FINAL PROJECT REPORT
WTFRC Project #: PH-02-249 **WSU ARC Project # 3055-3799**

Project Title: Relationships Between Horticultural Oil Application and Postharvest Behaviour of Apples

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OBJECTIVES

1. Determine the influence of a growing season-applied soybean oil spray on harvest quality and postharvest behaviour of apples.
   a. Ascertain the effects of a one-time soybean oil application on fruit quality parameters, ripening patterns, storability, and volatile aroma production capacity of 'Golden Delicious' and 'Gala' apples.
   b. Investigate the influence of application timing and the orchard location.

2. Determine the effects of a preharvest soybean oil application on colour development, fatty acid metabolism, and flavour regeneration capacity after controlled atmosphere storage and under shelf-life conditions.
   a. Inhibit ethylene responses of 'Golden Delicious' apples with 1-MCP to test ethylene dependence of apple response to soybean oil applications.

3. Describe and compare the development of epicuticular wax during maturation and storage of 'Golden Delicious' and 'Gala' apples.
   a. Determine the impact of a preharvest application of soybean oil emulsion on fruit morphology.
   b. Compare the rate of weight loss during storage and subsequent shelf life between untreated and oil-treated fruit.

SIGNIFICANT FINDINGS

1. No phytotoxicity was observed and fruit finish was not affected by a one-time soybean oil treatment.

2. None of the oil treatments significantly influenced storability of the fruit and no significant effect on the rate of fruit maturation (IEC, firmness, SSC, TA) was observed.

3. The rate of weight loss in storage and subsequent shelf life period was slowed down for apples that received the soybean oil. Fruit grown in a cooler climate and/or stored under sub-standard relative humidity conditions benefited the most from preharvest soybean oil treatments.

4. Surface wax and cuticular development was altered, depending on time of application, variety treated, storage conditions, and growing area. For example, the cuticle of ‘Golden Delicious’ apples developed cracks when approaching maturation. Soybean oil application reduced occurrence and severity of surface cracks.

5. Mean volatile aroma production of ‘Golden Delicious’ apples was consistently higher in apples treated with soybean oil 21 days before harvest (soy2) and apples treated with soy2 emitted more aldehydes (mainly hexanal). Oil applications closer to harvest (soy2, soy3) consistently yielded fruit with improved ester regeneration capacity after CA storage.

6. ‘Gala’ apples treated with the oil emulsion mid-season (soy1) had significantly higher alcohol and ester levels when compared to control fruit.

7. The flavour regeneration capacity of apples was improved, especially by late season soybean oil applications.

8. Delayed degreening was observed on ‘Golden Delicious’ apples after soy1 and soy2 treatment in 2003, but no treatment effect was noted in 2004.

RESULTS

In all experiments, the oil emulsion (1% food grade soybean oil emulsified with 0.1% Latron®, v/v) was sprayed at midseason (soy1), 21 days before harvest (soy2) and three days before harvest (soy3).

Ripening patterns. Initial studies in 2002 had indicated the potential of soybean oil emulsion sprays to slow down maturation of fruit. However, based on the results obtained during the 2003 and 2004 seasons we conclude that none of the oil treatments significantly influenced the storability of the fruit.

Respiration rates and ethylene evolution for ‘Golden Delicious’ from Yakima in 2003 were significantly higher at harvest for soy2 (3 days ahead in shelf-life) but all treatments leveled out the longer the storage lasted. The same variety in Pullman exhibited respiration/ethylene emission rates 3 days ahead of the control for soy1 at harvest and lower rates for soy3 after 6 months of storage (regardless whether RA/CA). No differences were observed in 2004.

Internal ethylene concentration was not significantly different between treatments for ‘Golden Delicious’ from Pullman and ‘Gala’ apples in 2003. However, after 6 months of CA the midseason soybean oil treatment (soy1) was significantly higher compared to all other treatments for ‘Golden Delicious’ from the Yakima valley. A similar trend was observed after 3 months in RA storage (but the fruit appeared greener than others). In 2004 no significant treatment effect was noted for all fruit.

