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Chromosome Numbers of *Rubus* Cultivars at the National Clonal Germplasm Repository

Maxine M. Thompson[1]
U.S. Department of Agriculture, Agricultural Research Service, National Clonal Germplasm Repository, 33447 Peoria Road, Corvallis, OR 97333

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Abstract. **Chromosome numbers were counted for 90 *Rubus* cultivars and selections maintained at the U.S. Dept. of Agriculture, Agricultural Research Service, National Clonal Germplasm Repository, Corvallis, Ore. To my knowledge, 37 of the counts are new, including five that are corrections of previously published counts, 30 that are confirmations of numbers that were previously published but assumed from their parentage rather than actually counted, and 23 that are confirmations of previous counts. The basic number was 7, and 2*n* numbers ranged from 2*x* to 14*x*, including odd-ploids and aneuploids.**

The U.S. Dept. of Agriculture, Agricultural Research Service, National Clonal Germplasm Repository (NCGR), Corvallis, Ore., has the responsibility to preserve *Rubus* species, cultivars, and selections that represent worldwide genetic diversity. In this genus, where chromosome numbers vary from 2*x* to 14*x*, including odd-ploids and aneuploids, chromosome counts are an important aspect of characterization of germplasm. Chromosome number can aid in establishing correct identity and is an important consideration when choosing parental combinations for breeding programs. Chromosome numbers of *Rubus* species at the NCGR have been published separately (Thompson, 1995). The objective of this study was to determine the chromosome number for cultivars and selections of blackberries, hybrid berries, and a few raspberries held at the NCGR. Although chromosome numbers have been published for many of the cultivars, verification was necessary to clarify some discrepancies in the literature, to confirm determinations for cultivars whose published numbers were assumed based on parentage rather than counts, and to establish the number for those not reported yet.

Materials and Methods

Plants used for this study are preserved as a living collection in screenhouses at the NCGR. Chromosome counts were made from squash preparations of pollen mother cells, shoot tips, or root tips. Snow's (1963) alcoholic hydrochloric acid–carmine staining method was used, with some modifications. Methods are described in greater detail in the Thompson (1995) study.

Results and Discussion

The chromosome numbers and ancestry of 90 *Rubus* cultivars and selections are arranged according to crop (blackberries/hybrid berries and raspberries) and within crop, according to increasing euploid chromosome number (Table 1). Aneuploid blackberry and hybrid berries are listed separately. The common term "hybrid berries" refers to cultivars that include blackberry and raspberry in their ancestry, for example, 'Loganberry', 'Tayberry', and 'Sunberry'. In the reference column, only the first report of chromosome number for a cultivar is cited. Specific references are not given for cultivars whose chromosome numbers have been assumed based on ancestry.

Blackberries and hybrid berries (euploids). Ten accessions are diploid, four of which are newly reported: 'Pink Crystal' and 'Snowbank' both of which, like 'White Pearl', are fruit color mutants derived from the 2*x* wild species, *R. allegheniensis* Porter; the North Carolina selection NC86-14-02, selected from the 2*x* species, *R. trivialis* Michx.; and 'Watlab', probably selected from *R. sanctus* Schreb., a 2*x* species related to *R. ulmifolius* Schott. Previously published counts for six 2*x* cultivars are confirmed.

The two triploid accessions are new counts: NC 87-04-01, a *R. trivialis* hybrid, and 'Philadelphia', possibly a selection of *R. canadensis* L. In natural populations, triploid forms of *R. canadensis* maintain their genetic integrity by being highly apomictic (Craig, 1960; Einset, 1951). This reproductive process may account for the fertility of these two 3*x* accessions.

The tetraploids counted in this study consist primarily of old cultivars, such as 'Eldorado' and 'Lawton', which were selected from eastern North American, wild species and newer cultivars developed in breeding programs. These two older 4*x* cultivars and several others reported as 4*x*, such as 'Snyder', 'Ancient Briton', and 'Taylor', were selected primarily from *R. allegheniensis*, a species known to be diploid (Darrow, 1937). This nonconcurrence of chromosome numbers of cultivars with those of the parent species serves as an example of the necessity of actually counting chromosomes of derivatives rather than making assumptions based on ancestry. Because unreduced gametes and spontaneous polyploidy are common in *Rubus*, individual plants selected from wild species for superior fruit or yield traits may have a different chromosome number than parents. Polyploidization itself may confer the superior traits for which the individuals are selected.

