

FRUIT PRODUCTION IN CRANBERRY (*ERICACEAE: VACCINIUM MACROCARPON*): A BET-HEDGING STRATEGY TO OPTIMIZE REPRODUCTIVE EFFORT¹

ADAM O. BROWN² AND JEREMY N. MCNEIL³

Department of Biology, Laval University, Quebec City, G1K 7P4 Canada

In the cultivated cranberry (*Vaccinium macrocarpon*), reproductive stems produce 1–3 fruit even though they usually have 5–7 flowers in the spring. We undertook experiments to test the hypothesis that this was an adaptive life history strategy associated with reproductive effort rather than simply the result of insufficient pollination. We compared fruit production on naturally pollinated plants with those that were either manually pollinated or that were caged to exclude insects. Clearly, insects are necessary for the effective pollination of cranberry plants, but hand pollination of all flowers did not result in an increase in fruit number. Most of the upper flowers, which had significantly fewer ovules than did the lower flowers, aborted naturally soon after pollination. However, when the lower flower buds were removed, the upper flowers produced fruit. This suggests that the upper flowers may serve as a backup if the earlier blooming lower ones are lost early in the season. Furthermore, the late-blooming flowers may still contribute to the plant's reproductive success as visiting pollinators remove the pollen, which could serve to sire fruit on other plants. These results are discussed in the context of their possible evolutionary and proximate causes.

Key words: abortion; Ericaceae; insect; pollination; Quebec; reproductive success; resource allocation.

In perennial plants, the investment of resources during periods of sexual reproduction can be considered as trade-offs between the immediate gains from the production of viable seeds and the costs of subsequent survival and future fecundity (Williams, 1966; Schaffer and Gadgil, 1975). Thus, at any given point in the plant's life, there is a limited amount of resources the plant can devote to the production of fruit and seeds, and this must be balanced with the need for vegetative growth and survival. However, in most perennial plants the relative investments appear to be plastic, varying as a function of environmental conditions, such as resource availability or access to pollinators (Gadgil and Sobrig, 1972; Westley, 1993).

In other words, perennial plants undergo selection to optimize their reproductive effort, defined as the ratio of resources devoted to sexual reproduction vs. vegetative growth over time (Stearns, 1976). Nevertheless, many plants produce more flowers than eventually develop into mature fruit (e.g., *Malus*: Quinlan and Preston, 1971; *Asclepias*: Willson and Price, 1977 and Wyatt, 1980; *Catalpa*: Stephenson, 1979), which may appear contradictory to the aforementioned strategy as this would seemingly increase reproductive effort without increasing reproductive success. Hypotheses on the selective advantages for the evolution of an over-production of flowers generally fall into three, not mutually exclusive categories (see

Burd, 1998): (1) the selection of optimal fruit and seed number, size, and quality via the abortion of inferior quality fruit and seeds (Janzen, 1977; Charnov, 1979); (2) compensation for losses arising from uncertain pollination (Stephenson, 1979), unpredictable resource availability (Willson and Price, 1977), climate effects such as frost or hail (Eaton, 1966) and herbivory or seed predation (Janzen, 1971); and (3) maximization of the plant's reproductive success via siring fruit on other plants (Janzen, 1977; Sutherland and Delph, 1984). A fourth hypothesis proposes that several flowers blooming at the same time may increase the reproductive success of the plant by increasing pollinator attraction (Podolsky, 1992).

The proportion of flowers that sets fruit can also be explained in terms of ultimate and/or proximate causes for the observed patterns (Stephenson, 1981; Diggle, 1995), which are also not mutually exclusive from one another. Because the development of flowers within an inflorescence is typically sequential, with the earlier, proximal positions having a higher incidence of successful fruit set, it is difficult to distinguish between spatial and temporal effects of resource allocation within the inflorescence. More specifically, the unequal allocation of resources to developing fruit may be controlled by proximate (temporal availability of resources) or ultimate, evolutionary constraints (a preferred floral position in which to invest). Furthermore, as the floral buds are often produced in the preceding fall, there may be preexisting constraints on the potential for distal fruit development due to factors such as unequal formation of meristems along plant axes (Jones and Watson, 2001).

Cranberry plants (*Vaccinium macrocarpon* Ait.) generally produce only 1–3 fruit per reproductive stem at the end of the growing season even though there are 2–7 flowers earlier in the year (Eaton, 1978; Baumann and Eaton, 1986; Birrenkott and Stang, 1990). The flower buds are formed in mid-season of the previous year (Eaton, 1978) and are distributed along the upright stem; the flowering phenology is acropetal, i.e., sequential from the lower positions, moving upwards. In most years, the lower, proximal flowers have a higher probability of setting fruit than do the distal ones (Baumann and Eaton,

¹ Manuscript received 10 August 2005; revision accepted 6 March 2006.

The authors thank I. Rodrigue, C. Pouliot, M. Maury, L. L'italien, and K. Levesque for their help in the field; W. Vincent for the use of the epifluorescence microscope, as well as G. Daigle for his help with the statistical analyses; M. Vézina of Manseau Farms, together with C. Turcotte and I. Drolet of CETAQ for their logistical help; and C. Cloutier, G. Houle, P. Kevan, S. Macfie, and two anonymous reviewers for their comments on earlier drafts of this manuscript. Funding for this study was provided by scholarships from UL and NSERC to A.O.B. as well as NSERC/CETAQ Industry and Ocean Spray Inc. research grants to J.N.M.

