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Cultivar Fruiting and Vegetative Response to Nitrogen Fertilizer in Cranberry

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Abstract. **Cranberry (*Vaccinium macrocarpon* Ait.) has the opportunity to partition resources into sexual and/or asexual (stolons) modes of reproduction. Nitrogen status has been shown to impact the degree of stoloniferous growth. To determine whether there is a genotypic response to varying nitrogen levels, six hybrid and four native cultivars were treated with three annual rates of nitrogen fertilizer (17, 34, or 67 kg·ha^{-1}) for 4 years. Fruit yield was determined each year and asexual vegetative growth (stolons) weight was removed and measured in all but the first year of the experiment. Cultivars exhibited different patterns of yield and stolon weight response over the three nitrogen rates. Not all cultivars exhibited significant yield decreases at the high N levels. Vegetative growth (stolon weight) generally increased with increasing N, however, not all cultivars responded similarly over three N rates. Partitioning between yield and stolon production favored fruit yield at the lower N rates in three of the four native cultivars studied ('Cropper', 'Early Black', and 'Howes'). Yield over N rates was more stable for four of the six hybrid cultivars, which may be the result of greater heterozygosity in hybrids than natives, and/or genetic gain from one breeding and selection cycle, offering increased tolerance to nitrogen stress. This study indicates that genetic variation exists for yield, yield stability, and stolon production relative to nitrogen level, and that genetic gain in cranberry is possible for these traits. Future studies involving cranberry physiology and nutrition should consider the genotypes used.**

Cranberry is a woody perennial with sexual and asexual (stolons) modes of reproduction. Flowers (fruit) are generally borne on vertical shoots called as uprights. Flower buds are set in late summer of the previous year, over winter, and flowering occurs the following spring. The partitioning of resources, e.g., nitrogen, to sexual versus asexual modes of reproduction may have a genetic component (Novy et al., 1996). Differences in overall vigor among cultivars have been noted (Dana, 1983).

The nitrogen fertilizer need for cranberry has been studied in several different cranberry growing regions in North America. These studies have focused on cultivars commonly grown in each region. Results indicate that nitrogen fertilizer can increase crop yield in cranberries. However, nitrogen application can also lead to increased fruit rot and higher than desirable vegetative (stolon) growth of the plant (Eck, 1976). Organic soils, particularly the highly decomposed muck soils, have been implicated in promoting excess stolon growth.

Work to date has shown some indications that yield differences may exist in cultivar response to fertilizer. In British Columbia, cultivars 'Ben Lear' and 'McFarlin' increased in yield with increasing N rate (Eaton, 1971; Eaton and Meehan, 1973). Hart et al. (1990), working on two commercial farms in Oregon, found a lack of response to N fertilizer after 2 years in 'Crowley' whereas 'Stevens' showed an increase in yield with N rates up to 66 kg·ha^{-1}. They attributed the response difference in the two cultivars to management history. The N response of 'Early Black' has been studied in Massachusetts and New Jersey where the yield response to N fertilizer has been positive and negative (Davenport, 1996; DeMoranville, 1992; Eck, 1976). Davenport (1996) studied five cultivars in four states and found that yield and fruit rot levels were related to N fertilizer treatments, but that the rates and timing of the fertilizer as well as the yield history of the bed influenced N response.

Commercially produced cranberries can be classified in two groups based on their genetic background: "natives", which are cranberry cultivars established from material selected from native wild populations in the 1880s and early 1900s; and hybrids, derived from crosses between native cultivars (Eck, 1990). Except for 'Ben Lear' the native cultivars are also characterized by smaller fruit.

The objectives of this study were to examine the impact of different application rates of nitrogen fertilizer on resource partitioning to reproductive versus vegetative weight in 10 cranberry cultivars grown in a replicated trial having uniform cultural condition and history. Specifically, we wanted to determine if there was a significant cultivar by N rate interaction for fruit yield and stolon weight accumulation across native and hybrid cultivars.

