Flowering and Fruiting Morphology of Primocane-Fruiting Blackberries

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Abstract
The flowering morphology of the erect, thorny primocane-fruiting blackberry (Rubus L. subgenus Rubus) cultivars Prime-Jan™ and Prime-Jim™ were studied in 2005 in Aurora, Ore., USA. Primocanes that were “soft-tipped” in early summer to 1 m were compared to un-tipped primocanes and floricanes. On average, soft-tipped primocanes for both cultivars developed five lateral branches, whereas un-tipped primocanes developed two lateral branches. Tipped canes developed almost twice the number of flowers as un-tipped canes. ‘Prime-Jan’ and ‘Prime-Jim’ began blooming on the branches of tipped canes in mid-July. Un-tipped primocanes began to bloom in late July. Apical branches on tipped canes bloomed earlier than branches on the mid and basal portions of the primocanes. Within a primocane inflorescence, the terminal or distal flower was always the first to open, followed by terminal flowers from axes located on the basal portion of the inflorescence. Flowers then opened acropetally within the inflorescence, with the exception of the most basal flower which was typically the last to open. In contrast to primocanes, floricanes developed two types of floral structures: short and long axial floral structures. Both types of floral structures developed below the spent primocane-fruiting apex of the un-tipped cane. Flowers on short floral structures began to open in early April while those on long floral structures began to open in mid-May. Days from anthesis to black fruit for soft-tipped and un-tipped primocanes averaged 46 to 52 d, depending on cultivar, and 57 d on floricanes. The blooming pattern within an inflorescence was the same for soft-tipped and un-tipped primocanes and floral structures on floricanes.

INTRODUCTION
Field observations revealed that erect primocane-fruiting morphology is different from that of erect florican-fruiting blackberry and primocane-fruiting raspberry (Strik, pers. commun.). Bloom pattern within an inflorescence and fruit maturity range for semi-erect blackberries has been reported (Takeda, 1987). Production guidelines for florican-fruiting blackberries are well established, however, to date there are few reports on management guidelines for primocane-fruiting types. Traditional cane management for erect, florican-fruiting blackberries includes summer topping of primocanes and winter pruning of floricanes. Tipping the upper portion of the primocanes in early summer removes apical dominance and encourages branching. Similarly, soft-tipping (removing the upper 5 cm) of primocane-fruiting types in early summer may be a feasible way to manage primocanes, to encourage branching and increase yield (Drake and Clark, 2003).

Currently, studies are underway to determine optimal cane management practices.

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in primocane-fruiting blackberry under mild climate conditions (Strik et al., 2006). Identifying the location of productivity within a primocane, bloom pattern among branches, and order of bloom within an inflorescence throughout the harvest season is necessary to optimize primocane management and precisely target harvest for off-season markets.

The objectives of this study were to: 1) characterize flowering location, inflorescence morphology, bloom pattern, and range of fruit maturation in primocanes and floricanes of ‘Prime-Jan’ and ‘Prime-Jim’; and 2) determine the impact of soft-tipping on flowering and fruit ripening patterns in primocanes.

MATERIALS AND METHODS

In June 2003, tissue-cultured plugs of ‘Prime-Jan’ and ‘Prime-Jim’ were established at the North Willamette Research and Extension Center (NWREC), Aurora, Ore., USA, 41 m above sea level under a mild winter climate (45°N). In May 2005, inflorescences in the apical, middle, and basal region were randomly flagged on three over-wintered floricanes for each cultivar. These floricanes were not tipped as primocanes the previous year. Floricanes had two types of inflorescences: 1) short axial floral structures: over-wintered, unopened primocane-developed floral buds that generally lacked compound leaves; and 2) long axial floral structures: florican-developed structures borne from a secondary bud that always developed compound leaves. Both types of floral structures developed below the spent, primocane-fruiting apex of the un-tipped canes. For each cultivar, order of bloom within an inflorescence, as described by Takeda (1987), short and long floral structure length, number of flowers and berries per inflorescence, and days from terminal bloom anthesis to shiny black fruit (Perkins-Veazie et al., 1996) for both fruiting structures were recorded.

Subsequently, in early Aug. 2005, three primocanes each of ‘Prime-Jan’ and ‘Prime-Jim’ under two cane management treatments were randomly chosen and flagged for observation: 1) primocanes “soft-tipped” (upper 2-5 cm removed) at 1 m, and 2) un-tipped primocanes. In treatment 1, primocanes were soft-tipped to 1 m on several occasions during the growing season, from 15–29 June 2005, to catch the various flushes of cane growth. In both treatments, only a primocane crop was harvested. Branches on flagged canes for both treatments and cultivars were labeled and photographed daily to observe bloom pattern. Number of branches, node position of branches, branch length, total node count for branches and main canes, number of fruiting nodes, number of fruiting sites, subsequent ripening among branches within a cane, and days from terminal bloom anthesis to shiny black fruit for each branch were recorded for each treatment and cultivar. For the purposes of this paper, data are presented as observational means with no analyses of variance.