Fruit firmness, soluble solids, acidity did not show a significant treatment effect for ‘Golden Delicious’ from Pullman in 2003. Generally, control fruit went into storage with slightly higher firmness (0.75lbs.), soluble solids and acidity, all of which were not significant. These differences were carried through storage. Interestingly, the type of storage itself had the most severe influence on fruit quality. For example, while fruit lost about one pound of pressure during the first three months of CA storage, firmness levels remained the same in the next three months. The effect was even more pronounced for RA. Firmness loss was 5lbs after 3months, with less than 1lb additional firmness loss after 6 months. Similar trends were observed for the ‘Golden Delicious’ and ‘Gala’ fruit from the Yakima valley in 2003 and 2004.

Fruit colour.The fruit colour did not match the perceived stage of ripeness after storage in 2003. For 'Golden Delicious' from both locations soy3 treated fruit appeared as yellow as the control, soy1 and soy2 treated fruit remained much greener, despite respiration and ethylene trends showing no differences among treatments. This suggested, that chlorophyll breakdown was delayed in soy1 and soy2 treated fruit in an ethylene independent manner.

Thus, in 2004 we investigated whether the delay in degreening of apples after soybean oil application was truly ethylene independent by utilizing the known ethylene action inhibitor 1-methylcyclopropene (1-MCP) in plants. During 'Golden Delicious' apple fruit ripening, as observed during at-harvest and post CA storage shelf-life studies, L*, a*, and b* values increased, resulting in decreased hue values, increased chroma values, and a visual colour change from green to yellow. Fruit treated with 1-MCP did not show changes in chroma and had a reduced loss of hue values after storage and during the subsequent shelf-life period. No significant treatment effects due to soybean oil application were noted.

Weight loss. The rate of weight loss was decreased for all soybean oil treated apples in storage and during subsequent shelf-life period (between 1-3 days of additional shelf-life before shrivel was visible) (Table 1). Overall, Soy2 fruit lost the least weight Fruit grown in a cooler climate and/or stored under sub-standard relative humidity conditions benefited the most from preharvest soybean oil treatments. Some of the apples from the Pullman trial in 2003 were stored in a CA room with low RH, conditions that shrivel apples. After 6 months CA, the occurrence and severity of shrivel was assessed. Untreated fruit had a higher incidence of shrivel, and even after 8 days on the shelf all fruit from soybean oil treatments still had not reached the level of shrivel observed in the control apples right out of storage.

Table 1. Moisture loss of stored apples as a function of soybean oil treatment

		Weight loss in storage as % loss											
		90d RA	180d RA	90d CA	180d CA	90d RA	180d RA	90d CA	180d CA	90d RA	180d RA	90d CA	180d CA
Treatment		*'Golden Delicious' from Pullman*				*'Golden Delicious' from Yakima*				*'Gala'*			
Control	(A)[a]	2.32 a	3.88	4.43	8.11 a	1.16	2.70	1.23	2.00	-	2.37	-	2.84
Soy1	(B)	2.05 b	3.72	3.50	6.25 b	1.21	2.51	1.26	1.69	-	2.22	-	2.63
Soy2	(B)	1.80 c	3.48	2.99	5.77 b	1.13	2.21	1.15	1.50	-	2.34	-	2.55
Soy3	(B)	1.91bc	3.34	3.31	6.60 b	1.20	2.24	1.40	2.20	-	2.36	-	2.60

[a]Capital letters in parenthesis indicate significant overall treatment effect.

Peel fatty acid concentration.The total fatty acid (FA) content of the fruit skin was measured for 'Golden Delicious' fruit in 2003 from Pullman only and expressed as % of total FA content based on the five FA included in the analysis. The most predominant FA in the apple fruit peel was linoleic acid (C18:2, around 50% of total). Untreated fruit showed a declining proportion of palmitic (C16:0) and linolenic (C18:3) acid, constant levels of stearic (C18:0) and oleic (C18:1) acid, and increasing proportions of linoleic (C18:2) acid during storage. The proportion of linoleic acid increased 30% during RA storage. The proportional decline of palmitic and linolenic acid in apples occurred faster during RA storage conditions. No significant treatment effects were determined, but untreated fruit had consistently higher linoleic acid contents compared to any oil-treated fruit, while soy3 treated apples had more linolenic acid (Table 2).

