al. 2005; Clark 2008). Clark (2008) also stated that several people had contacted him with comments about "primocane-fruiting" *Rubus* species, so that PSs may be more common in the wild in North America than hitherto believed.

Origin and frequency of PSs — The following conclusions were drawn from 52 excavated blackberries with PSs. (1) PSs originate from the rootstock only and never from roots. (2) PSs occur in plants established sexually from seeds (which develop a tap root; Rauh 1938; Fig. 5C) as well in plants established vegetatively by tip rooting (identified by an ellipsoid "tip body" with several larger roots radiating in all directions; Fig.1; to be published). (3) PSs do not spring from basal portions of canes and thus are independent stem entities with no obvious dependency on canes. (4) PSs often develop from separate domains of the rootstock in the absence of canes on this domain (Fig. 1, 3, 5B) or close to canes on the same stem domains of the rootstock (mixed stem domains; Fig. 5C). (5) The frequency of PSs in relation to primocanes ranged in more closely examined bushes of *Rubus rhombicus* and *R. scabrosus* mainly between 0.5–2. (6) Occasionally, root systems lacked active primocanes in the year of excavation and developed PSs only (seen in *R. caesius*, *R. elegans*, *R. exarmatus*, *R. rhombicus* and *R. scabrosus*; Fig. 5A). Four out of 17 excavated *R. caesius* plants (from N and S Germany) developed solely 1 or 2

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PSs and no primocane, seven plants solely 1–3 primocanes and no PSs, and six plants possessed both PSs and primocanes.

Life cycle of PSs — PSs spring from young (two-year-old) to more than ten-year-old root systems (determined by annual ring counts of root and rootstock; Fig. 5C). PSs can be the first independent type of stem (the first primocane of the daughter plant is not counted as an independent stem; see Introduction) arising from a vegetatively established two-year-old plant (seen in *Rubus caesius* and *R. scabrosus*). Like canes, PSs are usually biennial structures that in their second year develop multiple flowering laterals from the stem and from side branches but not from the former terminal panicle portions that always perish during winter (Fig.1, 6).

PSs in other Rubus *subgenera — Rubus idaeus* L. (raspberry, *R.* subg. *Idaeobatus*) has biennial stems that are erect and do not undergo tip rooting. They develop flowering laterals in the second year and do not form a terminal axial panicle. On a few occasions, the author collected first-year-flowering raspberries in the wild that had developed a terminal panicle and several axillary inflorescences along the stem very similar in appearance to the PS shown for *R. caesius* in Fig. 3. First-year-flowering raspberries were bred and are traded under the name "primocane-fruiting" (autumn-flowering) raspberries (Jennings 1988). All members of the related European, Russian and North American *R.* subg. *Chamaerubus* Focke and *R.* subg. *Cylactis* Raf. regularly develop flowering stems, which, however, are annual structures that perish in winter. In *R. arcticus* L., *R. chamaemorus* Focke, *R. humulifolius* C. A. Meyer and *R. stellatus* Sm., stems serve assimilation and sexual reproduction (1–3 flowers per stem). These species do not form canes but instead proliferate vegetatively by hypogeal stolons and adventitious root buds (Rauh 1938) like many other arctic herbaceous perennials (e.g. *Cornus suecica* L.). On the other hand, *R. saxatilis* L. (stone bramble, *R.* subg. *Cylactis*) develops in addition to annually flowering stems also annual stolon-like vegetative canes that are subject to root formation at terminal nodes and the tip. In this respect, *R. saxatilis* resembles other plants with stolons, such as members of the genus *Pilosella* Hill (hawkweed). Out of 44 *R. saxatilis* plants examined by the end of May 2018 (Gramschatz, N Bayern, Germany) 25 had flowering stems only, six plants displayed canes only, and 13 plants had developed both flowering stems and canes. In the latter case, flowering stems and canes emerged from separate rootstock domains. Thus, the two-stem architecture of growth is not a special feature of evolution confined to PS-forming blackberries except that blackberry canes develop flowering laterals (i.e. in PS-forming blackberries two different types of flowering stems) which is not the case in *R. saxatilis* and in other European perennials with stolons.

The dimorphic appearance of stems in other shrub species like *Hedera helix* L. (ivy) or members of the genus *Rosa* L. only reflects developmental stages of the same stem type from a non-flowering to a flowering stage. In *Hedera* L., the vertically climbing stems may eventually develop flowering laterals with differently shaped leaves. However, the vast majority of *Hedera* stems remain in a sterile stage and serve assimilation and vegetative proliferation. These developmental stages of the stem are comparable to the stages of stems of blackberries (primocane, floricane) with the exception that the flowering and non-flowering stages of the stems in *Hedera*, *Rosa* and other shrubs do not have a biennial life cycle but may last for several years in each of the stages.

Discussion

PSs are rootstock-borne first-year flowering shoots with a terminal panicle. In their second year they can develop flowering laterals from the stem and its side branches (see schematic drawing, Fig. 6C). They represent a hitherto overlooked independent type of stem that occurs in several members of all three European blackberry sections and can be considered a unique element of structural diversity of blackberries.

Terminology of stems — The term "stem" has been treated in this paper as collective term for all types of rootstock-borne stems and the term "cane" applied for the classical biennial stem type (Bailey 1932). As alternatives to the term "panicle shoot" (turio paniculatus), the names "flowering shoot" or "flowering stem" were considered, but both were discarded because flowering shoot is partly used in the literature as a synonym for flowering laterals (e.g. Bailey 1932; Takeda 2017) and flowering stem might be mistaken for the flowering stage of the cane (floricane). Recently developed cultivars of American erect blackberries that fruit on PSs (according to the definition of this paper) are traded as "primocane-fruiting" blackberries (Clark & al. 2005). However, as there are two possible types of first-year-flowering stems, i.e. (1) flowering primocanes with flowering laterals but no terminal panicle (Fig. 3, 6B) and (2) PSs, the ambiguous term "flowering (fruiting) primocane" was found anatomically incorrect as an alternative option for the term PS, because blackberry primocanes and floricanes lack a terminal panicle.