Almost all of the newer, eastern North American, blackberry cultivars developed from breeding programs are tetraploid, for example, 'Black Satin', 'Brison', 'Cherokee', 'Choctaw', 'Hull Thornless', 'Navaho', 'Raven', and 'Shawnee'. Common cultivars in their pedigrees include old, eastern North American, upright blackberries, for example, 'Eldorado', 'Brewer', and 'Lawton' (Darrow, 1937) and, from England, 4*x* 'Merton Thornless'. Based on this ancestry, tetraploidy would be expected in the progeny. For three of these cultivars ('Brazos', 'Humble', and 'Merton Thornless'), 28 chromosomes have been counted, whereas for most of them, the 4*x* number has been assumed. The 4*x* counts reported in this study for this group verify all those reported previously, actual and assumed numbers. I report a new 4*x* count for a Scottish Crop Research Institute selection (SCRI 74126), with one unknown parent and the other derived from North American cultivar crosses {['Chehalem' (6*x*) × 'Early Harvest' (2*x*)] × 'Thornfree' (4*x*)}, a cross that would be expected to be 4*x*.

'Perron's Black', previously reported as 3*x* (Hall, 1990), is 4*x*. This cultivar was originally described as being a selection of *R. canadensis* (Huber, 1987), so it might be assumed that it is 3*x*. However, based on both leaf characteristics and type of inflorescence, the plant at the NCGR is not *R. canadensis*, and the chromosome number is inconsistent with this origin.

The few European 4*x* blackberry cultivars and selections at the NCGR include 'Ashton Cross', selected from the wild species *R. bartonii* Newton and, to my knowledge, reported here for the first time. 'Merton Thornless', an important source of recessive thornlessness at the 4*x* level, is confirmed. Two selections from the breeding program in Kristianstad, Sweden, are newly reported tetraploids: Bru 82/1603-4 ('Hedrick' × 'Smoothstem') and Bru 86/1601-1 ('Smoothstem' × 'Valentina'). Because 'Valentina' was selected from the diploid *R.* ×*stellarcticus* G. Larsson (Thompson, 1995), it must be assumed that this parent contributed an unreduced gamete.

Although pentaploid wild species are known [for example, *R. wahlbergii* Arrh. (Gustafsson, 1942)] and at least one named cultivar ('Mertonberry') is 5*x* (Crane, 1953), no 5*x* cultivars were identified in this study. Waldo (1950) reported various percentages of fully fertile seedlings, presumably 5*x*, from

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[1]Collaborator.

crosses between 6*x* and 4*x* forms, so the existence of additional pentaploid cultivars is possible.

Cultivars with higher chromosome numbers (6*x* to 12*x*) are derived primarily from the western North American trailing blackberry (*R. ursinus* Schltdl.), while a few trace back to the eastern trailing blackberry (*R. flagellaris* Willd). *Rubus ursinus* consists of a polyploid complex with 6*x*, 8*x*, 9*x*, 10*x*, 11*x*, and 12*x* natural forms identified (Brown, 1943). High-quality cultivars, representing all ploidy levels found in the wild, except 11*x*, have been developed from this species, for example, 'Logan' (6*x*), 'Kotata' (7*x*), 'Douglass' (8*x*), 'Cascade' (9*x*), 'Tillamook' (10*x*), and 'Zielinski' (12*x*). Newly reported 6*x* forms include three Oregon–U.S. Dept. of Agriculture (ORUS) selections (ORUS 1122, 1465, and 1467) and 'McLeod', which was discovered in North Carolina on a farm whose owner had introduced many cultivars, including some from the western United States. Although the exact parentage of this cultivar is unknown, it appears to have some traits of 'Marion', a 6*x R. ursinus* derivative (J.R. Ballington, personal communication). 'Lincoln Logan', a genetically thornless cultivar derived from tissue-culture-manipulated chimeral 'Thornless Logan' by Hall et al. (1986), is 6*x*, the same as that reported for 'Logan' (Darrow and Longley, 1933). The new count of 7*x* for 'Kotata' differs from the 6*x* previously reported by Hall (1990). The parentage of 'Kotata' {[Pacific (9*x*) x Boysen (7*x*)] x [Jenner-1 (8*x*) x Eldorado (4*x*)]} also supports this 7*x* number. ORUS 1278, a *R. ursinus* derivative, also is 7*x*, a number expected based on its parentage. The New Zealand and Oregon clonal selections of 'Boysen' have the same 7*x* count reported for 'Boysen' (Britton and Hull, 1956).

