Dry Weight Partitioning in Three Phenotypes of Red Raspberry

Juanita Popenoe¹

West Virginia University, Division of Plant and Soil Sciences, Box 6108, Morgantown, WV 26506-6108

Additional index words. *Rubus idaeus*

Abstract. 'Heritage', 'Titan', and 'Boyne' red raspberries (*Rubus idaeus* L.) were grown for 3 years and plots were sampled annually for changes in growth. 'Heritage' is a primocane- and floricane-fruiting, strongly suckering cultivar; 'Boyne' is a floricane-fruiting, strongly suckering cultivar; and 'Titan' is a floricane-fruiting, weakly suckering cultivar. Each year in October, plants of each cultivar were dug from two 0.5-m² plots in each of four rows, separated into roots, crowns, canes (primocanes were harvested in October and floricanes were harvested in July), and leaves, and dried. Fruit were harvested, yields were recorded, and dry weights of subsamples were used to estimate total fruit dry weights. 'Heritage' fruit included the primocane and floricane harvests. 'Heritage' was more yield-efficient than 'Boyne' or 'Titan' in that it allocated a higher percentage of total dry weight to fruit and a lower percentage to vegetative parts. Although 'Titan' had fewer canes, cane diameter and length were greater. 'Boyne' allocated higher percentages of total dry weight to roots than other cultivars. The percentage of total dry weight allocated to fruit was similar for 'Boyne' and 'Titan' in 1992, but lower for 'Boyne' in 1991. Within the cultivars tested, phenotype for suckering did not indicate productivity.

Red raspberries spread by adventitious shoots or root suckers. In nature, this characteristic allows them to colonize an open area quickly and fruit before being out-competed for light by later successional, taller species (Whitney, 1982). In domestic production, this habit is not valued since narrow rows are desired for good light penetration (Braun et al., 1989; Wright and Waister, 1986) and ease of picking (Lawson and Wiseman, 1979). New cultivars have been selected that present less of a problem to the grower by producing fewer root suckers. Root suckers shade the floricanes (Fernandez and Pritts, 1993; Wright and Waister, 1984) and make picking difficult (Lawson and Wiseman, 1979, 1983), although they do not actually take photosynthate from the floricanes (Fernandez and Pritts, 1993). Growth regulators have been used to burn off the early root suckers to reduce competition with floricanes (Crandall et al., 1980), but this method is not practiced universally. New cultivars have been selected that produce fewer root suckers, potentially reducing cane competition and resulting in fewer canes with larger diameters; however, these new cultivars do not necessarily produce greater yields. Canes of greater diameter and length yield better on a per-cane basis but not on an area basis if density is low (Crandall et al., 1974). Suckering cultivars may allocate more C to producing suckers and less to fruit, with a resulting increase in intracane competition and reduced yield per cane. Or, the greater number of canes produced by suckering may increase fruit production on an area basis. The objective of this study was to determine how red raspberries with different phenotypes for suckering partition C between fruit and vegetative parts. Grain breeders have used dry weight partitioning to determine which cultivars maximize yields (Evans, 1975). This technique can offer much insight into productivity.

Received for publication 2 Nov. 1993. Accepted for publication 10 Mar. 1994. Approved for publication by the director of the West Virginia Agriculture and Forestry Experiment Station as scientific article no. 2409. This research was supported by Hatch funds allocated to the West Virginia Agriculture and Forestry Experiment Station. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

¹Present address: 7 Tri-City Rd., #507, Somersworth, NH 03878.

Materials and Methods

Three cultivars were selected for varying suckering ability and planted at the West Virginia Univ. Horticulture Farm in Morgantown. 'Heritage' is a primocane- and floricane-fruiting, strongly suckering cultivar; 'Boyne' is a floricane-fruiting, strongly suckering cultivar; and 'Titan' is a floricane-fruiting, weakly suckering cultivar (Handley, 1989). 'Heritage', 'Boyne', and 'Titan' plants were set 0.5 m apart in a randomized complete-block design of four 8-m sections for each cultivar in Spring 1990. The soil was a moderately well-drained Dormont fine-loamy, mixed, mesic Ultic Hapludalf (Wright et al., 1982). All plants received the same fertilizers and sprays based on current recommendations (Popenoe, 1993; Popenoe et al., 1993). Plants were grown as a hedgerow 0.5 m wide. Fall (primocane) and spring (floricane) crops were harvested for 'Heritage' plots. Harvested fruit were weighed for each 8-m plot and a representative sample was taken to determine dry weight. Total dry weight harvested was then calculated and divided by the appropriate number for reporting, and analysis was based on 0.5-m² subplots. Floricanes were removed from the 0.5-m² plots soon after spring harvest and dried and weighed separately. After harvesting 'Heritage' in the fall, two 0.5-m² subplots were dug from each plot and all roots were recovered with sieves. The plants were then washed and divided into canes, roots, and crowns. Primocanes and floricanes from each subplot were measured for height, diameter 20 cm from the base, and number of nodes. All plant parts were dried and weighed. An effort was made to recover all leaves, which were counted, dried, and weighed. Total leaf weight was calculated by establishing an average leaf weight for primocane and floricane leaves based on the leaves recovered. The total leaf weight was then derived by multiplying the number of nodes counted times the average dry weight for primocanes and floricanes separately, and the total was summed for both cane types. All nodes were assumed to have one leaf, and nodes on laterals and canes were counted.