Table 2. 'Golden Delicious' peel fatty acid profiles in relation to storage conditions and soybean oil treatment

Fatty acid	Treatment	At harvest	After Storage			
			RA		CA	
			Time in Storage (days)			
			90	180	90	180
16:0[a]	Control	21.7 ± 0.8	17.8 ± 1.7	14.5 ± 0.7	18.7 ± 0.6	16.6 ± 0.8
	Soy1	21.4 ± 0.8	18.1 ± 1.6	14.7 ± 0.7	19.2 ± 0.3	17.0 ± 0.9
	Soy2	22.1 ± 1.0	18.2 ± 1.5	15.4 ± 0.7	18.7 ± 0.3	17.7 ± 0.7
	Soy3	21.6 ± 1.2	17.3 ± 1.2	15.0 ± 0.3	18.9 ± 0.6	16.6 ± 0.3
18.0	Control	6.7 ± 0.7	6.8 ± 0.3	7.6 ± 0.3	7.0 ± 0.4	8.0 ± 0.3
	Soy1	6.9 ± 0.4	7.1 ± 0.3	8.2 ± 0.2	6.9 ± 0.2	8.1 ± 0.2
	Soy2	6.4 ± 0.8	7.4 ± 0.4	7.8 ± 0.5	7.5 ± 0.3	8.3 ± 0.5
	Soy3	6.2 ± 0.8	7.5 ± 0.5	8.0 ± 0.7	7.0 ± 0.8	8.1 ± 0.2
18.1	Control	5.4 ± 1.7	6.5 ± 1.6	6.5 ± 0.7	5.6 ± 0.5	6.5 ± 0.8
	Soy1	5.4 ± 1.6	5.9 ± 1.1	6.5 ± 0.6	5.4 ± 0.7	6.1 ± 1.0
	Soy2	5.5 ± 1.3	5.7 ± 1.0	6.4 ± 1.0	6.0 ± 0.3	5.9 ± 1.3
	Soy3	5.1 ± 1.3	6.7 ± 1.2	6.5 ± 0.5	5.5 ± 0.6	6.3 ± 0.4
18.2	Control	48.7 ± 2.7	59.5 ± 1.4	64.0 ± 0.9	58.3 ± 1.5	60.4 ± 0.9
	Soy1	48.6 ± 0.9	58.8 ± 1.5	62.7 ± 0.8	56.8 ± 1.3	61.0 ± 0.3
	Soy2	48.0 ± 1.1	59.2 ± 1.0	62.8 ± 0.4	56.7 ± 2.2	59.6 ± 1.2
	Soy3	48.8 ± 1.1	58.3 ± 0.7	62.3 ± 1.5	57.5 ± 0.9	59.7 ± 1.4
18.3	Control	17.5 ± 1.1	9.4 ± 1.2	7.4 ± 0.9	10.5 ± 1.4	8.5 ± 1.2
	Soy1	17.7 ± 0.8	10.1 ± 1.1	7.9 ± 0.7	11.7 ± 1.0	7.8 ± 0.5
	Soy2	18.0 ± 1.2	9.5 ± 0.6	7.6 ± 0.6	11.2 ± 1.8	8.5 ± 0.7
	Soy3	18.4 ± 1.0	10.3 ± 0.4	8.2 ± 1.7	11.1 ± 0.9	9.3 ± 1.7

[a]16:0, palmitic acid;
18:0, stearic acid;
18:1, oleic acid;
18:2, linoleic acid;
18:3, linolenic acid.