Materials and Methods

The experiment was initiated in May 1993 on a 10 cultivar field site at the Rutgers Blueberry–Cranberry Research and Extension Center in Chatsworth, NJ. Before May 1993 the bed was uniformly fertilized using local industry standards. The site was established in 1985 in a randomized complete block design consisting of four blocks with each containing 10 cranberry cultivars (3.3 × 10 m): 'Ben Lear', 'Cropper', 'Early Black', and 'Howes' representing "natives", and hybrid cultivars 'Crowley', 'Franklin', 'No. 35', 'Pilgrim', 'Stevens', and 'Wilcox'. Each plot was divided into three uniform subplots measuring ≈3.3 × 3.3 m.

Nitrogen fertilizer was applied in split applications at dosages of 40%, 40%, and 20% across three growth stages: peak bloom, fruit set, and bud set. Each subplot received one of three total

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season N applications of 17, 34, or 67 kg·ha^{-1} using the ammonium form of nitrogen. Blended fertilizers were used to allow for concurrent applications of phosphorus and potassium. Blends varied by treatment to provide constant P and K rates of 52 and 140 kg·ha^{-1}, respectively, across all plots. Fertilizer was shaken onto the plots without incurring any foot traffic on the plants.

At the end of each growing season, from 1993 through 1996, two fruit samples were hand picked from 900-cm^2 areas in each subplot. Samples were weighed and fruit counted to determine yield. After commercial harvest in 1994, 1995, and 1996, each subplot was hand pruned to remove stolon material growing above the fruit bearing uprights. This excess stolon growth differs by growth habit from the ground creeping stolons, which are required for long term plant production. The stolon prunings were weighed (fresh weight) to determine the biomass of excess vine material (stolon weight) removed from each plot.

Analysis of variance (ANOVA) with Type III sums of squares and multivariate analysis of variance (MANOVA) was conducted using PROC GLM of SAS (SAS Institute, Cary, N.C.). Block effects were considered a random factor. Nitrogen rate and cultivars were considered fixed factors. Appropriate interaction terms were employed as error terms to test for main effects.

Results

Yield measurements were taken in all four years of this experiment. Nitrogen fertilizer effect was not significant for the first year of the study (1993) across cultivars, nor was there a significant fertilizer × cultivar interaction effect on yield (data not given). Effect due to N was significant in the subsequent years 1994–96. Since there was no cultivar × N interaction, yield data were analyzed across these 3 years and year considered as a replication.

Cultivar, nitrogen rate and the N × cultivar interaction effects were all significant for yield and stolon weight from years 1994–96 (Table 1). The response of yield and stolon weight to N was largely linear, as demonstrated by linear effect (N_L) values accounting for most of the variability (sum of squares) in N response (Table 1). Only cultivar effects were significant for fruit weight (Table 1).

A negative, largely linear, yield response to nitrogen rate was observed for the native cultivars 'Ben Lear' (R^2 = 0.18, P < 0.05), 'Cropper' (R^2 = 0.28, P < 0.01), 'Early Black' (R^2 = 0.52, P < 0.001) and 'Howes' (R^2 = 0.41, P < 0.001), and the hybrid cultivars 'Stevens' (R^2 = 0.15, P < 0.05) and 'Wilcox' (R^2 = 0.46, P < 0.001) (Fig. 1). A significant, but lesser portion of the remaining variation could be accounted by a quadratic equation for 'Ben Lear', 'Howes' and 'Wilcox' (data not given), reflecting comparable yields at 17 and 34 kg·ha^{-1} nitrogen rates and declines in yield between 34 and 67 kg·ha^{-1} rates (Fig. 1). 'Cropper' appeared to be the only cultivar exhibiting a yield reduction between the 17 and 34 kg·ha^{-1} levels (Fig. 1). 'Ben Lear', 'Cropper', 'Howes', and 'Wilcox' exhibited the largest yield declines of 34%, 49%, 48%, and 63%, respectively, at the highest nitrogen level (Fig. 1). In contrast, no significant positive or negative relationship between nitrogen level and yield was found for 'Crowley', 'Franklin', 'No. 35' and 'Pilgrim' (Fig. 1).

