Journal of the American Pomological Society 65(2): 56-61 2011

U.P. Hedrick Award Winner 2010: Primocane-fruiting in Black Raspberry (*Rubus occidentalis* L.)

Michael Dossett[1] and Chad E. Finn[2]

Abstract

Production of fruit on first year canes, or primocane-fruiting in caneberries (*Rubus* L.) has proven to be an important trait, allowing production, particularly for the fresh market, to expand into new geographic areas and non-traditional seasons. While not a new trait, primocane-fruiting black raspberries have received new attention from breeders in recent years. Despite this, relatively little is known about primocane-fruiting in black raspberry because historical sources of the trait have been lost, and little has been written on the subject. Modern sources of primocane-fruiting include seedlings of floricane-fruiting black raspberry cultivars as well as wild black raspberry germplasm. Expression of primocane fruiting in these plants is variable, and further study on the genetic control of primocane fruiting and the effects of environmental influences on expression are needed.

Primocane-fruiting (PF), or the ability to produce fruit on the tips of first year canes, is a characteristic of many red raspberry (*Rubus idaeus* L.) cultivars. The trait has been recognized in red raspberries for over 200 years but has risen to a new level of importance in the last half-century. The introduction of improved PF red raspberry cultivars has revolutionized the red raspberry industry, allowing the expansion of red raspberry production into new areas and the development of new production systems. The recent release of the first PF blackberries (*Rubus* L.) from the University of Arkansas, 'Prime-Jim'®, 'Prime-Jan'® and 'APF-45' (Prime-Ark®- 45), promises to do the same for erect blackberry production (3, 5). While the black raspberry (*R. occidentalis* L.) industry is largely focused on the development of new floricane fruiting cultivars with better adaptation and disease resistance, PF satisfies a niche market by extending the season for fresh fruit, and may one day lead to industry expansion similar to other caneberries.

The PF trait in black raspberry has received attention since the species' domestication in 1832 (8); however, historical sources of PF germplasm have since been lost. New sources of PF black raspberry germplasm have only recently been discovered and are now beginning to be studied and characterized by breeders. Understanding the potential as well as the limitations of PF black raspberries will be critical to breeding progress and industry acceptance of new PF cultivars.

History of Primocane-Fruiting in Black Raspberry

The first black raspberry cultivar to be named, 'Ohio Everbearer' was selected and introduced in the fall of 1832 from a PF wild plant growing near the shore of Lake Erie (8). Other PF cultivars followed and by 1920, at least 19 were known (1). Many of these, including 'Grigg's Daily Bearing', 'Miller's Daily Bearing', and 'Lum's Autumn Black', were seedlings of 'Ohio Everbearer', though none ever reached prominence. Information on these early PF black raspberries is limited to short varietal descriptions indicating that most had small, soft fruit of poor quality and were kept merely for the novelty of fall production. 'Black Knight', introduced in 1973, from selfed fruit of 'Johnson Everbearing' is a more recent addition to the list of PF black raspberry cultivars (18). While 'Black Knight' is available through the USDA-ARS National Clonal Germplasm Repository, plants in the repository's field collection do not exhibit the PF trait in Corvallis, Oregon (M. Dossett, pers. observ.) and may not represent the original

[1] Department of Horticulture, Oregon State University, Corvallis, Oregon
[2] USDA-ARS, Horticultural Crops Research Laboratory, Corvallis, Oregon

'Black Knight'. None of the other historic PF black raspberry cultivars have been saved or are currently available.

Current Germplasm Sources

While strong, vigorous, fruiting laterals originating from near the crown of the plant are occasionally observed and may be confused with true primocanes, current black raspberry cultivars do not fruit reliably on primocanes. Genes for PF, however, have been recovered from this source. Dossett et al. (4) performed a diallel analysis of eight black raspberry cultivars, one wild accession, and a bulk pollen sample from *R. leucodermis* (Dougl. ex Torr. & Gray). Some degree of PF was observed in 13 of the 26 populations generated from this experiment. The percentage of plants expressing the trait in at least one year over a three year period ranged from 0-27% (Table 1). This is particularly surprising because Oberle and Moore (12), in their report on autumn fruiting in red and black raspberries, indicate that in their crosses between black raspberry cultivars none of the 6,600 seedlings evaluated were PF.

Primocane-fruiting has also been observed in wild black raspberries from a variety of sources. Wild *R. occidentalis* collected by J.R. Ballington (North Carolina State University, Raleigh) near Zebulon, NC in 1980s and selected for heat tolerance and resistance to fungal diseases, also express the PF trait both in North Carolina and Corvallis, Oregon (J.R. Ballington, pers. comm., M. Dossett, pers. observ.). One of these selections, NC 84-10-3 was used by Dossett et al. (4) in their diallel analysis and passed this trait to some of its progeny (Table 1). In 1986, a PF black raspberry was discovered in the wild near Poughkeepsie, NY by P. Tallman (16). Breeding with this germplasm has resulted in the naming and patenting of the first modern PF black raspberry cultivar, 'Explorer' (15). The success of 'Explorer' as a cultivar has been hindered by poor pollen fertility (P. Tallman, pers. comm.; M. Dossett, pers. observ.). However, 'Explorer' still represents an important step in breeding progress as well as raising awareness of PF in black raspberries.