2004: Generally, the most pronounced change in the FA profile of 'Golden Delicious' observed in this and previous studies was the loss of linolenic acid (C18:3) and the subsequent increase in the less unsaturated linoleic acid (C18:2). Linolenic acid was lost at a slower rate in fruit treated with 1-MCP, thus linoleic acid did not increase as fast (Figure 1). No significant treatment effects due to soybean oil application were determined when fatty acids were measured on fruit directly at harvest or after CA storage, validating results from previous work. Though not significant, soybean oil-treated fruit seemed to retain more fatty acid unsaturation during the shelf-life study following CA storage. Alternately, 1-MCP treated fruit with preharvest soybean oil application had higher oleic acid (C18:1) concentrations during the shelf-life period while C18:2 concentrations were lower compared to control fruit. This may indicate slightly increased metabolic activity due to soybean oil application while partially overcoming inhibitory effects due to 1-MCP treatment.

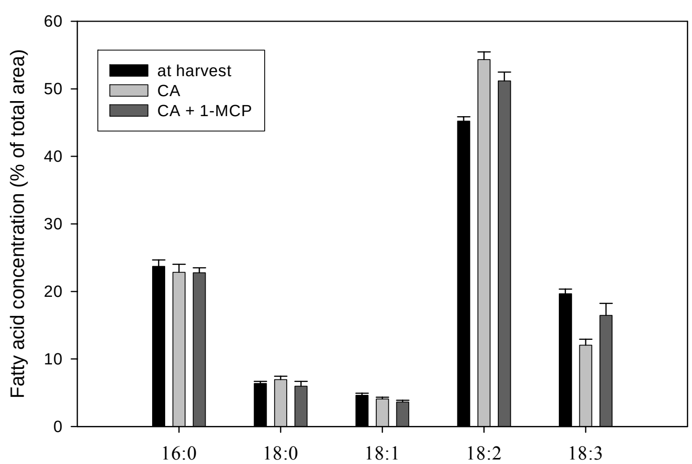

Figure 1. Changes in peel fatty acids of 'Golden Delicious' in response to MCP treatment and CA storage

Volatile aroma production. The apple volatile aroma emission was altered due to soybean oil application in 2003. For example, 'Golden Delicious' apples treated with soybean oil three weeks before harvest emitted more aldehydes (mainly hexanal), while fruit treated with the oil three days before harvest produced more esters at harvest and/or after storage. Overall, all soybean oil treated fruit had a higher aldehyde and mean volatile emission rate at harvest, a principal effect borne throughout the subsequent storage regimens (Table 3). Fruit grown in warmer conditions reacted with more pronounced changes within the volatile profile (only 'Golden Delicious' data from Yakima shown in Table 3). 'Gala' apples treated with soy1 had significantly higher alcohol and ester levels when compared to control fruit (Table 4).

Table 3. Volatile flavor compound production in 'Golden Delicious'after soybean oil treatment and storage.

Volatile group (µg ml^{-1})	Treatment		At harvest	After Storage			
				RA		CA	
				Time in Storage (months)			
				90	180	90	180
Overall means	Control		1.691	2.385 b	2.894	2.725	2.416
	Soy1		1.795	2.575ab	2.707	2.836	2.112
	Soy2		1.834	2.914 a	3.099	2.959	2.596
	Soy3		1.634	2.487 b	3.141	2.860	2.107
Aldehydes	Control	(B)[a]	1.627	1.475 b	0.433	2.368	2.163
	Soy1	(AB)	1.718	1.748ab	0.456	2.598	1.913
	Soy2	(A)	1.768	1.985 a	0.450	2.683	2.351
	Soy3	(B)	1.560	1.511 b	0.411	2.499	1.802
Alcohols	Control		0.050	1.391	1.276	0.273	0.203
	Soy1		0.061	1.479	1.129	0.186	0.161
	Soy2		0.051	1.140	1.314	0.215	0.196
	Soy3		0.058	0.856	1.453	0.283	0.236
Esters	Control	(AB)	0.014	0.309	1.184bc	0.084	0.050
	Soy1	(B)	0.016	0.267	1.122 c	0.052	0.038
	Soy2	(A)	0.015	0.324	1.335 a	0.061	0.049
	Soy3	(A)	0.017	0.342	1.277ab	0.078	0.069

[a]Capital letters in parenthesis indicate overall treatment effect.