All cultivars exhibited a positive linear response to nitrogen level for stolon weight (Fig. 1). Close to 50% of the variation in stolon weight was accounted for by the linear relationship for 'Cropper' (R^2 = 0.46), 'Early Black' (R^2 = 0.52) and 'Pilgrim' (R^2 = 0.50). 'Cropper' and 'Early Black' had ≈2-fold increases in stolon weight, whereas 'Ben Lear', 'Franklin', and 'No. 35' showed the smallest increases, 34%, 41%, and 45%, respectively (Fig. 1).

MANOVA of yield and stolon weight response at the three nitrogen levels provided six quantitative character traits (N subplots) for each main plot. Yields of subplots were only correlated with one another for the 17 versus 34 kg·ha^{-1} of N subplots (r = 0.32, P < 0.001). In contrast, stolon weight was positively correlated in all treatment comparisons (stolon weight: N at 17 vs. 34 k·ha^{-1}, r = 0.57, P <0.001; N at 17 vs. 67 kg·ha^{-1}, r = 0.20, P < 0.05; N at 34 vs. 67 kg·ha^{-1}, r = 0.32, P <0.001). There were significant differences among the varieties in their yield and vegetative response to nitrogen levels. The first three (of six) vectors were significantly variable accounting for 64.7%, 16.5%, and 9.3% of the variation, respectively, and accounted for 91.1% of the a total variation.

The variable yield, at all three N levels, and the variable stolon weight at 17 kg·ha^{-1} had positive coefficients, while the stolon weight variables at 34 and 67 kg·ha^{-1} had negative coefficients for the discriminant function vector Z1 (Table 2). The Z1 values increased when yields increased at all N levels, particularly at 67 kg·ha^{-1}, and when stolon weight decreased for the 34 and 67 kg·ha^{-1} rates. Thus, cultivars that are low yielding and responded to increasing N with the greatest yield declines or stolon weight increases had the lowest Z1 values. The Z2 values largely reflect patterns of stolon weight

Table 1. Analysis of variance (ANOVA) with Type III sums-of-squares (MS = mean square) for 10 cranberry cultivars under three N fertilizer rates for yield and plant biomass components across the second to fourth years of N treatments (1994–96).

		Yield (Mg·ha^{-1})		Avg berry wt (g)		Pruning wt (Mg·ha^{-1})	
Source	DF	MS	F	MS	F	MS	F
Block (B)	3	433	13.9**	0.185	1.5	1.26	8.4**
Cultivar (C)^z	9	969	9.3**	2.722	34.0**	0.97	1.4*
B × C	27	104	3.3**	0.080	0.67	0.21	6.4**
N^y	2	1289	99.2**	0.011	0.32	13.88	92.6**
N_l^y	1	2442	187.8**	0.005	0.15	27.37	185.6**
B × N	6	13	0.41	0.034	0.2	0.18	1.2
C × N^x	18	105	1.5	0.024	1.5	0.42	2.8*
C × N_L^x	9	165	2.3*	0.022	1.4	0.62	4.2**
B × C × N	54	71	2.3**	0.016	0.14	0.22	1.4*
Error	240	31		0.120		0.18	

^{z}Error term = block × cultivar mean square.
^{y}Error term = block × nitrogen mean square.
^{x}Error term = block × cultivar × nitrogen mean square.
*,**Significant at P = 0.10–0.01 or <0.01, respectively.