Hexaploid cultivars developed from species other than *R. ursinus* include 'Bedford Giant' and its thornless mutant 'Bedford Thornless'. The previously published 6*x* count for 'Bedford Giant' (Crane, 1935) is confirmed for both of these cultivars.

A few 7*x* and 8*x* cultivars were derived, at least in part, from *R. flagellaris* Willd, a species reported to be 8*x* by Einset (1947, 1951) but 9*x* by van Faasen and Nadeau (1976).

Table 1. Chromosome numbers of *Rubus* cultivars and selections at the U.S. Dept. of Agriculture, Agricultural Research Service, National Clonal Germplasm Repository, Corvallis, Ore.

Cultivar/ selection	NCGR inventory no.	Chromosome no.	Ancestry	References
		Blackberries and hybrid berries (euploids)		
Burbank Thornless	250.001	14	*R. ulmifolius inermis*	Darrow and Longley, 1933
Flordagrand	721.001	14	(Regal-Ness x *R. trivialis*) x Regal-Ness	Shoemaker and Sturrock, 1959
Hillquist	723.001	14[y]	*R. argutus* selection	
NC 86-14-02	988.001	14[z]	*R. trivialis* selection	
Oklawaha	720.001	14	(Regal-Ness x *R. trivialis*) x Regal-Ness	Sherman, 1968
Pink Crystal	980.001	14[z]	*R. allegheniensis* selection	
Snowbank	1389.001	14[z]	*R. allegheniensis* selection	
Watlab	26.001	14[z]	*R. sanctus* selection	
White Pearl	978.001	14[y]	*R. allegheniensis* selection	
Whitford Thornless	722.001	14	*R. argutus* selection	Hull, 1968
NC 87-04-01	981.001	21[z]	*R. trivialis* hybrid	
Philadelphia	207.001	21[z]	*R. canadensis* selection (?)	
Anderson	393.001	28[z]	Unknown, eastern U.S. erect type	
Arapaho	1726.001	28[y]	ARK 631(ARK 550 x Cherokee) x ARK 883 (ARK 593 x ARK 650)	
ARK Tree Blackberry	1781.001	28[z]	Unknown	
Ashton Cross	317.001	28[z]	*R. bartonii*	
Bailey	62.001	28	Unknown, probably *R. allegheniensis*, in part	Craig, 1960
Black Satin	151.001	28[y]	SIUS 47 (US 1482 x Darrow) x Thornfree	
Brazos	64.001	28	F_2 of Lawton x Ness-Berry	Sherman, 1968
Brison	65.001	28[y]	(F_2 of Brainerd x Brazos) x Brazos	
Cherokee	67.001	28[y]	Brazos x Darrow	
Chester Thornless	839.001	28[y]	SIUS 47 (US 1482 x Darrow) x Thornfree	
Cheyenne	68.001	28[y]	Brazos x Darrow	
Choctaw	1116.001	28[y]	ARK 526 (Darrow x Brazos) x Rosborough	
	1582.001	28[y]	ARK 526 (Darrow x Brazos) x Rosborough	
Comanche	69.001	28[y]	Darrow x Brazos	
Darrow	70.001	28[y]	N.Y. 15826 (Eldorado x Brewer) x Hedrick	
Dirksen Thornless	71.001	28[y]	SIUS 47 (US 1482 x Darrow) x Thornfree	
Ebano	833.001	28[y]	F_2 of Comanche x (Thornfree x Brazos)	
Eldorado	103.003	28	Possibly *R. allegheniensis* x *R. argutus*	Darrow, 1937
Hillenmeyer	252.001	28[z]	Unknown	
Hull Thornless	389.001	28[y]	SIUS 47 (US 1482 x Darrow) x Thornfree	
Humble	1780.001	28	Unknown	Sherman, 1968
Illini Hardy	1202.001	28[z]	Chester Thornless x NY 95 (derived from Hedrick, Eldorado, Brewer, and Buckeye)	
Kristianstad Bru 82/1603-4	1205.001	28[z]	Hedrick x Smoothstem	
Kristianstad Bru 86/1601-1	1206.001	28[z]	Smoothstem x Valentina (*R. ×stellarcticus*)	
Lawton	1201.001	28	Possibly *R. allegheniensis* x *R. frondosus*	Darrow, 1937
Merton Thornless	254.001	28	John Innes selfed x John Innes	Haskell and Tun, 1961
Navaho	1115.001	28[y]	ARK 583 (Thornfree x Brazos) x ARK 631 (ARK 550 x Cherokee)	
	1581.001	28[y]	ARK 583 (Thornfree x Brazos) x ARK 631 (ARK 550 x Cherokee)	
Perron's Black	1230.001	28[z]	Unknown, thornless eastern U.S. upright type	
Raven	77.001	28[y]	Dewblack x Eldorado	
SCRI 74126 RA8	853.001	28[z]	SCRI 6691/9 open-pollinated x [(Chehalem x Early Harvest) x Thornfree]	
Shawnee	836.001	28[y]	Cherokee x AR. 586 (Thornfree x Brazos)	
Smoothstem	80.001	28[y]	US 1482 [Merton Thornless x US 1411 (Eldorado x Merton Thornless)] open-pollinated	

