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Nitrogen uptake, partitioning and remobilization in 'Kotata' blackberry in alternate-year production

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SUMMARY
Mature 'Kotata' trailing blackberry plants growing in the alternate-year (AY) system in the field, were treated with ammonium sulfate depleted in ^{15}N in early April, 1997. Based on the whole plant, excluding roots, accumulation of new dry matter over the two year AY production cycle averaged 5.96 kg plant^{-1}. On average, 28, 64 and 8% of this new dry-matter accumulation could be attributed to harvested fruit; loss from the crop as prunings and leaf senescence; and increased dry matter in the crowns for the next growth cycle, respectively. On average, 46% of new dry matter accumulation occurred in the off-year (non-producing). Whole plant (excluding roots) accumulation of new N (labelled and non-labelled) over the two-year AY production cycle averaged 63.7 g N plant^{-1}. Over a two-year production cycle, 44% of new N accumulation occurred in the off-year. Of the newly accumulated N, 37% was in harvested fruit, 58% was lost from the crop as prunings, and 5% was accumulated in crowns for the next growth cycle. For both the on-year and the off-year plants fertilized with labelled N, near maximum nitrogen derived from fertilizer (NDFF) accumulation occurred by August. At this time, 45% of the applied fertilizer could be accounted for in the non-root portion of on-year plants. A portion of this maximum on-year accumulation was either lost from the system or translocated to the roots. At the time of maximum accumulation, 39, 37, 19, 3 and 2% of the accumulated NDFF was contained in the fruit, laterals, primocanes plus primocane leaves, floricanes, and crowns, respectively. Labelled N applied in the off-year was used primarily for primocane and primocane leaf growth. A large portion of the nitrogen stored in the off-year was used for early growth of floricanes, fruiting laterals and fruit in the following on-year. Excluding roots, by the end of the 1997 season, almost 30% of the applied fertilizer was accounted for in the non-root portion of off-year plants. There was also evidence of remobilization of N among plant tissues at different times during the production cycle. Results of this study suggest fertilizer N is an important N source for fruiting lateral and fruit growth in the on-year and for new primocane and primocane leaf growth in the off-year. N accumulated in the off-year is also an important source for early growth of floricanes, fruiting laterals and fruit the following year.

Appropriate nitrogen (N) fertilization is a key component in the achievement of optimum crop yield and quality in perennial horticultural crops. An understanding of crop N accumulation, partitioning and remobilization is critical for the development of N fertilization strategies for such crops. Very little information has been reported on these processes in *Rubus* spp.

Oregon is the leading producer of blackberry (*Rubus* L. subspecies *Rubus* Watson) worldwide. Primarily, trailing types such as 'Marion', 'Thornless Evergreen', and 'Kotata' are grown. Trailing blackberries have very long canes, requiring trellis support, and a lower planting density than erect and semi-erect blackberries (Moore and Skirven, 1990).

Roots and crowns are perennial in blackberry, whereas shoots are biennial. Blackberry shoots are vegetative the first year (primocanes), and reproductive the second year (floricanes), after which the floricanes die. Trailing blackberries are grown in either every-year (EY) or alternate-year (AY) production systems. In conventional EY production, fruit is produced every year, with primocanes and floricanes present on the plant (Strik, 1992). After harvest, floricanes are removed and primocanes are trained onto the trellis. In AY production, fruit is produced every other year. Only primocanes grow in the non-productive year (off-year); these over-winter, becoming floricanes the following year (on-year). In October, at the end of the season of the on-year, all the canes are removed, and a new cycle begins. Yield in AY production is 70 to 90% of yield in EY production over a two year cycle (Bullock, 1963; Sheets *et al.*, 1975), but can have lower production costs (Burt *et al.*, 1987; Eleveld *et al.*, 2001).

Yield of blackberry was highest at 67 kg N ha^{-1} for 'Thornless Evergreen' trailing blackberries in EY production in Oregon (Nelson and Martin, 1986), was not affected by N fertilization for 'Arapaho' erect blackberry in Arkansas (Naraguma and Clark, 1998), but increased with increasing N rate to 123 kg N ha^{-1} for 'Hull Thornless' semi-erect blackberries in Kentucky (Archbold *et al.*, 1989). In comparison, Oregon State University recommendations for trailing blackberries are 56 to 78 kg N ha^{-1} in spring (Hart *et al.*, 1992). Raspberry yield response to N fertilization has been limited and inconsistent (Dean *et al.*, 2000; Kowalenko, 1981). Lawson and Waister (1972) in Scotland found

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increased N fertilization increased yield in the first and second cropping year of raspberry production, but had no effect or decreased yield in later cropping years, suggesting that crop response varies with age of the stand.

Nitrogen accumulation in field-grown trailing blackberry has not been reported. In pot culture, N accumulation of 'Chester Thornless' blackberry was 0.9 and 2.1 g $plant^{-1}$, including roots, after one and two years of growth, respectively (Malik *et al.*, 1991). Nitrogen uptake for the above-ground portion of EY production raspberries in British Columbia ranged from 76 to 107 kg N ha^{-1} among N treatments (Dean *et al.*, 2000), and from 85 to 122 kg N ha^{-1} among years (Kowalenko, 1994). Similar quantities of N were accumulated in floricanes and primocanes.

In 'Chester Thornless' and 'Arapaho' blackberry in EY production, new fertilizer N was allocated primarily to new growth (primocanes, primocane leaves, and fruit), and fertilizer N accumulation continued in these tissues until late in the growing season (Malik *et al.*, 1991; Naraguma *et al.*, 1999). Little redistribution of the accumulated fertilizer N in the primocanes occurred in the subsequent growing season, therefore much of the stored N was recovered in the floricanes (previous year primocanes) the following season (Malik *et al.*, 1991).