Table 4. Volatile flavor compound production in 'Gala'after soybean oil treatment and storage.

Volatile group (µg ml^{-1})	Treatment		At harvest	After storage	
				180 days RA	180 days CA
Overall means	Control		2.040	2.943	1.573
	Soy1		2.173	3.520	1.681
	Soy2		1.951	3.212	1.595
	Soy3		1.940	3.078	1.583
Aldehydes	Control		1.097	0.929	1.472
	Soy1		0.823	1.288	1.555
	Soy2		1.031	1.071	1.475
	Soy3		1.076	1.031	1.472
Alcohols	Control	(B)[d]	0.639 b	1.133	0.078
	Soy1	(A)	0.861 a	1.396	0.100
	Soy2	(AB)	0.607 b	1.357	0.097
	Soy3	(B)	0.568 b	1.150	0.084
Esters	Control		0.304 b	0.880	0.024
	Soy1		0.489 a	0.835	0.026
	Soy2		0.312 b	0.783	0.024
	Soy3		0.296 b	0.896	0.026

[a]Capital letters in parenthesis indicate overall significant treatment effect.

Flavour regeneration capacity. Preliminary work in 2003 indicated that fruit from soybean oil applications close to the anticipated harvest date had higher alcohol and ester regeneration capacities after fruit were kept at 22 °C for seven days following CA storage. Consequently we evaluated the flavour regeneration capacity of 'Golden Delicious' fruit in 2004.

All ester regeneration capacity was improved for straight chain compounds due to soybean oil application (soy2). The branched chain ester 2-methyl-butyl acetate showed a significant treatment effect due to soybean oil application, regardless of storage treatment with the most pronounced response observed during the shelf-life period after CA storage (Figure 2). The increase in ester regeneration capacity was facilitated by the availability of necessary alcohol precursors, the concentration of which also increased during the shelf life. However, the increased capability to regenerate esters, particularly the branched chain ester 2-methyl-butyl acetate cannot be easily explained because alcohol emission rates did not show treatment effects due to soybean oil application. It seems possible that soybean oil application induced changes in the concentration of the acyl-CoAs by supplying fatty acids to the β-oxidation catabolic pathway. Apparently, the primary mode of action for soybean oil treatment is an increase in the supply of fatty acid precursors for volatile aroma synthesis.

Supplying additional FA to fruit can lead to incorporation into volatile aroma components. This would explain why no major changes in the FA profiles were observed, since additional substrate was metabolised immediately. The limiting factor in aroma production is thought to be substrate availability rather than enzyme activity. It is generally accepted that the enzymes required to catabolize FA (lipoxygenase, and/or beta oxidative enzymes), as well as downstream enzymes are not the limiting factors in aroma production.

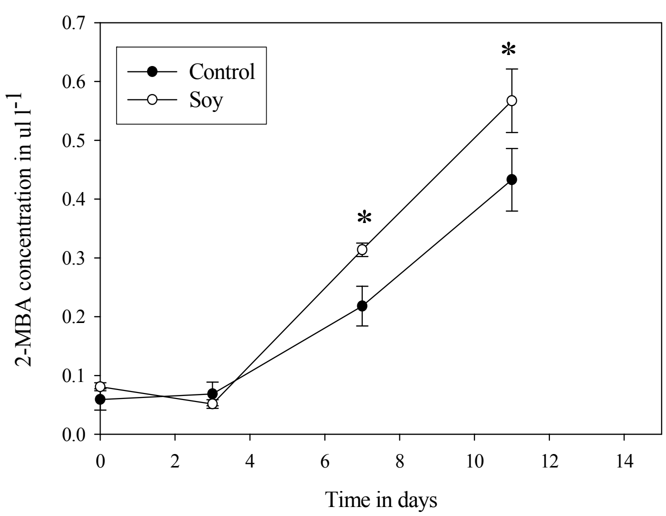

Figure 2. Influence of pre-harvest soybean oil application on 2-MBA (2-methyl-butyl acetate) emission of 'Golden Delicious' apples during a shelf-life period at 22 °C following 140 days of controlled atmosphere storage (CA). Vertical bars represent SE of means (n = 4).