² Author for correspondence (e-mail: adam.brown@lesbuissons.qc.ca), present address: Centre de recherche Les Buissons, 358 rue Principale, Pointe-aux-Outardes, Canada G0H 1H0

³ Present address: Department of Biology, University of Western Ontario, London, Canada N6A 5B7

1986). *Vaccinium macrocarpon* produces flowers biennially; however, as a cultivated plant, it has undergone intense selection for an increased yield and to minimize inter-year variability in fruit production. Cranberry farmers tend to attribute the limitation of fruit development to insufficient pollination, often renting honey and/or bumble bees to ensure maximum pollination levels (Kevan et al., 1983). However, this hypothesis has never been rigorously tested, and there is evidence that the abortion of later-forming fruit may be an adaptive life history strategy for cranberry. Birrenkott and Stang (1990) found that the removal of two lower flowers increased fruit set in upper positions compared to controls. Patton and Wang (1994) showed that plants with bigger terminal buds the previous fall produced more and bigger fruit than did plants with smaller buds, suggesting an inter-year linkage on resource use by leaves and fruit. Furthermore, although there are significant positive correlations between the number of leaves and the number of flowers and fruit per plant in the same and following years, there are negative correlations between number of leaves and fruit mass and seed number (Elle, 1996). In addition, while smaller plants produce less fruit than larger ones, their relative investment per fruit is greater (Elle, 1996). Together, these results suggest that *V. macrocarpon* employs a strategy that optimizes reproductive effort. However, more detailed studies are necessary to examine this hypothesis because most research on *V. macrocarpon* has been conducted from an agricultural point of view rather than from an evolutionary and ecological perspective.

We, therefore, undertook a series of experiments to determine the relative contribution of pollination vs. floral position with respect to fruit production and the abortion of developing fruit. Manual pollination treatments were used to separate variation in pollination effects from temporal or positional allocation of resources within plants, and flower removal treatments were used to determine the effects of positional factors. Our hypotheses were the following: (1) if pollination is the only limiting factor in the production of fruit, then manual pollination should result in 100% fruit set, and (2) if available resources are the only limiting factor, then each flower should have an equal probability of producing a fruit if there was a reduced number of flowers on the stem. However, when a full complement of flowers is present, there should be a temporal priority, favoring those that were first successfully pollinated, due to the hierarchical investment of the finite resources.

MATERIALS AND METHODS

Experiments were performed in a 1.3-ha field of 8-yr-old cranberry plants at Manseau Farms in Manseau-les-Bequets, Quebec, Canada (46°22' N, 72°00' W) in the spring and summer of 2001 and 2002. The cultivar Stevens, the result of a cross between cultivars McFarlin and Potter, was selected for its resistance to the blunt-nosed leafhopper, vigorous vine growth, and large fruit size (Roper, 2001). An estimate of inter-annual differences in natural pollination levels and resource allocation was obtained by comparing the fruit set, fruit mass, and seed number per fruit from 50 randomly selected flowering shoots from the open field.

To test whether or not insect pollination limits the production of fruit, in 2001 we compared the fruit set, fruit mass, and seed set of plants exposed to natural pollinator guilds with those from plants with either no or manual pollination. Plants for the manual and nonpollinated treatments were enclosed in insect-exclusion mesh cages (0.5 × 0.5 × 0.5 m) prior to the onset of flowering. Ten flowering shoots per cage were assigned randomly to each of the two different treatments, and the cages were replicated five times to give $N = 50$ per treatment. There were approximately 100 upright stems under each cage. Manual pollination was performed on both the second and third day of flowering.

Copious amounts of pollen were transferred by paintbrush from two flowers from two different sire sources, chosen randomly from plants in the open field.

To determine whether or not a cranberry plant differentially allocates resources to developing fruit based on floral position, we removed either the lower or upper three flowers on other flowering shoots that were caged prior to the onset of flowering. The remaining flowers were manually pollinated ($N = 50$ stems per treatment). At the end of the season, fruit set, fruit mass, and seed count per fruit were compared with data from manually pollinated, intact plants.

In 2002, we studied the timing of abortions relative to flowering and fruiting phenology, by tagging 50 randomly selected flowering shoots in the open field. We examined the plants every 4 d and recorded the following parameters for each floral position: (1) stage of flower development (hook, early, full, and late bloom; Fig. 3C), (2) stage of fruit development (pinhead, small, and large fruit; Fig. 3C), and (3) whether and when the flower or fruit aborted. Flowers or fruit with halted development and/or with visible wilting were classified as aborted. To ensure that the abortions were not caused by seasonal changes in pollinator activity, we collected 50 randomly selected aborted flowers and fruit from all possible positions (1–6) that still had the floral style attached. The styles were prepared for pollen tube analysis by rinsing them in NaOH and K_2PO_4 in a hot water bath prior to being dyed using aniline blue. The stained styles were mounted on slides, and pollen tubes reaching the base of the style were counted using an epifluorescence microscope.

We also examined floral morphology as a function of floral position on the stem. We randomly collected 50 flowers in full bloom from each position, at three different times in the flowering season (11, 15, and 19 July 2002) and stored them in 70% alcohol for subsequent dissection under a microscope. The number of ovules in each flower was counted and compared for flowers from the upper and lower three floral positions.

