Nitrogen Availability and Fruiting Influence Nitrogen Cycling in Strawberry

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ABSTRACT. As the primary nutrient applied to and used by strawberry, N allocation and cycling within the plant may play an important role in determining plant vigor and productivity. Our objectives were to determine 1) how N availability and fruit production affect N and fertilizer N (FN) partitioning among and within the vegetative tissues of 'Tribute' strawberry (*Fragaria × ananassa* Duch.) and 2) if the root N pool is temporary storage N. Plants were fed ¹⁵N-depleted NH₄NO₃ (0.001 atom percent ¹⁵N) for the initial 8 weeks, then were grown for 12 weeks with or without NH₄NO₃ with a natural ¹⁵N abundance (0.366 atom percent ¹⁵N), and were maintained vegetative or allowed to fruit. The vegetative tissues were sampled at 6 and 12 weeks. Neither N availability or fruiting had consistent effects on dry mass (DM) across all tissues at 6 or 12 weeks. At 6 weeks, the total N content of all tissues except the roots were higher with continuous N than with no N. Nitrogen availability was the dominant treatment effect on all plants at 12 weeks; continuous N increased leaflet, petiole, and total vegetative DM and total N of all tissues. Insoluble reduced N (IRN) was the major N pool within all tissues at 6 and 12 weeks regardless of treatment. Fruiting inhibited root growth and N accumulation at 6 weeks but had little effect at 12 weeks. The roots were a strong dry matter and N sink from 6 to 12 weeks. The FN pools, from the ¹⁵N-depleted FN supplied during the initial 8 weeks, exhibited changes similar to those of total N in plants not receiving N, in contrast to plants receiving continuous N where total leaflet and petiole N content increased while FN content declined. Total FN per plant declined nearly 26% over 12 weeks; the decline was greater in plants receiving N continuously than in those not receiving N, but the magnitude of the decline was not affected by fruiting. Increasing atom percent ¹⁵N values, primarily in plants receiving continuous N after the initial 8 weeks of receiving ¹⁵N-depleted FN, indicated that N cycling occurred through all tissues and N pools, proportionally more in the soluble reduced N pool but quantitatively more in the IRN pool. The root N pool was not a "temporary" N storage site available for re-allocation to other tissues, although N cycling through it was evident. Rather, leaflet N was primarily remobilized to other tissues.

Strawberry roots and leaves are sites of significant N accumulation (Archbold and MacKown, 1988, 1995; Long and Murmeek, 1937). The N is allocated to soluble reduced (SRN) and insoluble reduced (IRN) forms, and allocation patterns within the plant may be influenced by fruiting and time of year (Archbold and MacKown, 1995). During the growing season, leaves are the greatest repository of N, although the fruit crop removes significant amounts of N from the plant. Nitrogen accumulates in the roots of matted row-grown plants by early winter and declines during spring growth and fruiting, suggesting remobilization to other tissues. The root SRN pool is depleted most, while the root IRN pool remains large and relatively constant.

Storage N may be both soluble forms, such as nitrate and amino acids, and insoluble forms, such as protein (Millard, 1988). In our studies, the methanol-chloroform-water extraction protocol (Pace et al., 1982) yields an insoluble fraction consisting mostly of protein and nucleic acids and is referred to as IRN, while the SRN fraction contained in the methanol-water fraction consists mostly of amino acids and nucleotides. Evidence from ¹⁵N labeling studies

has indicated that N is cycled through the IRN pool of all vegetative tissues of strawberry including the roots (Archbold and MacKown, 1995). Thus, some proteins in the IRN pool of roots may be important for N storage, temporarily retaining N for eventual remobilization. In many herbaceous annual crop plants, the harvested component, such as a grain, mobilizes a significant proportion of the plant N from vegetative tissues that exhibit significant reductions in N concentration (Ta and Weiland, 1992; Van Sanford and MacKown, 1987). In contrast, vegetative tissues of perennial plants, herbaceous and woody, retain a significant proportion of the plant N year-round, although cycling of newly absorbed N and remobilization of N out of the vegetative tissues may occur (Archbold and MacKown, 1995; Cyr and Bewley, 1989; Titus and Kang, 1982). This cycling is especially evident in perennial tissues, such as roots and stems. The N in strawberry may be stored as proteins, but storage compounds have not been identified.