Analysis of data based on a split plot over time, with year as the main plot and cultivar as the subplot, indicated a significant year, cultivar, and year × cultivar interaction for most variables. Each year was analyzed separately based on a randomized complete-block design with subsampling. Analysis of variance (SAS's Proc

GLM) was used to test the effects of cultivar. Means were separated using Duncan–Waller mean separation. All percentage data were arcsin-transformed before analysis but are presented in original form.

Results and Discussion

This experiment used plants in the first 3 years of establishment, a period when plants are filling out their allotted space and have only approached full yield potential. Because of the different growth habits of the three cultivars, dry weight partitioning should be quite different at this stage of stand development. Plant parts were sampled at the time of year when dry weights should be greatest (Whitney, 1982) and would be only an estimate of a constantly changing value. All plant parts were measured for a 0.5-m² section and, therefore, do not reflect individual plants as much as a section of a solid row. Roots sampled may have been from adjoining plants but are an estimate of the biomass produced by raspberries in 0.5 m². Root, fruit, and shoot biomass were much greater in this study than in Whitney's (1982), but this is probably due to the use of cultivated plants rather than wild and the use of

cultural practices to remove growth limitations. Judging from the dry weights of single canes reported by Wright and Waister (1982), the cane dry weights in this experiment were much lower than would be expected, but again this could be due to cultivars and conditions. The canes in Wright and Waister's (1982) paper were much taller and conditions for growth were much different in a trellised hill system than the hedgerow used in the present experiment.

In raspberries, plant size and yield are determined by individual cane size and cane density. Within any cultivar, cane size, cane density, and yield can be compensatory. If the breeder attempts to increase yield by increasing either cane size or cane density, compensatory changes in the other factor must be avoided. In this study, plant size was similar among the three cultivars, despite their different growth habits, thus providing an excellent opportunity to examine the relationships among component plant parts. The allocation of biomass to shoots, roots, and crowns is hypothesized to differ between different growth habits, but yields should be similar if compensation occurs. This study illustrates that biomass partitioning to fruit varies between cultivars but does not seem to be related to growth habit.

Table 1. Dry-weight partitioning in 'Heritage', 'Titan', and 'Boyne' raspberry plants over 3 years in 0.5-m² plots.

Cultivar	Cane dry wt		Crown dry wt		Root dry wt		Fruit dry wt		Leaf dry wt		Total dry wt
	(g)	(%)	(g)	(%)	(g)	(%)	(g)	(%)	(g)	(%)	
1990											
Heritage	48.9 a ^z	19.8 b	16.7 a	6.8 c	39.6	16.2 b	91.9	37.0	50.0	20.1 c	247.1 a
Titan	42.0 a	32.2 a	16.2 a	12.9 a	34.7	28.2 a	---	---	35.1	26.7 b	128.0 b
Boyne	22.4 b	19.0 b	11.0 b	9.9 b	40.7	36.6 a	---	---	38.8	34.4 a	112.9 b
1991											
Heritage	210.3 a	40.2	61.7	11.5	57.1	11.1 b	120.4 a	24.4 a	70.8	12.8 b	520.2 a
Titan	167.5 ab	34.7	55.8	11.6	61.8	14.0 b	68.5 b	15.4 b	116.5	24.3 a	470.1 ab
Boyne	123.0 b	35.2	47.8	13.7	70.4	21.1 a	32.2 c	9.6 c	76.0	20.5 ab	349.4 b
1992											
Heritage	293.1	38.0 ab	96.8	5.1 b	99.4 b	14.0 b	87.0 a	12.5 a	170.6	22.9 b	746.9
Titan	352.5	40.3 a	125.5	10.2 a	139.0 a	16.6 ab	28.2 b	3.3 b	215.6	25.1 ab	860.7
Boyne	249.6	33.1 b	100.3	8.5 a	158.2 a	21.1 a	32.5 b	4.4 b	209.9	28.2 a	750.5

^zMeans within columns for each year followed by the same letter are not significantly different by Duncan–Waller mean separation at $P = 0.05$; $n = 4$.