RESULTS AND DISCUSSION

Primocane Branching Habit

Primocane emergence for ‘Prime-Jan’ and ‘Prime-Jim’ began in early February 2005 from adventitious buds on roots and the crown. On average, un-tipped primocanes of ‘Prime-Jan’ and ‘Prime-Jim’ developed two lateral branches. When present, branches were always located on nodes near the base of the cane. The un-tipped canes maintained apical dominance and were determinate in growth, thus fruiting sites were always found at the tips of the main cane and branches. Un-tipped primocanes of ‘Prime-Jan’ and ‘Prime-Jim’ averaged 1.8 and 2.0 m in length, respectively. Un-tipped primocanes (main cane + any branches) for ‘Prime-Jan’ averaged 95 total nodes; however, in the current season, only 26 of the total nodes were fruitful on average (Table 1). In ‘Prime-Jim’, total nodes averaged 98, with 19 of those fruitful (Table 1). Fruiting nodes were always located on the upper portion of the main cane and branches. Average branch length for un-tipped canes was 1.3 m for ‘Prime-Jan’ and 1.0 m for ‘Prime-Jim’.

In contrast, soft-tipped canes developed multiple lateral branches just below the...
site of tipping, resulting in an average of five branches per cane for both cultivars. The first three nodes below the site of tipping always developed a lateral branch. Other branches developed sporadically down the 1 m-long cane. Average branch length for soft-tipped canes was 63 and 52 cm for ‘Prime-Jan’ and ‘Prime-Jim’, respectively. On soft-tipped canes (branches only), the average total node number was 90 and 69, of which the average fruiting node number was 49 and 36 for ‘Prime-Jan’ and ‘Prime-Jim’, respectively (Table 1). The main cane on soft-tipped primocanes did not develop fruiting sites, as only lateral branches terminated in inflorescences.

**Primocane Bloom Pattern**

The greatest difference between primocane management techniques was the location of inflorescences and number of flowers per cane. Un-tipped canes and lateral branches on soft-tipped canes developed flowers on a panicle-like cyme (Judd et al., 1999), which terminated in an inflorescence and developed lower, secondary axial fruiting laterals. Bloom pattern for terminal inflorescences and lower fruiting laterals on un-tipped and soft-tipped primocanes was similar for both cultivars. Below the terminal inflorescence on un-tipped and soft-tipped primocanes, 4–7 secondary fruiting laterals generally developed, which were borne from nodes along the main cane or lateral branch.

In un-tipped canes, A1 will refer to the main cane or branch (Fig. 1). In soft-tipped canes, fruiting sites were always found on lateral branches and never on the main cane, thus A1 will refer only to branches (Fig. 1). The terminal flower on the main cane or branch, located on A1, was always the first to open for both cultivars (Fig. 1, “1”). This was followed by a terminal flower on a lower fruiting lateral located on an A2 axis near the basal portion of the inflorescence, agreeing with Takeda (1987). However, the most basal A2 axis in this study was often the last to bloom (Fig. 1, “8”). On soft-tipped and un-tipped primocane inflorescences, it was common to have A3 axes, and occasionally A4 axes. Blooming of A3 axes would begin simultaneously with the last opening of the flower on the upper most A2 axis, which was generally the flower located directly below the terminal flower on the A1 axis. The flower on the most basal A2 axis also opened at the same time, or just after, the opening of the most apical A2 axis flower. Most apical and basal A2 axes consisted of a single flower. The time between the opening of the A1 terminal flower and the first A2 flower was typically 1–3 d for both cultivars. Once the first A2 axis began to bloom, other A2 axes followed acropetally, opening at a constant rate of 2–3 flowers per day. For A2 axes with multiple A3 flowers, a 3–4 d period between A3 flower openings was typical. When present, A4 flowers opened last.