Influences on cuticle development.As observed by scanning electron microscopy (SEM), 'Golden Delicious' apples developed cracks that intensified with maturity (Figure 3, A-C), while 'Gala' apples retained a smooth surface. A thinning of the cutin caused the development of the cracks. The stretching of the cutin caused the epicuticular wax to collapse into the so-formed ridges, giving the fruit a cracked appearance (Figure 3, E). Under arid growing conditions, fewer cracks developed. The preharvest application of soybean oil emulsions decreased the occurrence and severity of cuticular cracks in susceptible varieties such as ‘Golden Delicious’ (Figure 3, E-F). Oil was less influential on ‘Gala’, a variety with innately smooth cuticle topography. The rate of weight loss during storage was directly related to the development of cracks. All apples showed altered wax crystallization patterns after soybean oil application.

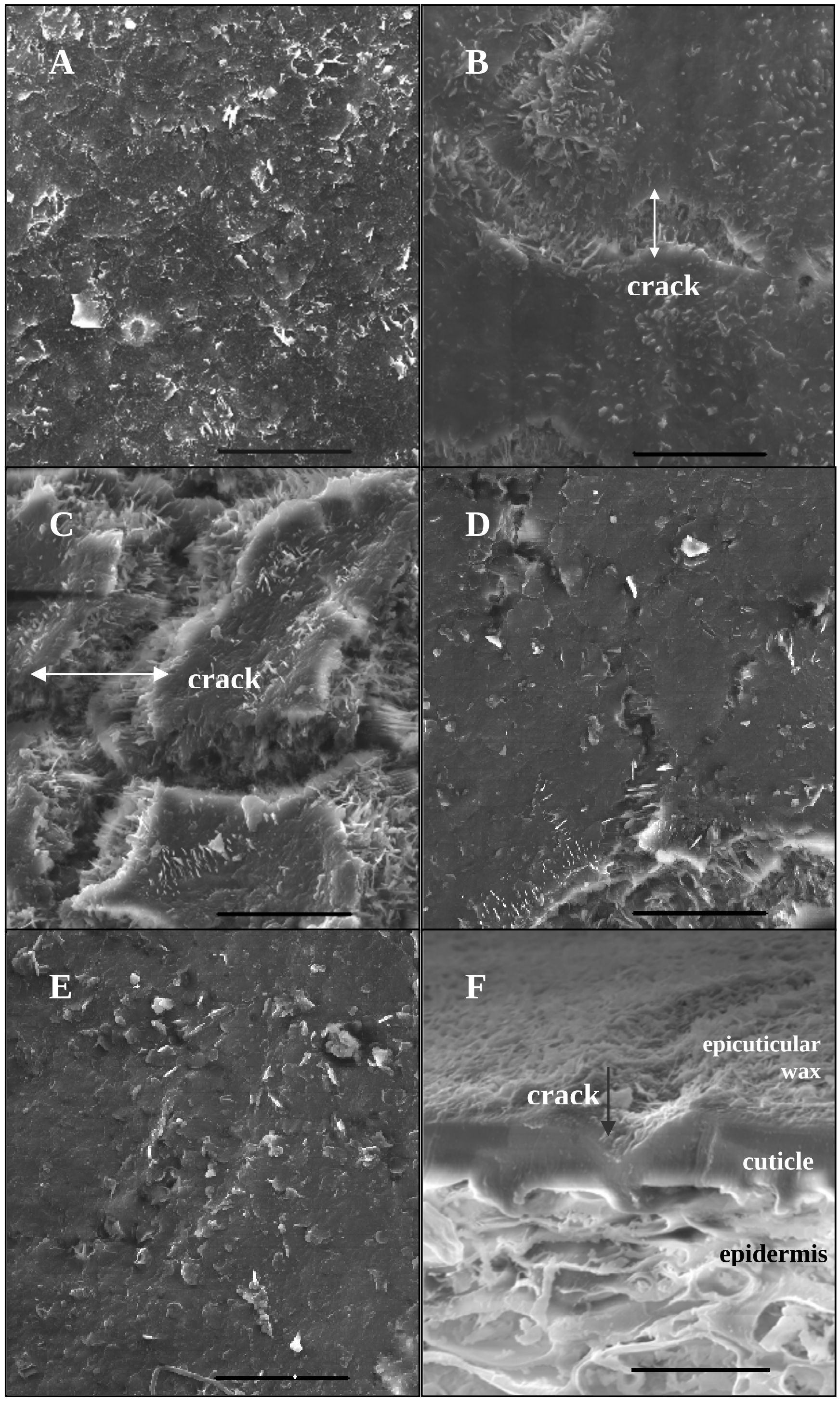

Figure 3. Cuticle structure of ‘Golden Delicious’ apples; A-C are untreated fruit, note cracks developing during maturation; D-E are soybean oil treated, minimizing crack severity; F is a cross-section of a surface crack.
Bar = 43 μm.

Additional observations. The fruit growth rate was not affected by a one-time soybean oil application (soy1, 'Golden Delicious' in Pullman). Due to high codling moth pressure in Pullman, about half the untreated fruit was lost due to insect damage. However, only half the amount of insect damage was observed on the oil-treated fruit.

After 6 months of RA storage, 'Golden Delicious' from Yakima had a high incidence of senescent breakdown. Fruit were scored for disorder incidence and severity and it was found that control fruit was most affected.

DISCUSSION

'Golden Delicious' and 'Gala' apples are important commercial apple varieties worldwide. Current thought links skin and peel related disorders of these varieties to epidermal structure, especially when compared to other cultivars. A better understanding of epicuticular wax structures, their seasonal changes in apples and the influence of hydrophobic surfactants on their development and function are essential for successful postharvest apple management. Every treatment that strengthens the fruit skin will diminish susceptibility for pathogen infection, as well as bruising, russeting and water loss.