Season and fruiting affect recovery of fertilizer N by strawberry grown in matted rows (Archbold and MacKown, 1995). Estimates of ¹⁵N recovery in field studies also have indicated a long-term recovery of N from the soil N pool (Archbold and MacKown, 1995). This N may enter all tissues and N pools, so it may obscure the role that the large root IRN pool plays in the internal N cycle. The leaflet IRN pool is larger than that of the root and also could be remobilized, as may occur during leaflet senescence preceding dormancy, but it is probably mostly rubisco (Millard, 1988) and is critical to maintaining photosynthesis and biomass production during active growth. Pulse labeling the N pool with ¹⁵N and tracking its pattern of distribution would permit determination of

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N partitioning of newly absorbed and storage N and potentially reveal the role of the root IRN pool in the internal N cycle. Our objectives were to determine 1) how N availability and fruiting affect N partitioning patterns in vegetative strawberry tissues and 2) if the root IRN pool is a temporary N storage site that can be remobilized to other tissues.

Materials and Methods

Commercially available dormant 'Tribute' strawberry plants were selected for uniformity of size and potted into 2.4-L containers using perlite as the rooting media. Plastic plates (20 cm in diameter and 1 cm deep) were placed under each container to capture and retain water. The plants were cultured in a greenhouse (temperature range 15 to 27 °C) and received only natural light. Plants were watered daily with deionized water until water collected in the plastic plates. After 7 d, the plastic plates were removed and four container volumes of deionized water were passed through each container to remove residual N. After the water had drained from the containers, the plastic plates were placed back in their original position. One day later, each plant received 300 mL of Hoagland's solution (Hoagland and Arnon, 1950) containing ^{15}N -depleted NH_4NO_3 (0.001 atom percent ^{15}N , Amersham Corp., Arlington Heights, Ill.) at $0.6 \text{ g}\cdot\text{L}^{-1}$, equivalent to full-strength N, while the other nutrients were supplied at half-strength. Thereafter, each plant received 300 mL of deionized

water every other day or as needed. The NO_3^- content of the solution in the plastic plate was monitored with NO_3^- test strips (EM Science, Gibbstown, N.J.) twice weekly, and 300 mL nutrient solution with ^{15}N -depleted NH_4NO_3 was re-applied when NO_3^- levels declined to $<100 \text{ mg}\cdot\text{L}^{-1}$ for 10% of the plants. During the initial 8 weeks, nutrient solution was re-applied at ≈ 2 -week intervals. Inflorescences and stolons were removed from all plants as they emerged and were discarded.

After the initial 8 weeks, the plastic plates were removed and the root zone and perlite were washed with more than five container volumes of deionized water, until NO_3^- in the runoff was no longer detected with the NO_3^- test strips. Five randomly selected plants were harvested for analysis. The plant roots were carefully separated from the perlite and washed thoroughly with deionized water. Each plant was separated into root, crown, petiole, and leaflet tissues. The component tissues from each plant were frozen, lyophilized, weighed dry, ground in a Wiley mill to pass a 40-mesh screen, and further pulverized to a fine powder in a ball mill. Dry tissues were stored in a desiccator over anhydrous CaCl_2 under vacuum until analyzed.

The remaining plants were assigned one of four treatments for the remaining 12 weeks: interrupted N supply with or without fruiting and continuous N supply with or without fruiting (Fig. 1). There were 10 plants per treatment arranged in a completely randomized design on the greenhouse bench. Plastic plates were placed under the containers. The interrupted N plants were fertilized with half-strength Hoagland's solution lacking N. The continuous N plants were fertilized with complete half-strength Hoagland's solution. Plants receiving N continuously were switched to NH_4NO_3 with natural ^{15}N abundance (0.366 atom percent ^{15}N). Fertilizer solutions were re-applied to all plants during the remainder of the study at ≈ 2 -week intervals, again when 10% of the plants receiving N exhibited NO_3^- levels $<100 \text{ mg}\cdot\text{L}^{-1}$. Emerging stolons were removed from all plants, emerging inflorescences were removed from those plants designated nonfruiting, and ripe fruit were harvested from fruiting plants. After 6 and 12 weeks, five plants of each treatment were randomly selected for analysis. Plants were washed and prepared as previously described. Stolon tissue, ripe fruit, and inflorescences were not saved for analysis. The few senescing and dead leaves were of minimal dry mass (DM) and so were included in the leaflet and petiole analyses.