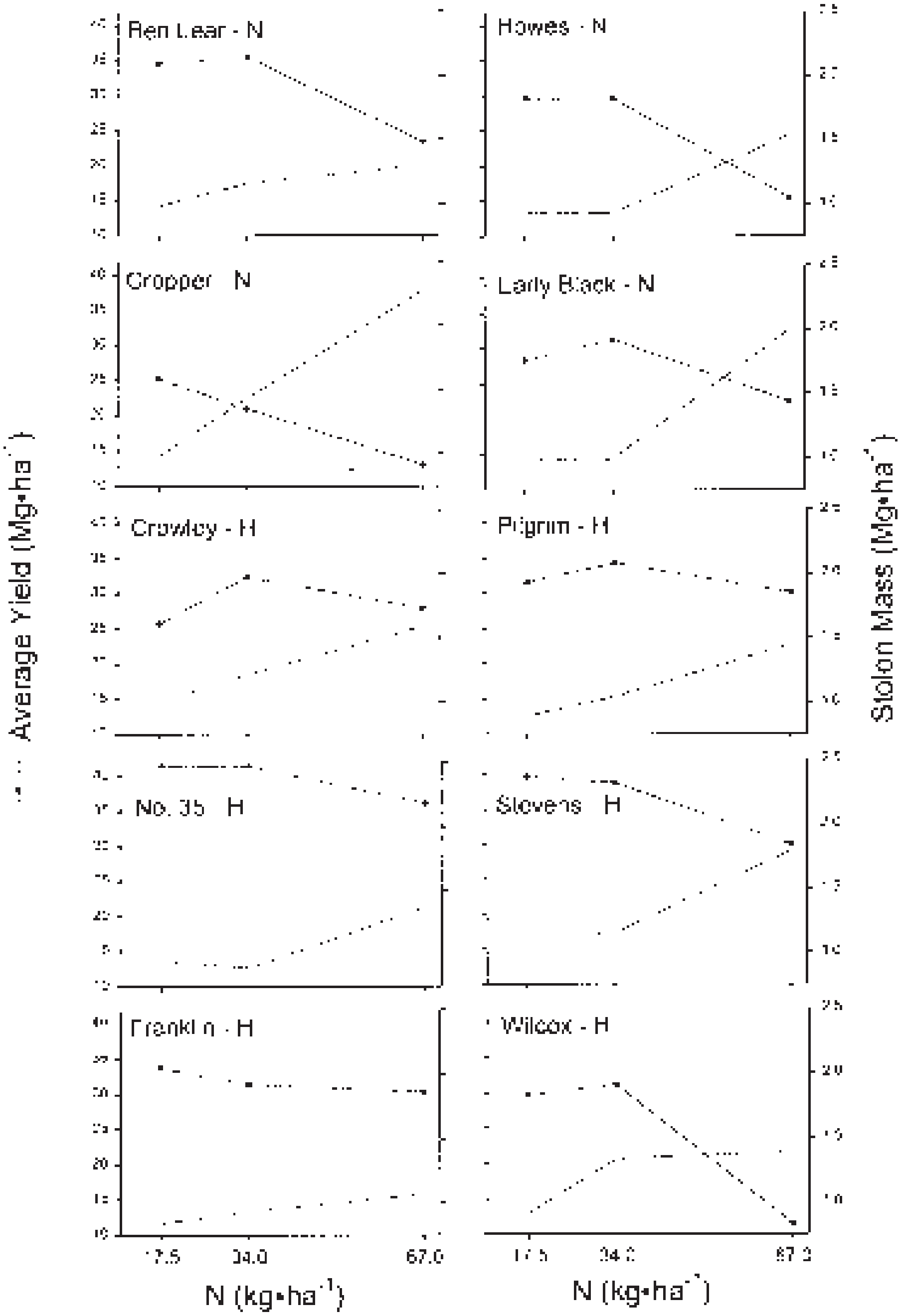

Fig. 1. Fruit and stolon partitioning in response to nitrogen fertilizer in four native cranberry cultivars and six hybrid cranberry cultivars, where N and H next to the cultivar names indicate native or hybrid, respectively.

response to N. Since cultivar stolon weight was not significantly different at the 17 kg·ha^{-1} rate, influence of stolon weight on the Z2 values reflects response at the other two N rates. Cultivars where stolon weight did not significantly increase between the 34 and 67 kg·ha^{-1} rates had the lowest Z2 values (Fig. 1, Table 2) as illustrated by 'Wilcox' and 'Ben Lear'. In contrast, 'Early Black' had the highest Z2 value, which reflects large stolon weight with 67 kg·ha^{-1} while yields were relatively moderate across N rates.