Distinguishing features of PSs — PSs can be mistaken for (1) flowering laterals originating from basal or underground parts of floricanes (Fig. 6) or (2) flowering laterals of prostrate canes covered with soil or fallen leaf material. A simple axial pull on the flowering structure may give a first hint. Flowering laterals arising from prostate floricanes are normally quite easily lifted up for some distance together with the adhering floricane. But, in most cases, PSs are much longer than flowering laterals (on average

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four times, see above) and possess a much larger and more elongated and often very complex inflorescence. Direct proof for PSs requires demonstration of their origin from the rootstock. In species with erect-growing canes, floricanes are readily distinguished from PSs by the absence of stem leaves and the absence of an apical axial panicle.

Taxonomic value — Taxonomy of *Rubus* subg. *Rubus* relies on a piece of the primocane ("no stem-piece, no name", Watson 1958) together with a stem leaf in combination with the upper two thirds of a flowering lateral of the floricane (e.g. Watson 1958; Weber 1995; Fig. 6A). If the inflorescence of a PS is collected instead of a flowering lateral of the cane, the correct determination of the species might be complicated because of mostly profound differences in shape and size seen in the two types of inflorescences. An example is illustrated for *R. rhombicus* in Fig. 2 showing small compact corymbose terminal heads of flowering laterals of the floricane but broad pyramidal and much larger terminal inflorescences of the PS. Fig. 4A shows an example of a PS of *R. scabrosus* with apical regions of the large panicles that are free of leaves up to 25 cm below the tip, whereas the inflorescences of flowering laterals of floricanes are much shorter and typically leafy up to the tip of the inflorescence (Müller 1859). Another example in this context is *R. fasciculatiformis* H. E. Weber, which does not develop PSs (own observations), whereas the most closely related species, *R. viridilucidus* and *R. visurgianus*, do possess PSs that may serve as additional distinguishing characters. To avoid any taxonomic problems, it is recommended to always include a piece of the floricane stem in herbarium specimens to be sure that the material was not collected from a PS. In addition, the saved pieces of the floricane stem allow to further answer the often even more relevant question whether the collected pieces of inflorescence and primocane (with leaf) belong to the same species (problem of mixed bramble shrubs).

Ecological aspects — Flowering laterals of prostate and trailing canes are frequently overgrown and suffocated by surrounding vegetation and by primocanes so that flowering laterals often die in early summer or do not successfully fruit (Fig. 5A). PSs, however, are generally much longer and mostly project out of the surface of thickets. This may help to improve the chance of successful pollination and fruiting and could explain why PSs mainly occur in species with prostate and trailing canes. Moreover, complex types of PSs can develop additional side branches during summer and autumn (Fig. 4), thereby prolonging the fruiting period considerably and potentially improving reproductive success.

Environmental and genetic aspects — The relative frequencies of PSs (in relation to primocanes) in *Rubus rhombicus* and *R. scabrosus* ranged mainly between 0.5–2 with no obvious modifications of the significantly varying weather conditions in the years of observation (2016–2018) with very cold and warm winters and very dry and wet springs/summers). Moreover, cutting the bushes of *R. rhombicus* and *R. scabrosus* down to the ground in January had no obvious effect on the frequency of PSs as compared to neighbouring intact bushes. This indicates a genetically controlled growth programme that appears to be hardly influenced by external factors. Genetic studies on PS-fruiting cultivars (crossings) of unnamed erect American blackberry species (Castro & al. 2013) demonstrated a recessive nature and tetrasomic inheritance of PS development with linkage to a certain locus (F) on a defined linkage group (LG 7). Identification of the genes involved in PS development may enable genetic approaches in the future to understand the molecular basis for expression of PSs in wild species.

Horticultural aspects — The "primocane-fruiting" blackberry cultivars 'APF-8' and 'APF-12', traded under the names 'Prime-Jan' and 'Prime-Jim', respectively (Clark & al. 2005; Clark 2008), develop PSs that possess a terminal panicle and two flowering side branches of the stem and hence can be classified as the complex type of PS (according to the definition of this study). If the tip is cut in spring to prevent development of the terminal panicle of the stem, two additional flowering / fruiting branches are formed resulting in average higher yields (Thompson & al. 2007; Strik 2017). In the second year, PSs of these cultivars fruit in late spring on their flowering laterals, and in summer the newly grown PSs begin to fruit so that the harvesting period is considerably extended. These PS cultivars may revolutionize commercial blackberry production.

Acknowledgements

I am grateful to Prof. Dr. Heinrich E. Weber (Bramsche, Germany) for enlightening discussions on diversity of blackberries and for valuable comments on the manuscript. I also wish to thank Prof. John Clark (University of Arkansas, Fayetteville, U.S.A.), Dr. Chad. E. Finn (US Dept. of Agriculture, Corvallis, U.S.A.) and Prof. Bernadine C. Strik (Oregon State University, Corvallis, U.S.A.) for detailed information on primocane-fruiting blackberries and for providing the relevant literature on this topic. Per Harald Salvesen (University of Bergen, Bergen, Norway) and Werner Jansen (Itzehoe, Germany) are also thanked for their reviews of the manuscript.

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Willdenowia
Open-access online edition bioone.org/journals/willdenowia
Online ISSN 1868-6397 · Print ISSN 0511-9618 · Impact factor 1.500
Published by the Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin
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