The objective of this study was to use a single rate of soil applied ^{15}N-depleted fertilizer to study the accumulation, partitioning and remobilization of N, over a two-year period in 'Kotata' blackberry plants grown in AY production. Use of AY production allows these N processes to be studied when the crop is primarily in vegetative (off-year) and in reproductive (on-year) growth.

MATERIALS AND METHODS

The experiment was conducted in 1997 and 1998 using a 'Kotata' blackberry planting established in 1987 at the North Willamette Research and Extension Center, Aurora, Oregon and grown in the AY system. Plants were spaced 2.4 m within rows spaced 3.0 m apart. Rows were oriented north to south on level ground. The trellis consisted of posts with two horizontal wires, one at the top (1.8 m) of the trellis and another at 1.2 m above the ground. The planting was on a Quatama series soil (fine-loamy, mixed mesic Aqualtic Haploxeralfs). Texture (pipette method) of the surface soil (0–15 cm) was 53% sand, 16% silt and 31% clay (sandy clay loam). Soil organic matter content (loss on ignition at 450°C) was 5.3, 5.1 and 4.0% and soil pH (1:2 soil: 0.01 M CaCl) was 5.4, 5.0, and 5.2, for 0–15, 15–30, and 30–60 cm depth, respectively. Weeds were managed using pre-emergent herbicides in spring and fall and hoeing where necessary. Irrigation was with overhead sprinklers at a rate of 3–5 cm once a week during the dry season. All plant parts above the crown were removed in October at the end of the on-year. Half the treated plots were in the on-year, and half were in the off-year, in any given year during the study.

On 5 April 1997, 80 plants, half in the on-year and half in the off-year, were given a soil application of 500 ml of a 40% (w/v) solution of ammonium sulfate depleted in ^{15}N (0.05 atom % ^{15}N) at a rate of 42 g N per plant (equivalent to 56 kg ha^{-1}). The labelled fertilizer was poured on and around each crown in a 0.5 m diameter circle, followed by 4 l of water to move the fertilizer into the root zone.

Throughout the 1997 growing season, four single on-year plant replicates were randomly selected and destructively harvested on each of five dates: three weeks after fertilizer application (24 April), flowering (12 June), fruit maturity (14 July), time of typical floricane removal in EY production systems (11 August), and late season (14 October). Four single off-year plant replicates were sampled on the same dates. On 17 March 1998, of the second year, only non-labelled ammonium sulfate was applied in the same manner and rate as in 1997, so that redistribution within the plant of the labelled N applied in 1997 could be measured. The 1998 sampling dates followed the same pattern as for 1997: 15 April, 18 June, 17 July, 12 August, and 13 October.

On each sampling date in both years, the sampled plants were partitioned into roots, crown, primocanes, primocane leaves, floricanes, fruiting laterals (with leaves), and immature and ripe fruit, if present. Due to the difficulty of accurately recovering the entire root system, a subsample was taken from the root tissues within 0.4 m of the crown. The separated tissues were dried at 60°C to a constant weight. Canes were cut into lengths of approximately 5 to 8 cm. Each tissue type was separately mixed and homogenized in a large paper bag, and a random 50–100 g subsample of tissue selected and ground to pass a 0.6 mm (40 mesh) screen. Woody crown tissue was subsampled by collecting the shavings from drilling 5–10 holes with a 14 mm bit which were then dried and ground as described above. Two gram sub-samples of each of the ground tissues were sent to Isotope Services (Los Alamos, NM) for analysis of total N concentration and ^{15}N by mass spectrometry.

On-year plant total fresh fruit yield was collected every 3–5 d throughout the harvest season. Total fruit dry matter was estimated from the fresh and freeze-dried weight of a ten fruit subsample from each harvest (n = 4). The freeze-dried fruit were ground and analysed for concentrations of total N and ^{15}N on each harvest date as described above. Average seasonal fruit N and ^{15}N concentrations were calculated.

Atom percent values were converted to the proportion of the nitrogen derived from fertilizer (NDFF), using standard conversions (Hauck and Bremner, 1976):

$$\text{NDFF} = \frac{(^{15}\text{N}_{\text{natural abundance}}) - (\text{atom \% }^{15}\text{N})_{\text{tissue}}}{(^{15}\text{N}_{\text{natural abundance}}) - (\text{atom \% }^{15}\text{N})_{\text{fertilizer}}}$$

The ^{15}N natural abundance was assumed equal to 0.366 atom percent.

The presence of any residual ^{15}N remaining in the soil was determined using barley (*Hordeum vulgare* L.) as an indicator plant. On 4 May 1998, 'Baronesse' spring barley was hand seeded directly in the areas where the last eight blackberry plants had been sampled in April, and on two bare soil check plots where no ^{15}N had been applied. The above-ground portion of the barley in a 0.5 m diameter circle chosen to match the location of fertilizer application was hand harvested on 17 July

TABLE I

Dry-matter accumulation (g) in 'Kotata' trailing blackberry by plant component and for the whole plant (excluding roots) in the off-year and on-year for two growing seasons