For crown, leaflet, and root tissues, the IRN and SRN pools were fractionated and assayed by a methanol-chloroform procedure as described by Pace et al. (1982). This procedure volatilizes NO_3^- in the soluble N fraction before Kjeldahl digestion. For ^{15}N determination, an acid trap diffusion technique (MacKown et al., 1987) was used to prepare the N in Kjeldahl digests for mass spectrometry. The ^{15}N diffusions of IRN and SRN fractions and samples of dried tissues were analyzed for total N and atom percent ^{15}N using a flash combustion mass spectrometer system (Europa Scientific, Cincinnati, Ohio).

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Fig. 1. Treatments and schedule of application to 'Tribute' strawberry plants.

Based on component tissue DM, total N, SRN, and IRN content, and the atom percent ^{15}N value, fertilizer N (FN) content was calculated for each tissue and the respective IRN and SRN pools (IRFN, SRFN) as described by Hauck and Bremner (1976). The FN content, thus, represents that N absorbed during the initial 8-week culture. Values for tissue DMs and for concentrations and total quantities of N and FN were analyzed by analysis of variance to determine the significance of the main effects of N availability, fruiting, and plant harvest date and the respective interactions. Single degree-of-freedom contrasts were used to compare harvest date means within the main effects of N availability and fruiting.

Results

At the initiation of the N and fruiting treatments, after the initial 8 weeks of labeling with ^{15}N -depleted NH_4NO_3 , leaflets comprised >60% of the plant DM (Table 1). The crown, root, and petiole tissues contributed roughly equal proportions to the remaining total DM. Leaflet tissue contained the greatest amount and concentration of N, followed by roots, crown, and petioles. The FN comprised >85% of the N of all plant tissues. The total IRN pool of each tissue analyzed contained >5-fold more N and FN than the total SRN pool.

After 6 weeks of N and fruiting treatments, leaflet DM was the largest component of the plant followed by root, petiole, and crown DM (Table 2). While there were no main effects of N availability or fruiting on DM across all tissues, continuous N increased petiole DM, and fruiting decreased petiole, root, and total DM of the vegetative tissues.

Only a small fraction of the total N was not accounted for by the IRN and SRN pools, as the sum of the IRN and SRN contents averaged $97.1\% \pm 7.7\%$ of the total N content across all tissues. More than 70% of the total N was in the IRN pool of all analyzed tissues. At 6 weeks, the total N content of all tissues except the roots was higher with continuous than with interrupted N availability, while fruiting reduced petiole and root N content (Table 2). Treatment effects on root IRN and SRN content generally paralleled effects on total N. However, root IRN and SRN concentration did not respond to fruiting in contrast to their reduction in total content. While the total content and concentration of leaflet IRN were higher with continuous N, fruiting resulted in higher leaflet IRN concentration but not total IRN content. Continuous N increased crown SRN concentration but not its total content. There were no N availability or fruiting effects on leaflet SRN content or concentration.

Fertilizer N at 6 weeks comprised 70% of the total N content of the vegetative tissues (Table 2). The total FN content of the crown was lower in plants receiving N continuously than in those with an interrupted supply, primarily a result of less IRFN. Although there was no effect of N availability on leaflet total FN or

IRFN, a continuous N supply reduced leaflet total SRFN. The total FN, IRFN, and SRFN content of roots was lower in plants continuously supplied with N than in those with an interrupted N supply. In addition, fruiting reduced leaflet total SRFN; total petiole FN; and root total FN, IRFN, and SRFN content. The atom percent ^{15}N values of the IRN and SRN pools, indicating the FN concentration, increased in the leaflets of plants receiving continuous N. Significant N availability by fruiting interactions on some crown IRN and SRN and root SRN atom percent ^{15}N values were evident at 6 weeks (data not shown). In plants with an interrupted N supply that fruited, the atom percent ^{15}N values decreased; in plants with a continuous N supply, fruiting increased the values.