To test for treatment effects on fruit set, pollination success via pollen tube analysis, as well as on abortion events, we employed binomial logit models, using the GENMOD procedure in SAS, version 8.1 (SAS Institute, 1996). A Poisson regression model was used for data in the form of discrete counts, such as seed set. When necessary, data were adjusted for over-dispersion by multiplying the standard error of estimates with a scaling factor, estimated as square root (χ^2/df), where χ^2 is the Pearson's goodness-of-fit statistic (Agresti, 1996). Differences in fruit mass were tested using ANOVAs by the generalized linear modeling (GLM) procedure. A posteriori tests for pairwise differences were made using the Waller–Duncan comparison.

RESULTS

There was no significant inter-year difference in the fruit ($df = 1$, $\chi^2 = 1.34$, $P = 0.2466$; Fig. 1A) or seed set ($df = 1$, $\chi^2 = 2.10$, $P = 0.1476$; Fig. 1C) of naturally pollinated plants. However, fruits had a significantly greater mass in 2001 than in 2002 ($df = 1$, 284, $F = 7.09$, $P = 0.0083$; Fig. 1B).

The exclusion of insects caused a significant decrease in fruit set ($df = 2$, $\chi^2 = 13.9$, $P = 0.001$; Fig. 2A), fruit mass ($df = 2$, 113, $F = 29.73$, $P < 0.0001$; Fig. 2B), and seed number per fruit ($df = 2$, $\chi^2 = 127.92$, $P < 0.0001$; Fig. 2C) compared to natural and manual pollination levels. The fruit set from plants with pollinators excluded may be attributed to wind pollination, as the sequential development of staminoïd and pistillate organs within the flowers would make self-fertilization unlikely. However, geitonogamy cannot be completely ruled out, as pistils from lower flowers may receive pollen from later-blooming flowers on the same stem. Thus, while insects are necessary for the effective pollination of *V. macrocarpon* flowers, manual pollination did not significantly increase fruit set or fruit mass compared to natural pollination (Fig. 2A, B). In both treatments there were approximately two fruit per plant, a value consistent with other studies (Baumann and Eaton, 1986; Birrenkott and Stang, 1990; Birrenkott et al., 1991). There were, however, more seeds per fruit in the open environment than in caged, hand-pollinated plants (Fig. 2C). This may reflect a greater diversity of sires, as we used only two male donors per flower pollination per day, but one cannot entirely rule out a cage effect.

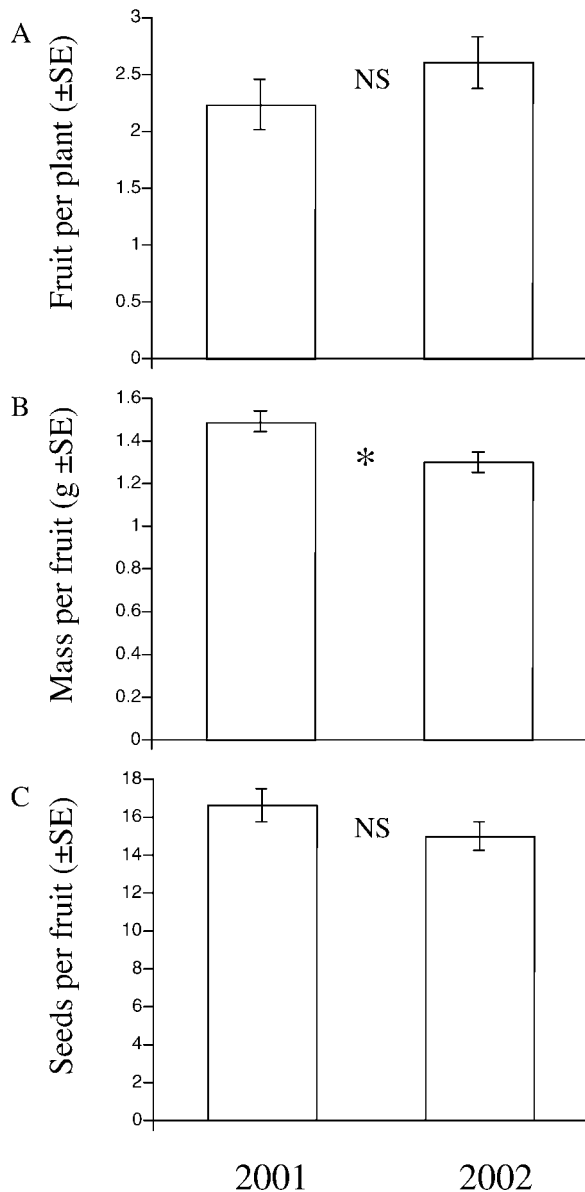


Fig. 1. Mean number of cranberry (*Vaccinium macrocarpon* Ait.) (A) fruit per plant, (B) fruit mass, and (C) number of seeds per fruit of plants at Manseau, Quebec, Canada, in 2001 and 2002. The fruit mass (B) differed significantly between years (protected least significant differences method, $P = 0.0083$). Differences in number of fruit per plant and number of seeds per fruit were not significant at $P = 0.05$.

No significant differences were found in the fruit set ($df = 2$, $\chi^2 = 2.09$, $P = 0.3512$; Fig. 2D) or fruit mass ($df = 2$, $F = 1.10$, $P = 0.3406$; Fig. 2E) from plants whose flowers were all pollinated vs. those with only three pollinated flowers (upper or lower). However, there were significantly fewer seeds in fruit from the treatment with flowers only in the upper three positions compared to those from the lower three, either on the manipulated or intact plants ($df = 2$, $\chi^2 = 189.55$, $P < 0.0001$; Fig. 2F).