	Off-year				On-year							
Month	Crown	Primo-cane	Primo-cane leaves	Above ground plant[Z]	Crown	Primo-cane	Primo-cane leaves	Flori-cane	Laterals	Unripe fruit	Ripe fruit	Above-ground plant[Z]
1997												
Apr.	756b[Y]	9e	16d	781d	854	7c	4c	1350	580bc	na	na	2794b
June	762b	459d	460c	1681c	690	174bc	198ab	1371	1113a	676	na	4222a
July	1010a	839c	897ab	2746b	847	307ab	244ab	1465	620b	543	271	4296a
Aug.	941ab	1193b	1020a	3153b	909	433a	306a	1169	1272a	na	na	4088a
Oct.	1091a	2056a	835b	3982a	868	339ab	178b	1600	351c	na	na	3336b
LSD	235	227	165	487	187	193	123	438	268	190	na	581
1998												
Apr.	889	10d	10b	910c	1108b	5c	1c	2004	462c	na	na	3578c
June	900	371cd	521a	1793b	1081b	105c	90bc	1753	816a	880a	na	4724ab
July	928	770ab	652a	2350ab	1175b	203bc	184ab	2034	771a	250b	297	4913a
Aug.	1059	693bc	556a	2309ab	1031b	339b	254a	1834	664ab	na	na	4122bc
Oct.	1282	1127a	729a	3138a	1776a	685a	234a	2125	557bc	na	na	5376a
LSD	352	387	289	865	330	206	99	481	188	286	na	667

[Z]Excludes roots.
[Y]Means followed by the same letter within a column are not significantly different (P>0.05) based on a protected LSD test.
na – not applicable.

1998, dried, ground, and analysed for concentrations of N and ^{15}N as described previously.

The experimental design was completely random. Individual plants were the experimental units with date of plant digging/analysis replicated four times. All plants were treated with the same rate of nitrogen, so the only "treatment" was date. Analysis of variance was performed for date effects separately for on-year and off-year plant variables in each calendar year using the general linear model procedure of SAS (SAS Institute Inc. 1990). The sampling date means were compared using a protected least significant difference (LSD) test.

RESULTS

Dry-matter accumulation

Total dry matter (excluding roots) increased during the off-year from April to October (Table I; Figure 1). Crown and primocane dry matter also increased throughout the growing season. Combined primocane and primocane leaf dry matter exceeded crown dry matter by June in both years (Table I).

In the on-years, total dry matter (excluding roots) increased from April to July, with maximum dry-matter accumulation measured in July of 1997 and in October of 1998 (Table I). Crown dry matter was relatively constant in 1997, but in 1998 an increase in crown dry matter occurred in October. Primocane dry matter increased from April to October. Dry-matter accumulation in fruiting laterals occurred early in the growing season, with near maximum accumulation in June. In contrast, floricane dry-matter accumulation did not vary significantly among sampling dates. Cumulative total yield of fruit, harvested every 3–5 d during the first three weeks in July for all on-year plants, was 9.4 and 10.0 kg plant^{-1} in 1997 and 1998, respectively, with a mean fruit mass of 3.5 g fresh wt. The two-year average cumulative total dry-matter yield of fruit was 1.6 kg plant^{-1} (Figure 1).

Based on the whole plant excluding roots, accumulation of new dry matter over the two year AY production cycle averaged 5.96 kg plant^{-1}, equivalent to 8.0 t ha^{-1} (Figure 1). On average, 28, 64 and 8% of the new dry-matter accumulation could be attributed to harvested

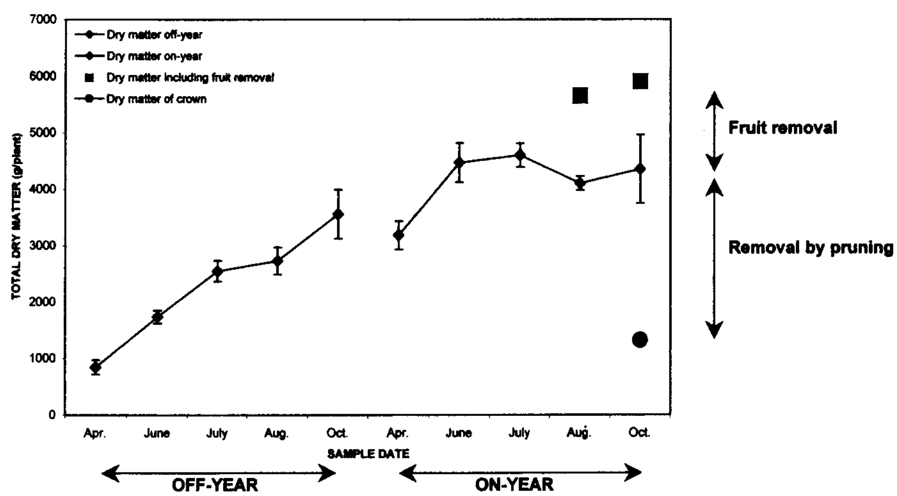

FIG. 1

Seasonal changes in total, non-root dry matter averaged over two years for 'Kotata' blackberry grown in an alternate-year production system. Plants were fertilized on 5 April 1997 and 17 March 1998 with 42 g N per plant as ammonium sulfate. Arrows on the figure indicate the amount of dry matter removed by fruit harvest and pruning.

TABLE II

Nitrogen concentration (g kg^{-1}) in 'Kotata' trailing blackberry by plant component and for the whole plant in the off-year and on-year for two growing seasons