The time from first to last open flower (A1 to A4, respectively) within an inflorescence averaged 17 d for both cultivars and treatments. Un-tipped canes in both cultivars had a similar number of fruiting sites, averaging 49 flowers per cane. Although ‘Prime-Jan’ and ‘Prime-Jim’ had a similar number of total flowers per cane, un-tipped ‘Prime-Jan’ primocanes had fewer fruiting nodes than un-tipped ‘Prime-Jan’ primocanes (Table 1). This may imply that ‘Prime-Jim’ tended to develop more A3 and A4 axes within an inflorescence. Soft-tipped canes, however, averaged 74 and 82 flowers per cane for ‘Prime-Jan’ and ‘Prime-Jim’, respectively. Again, ‘Prime-Jim’ had fewer total fruiting nodes than ‘Prime-Jan’, but a similar number of flowers.

On soft-tipped canes, the most apical lateral branches bloomed within one day of each other. Usually, the most basal of the three was the first to have the terminal flower on A4 fully open, followed by the branches above it, located at nodes 1 and 2 on the main cane. The number of days between branch three A1 and branch four A1 bloom ranged from 2 to 6 d for ‘Prime-Jim’ and ‘Prime-Jan’, respectively. Most of the canes studied had five branches and the number of days to bloom from branch one A1 to branch five A1 ranged from 18 to 21 d for ‘Prime-Jan’ and ‘Prime-Jim’, respectively. Branch bloom pattern on soft-tipped canes was similar for both cultivars.

Once the terminal flowers on upper branches opened, bloom rate and pattern were as described above for both cultivars. Although A1 flowers on the third branch tended to open earlier than the upper two branches, A1 bloom pattern for the remaining lower
branches was basipetal. In both cultivars, a few basal branches remained vegetative, while others were still blooming or fruiting when observations were stopped on 10 Oct., 2005.

In un-tipped primocanes, more variation occurred for branch A1 bloom pattern in both cultivars. In general, the A1 flower on the main cane opened before A1 flowers on basal lateral branches, when present. However, for 'Prime-Jan' one primocane had black fruit on all branches before the A1 flower on the main cane opened. The remaining canes for 'Prime-Jan' and 'Prime-Jim' typically had open basal branch A1 flowers 18–21 d after the A1 flower on the main cane had opened, similar to basal branches on tipped canes. As with soft-tipped primocanes, a few basal branches on un-tipped primocanes remained vegetative at the end of the growing season.

**Primocane Fruit Set and Ripening**

Days from anthesis to shiny black fruit for soft-tipped and un-tipped primocanes was similar, averaging 52 and 46 d for 'Prime-Jan' and 'Prime-Jim', respectively. Percent fruit set tended to be higher on un-tipped canes. 'Prime-Jan' had 83% fruit set on soft-tipped canes, while 'Prime-Jim' had 87% fruit set (Table 1). On un-tipped canes, 'Prime-Jan' had 90% fruit set, while 'Prime-Jim' had 88% fruit set (Table 1).

**Floricane Branching Habit**

Budbreak of overwintered floricanes occurred simultaneously with primocane emergence, in early February. Branches on floricanes were always located towards the basal portion of the main cane, when present. Fruiting sites that had developed the previous year were always found near the upper portion of the main cane and branches, likely because primocanes had not been tipped the previous season and thus maintained apical dominance. Average floricane branch number and branch length for 'Prime-Jan' and 'Prime–Jim' was four and two branches, and 43 and 35 cm, respectively. For 'Prime-Jan', total nodes per cane averaged 105, of which short floral structures accounted for an average of 16, while long floral structures accounted for 32 fruiting nodes (Table 1). For 'Prime-Jim', total nodes per cane averaged 76, of which short floral structures accounted for 25 fruiting nodes, while long floral structures accounted for 12 fruiting nodes (Table 1).

**Floricane Bloom Pattern**

Some floral structures, or short axial inflorescences, were able to overwinter and were always located below the determinate, spent primocane-fruiting tip from the previous year on the main cane and branches. Long axial inflorescences, or floral structures borne from a secondary bud, were sporadically interspersed among the short inflorescences along the main cane and branches and were always located below the determinate primocane-fruiting tip. Short and long inflorescences were borne on secondary axes (A2) located directly on the main cane or branch (A1).

On the main cane and branches, 'Prime-Jan' typically had more long floral structures than 'Prime-Jim'. However, there was no set pattern to the position of short and long floral structures along the main cane and branches identified for either cultivar. Average main cane length for 'Prime-Jan' and 'Prime-Jim' was 2.0 and 1.8 m, respectively.