At 12 weeks, N availability was the dominant treatment effect on all plants. A continuous N supply increased leaflet, petiole, and total vegetative tissue DM; total N of all tissues; and IRN and SRN content and concentrations and atom percent ^{15}N values of crown, leaflets, and roots (Table 3). A continuous supply of N decreased root and crown total FN and IRFN content, but it had no effect on the leaflet FN content. The reduction in crown IRN and SRN concentration by fruiting was the only effect of this treatment at 12 weeks. Significant N availability by fruiting interactions on crown and leaflet IRN and SRN concentrations and root SRN concentration occurred (data not shown). With an interrupted N supply, fruiting increased IRN and had no effect on SRN concentration; with a continuous N supply, fruiting decreased both IRN and SRN values.

All harvest date main effect means and many N availability by plant harvest date interaction means were significant for DM, total N, and total FN values (Table 4). There were no significant fruiting $\times$ plant harvest date interactions. All individual and total vegetative tissue DMs for N treatment increased from 0 to 6 and 6 to 12 weeks except leaflet DM, which declined from 6 to 12 weeks. The total N content of all tissues and their sum total from plants continuously receiving N increased over both intervals. In contrast, while total N content of crown, root, and petiole tissues increased in each interval, leaflet and total vegetative tissue N content declined in plants not receiving N. From 0 to 6 weeks, crown FN totals and leaflet FN levels in both N treatments

Table 1. Dry mass (DM), nitrogen (N), and labeled fertilizer N (FN) content and concentration in 'Tribute' strawberry vegetative tissues and their insoluble reduced N (IRN) and soluble reduced N (SRN) pools after 8 weeks of growth while fertilized with half-strength Hoagland's solution containing ^{15}N -depleted ammonium nitrate.

	Crown	Leaflet	Petiole	Root	Total
DM	1.04 ± 0.07^a	5.43 ± 0.09	1.07 ± 0.08	1.33 ± 0.05	8.87 ± 0.22
Total (μmol)					
N	795 ± 40	5850 ± 127	460 ± 30	1100 ± 53	8200 ± 196
FN	619 ± 36	5160 ± 117	369 ± 22	862 ± 45	7010 ± 158
IRN	533 ± 25	5780 ± 123	---	1040 ± 56	---
IRFN	414 ± 21	5190 ± 128	---	817 ± 50	---
SRN	106 ± 10	292 ± 13	---	78 ± 7	---
SRFN	81 ± 10	188 ± 7	---	47 ± 4	---
Concentration (DM basis) ($\mu\text{mol}\cdot\text{g}^{-1}$)					
IRN	518 ± 22	1060 ± 11	---	776 ± 19	---
SRN	106 ± 14	54 ± 2	---	58 ± 3	---
Atom percent ^{15}N ($\times 1000$)					
IRN	83 ± 1	38 ± 2	---	79 ± 3	---
SRN	88 ± 5	131 ± 6	---	144 ± 4	---

^aMean $\pm$ SE, $n = 5$. Dashes indicates petiole tissue not analyzed for IRN and SRN.

declined, while root and petiole FN contents increased. Only leaflet FN content fell from 6 to 12 weeks; all other tissues exhibited increases. Total plant FN content declined by 17% from 0 to 6 weeks and by 9% from 6 to 12 weeks.

Discussion

Since FN was not applied after the initial 8 weeks, allocation and mobilization of FN could be assessed directly as total plant FN would not increase. Prior field studies indicated that FN generally changed in parallel with total N (Archbold and MacKown, 1988, 1995). In this study, changes in FN content paralleled changes in total N in plants with an interrupted N supply but not N in plants receiving N continuously. In the latter treatment, total leaflet N values increased while total FN values declined at 6 and 12 weeks, revealing that leaflet FN was remobilized to other tissues while newly absorbed N was accumulated in the leaflets. Furthermore, these remobilization patterns of FN from one tissue to another differed due to N treatment. In plants with an interrupted N supply, roots accumulated >5-fold more FN from 0 to 6 weeks and >10-fold more FN from 6 to 12 weeks from the leaflet FN pool than in plants receiving continuous N.

Internal N cycling was altered by the treatments, indicated by differing atom percent ^{15}N values. Overall, the FN pool from the pulse of ^{15}N -depleted fertilizer application was diluted by the

normal ^{15}N -enriched fertilizer applied in the subsequent 12 weeks. The somewhat higher atom percent ^{15}N values of the SRN compared to the IRN pool in all tissues indicated a proportionally greater degree of N cycling through the SRN pool. However, the total amount of N cycled through the IRN pool would be greater because the IRN pool was much larger than the SRN pool, as much as 10-fold in leaflets.