	Off-year				On-year							
Month	Roots	Crown	Primo-cane	Primo-cane leaves	Roots	Crown	Primo-cane	Primo-cane leaves	Flori-cane	Laterals	Unripe fruit	Ripe fruit
1997												
Apr.	12.6ab[Z]	6.7a	30.7a	30.3a	13.9a	6.9	29.3a	33.6a	8.5a	28.9a	na	na
June	12.9a	5.5bc	16.7b	29.1a	12.6ab	6.3	11.6bc	28.1b	7.4ab	22.1b	28.5	na
July	10.9bc	5.0c	10.5c	22.6b	10.7b	6.5	9.9bc	23.0c	6.4b	20.2b	31.1	17.0
Aug.	10.4c	5.3c	8.7c	20.7bc	10.7b	6.3	12.4b	20.6d	7.4ab	16.2c	na	na
Oct.	9.4c	6.5ab	7.0c	18.3c	11.1b	7.2	9.5c	18.5d	4.7c	8.0d	na	na
LSD	1.7	1.0	3.6	3.6	2.4	0.9	2.8	2.1	1.4	2.2	9.8	na
1998												
Apr.	16.5a	8.6	29.7a	35.8a	17.7a	8.0a	31.3a	43.9a	10.6a	30.8a	na	na
June	14.9ab	7.7	14.4b	25.2b	11.5b	6.5b	12.5b	27.7b	7.5b	22.4b	29.1a	na
July	11.9bc	7.5	11.2c	20.5d	12.5b	5.9b	9.6c	21.8c	7.9b	18.9c	23.5b	14.2
Aug.	16.8a	7.5	9.8cd	23.4c	10.2b	6.2b	9.5c	19.8cd	6.9b	15.5d	na	na
Oct.	9.5c	8.3	7.8d	17.3e	11.2b	6.7b	9.1c	17.4d	6.8b	8.9e	na	na
LSD	3.7	1.4	2.4	1.6	4.1	0.9	2.1	2.9	1.2	2.6	1.5	na

[Z]Means followed by the same letter within a column are not significantly different (P>0.05) based on a protected LSD test.
na – not applicable.

fruit; loss from the crop as prunings and leaf senescence (could not be determined); and increased dry matter in the crowns for the next growth cycle, respectively. On average, 46% of new dry-matter accumulation occurred in the off-year (Figure 1).

Nitrogen accumulation

In the off-year, N concentration decreased during the growing season in primocanes and primocane leaves, but changed little in crowns (Table II). Root N concentration also generally decreased as the growing season progressed.

In the on-year, N concentration in primocanes, primocane leaves, floricanes and laterals generally decreased over the growing season, although N concentrations were generally lower and changed less over time for floricanes than for other plant tissues (Table II). As in the off-year, crown N concentration changed little over time, and root N concentration decreased slightly over time. Average fruit N concentration was 14 g kg^{-1}, with a significant increase during peak harvest to maximum values of 15 and 16 g kg^{-1} in 1997 and 1998, respectively.

In the off-year, whole plant (excluding roots) N accumulation increased from April to October (Figure 2), with maximum accumulation occurring by June of 1997 and by July of 1998 (Table III). Much of this increase occurred in the primocanes and primocane leaves (Table III).

In the on-year, average whole plant (excluding roots) N accumulation increased from April to June, then decreased in October (Table III; Figure 2). A total of 24.8 g N plant^{-1} in 1997, and 22.4 g N plant^{-1} in 1998 were harvested in fruit from on-year plants. In June, an average of 33, 32, 17, 9 and 8% of the accumulated N was in the fruit, laterals, floricanes, crowns, and primocanes plus primocane leaves, respectively.

Based on the two-year average, 37% of the new accumulated N could be attributed to harvested fruit, 58% was removed from the plant as prunings, and 5% was accumulated in crowns for the next growth cycle. On

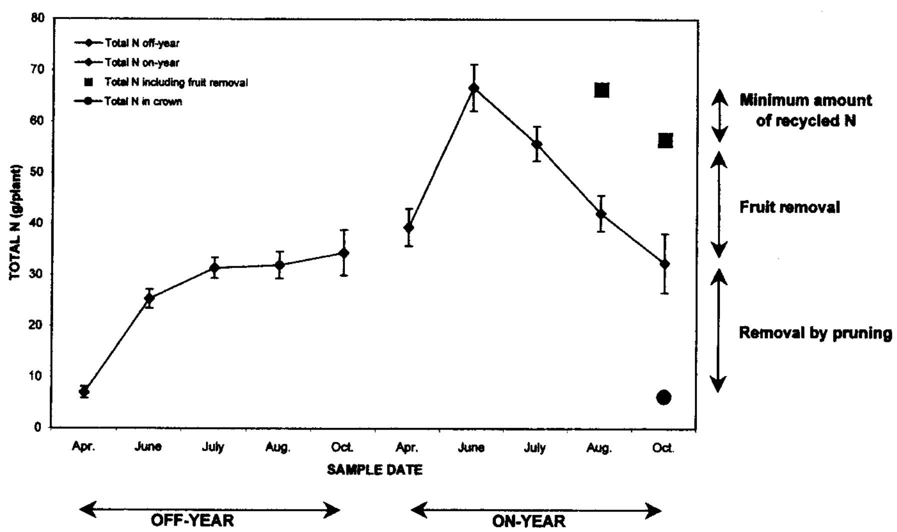

FIG. 2

Seasonal change in total, non-root N averaged over two years for 'Kotata' blackberry grown in an alternate year production system. Plants were fertilized on 5 April 1997 and 17 March 1998 with 42 g N per plant as ammonium sulfate. Arrows on the figure indicate a minimum estimate of recycled N, the amount of N removed by fruit harvest and the amount of N removed at post-harvest pruning.