The flowering phenology of *V. macrocarpon* was staggered over several weeks, and most pollinated flowers had initiated fruit set by 3–4 wk after the onset of bloom (Fig. 3A). Fruit

development was initiated ~ 1 wk later. Ninety-three percent ($N = 508$) of the abortions took place after the onset of fruit development, with only 7% ($N = 38$) occurring during flowering (Fig. 3B). Pollen tube analysis suggests that flower abortion was related to pollination because there were significantly fewer tubes in the styles of aborted flowers than in aborted fruit of all positions ($df = 1$, $\chi^2 = 5.14$, $P = 0.0234$). In addition, there were no differences in the number of pollen tubes between the upper and lower aborted flowers ($df = 1$, $\chi^2 = 0.32$, $P = 0.571$; Table 1). However, the number of pollen tubes in aborted upper fruits was higher than in lower ones, and the difference was marginally significant ($df = 1$, $\chi^2 = 3.63$, $P = 0.0567$), suggesting fruit abortion in upper fruit may be independent of pollination.

On intact plants, flowers and fruit from the upper three positions aborted significantly more often than did those from the lower positions ($df = 1$, $\chi^2 = 36.54$, $P < 0.0001$; Fig. 4A). When upper flowers were removed, the incidence of abortions of those remaining increased slightly, possibly due to the trauma of the experimental manipulation, but was not significantly different from those in the lower positions on intact plants ($df = 1$, $\chi^2 = 2.48$, $P = 0.1153$; Fig. 4B). However, when competing lower flowers were removed, the remaining upper flowers aborted significantly less often than those from the same positions on intact plants ($df = 1$, $\chi^2 = 19.87$, $P < 0.0001$; Fig. 4C). Furthermore, despite any potential traumatic effects of manipulation, when only the upper buds were left, the flower and fruit abortion patterns were similar to those seen when only the lower buds were left (60 vs. 57%; Fig. 4B, C).

There were significantly fewer ovules in flowers from the upper three positions ($N = 76$) than in those in the lower three positions ($N = 78$) on the stem (35.5 ± 0.62 vs. 39.3 ± 0.87 ovules, respectively [means \pm SE]; $df = 1$, $t = 4.57$, $P < 0.0001$). In all cases, the number of seeds per fruit (Fig. 2C) is $< 50\%$ of the ovules present in the flower. However, the disparity between the number of ovules and seeds in the different positions (the ratio of seeds to ovules was 0.39 in lower flowers and only 0.19 in upper flowers) indicates that some other factor is limiting the production of quality fruit in the upper positions.

DISCUSSION

The results of this study clearly show that pollination levels alone do not explain the pattern of fruit set in *V. macrocarpon*. While pollinators are essential for fruit production (as seen in our exclusion studies), reduced fruiting success of distal flowers can be explained by a combination of resource limitation and developmental or architectural constraints.

Our experiments support three of four hypotheses about why some plants produce more flowers than will set fruit. In the case of *V. macrocarpon*, we could discount the hypothesis that the presence of several flowers on the same plant would increase the attraction of pollinators because blooming is sequential, rather than simultaneous. We did find evidence supporting the other three hypotheses: selective abortion of inferior fruit when resources are limited, production of late flowers that could develop fruit if the earlier flowers failed, and later flowers contributing to the plant's fitness primarily through pollen dispersal.

The idea that *V. macrocarpon* uses a selective abortion strategy to optimize reproductive effort is supported by the fact that manual pollination did not increase fruit set, and most fruit