In 2006, we began an effort to collect and evaluate wild *R. occidentalis* germplasm from across the native range by soliciting wild-collected fruit from friends and colleagues living in eastern North America. This was followed by collecting trips in 2007 to the southeast and Great Plains (6). Seedlings from these collections are currently being evaluated in the field in Corvallis, Oregon. To date, PF has been observed in many of these populations from

Table 1. Summary of primocane-fruiting in black raspberry diallel populations studied by Dossett et al. (4) including cross identification (ORUS) number and percentage of progeny carrying some primocane fruit in at least one year from 2004-2006.

ORUS number	Parents			%
ORUS 3012-0	'Black Hawk'	x	'Hanover'	25
ORUS 3013-0	'Black Hawk'	x	'John Robertson'	9
ORUS 3014-0	'Black Hawk'	x	'Munger'	9
ORUS 3015-0	'Black Hawk'	x	NC 8410-3	20
ORUS 3016-0	'Dundee'	x	NC 8410-3	13
ORUS 3018-0	'Hanover'	x	'John Robertson'	9
ORUS 3021-0	'Jewel'	x	NC 8410-3	9
ORUS 3022-0	'John Robertson'	x	NC 8410-3	13
ORUS 3028-0	'Mac Black'	x	NC 8410-3	27
ORUS 3030-0	'Mac Black'	x	*R. leucodermis*	15
ORUS 3031-0	'Munger'	x	'Dundee'	6
ORUS 3032-0	'Munger'	x	'Hanover'	6
ORUS 3039-0	'New Logan'	x	'Hanover'	3

across the range (Table 2). This germplasm may prove to be a valuable additional source of this trait for future breeding.

Expression and Genetic Control of Primocane-Fruiting

In black raspberries, expression of PF within a plant is variable in the length of the primocane that initiates flower buds, as well as the number of primocanes or primocane branches that flower. Both are important factors in determining total yield and should be selected for in breeding. Primocane fruit may be produced on the tips of some or all branches on a single primocane or on a high percentage of primocane branch tips throughout the plant. This may also vary with year as some weakly PF plants may express this trait in some years and not others (M. Dossett, pers. observ.). Both of these characteristics were also noted in red raspberry by Keep (9) who considered it to be related to timing of flower bud initiation interacting with factors that influence cane elongation to determine timing of flowering

Table 2. USDA-ARS plant introduction (PI) number, breeding program cross identification (ORUS) number, and general provenance of primocane-fruiting seedlings in wild black raspberry germplasm collected in 2006 and 2007 and evaluated in the field in Corvallis, Oregon in 2008 and 2009.

PI #	ORUS number	Provenance
PI 653327	ORUS 3779	Litchfield County, CT
PI 652975	ORUS 4117	Clayton, GA
PI 652976	ORUS 4119	Clayton, GA
PI 653332	ORUS 3797	Hendricks County, IN
PI 653336	ORUS 3801	southern IN
PI 651846	ORUS 4130	Minneapolis, KS
PI 653337	ORUS 3803	Berkshire County, MA
PI 653343	ORUS 3811	Allegany County, MD
PI 653344	ORUS 3812	Anne Arundel County, MD
PI 653350	ORUS 3821	Camden, ME
PI 653347	ORUS 3817	Gardiner, ME
PI 653345	ORUS 3814	Orono, ME
PI 653346	ORUS 3816	West Kennebunk, ME
Not in GRIN	ORUS 4110	Benton Harbor, MI
Not in GRIN	ORUS 4112	Okemos, MI
PI 653351	ORUS 3823	Cass County, MN
PI 653353	ORUS 3826	Ramsey County, MN
PI 653307	ORUS 4135	Victoria Springs State Recreation Area, NE
PI 653363	ORUS 3843	Columbia County, NY
PI 653361	ORUS 3840	Ontario County, NY
PI 653370	ORUS 3852	Greene County, PA
PI 652971	ORUS 4113	Glassy Mountain, SC
PI 652973	ORUS 4114	Glassy Mountain, SC
PI 653375	ORUS 3859	Davidson County, TN
PI 653376	ORUS 3864	Davidson County, TN
PI 653377	ORUS 3867	DeKalb County, TN
PI 653392	ORUS 3910	Van Buren County, TN
PI 653394	ORUS 3912	Van Buren County, TN
PI 653399	ORUS 3926	Columbia County, WI

and fruiting. Environmental and production factors influencing cessation of cane elongation may help to explain differences in PF expression from year to year and on separate canes within a plant, and the possibility of environmental influence on expression of the trait rather than just on timing of ripening should be examined more closely. Slate (13), Waldo and Darrow (19), and Jennings (8) all emphasize the effect of environment on the expression of PF in red raspberry. Card (1) and Hedrick (7) also hint at the possibility of environmental effects on the expression of PF in black raspberry, noting that 'Mystery' which was selected as a PF variety in Kentucky, was "not autumn fruiting in Minnesota" (7).