TABLE III
Nitrogen accumulation (g plant^{-1}) in 'Kotata' trailing blackberry by plant component and for the whole plant (excluding roots) in the off-year and on-year for two growing seasons

	Off-year				On-year							
Month	Crown	Primo-cane	Primo-cane leaves	Above ground plant[Z]	Crown	Primo-cane	Primo-cane leaves	Flori-cane	Laterals	Unripe fruit	Ripe fruit	Above-ground plant[Z]
1997												
Apr.	4.9b	0.3d	0.5d	5.7c	5.9a	0.2c	0.1c	11.5	16.7bc	na	na	34.4c
June	4.2b	7.7c	13.4c	25.3b	4.4b	2.0b	5.4ab	10.1	24.6a	19.1	na	65.7a
July	5.0b	8.9bc	20.2ab	34.1a	5.5ab	2.9b	5.6ab	9.4	12.5c	17.6	4.6	58.1a
Aug.	4.9b	10.4b	21.1a	36.4a	5.7a	5.3a	6.3a	8.6	21.0ab	na	na	46.9b
Oct.	7.1a	14.4a	15.5bc	37.0a	6.2a	3.2b	3.3b	7.4	2.8d	na	na	22.9d
LSD	1.4	2.5	4.9	7.2	1.2	1.5	2.5	3.2	6.5	11.0	na	8.7
1998												
Apr.	7.6	0.3c	0.4b	8.3b	8.9b	0.2c	0.03c	21.2a	14.1ab	na	na	44.4bc
June	6.8	5.3b	13.1a	25.3a	7.0b	1.3bc	2.5b	13.1b	18.3a	25.5a	na	67.7a
July	6.9	8.4a	13.3a	28.7a	6.9b	1.9bc	4.1ab	16.0b	14.5ab	5.9b	4.2	53.5b
Aug.	8.0	6.8ab	12.7a	27.5a	6.3b	3.1b	5.0a	12.6b	10.3b	na	na	37.4c
Oct.	10.5	8.6a	12.6a	31.8a	12.0a	6.5a	4.0ab	14.4b	4.9c	na	na	41.9c
LSD	2.7	3.0	5.4	8.6	2.7	2.5	2.2	5.1	4.6	6.8	na	9.4

[Z]Excludes roots.
[Y]Means followed by the same letter within a column are not significantly different (P>0.05) based on a protected LSD test.
na – not applicable.

average, 44% of new N accumulation occurred in the off-year.

Crop nitrogen derived from fertilizer

Year of fertilizer application: Following fertilization of off-year plants with ^{15}N-depleted fertilizer in early April 1997, the percentage of the N which was derived from fertilizer (%NDFF) increased during the growing season for all plant tissues (Table IV). The %NDFF was highest for primocanes and primocane leaves, intermediate for roots, and lowest for crowns. For plants in the on-year in 1997, %NDFF increased over the growing season for all tissues except the primocanes and fruit (Table IV). A large increase in %NDFF occurred between the April and June sampling dates for primocane leaves and laterals, whereas much of the increase in %NDFF for floricanes, crowns and roots occurred after July.

The mass of NDFF accumulated in the whole plant (excluding roots) in the off-year increased over the growing season with a maximum value of 13.0 g plant^{-1} measured in August (Table V; Figure 3). A large increase in NDFF accumulation occurred between April and June, primarily in primocanes and primocane leaves, immediately after fertilizer application (Table V).

In the on-year, NDFF in plants increased rapidly from April to June, reached a plateau in June and July, and then decreased from July to October (Table V; Figure 4). On the June sampling date, 39, 37, 19, 3 and 2% of the accumulated NDFF was contained in the fruit, laterals, primocanes plus primocane leaves, floricanes, and crowns, respectively. Fruit harvested from on-year plants averaged 30.5 %NDFF, and contained an average of 7.6 g NDFF plant^{-1} (data not presented).

On average, 0.01 %NDFF was measured in barley grown in 1998, following blackberry plants which had received ^{15}N depleted fertilizer in April of 1997 and were harvested in October 1997. Barley grown on soil which had not received ^{15}N depleted fertilizer in 1997 or 1998 had <0.01 %NDFF. It was therefore assumed for the purposes of this study that the quantity of ^{15}N depleted fertilizer applied in spring of 1997 which was supplied to blackberry plants in 1998 from the soil was negligible. Consequently, it is also assumed that all

TABLE IV
Percentage of accumulated N in 'Kotata' trailing blackberry, derived from fertilizer applied to off-year and on-year plants in spring of 1997, by plant component for two growing seasons

	Off-year				On-year							
Month	Roots	Crown	Primo-cane	Primo-cane leaves	Roots	Crown	Primo-cane	Primo-cane leaves	Flori-cane	Laterals	Unripe fruit	Ripe fruit
1997												
Apr.	7b[Z]	7bc	26c	25b	10d	8b	18	16b	3c	5b	na	na
June	18a	6c	28bc	27b	15cd	7b	39	33a	4bc	19a	28	na
July	19a	7c	31bc	33ab	18c	7b	38	44a	6bc	23a	28	29
Aug.	24a	10b	38a	40a	26b	14a	43	39a	14a	21a	na	na
Oct.	25a	13a	35ab	38a	36a	13a	40	43a	10ab	21a	na	na
LSD	7	3	6	8	7	2	17	12	7	10	27	na
1998												
Apr.	28a	13	23a	26a	32a	15	27a	22a	35	34a	na	na
June	29a	11	13b	13b	23bc	15	18b	15b	30	23b	20	na
July	23ab	8	11b	14b	30ab	9	17bc	14b	32	22b	25	19
Aug.	18bc	7	10b	11b	24abc	13	19b	12b	32	18b	na	na
Oct.	15c	10	10b	10b	20c	13	13c	14b	37	25b	na	na
LSD	8	5	6	8	8	5	5	5	7	8	11	na

[Z]Means followed by the same letter within a column are not significantly different (P>0.05) based on a protected LSD test.
na – not applicable.