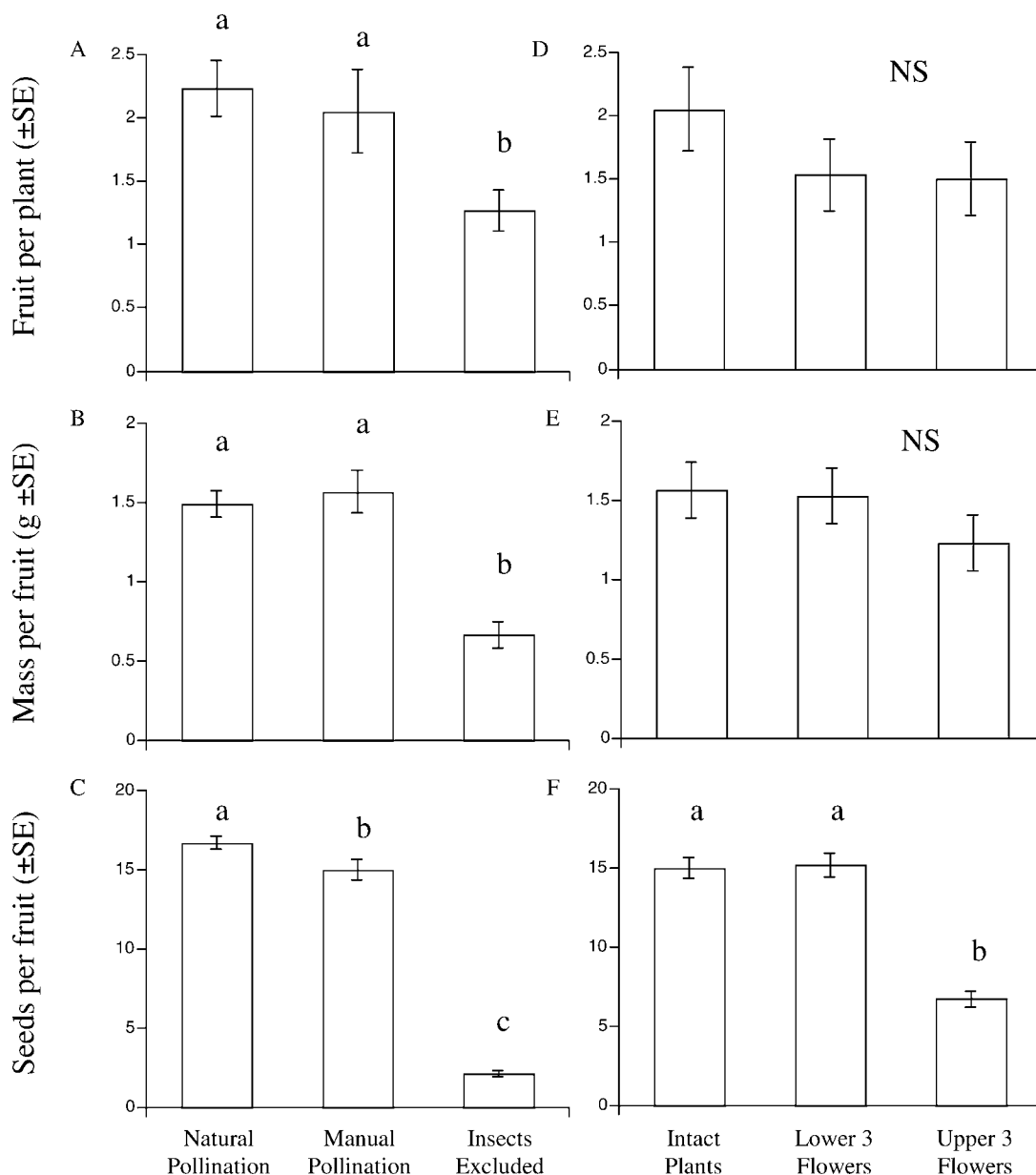


Fig. 2. Mean number of cranberry (*Vaccinium macrocarpon* Ait.) (A, D) fruit per plant, (B, E) fruit mass, and (C, F) numbers of seed per fruit at Manseau, Quebec, Canada, in 2001. Treatments of natural pollination, manual pollination, and pollination with insects excluded are shown in panels (A), (B), and (C). Treatments from manual pollination of intact plants or plants with only the lower or upper three flowers (with the other three removed) are shown in panels (D), (E), and (F). Bars within each panel with different letters are significantly different ($P < 0.05$) using the protected least significant differences method.

came from the early-blooming flowers (discussed later), while those blooming later aborted. This is consistent with other studies that show that for plants with variation in within-plant flowering timing, the earlier flowers have a higher probability of setting fruit (e.g., Stephenson, 1979). Flowers from the upper positions are typically of lower quality, as evidenced by their significantly fewer ovules, which is the ultimate limitation on seed set (Stephenson, 1981). Furthermore, they have a lower seed to ovule ratio compared with the earlier emerging ones found lower on the stem; in our study, later flowers had half as many seeds per ovule. This indicates that some internal plant regulator is limiting seed production in the upper positions

(Wiens, 1984), such as selection for optimal seed size (Smith and Fretwell, 1974; Lloyd, 1987; Zhang, 1998), which may also be limited by access to resources (Schemske et al., 1978). We found little or no evidence of fruit or seed predation, probably because the fields were sprayed with insecticide against the principal pest in the region, the cranberry fruitworm (*Acrobasis vaccinii* Riley, Lepidoptera: Pyralidae).

The fact that upper flowers do give rise to fruit when the lower, competing flowers are removed provides further support for the resource limitation hypothesis. The abortion of later-developing fruit is probably modulated by the production of growth inhibitors (Nitche, 1970; Bangerth, 2000) and would

