character persists in grafted trees, their natural dwarfting tendency could prove valuable, since commercially acceptable dwarfing rootstocks have not been developed for cherries.

No ploidy differences were observed in the variants. The normal chromosome number ($2n = 32$) was found in L-II of all variants and in L-III of those variants which produced adventitious roots. Stomatal size was the same in all cases. None of the variants exhibited any traits characteristic of increased ploidy or cytochimerism (5).

L-I does not produce enough tissue to account for the changed phenotypes of the variants; therefore L-II and/or L-III must be involved. Since L-II gives rise to reproductive tissue, changes in this layer may explain changes in fruiting characteristics. Changes involving both spur-type growth and fruit characters ('RM-409' and 'MC-14') probably involve both L-II and L-III.

Based on quantitative measurements and visual observations we conclude that 'MC-13', 'MC-14', 'MC-15', 'AE-408', 'AE-414', 'HN-418', and 'RM-409' are different from the standard commercial strain of 'Montmorency'. The difference, however, is not due to a change in ploidy level but to other genetic changes.

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Unilateral Incompatibility between Red and Black Raspberries[1]

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Additional index words. Rubus occidentalis, Rubus idaeus, fruit breeding

***Abstract.* The discrepancy in seed set observed in reciprocal crosses of red (*Rubus idaeus* L.) and black (*R. occidentalis* L.) raspberries verifies unilateral incompatibility. The strength of the incompatibility varies between cultivars; some red x black crosses yield a small percentage of seed set by simple cross-pollination, while others produce almost no seed. Although black cultivars have shorter pistils than red cultivars, the role of this factor in incompatibility is unknown. Bud pollination and heat treatments increased seed set in some normally incompatible red x black crosses.**

The purple raspberry is an interspecific hybrid of the red raspberry, *Rubus idaeus*, and the black raspberry, *R. occidentalis* (1). Hybrid purple raspberries typically more closely resemble the black raspberry in a number of characteristics including growth habit, tip layering tendency, response to pinching, type of prickles, pubescence on the fruit surface, and hardiness (4). Purple raspberries are produced when the pollen parent is a red raspberry (3, 5, 7, 9, 10). If the black raspberry is used as the pollen parent, seed set usually fails, although a few reports indicated limited success (2, 6, 8). This problem of unilateral incompatibility is confounded in the oldest literature because the researchers often failed to describe the characteristics of their hybrids.

Unilateral incompatibility between raspberries has been investigated histologically by Zych (10), who found that in incompatible crosses of red x black raspberries (seed parent is always expressed first) restricted pollen tube growth occurs within the style. Black raspberry pollen tubes never grew more than one-third of the way down the styles of red raspberry flowers. Normal pollen tube growth was observed in the reciprocal crosses.

One of the authors (A. G. Otterbacher) observed that the pistils of black raspberry cultivars appeared to be slightly shorter than those of red raspberry cultivars. It was hypothesized that incompatibility may be due to the inability of pollen tubes of black raspberry to grow the entire length of red styles.

The objective of this investigation was to investigate unilateral incompatibility between red and black raspberry.

Materials and Methods

Flowers for pistil measurement were obtained in 1977 and 1978 by randomly collecting 10 flowers from each of the fall-bearing red raspberry cultivars 'Fallred', 'September', 'Heritage', 'Fallgold', and the black raspberry cultivars 'Bristol', 'New Logan', 'Plum Farmer', 'Allen', 'Black Hawk', 'Lowden', and 'Domack'[3]. Ten pistils from each flower were excised and measured from the tip of the stigma to the base of the ovary.

Field-grown 'Fallred' and 'Heritage' red raspberry and 'Allen' and 'New Logan' black raspberry plants were dug in the fall

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[3]Not a commercially released cultivar.

and stored at 3°C for 9 weeks to break dormancy. Plants were moved to a greenhouse and flowered within a few weeks. Flowers were emasculated 1 to 2 days prior to anthesis. Pollination was performed 2 to 3 days after emasculation. Pollen was obtained by collecting fresh flowers daily and allowing them to dry overnight. The following morning anthers dehisced fully and pollen was collected and stored in Petri dishes at about 15°. The bottom of the Petri dish was used to apply pollen in most crosses.

The following treatments were used in red x black crosses in an attempt to overcome incompatibility:

1) *Bud pollination.* Flower buds were emasculated about 1 to 3 days prior to anthesis and pollinated immediately.