Table 2. Cane measurements of 'Heritage', 'Titan', and 'Boyne' raspberry plants over 3 years in 0.5-m² plots.

	No. of nodes ^z	No. of canes	Avg cane length (cm)	Total cane length (cm)	Avg cane diam (mm)
Treatment					
1990					
Heritage	106.9	7.3 a ^y	60.7 b	443.5 a	5.9 b
Titan	82.6	2.9 b	81.0 a	235.0 b	8.3 a
Boyne	87.6	3.1 b	70.6 b	218.9 b	6.3 b
1991					
Heritage	646 a	36.5 a	52.4 a	1913.0 a	4.0 b
Titan	430 b	18.5 b	54.1 a	1000.5 b	4.6 a
Boyne	548 ab	35.3 a	33.3 b	1175.3 b	3.5 c
1992					
Heritage	827.5	34.1 a	75.5 ab	2575.3	6.7 b
Titan	621.1	17.3 b	98.7 a	1708.0	8.5 a
Boyne	850.4	33.0 a	65.6 b	2163.7	6.4 b

^zIncludes laterals.

^yMeans within columns for each year followed by the same letter are not significantly different by Duncan–Waller mean separation at $P = 0.05$; $n = 4$.

'Heritage' plants had consistently greater total and fruit dry weights and a higher percentage of total dry weight in fruit per 0.5-m² section (Table 1). 'Heritage' also consistently had the lowest percentage of total dry weight allocated to roots and crowns. The commercial popularity of 'Heritage' (Daubeney et al., 1992) may be due to the fact that it consistently outyields the other cultivars by allocating nearly twice as much dry weight to fruit production. 'Heritage' produces a crop in the fall on the tips of the primocanes and in the spring on the remaining length of these canes (floricanes). In this experiment, 56% and 89% of the crop was produced on the primocanes in 1991 and 1992, respectively. This should not bias the estimate of C partitioning, because the number of fruiting sites is determined by the number of nodes on the canes and not by the season in which the fruit is borne. In areas with shorter growing seasons, 'Heritage' fruits mainly on the floricanes (Skirvin and Otterbacher, 1979).

'Titan' had the least number of canes; however, the canes had the greatest lengths and diameters (Table 2). Thus, the total cane dry weights were not very different from the strongly suckering 'Heritage' and 'Boyne' (Table 1). A weakly suckering cultivar such as 'Titan' may allocate a higher percentage of total dry weight to fruit rather than canes to compensate for the reduced number of canes (Crandall et al., 1974); however, 'Titan' canes were of greater diameter and longer than those of the other cultivars tested, traits associated with greater yield per cane. However, on a 0.5-m² basis, 'Boyne' and 'Titan' had similar yields, especially as the 'Boyne' canes filled in the row in the third year, illustrating yield compensation between cane density and cane size.

'Boyne' and 'Heritage' are strongly suckering cultivars that may increase the percentage of total dry weight allocated to roots and crowns compared to weakly suckering cultivars (Whitney, 1982), because an extensive root system can rapidly exploit allotted space. 'Boyne' allocated the lowest percentage of dry weight to canes and the highest percentage to roots of the three cultivars tested (Table 1). 'Heritage' did not fit the hypothesis, however, allocating less to roots and crowns than 'Boyne' and 'Titan'. 'Boyne' allocated a lower percentage of total dry weight to fruit than 'Heritage', although 'Boyne' is considered to yield well (Handley, 1989). Strongly suckering cultivars do not necessarily have greater biomass partitioning to the roots and crowns.

'Heritage' was the most productive cultivar, allocating a higher percentage of total dry weight to fruit than the other cultivars tested, although plant size was similar, the reasons for which should be investigated further. 'Heritage' may be more efficient photosynthetically, or the effect of a fruit sink demand in the summer and fall may increase photosynthesis. Alternatively, light interception or canopy architecture may be somewhat different in this cultivar.