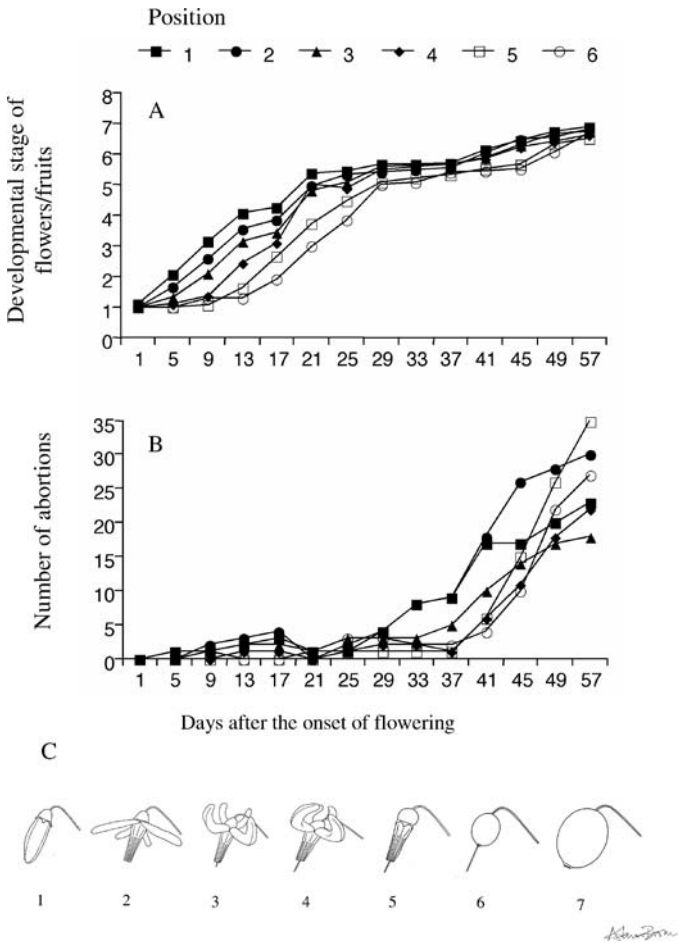


Fig. 3. The phenology of cranberry (*Vaccinium macrocarpon* Ait.) (A) flower and fruit development and (B) abortions as a function of relative position on the stem at Manseau, Quebec, in 2002. Position 1 is the most proximal and position 6 is the most distal. The flowering period started on 1 July. (C) Diagrams of various stages of cranberry flower and fruit development used in the phenology study in 2002: 1, flower hook; 2, early bloom; 3, full bloom; 4, late bloom; 5, fruit set (pinhead); 6, small fruit; and 7, large fruit.

allow the plant to recover some of the nutrients invested in them (Mooney, 1972; Rocheleau and Houle, 2001). Studies on other species have found similar results to ours (Gutián, 1994; Medrano et al., 2000), suggesting the production of fruit may be governed by architectural constraints in the plant's evolved reproductive strategy, such as fewer ovules or decreased vascular flow in distal flowers (Diggle, 1995), as well as by limitations from a number of other factors, such as insufficient pollination or resource availability.

TABLE 1. The number of pollen tubes found in the styles of aborted flowers and fruit based on their position on the reproductive stem of cranberry, *Vaccinium macrocarpon* Ait., plants at Manseau, Quebec, Canada, in 2002 ($N = 208$; data are means with SE in parentheses).

Position	Flowers	Fruit
Lower	22.81 (4.85)	25.86 (4.82)
Upper	26.96 (3.07)	36.35 (2.87)

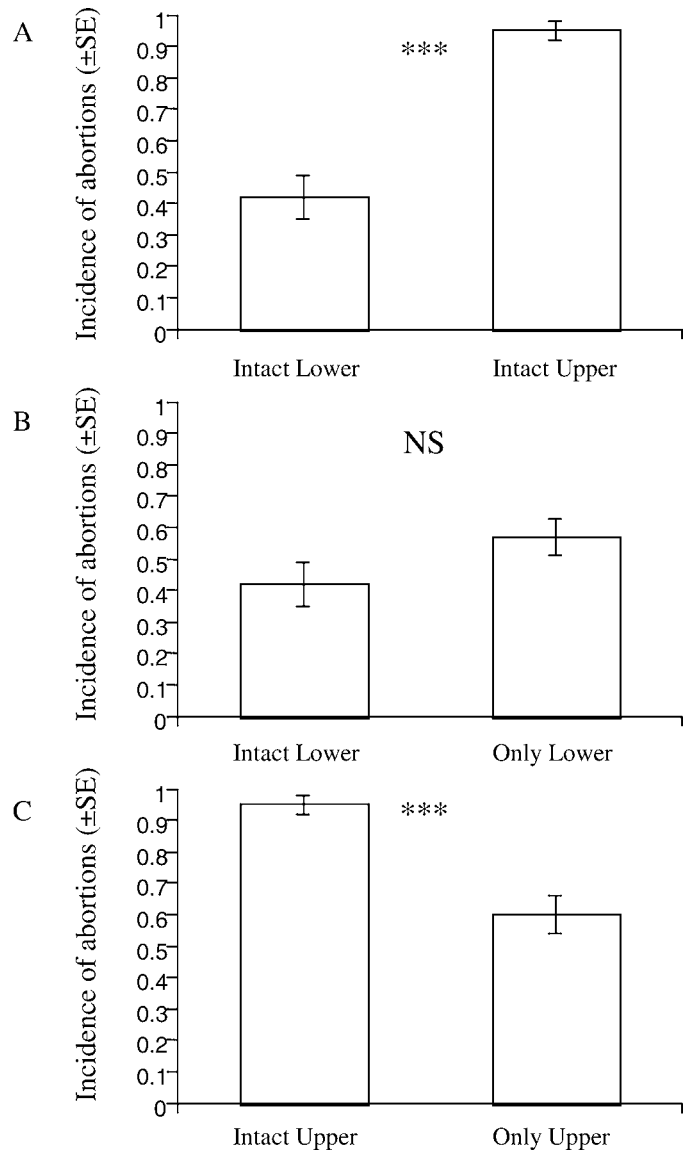


Fig. 4. The incidence of abortions in cranberry (*Vaccinium macrocarpon* Ait.) flowers and fruit relative to their position on either intact plants or those with competing flowers removed at Manseau, Quebec, in 2002. Bars denoted with asterisks are significantly different ($P < 0.0001$) using the protected least significant differences method.

The second hypothesis, that the plant is pre-adapted to take advantage of “good years” of pollination and resource availability by favoring the first flowers and using later flowers as insurance, is supported by data obtained from the between-year comparisons. Even though cool temperature delayed flowering for several weeks in 2002 compared with 2001, fruit set was similar in both years, indicating that pollinators were not limiting in either season. However, in 2002 only 64.1% of all fruit produced under conditions of natural pollination came from the lower three positions on the stem compared with 97.4% in 2001. There were more rainy days during the first 2 weeks of flowering in 2002, and this appeared to have negatively impacted pollinator activity when the earlier blooming flowers were receptive. This is supported by the

fact that, among aborted flowers, there were fewer pollen tubes in earlier, proximal flowers as compared to later, distal flowers (Table 1). Such a bet-hedging strategy for fruit production may be adaptive for a northern plant because flowering, even though staggered, occurs early in the season when variable and extreme conditions of temperature, rain, frost, and hail may all be deleterious to pollination and fruit production.