Cultivar mean separation of Z1 vectors yielded six groupings, whereas, means for Z2 vector partitioned the cultivars into four groups (Table 2). Z1 differentiated 'No. 35' as unique in response to nitrogen rate from the remaining cultivars (Table 2, Fig 1). The remaining varieties appear to represent a response continuum. 'Wilcox' also appears to be somewhat unique in that stolon weight response reached a maximum at 34 kg·ha^{-1} (Fig. 1), although yield declined drastically with the highest N rate. 'Wilcox' can be separated from all other cultivars based on Z1 and Z2 groupings (Table 2).

Discussion

The lack of yield response to N during the first application year was expected since flower buds were set the previous year, before the N treatments were imposed. Other studies on the impact of nitrogen on cranberry production have shown that there is rarely a yield response to changing fertilizer practices during the first year of the treatments (Davenport, 1996; DeMoranville, 1992; Hart et al., 1990). As a result, yield relationships with fertilizer treatment represent second through fourth year data. Since there was no significant effect of nitrogen treatment on individual berry weight, yield is a function of fruit number per unit area.

Different cultivar responses of fruit yield and stolon weight to nitrogen rate suggests that there is genotypic variation for nutrient assimilation and/or utilization in cranberry. The cultivars in this study appeared to represent a response continuum to nitrogen rates, although some, like 'No. 35' and 'Wilcox', appear to be distinct.

Previous studies conducted on 'Early Black' and 'Howes' have given rise to the belief that all cranberry cultivars respond to increasing N by yield by increased stolon weight production and concurrent yield reduction (DeMoranville, 1992). The hypothesis appears valid for all native cultivars except 'Ben Lear'. Although 'Ben Lear' yield was reduced, there was minimal stolon proliferation at the highest nitrogen rate, a finding that is consistent with industry observations. The response of 'Wilcox' was similar to that of 'Ben Lear' suffering drastic yield reduction without a concomitant increase in stolons as N rate increased.

Our study also suggests that phenotypic plasticity for sexual and asexual reproductive traits to nitrogen environment is a function of genotype. Genotypes having the ability to tolerate high nitrogen environments exist (e.g., 'No. 35'). In general, hybrid cultivars ('Franklin', 'Pilgrim', 'Stevens', and 'No. 35') appear to be more stable for yield across N environments. It also appears that hybrid cultivars may be more stable across varying environments in general. 'No. 35' and 'Stevens' have been the most productive varieties in the test over the course of 5 years before this experiment as well as in 1997 (unpublished data). It is likely that the hybrid cultivars have higher levels of heterozygosity than cultivars derived from native populations, where inbreeding is possible (Bruederle et al., 1996). Since it has been observed that environmental variance for traits is greater in inbreds than noninbred individuals (Falconer, 1981), heterozygosity in cranberry may offer increased tolerance to environmental stresses including nutritional stresses. Although the level of heterozygosity of the native cultivars in this study is not known, progenies of all 'native'

Table 2. Mean separation of cultivars for vectors Z1 and Z2 derived from MANOVA.