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Table 1. Continued.

Cultivar/ selection	NCGR inventory no.	Chromosome no.	Ancestry	References
Thornfree	105.002	28[y]	US 1410 (Brainerd x Merton Thornless) x US 1414 (Merton Thornless x Eldorado)	
	114.001	28[y]	US 1410 (Brainerd x Merton Thornless) x US 1414 (Merton Thornless x Eldorado)	
Womack	205.001	28[y]	(F_2 of Brainerd x Brazos) x Brazos	
Bedford Giant	312.002	42	Veitchberry selfed	Crane, 1935
Bedford Thornless	857.001	42[y]	Thornless mutant of Bedford Giant	
Chehalem	761.001	42	Santiam x Himalaya	Britton and Hull, 1957
Lincoln Logan	81.001	42[y]	Thornless loganberry tissue-culture-manipulated for genetic thornlessness	
	737.001	42[y]	Thornless loganberry tissue-culture-manipulated for genetic thornlessness	
	1394.001	42[y]	Thornless loganberry tissue-culture-manipulated for genetic thornlessness	
Marion	385.001	42[y]	Chehalem x Olallie	
Mcleod	108.001	42[z]	Unknown, chance seedling, McLeod farm, N.C.	
Olallie	76.001	42	Black Logan x Young	Britton and Hull, 1957
ORUS 1122	342.001	42[z]	OSC 878 (Eldorado x Jenner-1) x Marion	
ORUS 1465	350.001	42[z]	OSC 998 (Eldorado x Jenner-1) x Olallie	
ORUS 1467	345.001	42[z]	OSC 998 (Eldorado x Jenner-1) x Olallie	
Silvan	633.003	42[y]	ORUS 742 (Pacific x Boysen) x Marion	
Sunberry	855.001	42[y]	*R. ursinus* x Malling Jewel (4*x*) selfed seedling	
Tayberry	1216.001	42[y]	Aurora x *R. ideaus* (4*x*)	
Tummelberry	854.001	42[y]	Tayberry x Tayberry sib	
Waldo	983.001	42[y]	ORUS 1122 [Marion x OSC 878 (Jenner-1 x Eldorado)] x ORUS 1367 (ORUS 1083 x NC 37-35-M2)	
Boysen (New Zealand selection)	1025.001	49	Clonal selection of Boysen (*R. ursinus*, in part)	Britton and Hull, 1956
Boysen 43 (Oregon selection)	1108.001	49	Clonal selection of Boysen (*R. ursinus*, in part)	Britton and Hull, 1956
Kotata	359.001	49[z]	OSC 743 (Pacific x Boysen) x OSC 877 (Jenner-1 x Eldorado)	
Kotata	637.001	49[z]	OSC 743 (Pacific x Boysen) x OSC 877 (Jenner-1 x Eldorado)	
	992.001	49[z]	OSC 743 (Pacific x Boysen) x OSC 877 (Jenner-1 x Eldorado)	
Lucretia	74.001	49	*R. flagellaris*, in part	Britton and Hull, 1957
ORUS 1278	458.001	49[z]	Austin Thornless x ORUS 1063 (Chehalem x OSC 743)	
Young	131.001	49	Austin Mayes x Phenomenal	Britton and Hull, 1956
Austin Thornless	357.001	56	Sport or open-pollinated seedling of Austin Mayes, a selection of *R. flagellaris*	Britton and Hull, 1957