The third hypothesis is supported by pollen tube analysis, which showed that the late-blooming flowers were actively visited by pollinators and, thus, could have served as pollen donors. Therefore, the flowers on the upper stem, even though they do not develop mature fruit, could increase the plant's reproductive success by siring seeds in the flowers of less phenologically advanced plants present in the habitat (Harder et al., 2000).

Thus, the proximate cause for the low fruit set in distal cranberry flowers under natural conditions appears to be resource competition between developing fruits, whereas the ultimate or evolutionary causes for the over-production of flowers in cranberry may (1) allow selection for optimal fruit and seed size and/or quality through selective abortion, (2) result in additional fruit set in years of high resource availability, (3) serve as pollen sources to sire fruit on other plants, and (4) provide an assurance policy for fruit lost to unpredictable events (Ehrlén, 1992; Guitián et al., 2001).

Because the Stevens cultivar was, in part, chosen for its large fruit size, it is possible that the strategy of producing fewer larger fruits over a greater number of smaller ones was inadvertently selected for. However, the wild sister species, *Vaccinium oxycoccos*, also has only about 12% fruit set under experimental conditions of maximal pollination (Fröberg, 1996), indicating that selective abortion of distal fruit may be an ancestral trait. In addition, if the over-production of flowers might allow for extra fruit production in years of high resources, then cultivated plants in agro-ecosystems should set more fruit because they experience intense fertilization regimes. The fact that they do not have a higher fruit set adds support to the notion that the abortion of distal fruit in cranberry is, at least in part, due to evolved architectural constraints.

Our results show that *V. macrocarpon* strategically allocates resources to fruit production within a given year. The long-term inter-year dynamics of resource allocation as it relates to growth and sexual reproduction remain to be exploited. Further studies must be conducted on the role of leaf growth on resource availability within the plant and the effect of vegetative growth on fruiting (e.g., Roper et al., 1992). From a practical perspective, our results show that cranberry farmers should not expect 100% fruit set from their plants, and they may be able to reduce the intensity of their management of pollinators. Although the activity of natural pollinators was not limiting fruit production during our study, this may vary among years and populations (Ehrlén, 1992). This study, along with others showing the superior effectiveness of native pollinators over honeybees at cranberry pollination (Kevan et al., 1983; MacKenzie, 1994), suggests that if the habitat surrounding the cranberry bogs is managed to sustain populations of natural insect pollinators, farmers may not need to rent hives every year. Adequate native insect biodiversity around cranberry farms could provide sufficient pollination and control of pests through predation or parasitism (Landis et al., 2000; Kremen et al., 2002).

LITERATURE CITED

- AGRESTI, A. 1996. An introduction to categorical data analysis. John Wiley, New York, New York, USA.
- BANGERTH, F. 2000. Abscission and thinning of young fruit and their regulation by plant hormones and bioregulators. *Plant Growth Regulation* 31: 43–59.
- BAUMANN, T. E., AND G. W. EATON. 1986. Competition among berries on the cranberry upright. *Journal of the American Horticultural Society* 11: 869–872.
- BIRRENKOTT, B. A., C. A. HENSON, AND E. J. STANG. 1991. Carbohydrate levels and the development of fruit in cranberry. *Journal of the American Society of Horticultural Science* 166: 174–178.
- BIRRENKOTT, B. A., AND E. J. STANG. 1990. Selective flower removal increases cranberry fruit set. *Hortscience* 25: 1226–1228.
- BURD, M. 1998. “Excess” flower production and selective fruit abortion: a model of potential benefits. *Ecology* 79: 2123–2132.
- CHARNOV, E. L. 1979. Simultaneous hermaphroditism and sexual selection. *Proceedings of the National Academy of Sciences, USA* 76: 2480–2484.
- DIGGLE, P. K. 1995. Architectural effects and the interpretation of patterns of fruit and seed development. *Annual Review of Ecology and Systematics* 26: 531–552.
- EATON, G. W. 1966. The effect of frost upon seed number and berry size in the cranberry. *Canadian Journal of Plant Sciences* 46: 87–88.
- EATON, G. W. 1978. Floral induction and biennial bearing in the cranberry. *Fruit Varieties Journal* 32: 58–60.
- EHLÉN, J. 1992. Proximate limits to seed production in a herbaceous perennial legume, *Lathyrus vernus*. *Ecology* 73: 1820–1831.
- ELLE, E. 1996. Reproductive trade-offs in genetically distinct clones of *Vaccinium macrocarpon*, the American cranberry. *Oecologia* 107: 61–70.
- FRÖBERG, H. 1996. Pollination and seed production in five boreal species of *Vaccinium* and *Andromeda* (Ericaceae). *Canadian Journal of Botany* 74: 1363–1368.
- GADGIL, M., AND O. SOBRIG. 1972. The concept of r- and K-selection: evidence from wildflowers and some theoretical considerations. *American Naturalist* 106: 14–31.
- GUITIÁN, J. 1994. Selective fruit abortion in *Prunus mahaleb* (Rosaceae). *American Journal of Botany* 81: 1555–1558.
- GUITIÁN, J., P. GUITIÁN, AND M. MEDRANO. 2001. Causes of fruit set variation in *Polygonatum odoratum* (Liliaceae). *Plant Biology* 3: 637–641.
- HARDER, L. D., S. C. H. BARRETT, AND W. W. COLE. 2000. The mating consequences of sexual segregation within inflorescences of flowering plants. *Proceedings of the Royal Society of London, B, Biological Sciences* 267: 315–320.
- JANZEN, D. H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* 2: 465–492.
- JANZEN, D. H. 1977. A note on optimal mate selection by plants. *American Naturalist* 111: 365–371.
- JONES, C. S., AND M. A. WATSON. 2001. Heteroblasty and preformation in mayapple, *Podophyllum peltatum* (Berberidaceae): developmental flexibility and morphological constraint. *American Journal of Botany* 88: 1340–1358.
- KEVAN, P. G., R. M. GADAWSKI, S. D. KEVAN, AND S. E. GADAWSKI. 1983. Pollination of cranberries, *Vaccinium macrocarpon*, on cultivated marshes in Ontario. *Proceedings of the Entomological Society of Ontario* 114: 45–53.
- KREMEN, C., N. M. WILLIAMS, AND R. W. THORP. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences, USA* 99: 16812–16816.
- LANDIS, D. A., S. D. WRATTEN, AND G. M. GURR. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45: 175–201.
- LLOYD, D. G. 1987. Selection of offspring size at independence and other size-versus-number strategies. *American Naturalist* 129: 800–817.
- MACKENZIE, K. E. 1994. The foraging behaviour of honey bees (*Apis*