There was a general decline in total plant FN content of 26% over the 12 weeks of this study. While most of the decline in fruited plants could be attributed to the harvest of ripe fruit, the reason for the decline in nonfruited plants is unclear. This loss may have been due to removal of emerging stolons and inflorescences in the nonfruited plants and exclusion of these tissues from the analyses. Loss of FN by senescing roots was probably insignificant because the plates beneath each container would have captured N leached from the pots for reabsorption. Microbes in the containers also may have immobilized N released from the roots, but quantitatively, this loss would have been small. While logistical problems prevented collection and analysis of the excluded tissues, identifying the cause(s) of the decline in FN warrants further study. To our knowledge, loss of N by volatilization has not been studied in strawberry, but it accounts for measurable losses of N in some species (Stutte et al., 1979) and should be considered in future work on N recovery and allocation in strawberry.

The IRN and SRN concentrations in the respective tissues of

Table 2. Overall and statistically significant main effect means ($P \leq 0.05$) of the influence of nitrogen availability ($\pm \text{N}$) and fruiting ($\pm \text{B}$) on 'Tribute' strawberry vegetative tissue dry mass (DM) and on nitrogen (N) and labeled fertilizer N (FN) content and concentration of the total N, insoluble reduced N (IRN, IRFN), and soluble reduced N (SRN, SRFN) pools after 6 weeks of treatment.

Means	Total (μmol)							Concn ($\mu\text{mol} \cdot \mu\text{g}^{-1} \text{DM}$)		Atom percent ^{15}N	
	DM (g)	N	FN	IRN	IRFN	SRN	SRFN	IRN	SRN	IRN	SRN
<i>Crown</i>											
Overall	1.43	899	548	650	403	154	65	452	107	135	157
+N	---	1000	480	709	350	---	---	478	122	186	212
-N	---	798	616	591	457	---	---	425	92	84	104
<i>Leaflet</i>											
Overall	7.35	5410	3640	5300	3650	343	182	721	57	108	171
+N	---	6380	---	6280	---	---	166	810	---	160	196
-N	---	4440	---	4380	---	---	200	631	---	55	146
+B	---	---	---	---	---	---	158	772	---	---	---
-B	---	---	---	---	---	---	206	670	---	---	---
<i>Petiole</i>											
Overall	1.83	658	417	---	---	---	---	---	---	---	---
+N	2.03	772	---	---	---	---	---	---	---	---	---
-N	1.62	544	---	---	---	---	---	---	---	---	---
+B	1.64	582	362	---	---	---	---	---	---	---	---
-B	2.02	734	473	---	---	---	---	---	---	---	---
<i>Root</i>											
Overall	2.84	1780	1170	1540	1040	140	68	551	49	120	189
+N	---	---	962	---	846	---	50	---	---	---	---
-N	---	---	1370	---	1230	---	87	---	---	---	---
+B	2.42	1540	1010	1340	898	118	59	---	---	---	---
-B	3.26	2020	1320	1750	1180	161	78	---	---	---	---
<i>Total</i>											
Overall	13.5	8750	5770	---	---	---	---	---	---	---	---
+N	---	10000	---	---	---	---	---	---	---	---	---
-N	---	7500	---	---	---	---	---	---	---	---	---
+B	12.4	---	---	---	---	---	---	---	---	---	---
-B	14.6	---	---	---	---	---	---	---	---	---	---

^aDash indicates that means were not significant at $P \leq 0.05$, except for the IRN and SRN fractions of petiole tissue, which were not analyzed.

Table 3. Overall and statistically significant main effect means ($P \leq 0.05$) of the influence of nitrogen availability ($\pm N$) and fruiting ($\pm B$) on 'Tribute' strawberry vegetative tissue dry mass (DM), and on nitrogen (N) and labeled fertilizer N (FN) content and concentration of the total N, insoluble reduced N (IRN, IRFN) and soluble reduced N (SRN, SRFN) pools after 12 weeks of treatment.