The genetic control of PF in black raspberry including how genetics and environment influence expression of this trait needs to be further studied. Unlike PF in tetraploid erect blackberries (11), PF in black raspberries does not appear to be a simply inherited trait. Segregation for PF in crosses between floricane-fruiting cultivars may be explained by recessive alleles at one or more loci. However, in October 2004, open-pollinated (OP) primocane fruit was collected from the plant with the highest degree of PF trait expression in six of the diallel populations studied by Dossett et al. (4). The resulting seedlings continued to segregate for PF, and in some populations, nearly all PF seedlings expressed the trait to a greater degree than their parent. This continued segregation for and intensification of PF expression observed in populations derived from fall-collected OP fruit of PF selections cannot be explained by the model of simple inheritance as these seedlings should all be the result of selfing or crossing with other PF plants. These observations suggest that PF is under the control of many loci acting in an additive or complementary manner as suggested by Keep (9) for the control of PF in red raspberry. In working with PF from his original wild selection from New York, Tallman (16) noted that in crosses between PF black raspberries and 'Jewel' and 'Allen', as well as a floricane-fruiting wild selection from Arkansas, it was unusual to observe PF in F_1 populations but that they reappear in the F_2 generation. Primocane-fruiting plants are, however, recovered from the F_1 generation in crosses with 'Haut'. These observations are not necessarily inconsistent with the hypothesis of quantitative genetic control.

Timing of Primocane-Fruiting

Primocane fruit of 'Explorer' ripen in mid-late August in Longmont, Colorado and continue until frost (15). This is similar to the timing of ripening in western Oregon of PF selections derived from cultivated germplasm (M. Dossett., pers. observ.). Primocane fruit from the material collected by J.R. Ballington in North Carolina begin ripening 2-3 weeks after these PF selections in western Oregon. Primocane-fruiting plants from other wild sources have not been under observation long enough to establish patterns in the timing of ripe fruit, but wide variation has been noted. Hedrick (7) indicates that some PF black raspberries may begin ripening in August while others do not start until October. Development of earlier PF black raspberries should be a breeding objective. This would not only help fill the seasonal gap from floricane-fruiting types, but may also lead to higher yields of fall fruit because a higher proportion of the cane will have time to ripen fruit before frost or poor weather end the season. Keep (9) considered PF potential in red raspberries to be strongly correlated to earliness of ripening. This association is supported by the development of earlier ripening PF red raspberry genotypes (14). Selecting and crossing promising PF selections with earlier floricane-fruiting genotypes has worked well in red raspberry (8, 10) and is the approach currently being taken in PF blackberries (2) to meet this objective.

Current Efforts and Future Prospects

In noting the occasional appearance of PF in red raspberry seedling lines which were not known to carry the trait, Keep (9) notes, "It is probable that chance selection during inbreeding had built up minor-gene

complexes sufficient in both cases to induce autumn-fruiting." This seems like a plausible explanation for the observations on inheritance of PF in black raspberry and its occurrence in some wild populations. With this in mind, crosses between different sources of PF in black raspberry are starting to take place. The primary objective of this approach is to mitigate possible deleterious effects of inbreeding that may be associated with maintaining PF from a single source as well as identify recombinants for PF genes from different sources that express PF more strongly. This work is being pursued primarily in Corvallis, Oregon at the USDA-ARS/Oregon State University cooperative breeding program and in a private breeding program in Longmont, Colorado. Currently the most advanced selection from either of these programs is PT-2A4, originating from the program in Longmont, Colorado. This selection is being evaluated in trials at a number of locations across the U.S. and boasts larger fruit and smaller seeds than 'Explorer', which it is intended to replace (P. Tallman, pers. comm.). The first selections from the breeding program in Oregon are a few years behind this.

The effects of training and tip pruning on the timing and extent of PF have not yet been closely studied in black raspberry. Even small scale controlled studies in this area would be highly beneficial to allow breeders and others working with PF black raspberries to know how to treat plants for evaluation. Understanding the relationship between cane tipping and the timing of PF, the number of cane branches with primocane fruit, the extent of PF on those branches, and the size of primocane fruit will also be an essential component for commercial acceptance of PF black raspberries. Pruning tips of primocanes to force branching may delay primocane-flowering in black raspberry (16). In blackberries, cane tipping at 0.6 m stimulates lateral bud break and subsequent flowering early in the summer, thereby allowing the bulk of the crop to ripen before frost and greatly increasing the commercial yield (17). While soft tipping of primocanes to induce branching is a production practice common to floricane-fruiting black raspberry and erect blackberries, control and expression of PF in black raspberry appears to be more similar to red raspberry, in which cane tipping is not advantageous, and caution should be exercised when drawing comparisons without further study.