Bodega Bay	367.001	56	*R. ursinus* selection	Fischer et al., l941
Douglass	1416.001	56[z]	Sander x Lawrence (both parents derived primarily from *R. ursinus* and, remotely, Austin Thornless)	
Jenner	137.001	56	*R. ursinus* selection	Zielinski and Galey, 1951
Cascade	66.001	63	Zielinski x Logan	Fischer et al., 1941
Lincoln	1140.001	63[z]	*R. ursinus*, in part	
Long Black	Quarantine	70[z]	Derived from Marion, Lincoln, and unnamed *R. ursinus* selections	
Tillamook	1228.001	70[z]	*R. ursinus*, in part	
Dyke	139.001	84[z]	*R. ursinus* selection	
Zielinski	356.001	84	*R. ursinus* selection	Fischer et al., l941
Keriberry	1720.001	98[z]	*R. rugosus* selection	
			Blackberries and hybrid berries (aneuploids)	
Tayberry seedling	227.001	44[z]	Open-pollinated seedling of Tayberry	
Carolina	102.005	53	Austin Thornless x Lucretia	Britton and Hull, 1957
Aurora	101.001	58[z]	ORUS 616 (Zielinski x Logan) x ORUS 73 (Logan x Austin Thornless)	
Aurora	134.001	58[z]	ORUS 616 (Zielinski x Logan) x ORUS 73 (Logan x Austin Thornless)	
Santiam	79.001	61[z]	*R. ursinus*, in part	
			Raspberries	
Bababerrry	1123.001	14[z]	*R. ideaus* chance seedling	
Benenden	816.001	14[z]	*R. trilobus* x *R. deliciosus*	
Columbian	1030.001	14[z]	Cuthbert red raspberry x *R. occidentalis* cv. Gregg	
Dorman Red	388.001	14[z]	Dorsett [Van Fleet (*R. kuntzeanus* x Cuthbert red raspberry) x *R. parvifolius*] x *R. parvifolius*	
Jingu Juegal	267.001	14[z]	*R. crataegifolius* selection	
Jokdal	449.001	14[z]	*R. crataegifolius* selection	
Mandarin	743.001	14[z]	(*R. parvifolius* x Taylor) x *R. ideaus* cv. Newburgh	
Malling Exploit (4*x*)	987.001	28	Tetraploid form of Malling Exploit	

[z]New report or different from previous reports.
[y]Previously reported, but chromosome number assumed based on parents' numbers rather than counted.

However, this discrepancy in reported numbers for this species could not be clarified because no plants were available at the NCGR. The cultivars include 'Austin Mayes' (8*x*); 'Austin Thornless' (8*x*), an important source of dominant genetic thornlessness (Darrow, 1937); 'Young' (7*x*); and 'Lucretia' (7*x*), previously reported to be 6*x* by Darrow and Longley (1933) but reported as 7*x* by Britton and Hull (1957) and confirmed here. The 7*x* count for 'Lucretia' suggests that, like 'Young', it may also be a hybrid of the 8*x R. flagellaris* with a 6*x* cultivar.