Means	Total (μmol)							Concn ($\mu\text{mol} \cdot \mu\text{g}^{-1} \text{DM}$)		Atom percent ^{15}N	
	DM (g)	N	FN	IRN	IRFN	SRN	SRFN	IRN	SRN	IRN	SRN
<i>Crown</i>											
Overall	2.09	1460	706	1020	513	337	132	488	160	169	192
+N	--- ^z	1790	555	1200	384	467	---	404	221	250	278
-N	---	1120	856	840	642	207	---	572	98	89	106
+B	---	---	---	---	---	---	---	464	140	---	---
-B	---	---	---	---	---	---	---	512	179	---	---
<i>Leaflet</i>											
Overall	7.52	6050	2690	5780	2701	342	129	730	43	149	204
+N	9.72	9170	---	8530	---	500	---	878	52	248	260
-N	5.32	2940	---	3040	---	182	---	582	34	50	148
<i>Petiole</i>											
Overall	2.36	876	396	---	---	---	---	---	---	---	---
+N	3.02	1200	---	---	---	---	---	---	---	---	---
-N	1.71	546	---	---	---	---	---	---	---	---	---
<i>Root</i>											
Overall	4.40	2620	1350	2140	1182	435	152	490	342	157	208
+N	---	3070	994	2360	819	624	---	544	143	240	285
-N	---	2170	1700	1930	1546	246	---	436	541	74	130
<i>Total</i>											
Overall	16.4	11000	5140	---	---	---	---	---	---	---	---
+N	19.2	15200	---	---	---	---	---	---	---	---	---
-N	13.5	6780	---	---	---	---	---	---	---	---	---

^zDash indicates means not significant at $P \leq 0.05$, except for the IRN and SRN fractions of petiole tissue, which were not analyzed.

this study are similar to that observed in field studies with 'Tribute' (Archbold and MacKown, 1995). Thus, strawberry plant growth and N use of container-grown plants may be similar to events occurring in the field. As previously noted, our objective was to determine if the root IRN content could be remobilized for use by other tissues. While fruiting inhibited root growth during the first 6 weeks and root N and FN content was lower in fruiting plants, the roots were a strong N sink, acquiring additional labeled FN by 12 weeks from the leaflet. This fact was particularly evident in plants with an interrupted N supply. These results showed that leaflet FN was most readily mobilized to other tissues. Thus, root N, specifically the large root IRN pool, does not seem to be a "temporary" storage site, although some N cycling through it did occur as indicated by increasing atom percent ^{15}N values of root IRN and SRN pools over time in fruiting plants.

More significantly, the results indicate that adequate N fertilization is critical to maintenance of leaflet area. In plants with an interrupted N supply, leaflet DM declined and leaflet N rather than root N was remobilized to other tissues. Thus, declining N availability in the field or cessation of fertilizer N application during the production cycle on easily leached soils might result in declining leaflet area, biomass production, and yield. The sensitivity of strawberry plant productivity to levels and patterns of N availability during a production cycle warrants further investigation.

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Table 4. Overall and statistically significant differences ($P \leq 0.05$) in tissue dry mass (DM), total N content, and total fertilizer N (FN) content between plant harvest dates within the main treatments of N availability. Plants were harvested for analysis initially (0 weeks) and after 6 and 12 weeks.

Mean	DM change (g)		Total N change (μmol)		Total FN change (μmol)	
	Weeks		Weeks		Weeks	
	0-6	6-12	0-6	6-12	0-6	6-12
<i>Crown</i>						
Overall	0.39	0.66	104	556	-71	158
+N	0.42	0.66	205	790	---	---
-N	0.36	0.65	3	322	---	---
<i>Leaflet</i>						
Overall	1.92	0.16	-442	645	-1520	-955
+N	2.32	1.96	530	2790	-1660	-567
-N	1.52	-1.63	-1420	-1500	-1370	-1340
<i>Petiole</i>						
Overall	0.76	0.54	198	218	48	21
+N	0.96	0.98	312	433	---	---
-N	0.55	0.09	84	2	---	---
<i>Root</i>						
Overall	1.51	1.56	682	835	304	184
+N	1.47	1.55	750	1220	100	33
-N	1.56	1.58	615	455	508	330
<i>Total</i>						
Overall	4.60	2.90	558	2260	-1240	-635
+N	5.23	5.15	1820	5230	-1680	-490
-N	3.98	0.69	-705	-720	-787	-780

^zDash indicates differences not significant at $P \leq 0.05$.

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