TABLE V

Mass of accumulated N (g plant^{-1}) in 'Kotata' trailing blackberry, derived from fertilizer applied to off-year and on-year plants in spring of 1997, by plant component and for the whole plant (excluding roots) for two growing seasons

	Off-year				On-year							
Month	Crown	Primo-cane	Primo-cane leaves	Above ground plant[Z]	Crown	Primo-cane	Primo-cane leaves	Flori-cane	Laterals	Unripe fruit	Ripe fruit	Above-ground plant[Z]
1997												
Apr.	0.36bc[Y]	0.06c	0.12d	0.55d	0.45b	0.04d	0.02c	0.32	0.88b	na	na	1.71b
June	0.25c	2.14b	3.63c	6.01c	0.29b	0.72c	1.84ab	0.42	4.85a	5.14	na	13.25a
July	0.36bc	2.61b	6.77ab	9.74b	0.39b	1.02bc	2.44a	0.61	2.80ab	5.25	1.39	13.89a
Aug.	0.51b	4.01a	8.44a	12.95a	0.80a	2.21a	2.33ab	1.21	4.60a	na	na	11.15a
Oct.	0.99a	5.22a	6.72bc	12.93ab	0.84a	1.26b	1.39b	0.81	0.57b	na	na	4.87b
LSD	0.19	0.99	2.3	3.18	0.18	0.52	1.01	0.76	2.35	7.54	na	4.29
1998												
Apr.	1.02	0.07	0.10b	1.19	1.38a	0.04c	0.01b	7.34a	4.79a	na	na	13.56ab
June	0.80	0.67	1.69a	3.15	1.05ab	0.24c	0.37a	3.95b	4.05ab	5.12a	na	14.77a
July	0.55	0.91	1.85a	3.31	0.59b	0.34bc	0.58a	5.11b	3.19b	1.39b	0.80	12.00b
Aug.	0.55	0.75	1.41a	2.71	0.79b	0.59ab	0.57a	4.05b	1.82c	na	na	7.81c
Oct.	1.09	0.99	1.28a	3.35	1.55a	0.81a	0.56a	5.26b	1.20c	na	na	9.37c
LSD	0.50	0.71	1.03	1.79	0.51	0.32	0.36	1.72	1.12	1.77	na	2.58

[Z]Excludes roots.
[Y]Means followed by the same letter within a column are not significantly different (P>0.05) based on a protected LSD test.
na – not applicable.

NDFF present in plants in 1998 was attributed to uptake of NDFF during 1997.

Year following labelled fertilizer application: The %NDFF for plants in the off-year in 1998 decreased over the growing season for roots, decreased between the April and June sampling dates then remained unchanged for the remainder of the growing season for primocanes and primocane leaves, and did not change for crowns (Table IV). The %NDFF for plants in the on-year in 1998 decreased between the April and June sampling dates then remained unchanged for the remainder of the growing season for primocane leaves and laterals (Table IV). A similar pattern was observed for primocanes except that %NDFF was lowest in October. The %NDFF did not differ among sampling dates for crowns or floricanes.

Mass of accumulated NDFF in the whole plant (excluding roots) in the off-year in 1998 averaged 2.7 g plant^{-1} and did not differ among sampling dates (Table V; Figure 4). The mass of NDFF increased between the April and June dates for primocane leaves, but was not significantly different among sampling dates for primocanes or crowns (Table V).

The mass of NDFF in the whole plant (excluding roots) in the on-year in 1998 reached a maximum value of 14.8 g plant^{-1} in June, and decreased as the growing season progressed (Table V; Figure 3). The mass of NDFF generally increased during the growing season for primocanes and primocane leaves, and decreased over the growing season for crowns, floricanes, and laterals (Table V). For the June sampling date, approximately 35, 27, 27, 7 and 4% of the accumulated NDFF was contained in the fruit, laterals, floricanes, crowns, and primocanes plus primocane leaves, respectively. Fruit harvested from on-year plants in 1998 averaged 20 %NDFF and contained an average of 4.5 g NDFF plant^{-1} (data not presented).

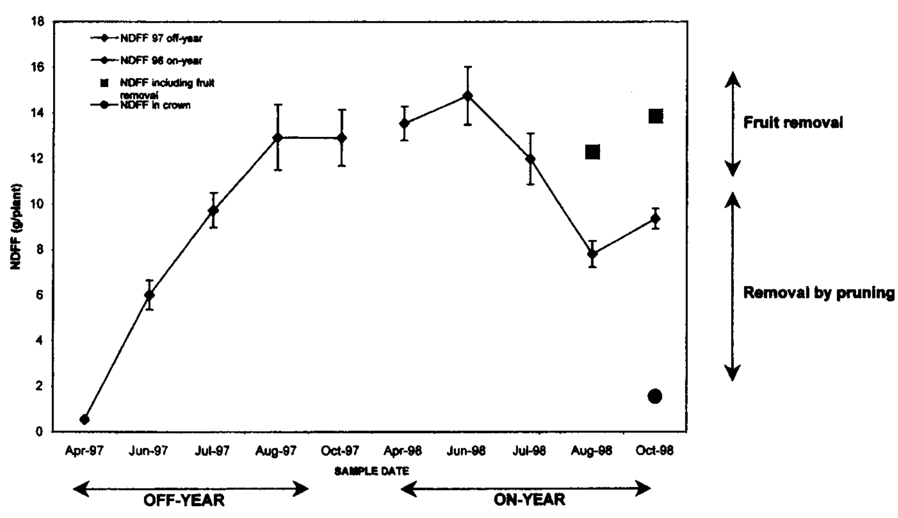

FIG. 3

Seasonal changes in nitrogen derived from the fertilizer (NDFF) in non-root tissues for 1997 off-year (fertilized with 42 g N per plant as depleted ^{15}N ammonium sulfate in April 1997) and 1998 on-year 'Kotata' blackberry (fertilized with 42 g N per plant unlabelled ammonium sulfate in March 1998) grown in an alternate-year production system. All of the fertilizer N accumulated in the off-year was assumed to be available in the following on-year. N lost due to leaf senescence could not be estimated. Arrows on the figure indicate the amount of ^{15}N removed by fruit harvest and the amount of ^{15}N removed at post-harvest pruning.