The rediscovery of PF in black raspberry over the last 20 years is an exciting development in the evolution of this crop. Fresh black raspberry fruit in late summer and early fall has the potential to be a high-value crop, particularly in regions where fresh market demand for black raspberry already exists. A lack of understanding of the genetics controlling PF and its variable expression, as well as the best management practices for production could become barriers to the adoption of this crop. Significant disease problems hampering production of traditional floricane-fruiting black raspberries will need to be addressed in PF black raspberries as well. Observations of PF black raspberries over the last several years have helped those working with the plants to begin to gain an understanding of PF, but there is still a great deal to be learned and the success of PF black raspberries in the future will depend on studies that address these questions.

Acknowledgements

The authors wish to thank Pete Tallman (Longmont, CO) for discussions and correspondence making this review possible.

Literature Cited

1. Card, F. W. 1920. Bush-fruits. MacMillan, New York, NY.
2. Clark, J. R. 2008. Primocane-fruiting blackberry breeding. HortScience 43:1637-1639.
3. Clark, J. R., J. N. Moore, J. Lopez-Medina, C. E. Finn and P. Perkins-Veazie. 2005. 'Prime-Jan'('APF-8') and 'Prime-Jim'('APF-12') primocane-fruiting blackberries. HortScience 40:852-855.
4. Dossett, M., J. Lee, and C. E. Finn. 2008. Inheritance of phenological, vegetative, and fruit chemistry traits in black raspberry. J. Am. Soc. Hort. Sci. 133:408-417.
5. Finn, C. E., J. R. Clark and S. Sleezer. 2010.

Blackberry. Pp. 720-721. In: Clark, J. R. and C. E. Finn (eds.). Register of new fruit and nut cultivars, list 45. HortScience 45.
6. Hall, H., K. E. Hummer, A. Jamieson, S. Jennings and C. Weber. 2009. Raspberry breeding and genetics. Plant Breeding Rev. 32:39-382.
7. Hedrick, U. P. 1925. The small fruits of New York. N.Y. State Agric. Expt. Station. J.B. Lyon, New York, NY.
8. Jennings, D. L. 1988. Raspberries and blackberries: their breeding, diseases and growth. Academic Press, San Diego, Calif.
9. Keep, E. 1961. Autumn-fruiting in raspberries. J. Hort. Sci. 36:174-185.
10. Keep, E. 1988. Primocane (autumn)-fruiting raspberries: a review with particular reference to progress in breeding. J. Hort. Sci. 63:1-18.
11. Lopez-Medina, J., J. N. Moore and R. W. McNew. 2000. A proposed model for inheritance of primocane fruiting in tetraploid erect blackberry. J. Amer. Soc. Hort. Sci. 125:217-221.
12. Oberle, G. D., and R. C. Moore. 1952. Transmission of the autumn-fruiting character in crosses of red and black raspberries. Proc. Amer. Soc. Hort. Sci. 60:235-237.
13. Slate, G. L. 1939. Breeding autumn-fruiting raspberries. Proc. Amer. Soc. Hort. Sci. 37:574-578.
14. Slate, G. L. and J. Watson. 1964. Progress in breeding autumn-fruiting red raspberries. Farming Res. 30:6-7.
15. Tallman, P. 2007. Black raspberry plant named 'Explorer'. U.S. Plant Patent 17,727, filed April 27, 2005, and issued May 15, 2007.
16. Tallman, P. 2007. Primocane-fruiting black raspberry breeding program. Pp. 7-14. In: Proc. North Amer. Bramble Conf., 15-17 Jan. 2007, Columbus, Ohio.
17. Thompson, E., B. C. Strik, J. R. Clark and C. E. Finn. 2007. Flowering and fruiting patterns of primocane-fruiting blackberries. HortScience 42:1174-1176.
18. United State Dept. of Agric., Agric. Res. Serv. National Genetic Resources Program. 2010. Germplasm Resources Information Network - (GRIN). [Online Database] National Germplasm Resources Laboratory, Beltsville, Maryland. Available: http://www.ars-grin.gov/cgi-bin/npgs/acc/search.pl?accid=%20PI+553754 <<Accessed 15 May 2010>>
19. Waldo, G. F., and G. M. Darrow. 1941. Breeding autumn-fruiting raspberries under Oregon conditions. Proc. Amer. Soc. Hort. Sci. 39:274-278.