Since fatty acids are known precursors for apple volatile aroma components, the application of soybean oils, rich in fatty acid aroma precursors, during the growing season has shown promise to improve the retention and regeneration capacity of important volatile compounds contributing to the aroma of apples. Hence, the use of non-traditional, plant-based horticultural oils has the potential to benefit the growth, development, and storage longevity of apples. Plant oil application could be beneficial in organic as well as in integrated pest management programs. Approved chemicals for summer applications are becoming more limited every year due to development of resistance and loss of regulatory agency approval. No species of insects or mites are known to have developed resistance against oils.

In response to increased consumer pressure for a more wholesome product, use of non-toxic materials, such as soybean oil, could provide increased marketing opportunities to a growing sector of fruit buyers while contributing to the long-term sustainability of the fruit-growing enterprise.

In conclusion, field-applied soybean oil emulsions have demonstrated potential to improve postharvest quality of apples by stimulating volatile aroma emission of fruit, delaying weight loss in storage and the improvement of cuticular structures.

Suggestions for further study. The 1% oil concentration appears too low to sustain any effects. Consequently, a combination of two oil treatments within three weeks of harvest might result in even higher and more pronounced volatile aroma retention capacities. Additionally, the 1% concentration used in the field might not have been high enough to cause major physiological changes, as other groups have observed when using higher concentrations (5 or 10%) in a postharvest application. Higher concentrations should be field-tested, especially to determine threshold levels for phytotoxicity, with the goal to amplify any underlying physiological phenomena.

One of the most pronounced effects of soybean oil application was the reduction of weight loss during storage and subsequent shelf-life periods. The exact mechanism of this waterproofing is presently unknown. However, the mode of action of soybean oil applications appears unique, since weight loss was reduced without affecting other quality parameters as observed elsewhere after application of traditional antitranspirants.