The order of bloom within an inflorescence was similar for short and long floral structures for each cultivar. The average number of blooms for short, axial inflorescences for both 'Prime-Jan' and 'Prime-Jim' was eight flowers. In contrast, long inflorescences averaged 11 flowers within the floral structure for 'Prime-Jan' and eight flowers for 'Prime-Jim'. Short and long inflorescences were A2 axes borne from nodes located on the main cane or branch, and always terminated in a flower (Fig. 2). Once the terminal flower on A2 had opened, the A3 flowers within the inflorescence opened acropetally, with the exception of the most basal flower, which was typically the last to open (Fig. 2, “7”). The most basal flower would begin to open once two-thirds of the remaining flowers within the inflorescence had opened, followed by A4 flowers, if present. This differs from what
has been reported for floricane bloom pattern of semi-erect blackberries, in which the most basal A2 axis was always the second to open after the terminal flower on A1 (Takeda, 1987). Short and long inflorescences bloomed over a 12-15 d period, depending on the number of flowers within an inflorescence.

Floricane Fruit Set and Ripening

Short floral structures in both cultivars tended to lack leaves, unlike long floral structures. With limited photosynthetic capacity within short floral structures, it is assumed that nutrients for ripening fruits were allocated from cane or root stores or from newly developed leaves on the long floral structures. The earliest observed short structures began blooming in early April, but ovule viability was poor, with fruit set averaging 57 and 47% for ‘Prime-Jan’ and ‘Prime-Jim’, respectively (Table 1). In long floral structures, bloom began in mid-May and fruit set averaged 94 and 87% for ‘Prime-Jan’ and ‘Prime-Jim’, respectively (Table 1). The time from anthesis to black fruit was similar for both cultivars and floral structure types, averaging 57 d. Short floral structures thus had fruit ripening in early to mid-June while fruit on long floral structures ripened in mid-July.

CONCLUSIONS

Short floral structures on floricanes had a lower fruit set than did long floral structures. However, long floral structures on floricanes had a somewhat higher fruit set than did fruiting structures on un-tipped and soft-tipped primocanes. More branches were observed on un-tipped (double-cropped) floricanes compared to un-tipped primocane-only cropped canes. This may be due to better light penetration around the base of floricanes due to fewer vegetative growth flushes common in primocane-only cropping systems.

For both cultivars, soft-tipping primocanes to 1 m nearly doubled the number of flowers per cane compared to un-tipped primocanes, which consistently reached 2 m in length. Although flowers were more abundant in soft-tipped primocanes, percent fruit set was lower than in un-tipped primocanes.

Days from anthesis to shiny black fruit was shorter for primocane-only cropping systems than for double-cropped floricanes. This may be due to warmer temperatures during fruit ripening, as primocanes bloomed in early to mid-August, whereas floricanes bloomed in early to mid-May. Soft-tipped and un-tipped primocane-fruiting structures were more similar to semi-erect floricane-fruiting structures than inflorescences on floricanes of ‘Prime-Jan’ and ‘Prime-Jim’.

Literature Cited


Tables

Table 1. Fruiting characteristics under different cane management techniques and percent fruit set for ‘Prime-Jan’ and ‘Prime-Jim’.

<table>
<thead>
<tr>
<th>Cane management</th>
<th>Avg. frueling nodes/cane&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Avg. # flowers/cane&lt;sup&gt;b&lt;/sup&gt;</th>
<th>% Fruit set</th>
<th>Avg. frueling nodes/cane&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Avg. # flowers/cane&lt;sup&gt;b&lt;/sup&gt;</th>
<th>% Fruit set</th>
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<tr>
<td>Un-tipped primocane</td>
<td>26</td>
<td>50</td>
<td>90</td>
<td>19</td>
<td>48</td>
<td>88</td>
</tr>
<tr>
<td>Soft-tipped primocane</td>
<td>49</td>
<td>74</td>
<td>83</td>
<td>36</td>
<td>82</td>
<td>87</td>
</tr>
<tr>
<td>Floricane: short inflorescence</td>
<td>16</td>
<td>48</td>
<td>57</td>
<td>25</td>
<td>72</td>
<td>47</td>
</tr>
<tr>
<td>Floricane: long inflorescence</td>
<td>32</td>
<td>70</td>
<td>94</td>
<td>12</td>
<td>21</td>
<td>87</td>
</tr>
</tbody>
</table>

<sup>a</sup>total number of nodes/cane (including any branches) that produced an inflorescence or flowering lateral (n=3).

<sup>b</sup>average of total flowers/cane (including any branches) (n=3).
Fig. 1. Structure of bloom pattern of an inflorescence on soft-tipped and un-tipped primocanes. Order of bloom is designated as "1" through "8". Numbered flowers preceded lettered flowers.

Fig. 2. Structure and bloom pattern of short and long floral structures on floricanes. Order of bloom is designated as "1" through "7". Numbered flowers preceded lettered flowers.