Type	Cultivar	Z1[z]	Z2
Hybrids	No. 35	0.53 a[y]	0.008 bc
	Stevens	0.42 b	0.006 bc
	Franklin	0.39 bc	–0.032 bc
	Pilgrim	0.38 bc	–0.014 bc
	Crowley	0.33 cd	0.018 b
	Wilcox	0.22 e	–0.140 d
Native	Ben Lear	0.36 bc	–0.067 cd
	Howes	0.26 de	0.004 bc
	Early Black	0.24 e	0.098 a
	Cropper	0.10 f	0.014 b

[z]Z1 = 0.003 (YN1) + 0.005 (YN2) + 0.007 (YN3) + 0.146 (SN1) – 0.099 (SN2) – 0.080 (SN3), where Y = yield, S = stolon weight, N1 = N at 17 $kg\cdot ha^{-1}$, N2 = N at 34 $kg\cdot ha^{-1}$, and N3 = N at 67 $kg\cdot ha^{-1}$.
[y]Z2 = –0.003 (YN1) – 0.004 (YN2) + 0.005 (YN3) + 0.137 (SN1) – 0.212 (SN2) + 0.123 (SN3), where Y = yield, S = stolon weight, N1 = N at 17 $kg\cdot ha^{-1}$, N2 = N at 34 $kg\cdot ha^{-1}$, and N3 = N at 67 $kg\cdot ha^{-1}$.
[x]Mean separation BY LSD AT $P < 0.05$.

cultivars of this study segregate for RAPD markers when self pollinated, indicating at least some level of heterozygosity (Vorsa, unpublished data).

The hybrid cultivar ‘Wilcox’ did not follow the same pattern of the other hybrids. ‘Wilcox’ is a translocation heterozygote and exhibits reduced seed set, and fruit size is generally observed to be correlated with seed number (Sarracino and Vorsa, 1991). It is also of interest to note that ‘Wilcox’ and ‘No. 35’ are full sibs from a ‘Howes’ x ‘Searles’ cross (Dana, 1983) with ‘No. 35’ lacking the translocation. ‘Wilcox’ apparently inherited the translocation from ‘Howes’ (Vorsa, 1987). The N response of fruit yield by ‘Wilcox’ and ‘Howes’ is similar, suggesting perhaps the response is associated with the translocated region.

The cultivar ‘Crowley’ fell at the lower end of the hybrids for Z1 values (Table 2). There is some question as to the genetic identity of ‘Crowley’. Of the eight ‘Crowley’ accessions available, RAPD profiles indicate at least six distinct genotypes are represented by the name ‘Crowley’ (unpublished data). In addition, ‘Crowley’ is the only cultivar in this study that was selected from the Pacific Northwest and may reflect adaptation to a different environment. Due to the uncertainty of the genotype representing ‘Crowley’ its response to N compared to the other hybrids was not surprising.

Previous work comparing N response in the cultivars ‘Stevens’ and ‘Crowley’ suggested that the lack of an N response in ‘Crowley’ could be related to previous management history (Hart et al., 1990). The results of this study support the lack of N response in ‘Crowley’ but instead suggest that the cultivars differ in their response to nitrogen rates due to genotypic differences (Table 2) rather than environmental factors.

Of the six hybrid cultivars, five (excluding ‘Crowley’) in this study were originally selected in New Jersey in the 1940s (Chandler et al, 1950; Chandler and Demoranville, 1961). This was before the regular management practice of adding sand to the soil surface, which has since resulted in sandier soils in NJ (Eck, 1990). Thus, the selections were made on organic, high N soils. It is possible that these selection criteria provided increased production stability under higher N environments.

In conclusion, this study illustrates that genotypic variation for reproductive and vegetative response to nitrogen. The greater stability for yield by cultivars derived from one generation of breeding and selection (hybrids) indicates genetic gain for yield and yield stability is possible in cranberry. This is reflected by the increased popularity of the hybrid cultivar Stevens for new planting throughout North America across an array of environmental conditions (Ocean Spray Cranberries, unpublished data). However, it may be argued that heterosis contributed to increased yield and stability in the hybrid group. The effects of genetic gain versus heterosis are confounded in this study. Nevertheless, the hybrids may be more adaptable to varying N management practices. Differences in cultivar response to nitrogen management in this study suggests that future studies on cranberry response to manipulation of environmental factors (e.g., N) should consider genotype.

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