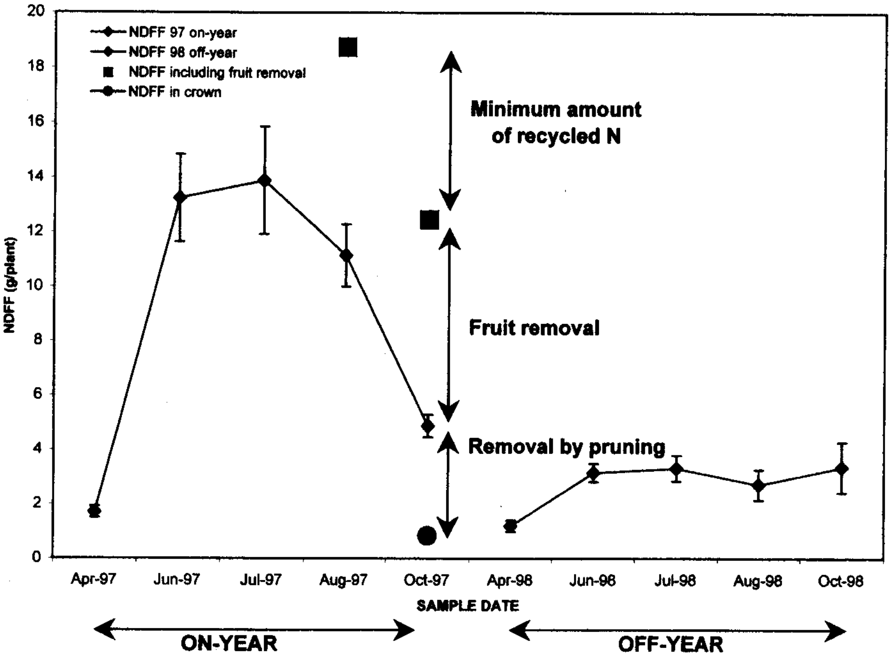

FIG. 4

Seasonal changes in nitrogen derived from the fertilizer (NDFF) excluding roots for the on-year (fertilized with 42 g N per plant as depleted ^{15}N ammonium sulfate in April 1997) and off-year 'Kotata' blackberry (fertilized with 42 g N per plant unlabelled ammonium sulfate in March 1998) grown in an alternate year production system. Arrows on the figure indicate the amount of recycled ^{15}N, the amount of ^{15}N removed by fruit harvest.

Fertilizer nitrogen recovery

For fertilizer N applied in the off-year, accumulation of new fertilizer N in the whole plant (excluding roots) averaged 12.9 g plant^{-1}, equivalent to 30.7% of the applied fertilizer N. Maximum accumulation of labelled fertilizer occurred in October (Table V; Figure 3). Of the NDFF present in the plant in the on-year, approximately 32, 56, and 12% were attributed to fruit, loss as pruning and leaf senescence (could not be determined), and retained for the next growth cycle, respectively.

For fertilizer N applied in the on-year, average NDFF accumulation in non-root tissues was 11.2 g plant^{-1} in August (Table V). If the August value is added to the 7.6 g in fruit an estimated maximum accumulation of fertilizer N in the non-root tissues was 18.8 g plant^{-1}, equivalent to 44.8% of the applied fertilizer N (Figure 4). Fertilizer N declined in the non-root portion of on-year plants late in the season, with 33% of the fertilizer N in the plant during August being unaccounted for in October.

DISCUSSION

In this study, dry matter and N accumulation of trailing blackberry was relatively low, averaging 4.8 or 5.3 t ha^{-1} yr^{-1} and 46 or 45 kg N ha^{-1} yr^{-1} for the whole plant (excluding roots) in the off- or on-year, respectively. The low accumulation probably reflects the wide row spacing required to accommodate equipment access, and the wide within-row spacing to accommodate the long canes produced by trailing blackberry. In comparison, dry matter measured in the above-ground portion of red raspberry in EY production averaged 7.3 t ha^{-1} and N accumulation averaged 99 kg N ha^{-1} (Dean *et al.*, 2000).

Over the two-year AY production cycle, approximately 28% of the dry matter and 37% of the N accumulated by trailing blackberry in this study was harvested in fruit. Dry matter and N accumulation in roots cannot be determined in this study because only a fraction of the root system was harvested. Roots contain a substantial proportion of whole plant dry matter for blackberry. Malik *et al.* (1991) found that roots contained 41% of the total dry matter for potted semi-erect 'Chester Thornless' blackberries in EY production whereas Naraguma *et al.* (1999) found roots contained 26% of the total dry matter (excluding fruit) of 'Arapaho' erect blackberry grown in EY production. Greater N was allocated to the roots of de-fruited than of fruiting apple trees (Hansen, 1980), hence, greater allocation of dry matter and N to roots may also occur in off-year blackberry plants, where the fruit sink is absent. Therefore, the estimates of whole plant dry matter and N accumulation may be substantially underestimated because of the lack of root information, particularly in the off-year.

Even allowing for significant root N accumulation, the plant N accumulation was similar to the quantity of N supplied by fertilizer (42 g N plant^{-1}). In addition, based on accumulation of soil inorganic N in bare soil plots adjacent to this experiment, soil N mineralization in 1998 was conservatively estimated at 53 g N plant^{-1} (70 kg N h^{-1}, unpublished data). Other studies on non-manured soils in a similar climatic region have reported similar or higher soil N mineralization (Dean *et al.*, 2000; Kowalenko and Hall, 1987). Therefore the combined mineralization and fertilizer additions greatly exceed the amount of N that one could expect the plants to utilize. Primocane growth occurred throughout the growing season in both off- and on-years, with 45%

and 50% of primocane growth occurring after fruit harvest, respectively. Similarly, Cortell and Strik (1997) reported 45% of primocane growth occurred after fruit harvest for 'Marion' trailing blackberry in EY production, whereas Waister and Wright (1989) reported 25% of primocane growth occurred after fruit harvest for red raspberry.