Growth habit does not indicate biomass efficiency. 'Boyne' had high allocations of total dry weight to roots and crowns and reduced allocations to fruit during this experiment. 'Boyne', released in 1960, is an older cultivar that seems to be more closely related to an aggressively colonizing wild type, a trait very useful for marginal climates. 'Titan' had reduced cane numbers with increased cane diameter and length, resulting in similar cane dry weights as the other cultivars. Percentage of total dry weight allocated to fruit was similar to that of the strongly suckering 'Boyne' in 1992 (although intermediate in 1991). 'Titan' was produced in 1986 from the same breeding program that produced

'Heritage' in 1969 (Dale et al., 1993) and is popular for its exceptional fruit size, although it does not exhibit higher dry weight partitioning to fruit. 'Heritage', a strongly suckering cultivar, was the most yield efficient. Selecting cultivars for increased partitioning to fruit may be time consuming, but could be useful to *Rubus* breeders screening new cultivars with greater yields. Although compensation between cane size and cane density occurs, plant genotypes differ greatly in allocation to fruit, shoots, canes, and crowns. From this small population, it can be seen that genotypes that allocate a higher percentage of biomass to fruit are not necessarily smaller plants nor are their growth habits different from other, less-efficient cultivars.

Literature Cited

- Braun, J.W., J.K.L. Garth, and C.A. Brun. 1989. Distribution of foliage and fruit in association with light microclimate in the red raspberry canopy. *J. Hort. Sci.* 64:565-572.
- Crandall, P.C., D.F. Allmendinger, J.D. Chamberlain, and K.A. Biderbost. 1974. Influence of cane number and diameter, irrigation, and carbohydrate reserves on the fruit number of red raspberries. *J. Amer. Soc. Hort. Sci.* 99:524-526.
- Crandall, P.C., J.D. Chamberlain, and J.K.L. Garth. 1980. The effects of chemical primocane suppression on growth, yield, and chemical composition of red raspberries. *J. Amer. Soc. Hort. Sci.* 105:194-196.
- Dale, A., P.P. Moore, R.J. McNicol, T.M. Sjulín, and L.A. Burmistrov. 1993. Genetic diversity of red raspberry varieties throughout the world. *J. Amer. Soc. Hort. Sci.* 118:119-129.
- Daubeney, H., K. Maloney, and G.R. McGregor. 1992. 'Heritage' red raspberry. *Fruit Var. J.* 46:2-3.
- Evans, L.T. 1975. Crops and world food supply, crop evolution, and the origins of crop physiology, p. 1-22. In: L.T. Evans (ed.). *Crop physiology*. Cambridge Univ. Press, Cambridge, U.K.
- Fernandez, G.E. and M.P. Pritts. 1993. Canopy manipulation effects on vegetative and reproductive growth of 'Titan' red raspberry. *HortScience* 28:259. (Abstr.)
- Handley, D. 1989. Plant selection, p. 27-36. In: M. Pritts and D. Handley (eds.). *Bramble production guide*. Northeast Regional Agr. Eng. Serv.
- Lawson, H.M. and J.S. Wiseman. 1979. Effects of raspberry suckers, growing in the alleys between the rows, on cane and fruit production in a non-cultivated plantation. *Hort. Res.* 19:63-74.
- Lawson, H.M. and J.S. Wiseman. 1983. Techniques for the control of cane vigour in red raspberry in Scotland; effects of timing and frequency of cane removal treatments on growth and yield in cv Glen Cova. *J. Hort. Sci.* 58:247-260.
- Popenoe, J. 1993. Growing brambles in West Virginia. *West Virginia Univ. Ext. Serv. Publ.* 845.
- Popenoe, J., P. Powell, and J. Baniecki. 1993. *West Virginia commercial small fruit and grape spray guide*. West Virginia Univ. Ext. Serv. Publ. 865.
- Skirvin, R. M. and A. G. Otterbacher. 1979. Effects of single and double cropping on yields of fall bearing raspberries. *Fruit Var. J.* 33:144-148.
- Whitney, G. 1982. The productivity and carbohydrate economy of a developing stand of *Rubus idaeus*. *Can. J. Bot.* 60:2697-2703.
- Wright, E.L., C.H. Delp, K. Sponaugle, C. Cole, J.T. Ammons, J. Gorman, and F.D. Childs. 1982. Soil survey of Marion and Monongalia counties, West Virginia. U.S. Dept. of Agr., Soil Conservation Serv.
- Wright, C.J. and P.D. Waister. 1982. Within-plant competition in the red raspberry. II. Fruiting cane growth. *J. Hort. Sci.* 57:443-448.
- Wright, C.J. and P.D. Waister. 1984. Light interception and fruiting cane architecture in the red raspberry grown under annual and biennial management systems. *J. Hort. Sci.* 59:395-402.
- Wright, C.J. and P.D. Waister. 1986. Canopy structure and light interception in the red raspberry. *Acta Hort.* 183:273-283.