2) *Bud pollination with raspberry pollen germination medium.* In order to mimic the pollen germination stimulus of stigmatic fluids on immature stigmas, a *raspberry pollen germination medium* (RPGM) developed by Otterbacher (unpublished) consisting of (qty/liter) $MgSO_4 \cdot 7\ H_2O$ (100 mg), KNO_3 (50 mg), $Ca\ (NO_3)_2 \cdot 4H_2O$ (150 mg), H_3BO_3 (50 mg), and raffinose (200 g) was used. A single drop of a liquid RPGM was mixed with a generous amount of pollen and applied to the stigmas of pre-anthesis stage buds with a camel's hair brush. Evaporation of the medium was retarded by misting the surrounding leaves with water and enclosing the shoot and buds within polyethylene film.

3) *Bud pollination with agar RPGM.* Solid RPGM was obtained by adding 8 g/liter agar to the medium. Pollen was spread over the 1–2-mm-thick agar medium and allowed to germinate for 2 hr at room temperature (23°C). A small square of the medium with germinating pollen was removed with a scalpel and immediately placed on the stigmas. Polyethylene film was used to maintain humidity and minimize drying.

4) *Style shortening.* Flower buds were emasculated prior to anthesis. Two to 3 days later, styles were cut to less than one-third of normal length and pollen was immediately applied.

5) *Style shortening with liquid RPGM.* Shortened styles were pollinated with liquid RPGM and pollen, using the procedures described for bud pollination.

6) *Style shortening with agar RPGM.* Shortened styles were pollinated with pollen growing on agar RPGM medium, using the procedures described for bud pollination.

7) *Heat treatment of styles.* Two to 3 days after emasculation clusters of buds were submerged in a hot water bath of 45°C for 5 min. Pollination was completed immediately after the pistils had dried.

8) *Emasculation, no pollination (control).* Flower buds were emasculated just prior to anthesis using the normal procedure.

9) *Self-pollination (control).* In each of the treatments 1–8, some of the flowers of 'Fallred' and 'Heritage' red raspberries received their own pollen (selfing) instead of black raspberry pollen. These self-pollinations were designed to determine the effect of the various treatments on potential seed set.

The percentage of seed set was obtained by first counting the pistils in a sample of 30 flowers for each cultivar. Later, when the crosses were all completed and the fruits were harvested, the total number of plump seeds per fruit was determined. The success of our various treatments was assessed as percentage seed set [seed set = (total number of plump seeds/total number of pistils per flower) × 100].

Results and Discussion

Red raspberry cultivars had significantly longer pistils than black raspberry cultivars (Table 1) in 1977 and 1978. The overall pistil length of the cultivars in 1978 was longer than in 1977.

Table 1. Mean pistil length of 11 raspberry cultivars in 1977 and 1978.

Type	Cultivar		Pistil length (mm)[z] 1977	1978
Red	Fallred		4.14a	5.05b
	September		4.04b	5.13a
	Heritage		3.66c	4.75c
	Fallgold		3.58d	4.27e
		Avg	3.86	4.80
Black	Bristol		3.51e	4.29e
	New Logan		3.25f	4.24e
	Plum Farmer		3.15g	---
	Lowden		3.15g	---
	Allen		3.05h	4.37d
	Black Hawk		3.05h	3.76g
	Domack		3.02h	3.84f
		Avg	3.17	4.10

[z]Means within columns followed by different letters are significantly different by Duncan's multiple range test, 5% level.

Since pistils of black cultivars were shorter than those of red cultivars, their pollen tubes conceivably lack the ability to affect pollination in the longer styles of red raspberry, especially if pollen tube growth is inhibited by an incompatibility reaction in a style of red raspberry as suggested by Zych (10).

A strong unilateral incompatibility between the red and black species was confirmed. Seed set of black x red crosses was 35.6 to 54.0% (Table 2), while the reciprocal red x black crosses was 0.0 to 2.5%. The strength of the incompatibility in red x black crosses varied with cultivars. 'Fallred' produced 1.5 and 2.5% seed set when pollinated by 'Allen' and 'New Logan', respectively. When 'Heritage' was pollinated by the same 2 black cultivars, the only seed set obtained was from 'New Logan' (0.1%).

The results of treatments to overcome incompatibility in red x black crosses are shown in Table 3. In the cross 'Heritage' x 'New Logan', no treatments produced a statistically significant increase in seed set over that obtained by either ordinary pollination or the pollinated control. However, bud pollination significantly increased seed set in 'Heritage' x 'Allen' (0.57%). No seed set had been obtained when this cross was performed using ordinary pollinations.

Table 2. Percentage seed set of interspecific crosses between red and black raspberries, 1979.