In comparison, reproductive growth occurs early in the growing season with significant lateral growth already present in April, and fruit harvest complete in July. Red raspberry grown in the EY system shows a similar pattern to on-year blackberry plants, where primocanes and primocane leaves accumulate dry matter throughout the season into the fall, while floricane and lateral growth is completed early in the season (Kowalenko, 1994).

Dry-matter accumulation in off-year primocanes and primocane leaves was 2–5 times higher than for the same plant tissues in the on-year. Vegetative (primocane) and reproductive (floricane, lateral, and fruit) tissues are known to compete for resources in trailing blackberry (Cortell and Strik, 1997) and red raspberry (Waister *et al.*, 1977). As a result, reduced dry-matter partitioning to vegetative growth would be expected in the on-year. The much larger dry-matter accumulation in fruit and laterals compared with primocanes and primocane leaves suggests that reproductive growth is a stronger sink than vegetative growth in trailing blackberry. In contrast, the quantity of dry matter and N contained in primocanes plus primocane leaves was similar to or greater than in floricanes plus floricane leaves plus fruit for semi-erect blackberry (Malik *et al.*, 1991; Naraguma *et al.*, 1999) and red raspberry (Kowalenko, 1994).

Excluding roots, almost 30% of the applied fertilizer was accounted for in off-year plants by the end of the 1997 season, and 45% was accounted for during maximum uptake in on-year plants. Due to the extensive root system, and to the high root %NDFF found in this study, these values probably significantly underestimate recovery of fertilizer N by the whole plant. In addition, a significant portion of the labelled N which was not recovered may have been incorporated into the soil organic fraction. Naraguma *et al.* (1999) recovered 31–51% of labelled N, surface applied as ^{15}N-enriched urea, in the soil organic fraction. It is also possible that some of the labelled N was taken up by the inter-row cover crop, although this is expected to be small based on the small area of fertilizer application relative to width of the herbicide strip. Based on other studies in a similar climatic region, losses of the labelled N by denitrification (Paul and Zebarth, 1997) and leaching (Kowalenko, 1987) are expected to be low during the growing season for this non-manured soil.

Within the crop, new fertilizer N was used primarily for "new" growth; primocane and primocane leaf growth in the off-year, and fruit, fruiting lateral, primocane and primocane leaf growth in the on-year. This is consistent with the finding of Malik *et al.* (1991) that predominately new fertilizer N is used for primocane growth in 'Chester Thornless' blackberry. This agrees with previous reports on the preferential partitioning of new fertilizer N into the fruits and new growth in other fruiting plants, including grapes (Hanson and Howell, 1995), pears (Sanchez *et al.*, 1991), apples (Atkinson *et al.*, 1980; Grasmanis and Nicholas, 1971), and 'Marion' blackberry (Mohadjer, 1999). Very little stored N was allocated to the primocanes and primocane leaves of the on-year plants. Results of this study suggest the need for fertilizer N in both the on-year, for fruiting lateral and fruit growth, and in the off-year, for new primocane and primocane leaf growth.

There was evidence of remobilization of N among plant tissues at different times during the production cycle. The relatively high percentage of labelled N from the off-year application that was found in the following on-year fruit (20%) suggests that reserves accumulated in the off-year are an important source for on-year growth. In the on-year of 1998, remobilization of crown and root N to fruiting laterals and fruit occurred. Root %NDFF decreased in June during fruit growth, and crown %NDFF decreased during fruit ripening in July, suggesting that movement of N to fruit had occurred. Storage of NDFF from an on-year to an off-year can only be in the crown and roots, since the rest of the plant tissue is removed. The 12.9 g NDFF that was accounted for as potential non-root reserves (crown, primocanes and primocane leaves) in the 1997 off-year plant, produced 13.6 g NDFF in the on-year plant the following April. Therefore, at least 0.7 g NDFF and whatever portion of the 6.7 g NDFF found in the leaves the previous October that was not remobilized prior to senescence came from reserves. Only 0.8 g NDFF was accounted for in the 1997 on-year crowns that produced a total of 3.4 g NDFF in the off-year plant the following year. Average root NDFF decreased from 29.8% in April to 17.3% in October. This suggests a large N resource in the roots capable of being remobilized to new growth.

There was also significant remobilization of N from senescing tissues into the roots and crown. In the off-year of 1997, primocane leaf N content decreased while crown and primocane N content increased between July and October. In 1998, however, primocane and crown N content increased, but primocane leaf N content showed no change. Since leaves had not yet senesced, remobilization of N from primocane leaves could have occurred after the mid-October sampling date. Crown stored NDFF in the 1998 on-year started higher (1.4 g) than the previous October (1.0 g), possibly due to remobilization of N from other tissues after the October sampling date.

In the on-year of 1997, floricane and fruiting lateral N content decreased from a mean of 28.6 g in August to 10.2 g in October, and NDFF greatly decreased from 5.8 to 1.4 g in this same time period. This supports remobilization of N from the floricanes to the roots, crown, and/or primocanes before they were lost from the plant.

Floricane and lateral N decreased from August to October. This then suggests that in EY production, growers could reduce crop N loss by removing dead floricanes in October (2.8 g lost) instead of the customary August (21.0 g lost) date. Presumably, this N would go to the crown and/or roots to support early season primocane growth, and may be important for yield potential.

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