- mellifera* L.) and bumblebees (*Bombus* spp.) on cranberry (*Vaccinium macrocarpon* Ait.). *Apidologie* 25: 375–383.
- MEDRANO, M., P. GUITIÁN, AND J. GUITIÁN. 2000. Patterns of fruit and seed set within inflorescences of *Pancreatium maritimum* (Amaryllidaceae): nonuniform pollination, resource limitation, or architectural effects? *American Journal of Botany* 87: 493–501.
- MOONEY, H. A. 1972. The carbon balance of plants. *Annual Review of Ecology and Systematics* 3: 315–346.
- NITSCH, J. P. 1970. Hormonal factors in growth and development. In A. C. Hulme [ed.], *The biochemistry of fruits and their products*, 427–472. Academic Press, New York, New York, USA.
- PATTON, K. D., AND J. WANG. 1994. Leaf removal and terminal bud size affect the fruiting habits of cranberry. *HortScience* 29: 997–998.
- PODOLSKY, R. D. 1992. Strange floral attractors: pollinator attraction and the evolution of sexual systems. *Science* 258: 791–793.
- QUINLAN, J. D., AND A. P. PRESTON. 1971. The influence of shoot competition on fruit retention and cropping of apple trees. *Journal of Horticultural Science* 46: 525–534.
- ROCHELEAU, A.-F., AND G. HOULE. 2001. Different cost of reproduction for the males and females of the rare dioecious shrub *Corema conradii* (Empetraceae). *American Journal of Botany* 88: 659–666.
- ROPER, T. R. 2001. 'Stevens' cranberry. *Journal of American Pomological Society* 55: 66–67.
- ROPER, T. R., E. J. STANG, AND G. M. HAWKER. 1992. Early season leaf removal reduces fruit set and size in cranberry (*Vaccinium macrocarpon* Ait.). *HortScience* 27: 75.
- SAS INSTITUTE. 1996. SAS, version 8.1. SAS Institute, Cary, North Carolina, USA.
- SCHAFFER, W. M., AND M. D. GADGIL. 1975. Selection for optimal life histories in plants. In M. L. Cody and J. Diamond [eds.], *Ecology and evolution of communities*, 142–157. Belknap Press, Cambridge, Massachusetts, USA.
- SCHEMSKE, D. W., M. G. WILLSON, M. N. MELAMPY, L. J. MILLER, L. VERNER, K. M. SCHEMSKE, AND L. B. BEST. 1978. Flowering ecology of some spring woodland herbs. *Ecology* 59: 351–366.
- SMITH, C. C., AND S. D. FRETWELL. 1974. The optimal balance between size and number of offspring. *American Naturalist* 108: 499–506.
- STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51: 3–47.
- STEPHENSON, A. G. 1979. An evolutionary examination of the floral display of *Catalpa speciosa* (Bignoniaceae). *Evolution* 33: 1200–1209.
- STEPHENSON, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* 12: 153–279.
- SUTHERLAND, S., AND L. F. DELPH. 1984. On the importance of male fitness in plants. *Ecology* 65: 1093–1104.
- WESTLEY, L. C. 1993. The effect of inflorescence bud removal on tuber production in *Helianthus tuberosus* L. (Asteraceae). *Ecology* 74: 2136–2144.
- WIENS, D. 1984. Ovule survivorship, brood size, life history, breeding systems, and reproductive success in plants. *Oecologia* 64: 47–53.
- WILLIAMS, G. C. 1966. *Adaptation and natural selection*. Princeton University Press, Princeton, New Jersey, USA.
- WILLSON, M. F., AND P. W. PRICE. 1977. The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). *Evolution* 31: 495–511.
- WYATT, R. 1980. The reproductive biology of *Asclepias tuberosa*. I. Flower number, arrangement, and fruit-set. *New Phytologist* 85: 119–131.
- ZHANG, D. Y. 1998. Evolutionarily stable reproductive strategies in sexual organisms. IV. Parent–offspring conflict and selection of seed size in perennial plants. *Journal of Theoretical Biology* 192: 143–153.