Cross	Cultivars: Seed parent x Pollen parent	Seed set[z] (%)
Red self	Fallred x Fallred	60.0
	Heritage x Heritage	66.5
Black self	Allen x Allen	79.1
	New Logan x New Logan	81.4
Black x red	Allen x Fallred	41.8
	Allen x Heritage	37.2
	New Logan x Fallred	54.0
	New Logan x Heritage	35.6
Red x black	Fallred x Allen	1.5
	Heritage x Allen	0.0
	Fallred x New Logan	2.5
	Heritage x New Logan	0.1

[z]% seed set = (no seeds per flower/avg pistil count per flower) × 100.

Table 3. Seed set obtained in interspecific crosses of red and black raspberry, using several hybridization techniques with 2 red raspberry cultivars as seed parents.

	Heritage (red) ♀ ×						Fallred (red) ♀ ×					
	New Logan (black) ♂			Allen (black) ♂			New Logan (black) ♂			Allen (black) ♂		
Hybridization technique	No. crosses	No. seed set	Seed set[z] (%)	No. crosses	No. seed set	Seed set[z] (%)	No. crosses	No. seed set	Seed set[z] (%)	No. crosses	No. seed set	Seed set[z] (%)
Emasculation, no polln. (control)	40	0	0.00a[y]	40	0	0.00a[y]	38	13	0.41a[y]	38	13	0.41a[y]
Simple pollination	30	1	0.05a	30	0	0.00a	30	64	2.54b	29	37	1.52a
Shortened styles	40	0	0.00a	40	2	0.07a	30	1	0.04a	29	7	0.29a
+ liquid medium	25	0	0.00a	---[x]	---	---	30	9	0.36a	21	0	0.00a
+ agar medium	36	0	0.00a	---	---	---	32	12	0.45a	---	---	---
Bud pollination	30	4	0.19a	30	12	0.57b	30	8	0.32a	30	2	0.08a
+ liquid medium	12	0	0.00a	---	---	---	15	0	0.00a	---	---	---
+ agar medium	25	0	0.00a	---	---	---	20	0	0.00a	---	---	---
High (45°C) temperature	30	11	0.52a	30	3	0.14a	30	0	0.00a	27	16	0.71a

[z]% Seed set = (no. seeds per flower/avg pistil count per flower) × 100

[y]Means within columns followed by different letters are significantly different by Duncan's multiple range test, 5% level.

[x]Due to shortage of flowers these hybridization techniques were not completed.

No treatments increased the rate of seed set in all crosses with 'Fallred' (Table 3). Only ordinary pollinations of 'Fallred' x 'New Logan' gave significantly greater seed set than the unpollinated control.

These pollination treatments greatly reduced self seed set in normally self-compatible red cultivars (Table 4). Both red cultivars produced many seeds when self-pollinated using ordinary pollination techniques, while bud pollination and heat treatment reduced the mean seed set by at least one-half. Other treatments reduced the seed set even more severely and several treatments failed to produce any seeds.

The seed set observed in the unpollinated control showed that there was a small amount of contamination among the treatments. Since many of the hybridization treatments did not differ significantly from the unpollinated control, the seeds obtained from all crosses were germinated in the greenhouse and samples of each cross were field evaluated at Urbana, Ill.

A total of 11 red x black seedlings germinated and were planted in the field in 1980. Of these only 1 plant ('Heritage' x 'Allen' from bud pollination) survived the winter. This plant had purple fruit, was vigorous, had a growth habit similar to a red raspberry, prickles like a black raspberry, and had a glaucous stem. All of the compatible black x red offspring that were planted in the field proved to be purple hybrids. Selfed reds which were planted as controls with our suspected hybrids germinated poorly, grew little in the field, and most of them eventually either died or were very weak. It appears, therefore, that most of the seeds that resulted from red x black hybridization were probably the result of accidental selfing, since both selfs and contaminants performed poorly in the field. However, we did confirm that a true purple-fruited hybrid from a normally incompatible cross of red x black raspberry could be obtained through bud pollination.

Table 4. Mean seed set obtained by self-pollinations of 2 red raspberry cultivars using several hybridization techniques.

	Seed set (%)[z]	
Hybridization technique	Fallred	Heritage
Simple pollination	50.3a[y]	46.8a
Heat treatment (45°C)	23.5b	5.0c
Bud pollination	22.9b	20.9b
+ liquid medium	2.5c	4.5cd
+ agar medium	0.1c	0.0d
Shortened styles	0.7c	0.0d
+ liquid medium	0.0c	0.0d
+ agar medium	0.0c	0.0d
Control[x]	0.3c	0.0d

[z]Seed set = (no. seeds per flower/avg pistil count per flower)²Seed set = (no. seeds per flower/avg pistil count per flower) × 100.

[y]Means within columns followed by different letters are significantly different by Duncan's multiple range test, 5% level.

[x]Emasculation with no pollination.