A largely unexplored aspect of the development of cuticular cracks is the lack of a clear description of the involvement of the different epicuticular layers like epicuticular wax and/or cutin. In results reported here, cracks appeared to be due to changes in the thickness of the cutin without changes in the epicuticular wax fraction. This is plausible, as cutin functions as the principal barrier against water loss. Furthermore, the development of cracks has been attributed to rapid fruit growth, which does not explain why cracks continue to enlarge during storage of apples. In light of the present study it seems possible to improve cuticular characteristics through application of materials rich in fatty acids. If and how these compounds are incorporated remains unknown.

Soybean oil application also altered epicuticular wax crystallization patterns. It would be intriguing to study relationships between soybean oil application and light reflection, water repellence, cuticular sorption of agrochemicals, and plant insect interactions, since all these processes are tightly linked to epicuticular wax crystallization patterns.

Publications and Presentations resulting from this study

Manuscripts:

Müller, I., Fellman, J.K., Mattinson, D.S. 2004. Relationships between horticultural oil application and postharvest behaviour of 'Golden Delicious' apples: Effects on volatile aroma production. Acta Horticulturae (paper in press).

Müller, I., 2005. Relationships between horticultural oil application and postharvest behaviour of apples. Dissertation, Washington State University, USA.

Müller, I., Mattinson, D.S., Fellman, J.K., 2005. Apple postharvest performance as influenced by preharvest soybean oil application (manuscript in preparation).

Müller, I., Fellman, J.K., 2005.Preharvest soybean oil application alters epicuticular wax crystallization patterns and resistance to weight loss in storage (manuscript in preparation).

Presentations:

Müller, I., D. Scott Mattinson and John K. Fellman "Preharvest Horticultural Oil and postharvest 1-methylcyclopropene (1-MCP) Application to 'Golden Delicious' Apples: Volatile Aroma Production After 4 Months Controlled Atmosphere Storage and Shelf-Life Regeneration". 9th International CA research conference, E.Lansing, Michigan, 2005.

Müller, I., Fellman, J.K., Mattinson, D.S. 2005. Field-applied soybean oil alters postharvest behaviour of apples. 9th International CA research conference, E.Lansing, Michigan, 2005 (poster presentation).

Müller, Ines, D. Scott Mattinson and John K. Fellman Relationships between horticultural oil application and postharvest behaviour of 'Golden Delicious' apples. Postharvest 2004 ISHS. Verona, Italy, 2004 .

BUDGET

Project duration: 2003-2005 No additional funds requested
Project total (3 years):

Item	Year 1 (2003)	Year 2 (2004)	Year 3 (2005)	**Total**
Salaries				
0.1 FTE DS Mattinson	3,181	3,402	3,538	**10,121**
APA Ines Müller	17,870	19,137	19,902	**56,909**
Benefits				
40% (Mattinson)	1,082	1,128	1,174	**3,384**
1.5% Müller	268	279	290	**837**
Health Insurance	1,224	1,441	1,499	**4,164**
Wages	4,500	5,000	5,500	**15,000**
Benefits 9%	405	450	495	**1,350**
Equipment	0	0	0	**0**
Supplies	2,421	3,500	4,000	**9,921**
Travel	0	0	0	**0**
Miscellaneous	0	500	500	**1000**
Total	30,951	35,078	35,559	**101,588**

Budget justification: Salary is for partial support of Scott Mattinson, Postharvest Physiology Research Associate. Other support for his salary comes from WSU and USDA Special Grant funds. Salary is also requested for an Agricultural Project Associate, Ines Müller, who will have principal task management and implementation responsibility. Wages are for part-time student helpers. Principal supply costs include maintenance and operation of orchard and CA storage facility, purchase of chemicals, cylinder gases, GC columns, and liquid nitrogen. Miscellaneous costs include publication, graphics and computer support.

For further information please refer to the dissertation from Ines Müller, which is available by the author upon request as a PDF and has been submitted as supporting material to the TFREC.