The 8*x* cultivars derived from *R. ursinus* include 'Bodega Bay' and 'Jenner', both selections from the wild species in central California, and 'Douglass', a new thornless cultivar, developed and recently patented (U.S. plant patent 8423) by Barney Douglass, a private breeder in Oregon. Its complex ancestry, given in the patent description, includes several of Douglass' *R. ursinus* selections from Oregon as well as 'Boysen', 'Marion', 'Austin Thornless', and 'Chehalem'.

The 9*x* count for 'Cascade' was confirmed; it is the number expected from the parents 'Zielinski' (12*x*) x 'Logan' (6*x*). A new count of 9*x* for 'Lincoln', a chance seedling selected in Oregon, supports the purported hybrid origin for this cultivar (Waldo, 1968). Most likely, it also was a cross of the local 12*x R. ursinus* with a 6*x* cultivar.

The new count of 10*x* for 'Tillamook', a selection from the wild in northern Oregon, supports its hybrid origin, which had been suspected based on its having perfect flowers (compared to dioecy in the wild species) as well as the fact that neither 8*x* nor 10*x* forms of the wild species have been found this far north. It is probably a cross of the local 12*x R. ursinus* and an 8*x* cultivar. 'Long Black', newly reported as 10*x*, was selected in Oregon by Barney Douglass. Its ancestry involved 'Marion', 'Lincoln', and a few unnamed *R. ursinus* selections (C. Finn, personal communication).

'Dyke' (12*x*) is a new count, and 'Zielinski' (12*x*) was confirmed. Both were selected from wild *R. ursinus* in Oregon.

The count of 14*x* for 'Keriberry', a New Zealand cultivar selected from *R. rugosus* Smith, is consistent with that reported for the wild species from Sri Lanka by Nybom (1980).

Blackberries and hybrid berries (aneuploids). New counts are given for three of the four aneuploid cultivars and selections, all of which are above 6*x*. A 'Tayberry' open-pollinated seedling (6*x* + 2) most likely resulted from a cross with a 7*x* form. The count for 'Aurora' (8*x* + 2) differs from that reported by Hall (1990) but would be expected based on its parentage, [Zielinski (12*x*) x Logan (6*x*)] x ['Logan' x 'Austin Thornless' (8*x*)], a cross between 9*x* and 7*x* selections. 'Santiam', previously considered to be 8*x* (Waldo, 1950), is in fact 8*x* + 5, or 9*x* – 2. Waldo (1968) suspected that 'Santiam' was not pure *R. ursinus* because of its perfect flowers as well as other traits. This aneuploid chromosome number supports the suspicion of hybridity, possibly a cross of the native 12*x R. ursinus* x a 6*x* cultivar, with the loss of two chromosomes. The occurrence of fully fertile, aneuploid cultivars demonstrates that these unbalanced numbers (at least above 6*x*) may have no adverse effect on fertility. Waldo (1950) and Lawrence (1976) have used these high and irregular chromosome-number forms extensively in breeding.

Raspberries. With the exception of 'Bababerry', chromosome numbers of raspberry accessions were determined only if a cultivar had been received as a 4*x* form or if it had been developed from species other than *R. ideaus* or *R. strigosus*, both diploid species. Seven of the eight raspberry cultivars counted were 2*x*, as would be expected based on their diploid species ancestry. The fourth, 'Malling Exploit' (4*x*) was counted to confirm that the plants held at the NCGR were indeed tetraploid.

The new chromosome numbers presented in this study provide additional information about the cytologically complex *Rubus* genus. Discrepancies in published chromosome numbers arise from misidentified plants and inaccurate counting, especially with the higher ploidy levels and aneuploidy. Knowledge of the chromosome number is important for breeders considering parental combinations because of possible reduced fertility in offspring with unbalanced chromosome numbers, especially at the lower ploidy levels. Because the counts that I reported are associated with voucher plants in a permanent living collection, it will be possible to verify the identity of each plant or to reconfirm its chromosome number.

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