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Mineral Composition of Radish in Response to Nitrapyrin and Nitrogen Sources

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Additional index words. Raphanus sativus, nitrification, mineral nutrition, ammonium toxicity

Abstract. **The relationship between nitrapyrin [2-chloro-6-trichloromethyl)pyridine, a nitrification inhibitor], and the growth and the mineral composition of 'Cherry Belle' radish (*Raphanus sativus* L.) was determined with sewage sludge as the N carrier in a greenhouse study. Plant growth fell sharply as nitrapyrin was increased in concentration from 1 to 10 ppm. The concentrations of Ca, Mg, and NO_3^- in the plants fell with this range of treatment, whereas that of K rose. The mineral composition of shoots was altered much more than that of roots. Increasing nitrapyrin concentrations to 50 ppm had little added effects on growth or composition relative to the 10-ppm level. Some of the phytotoxicity due to nitrapyrin addition appeared to be ammonium toxicity imparted by the accumulation of ammonium-N from the mineralization of the sewage. Another greenhouse study with nitrapyrin at 10 ppm, but with KNO_3, $(NH_4)_2SO_4$, and sewage sludge as the N carriers, showed that a depression in growth was correlated with the accumulation or retention of ammonium-N in the medium.**

Nitrapyrin is used as a nitrification inhibitor to delay the conversion of NH_4^+ to NO_3^- by *Nitrosomonas* sp (4). Its application to soils may decrease leaching of N and may decrease the number of applications to fertilizer needed to provide N to plants. Small increases in yield have been noted with the use of nitrapyrin in conjunction with ammoniacal fertilizers.

Welch et al. (17) found that the addition of nitrapyrin aided in growth and development of lettuce, celery, and strawberries. Yield increases in cotton, corn, and sugar beets have been demonstrated with the inhibitor as an additive to NH_4^+ fertilizers (15). On the other hand, Hendrickson et al. (8) reported a decrease in total potato tuber yield and quality with nitrapyrin and NH_4^+ fertilizers, which was attributed to ammonium toxicity. English et al. (6) found lower Ca and Mg concentrations in corn leaves from plants grown with sludge, $(NH_4)_2SO_4$, or KNO_3 fertilization in the presence of nitrapyrin than in its absence. Such changes in plant composition are associated with NH_4^+ toxicity (2, 18). However, Zawistowska et al. (19) demonstrated that nitrapyrin was inhibitory on the uptake of K^+, Ca^{++}, Mg^{++}, and NO_3^- from nutrient solutions by cucumber seedlings. Dibb and Welch (5) found a lowering of Ca and Mg and an elevation of K in corn grown with nitrapyrin and NH_4 nutrition in relation to plants grown with no nitrapyrin in greenhouse studies. Under field conditions, NH_4^+ fertilizers caused a restriction in cation accumulation in sweet corn leaves whereas nitrapyrin had little effect on tissue composition (16).

Dibb and Welch (5) did not note toxicity to corn with nitrapyrin at 50 ppm or lower in the soil. However, several studies (7, 12, 13, 14) have shown that nitrapyrin has effects on plant growth unassociated with NH_4^+ toxicity. Some of the effects have properties similar to those produced by auxin injury (13, 14), and others are characterized by restricted growth (7, 12). Most investigations have been conducted at very low or high levels of nitrapyrin addition. The low levels are used to characterize field rates of application, whereas high concentrations are used to give a long-lived effect of the inhibitor.

The combination of an organic fertilizer such as sewage sludge, which is slow to mineralize, and a nitrification inhibitor was considered as a means of controlling nitrate accumulation in vegetables. However, poor plant growth has been observed with this combination. This study investigated the effects of nitrapyrin on the mineral composition and growth of radish and on NH_4-N accumulation in the soil under various N regimes.

Materials and Methods

This study was conducted under greenhouse conditions in the falls of 1979 and 1980. 'Cherry Belle' radish seeds were planted in 15-cm plastic azalea pots containing 1200 g of a potting mix of loam, sand, and peat in a proportion of 7:3:2, respectively, by volume. In 1979, sewage sludge (Milorganite, Milwaukee Sewerage District, Milwaukee, Wis.) provided N at 670 ppm in the soil mass with five replications. Nitrapyrin was added at 0, 1, 5, 10, and 50 ppm of the active ingredient. All materials were incorporated with a rotary mixer. Two weeks after seeding, plants were thinned to 7 per pot, and the following week to a final population of 5 per pot. Pots were irrigated with tap water. Harvesting occurred when the control plants had produced radishes about 2.5 cm in diameter, 38 days after seeding. Plants were pulled from the pots and rinsed with tap water and with

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