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Review

Russeting of Fruits: Etiology and Management

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Abstract: The skin of a fruit protects the vulnerable, nutrient-rich flesh and seed(s) within from the hostile environment. It is also responsible for the fruit's appearance. In many fruitcrop species, russeting compromises fruit appearance and thus commercial value. Here, we review the literature on fruit russeting, focusing on the factors and mechanisms that induce it and on the management and breeding strategies that may reduce it. Compared with a primary fruit skin, which is usually distinctively colored and shiny, a secondary fruit skin is reddish-brown, dull and slightly rough to the touch (i.e., russeted). This secondary skin (periderm) comprises phellem cells with suberized cell walls, a phellogen and a phelloderm. Russeted (secondary) fruit skins have similar mechanical properties to non-russeted (primary) ones but are more plastic. However, russeted fruit skins are more permeable to water vapor, so russeted fruits suffer higher postharvest water loss, reduced shine, increased shrivel and reduced packed weight (most fruit is sold per kg). Orchard factors that induce russeting include expansion-growth-induced strain, surface wetness, mechanical damage, freezing temperatures, some pests and diseases and some agrochemicals. All these probably act via an increased incidence of cuticular microcracking as a result of local concentrations of mechanical stress. Microcracking impairs the cuticle's barrier properties. Potential triggers of russeting (the development of a periderm), consequent on cuticular microcracking, include locally high concentrations of O_2, lower concentrations of CO_2 and more negative water potentials. Horticulturists sometimes spray gibberellins, cytokinins or boron to reduce russeting. Bagging fruit (to exclude surface moisture) is also reportedly effective. From a breeding perspective, genotypes having small and more uniform-sized epidermal cells are judged less likely to be susceptible to russeting.

Keywords: disorder; periderm; repair mechanism

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1. Introduction

The skin of a fruit lies at the interface between the vulnerable, nutrient-rich fleshy tissues and seed(s) inside and the surrounding 'hostile' environment outside. The fruit skin is exposed to a broad range of abiotic and biotic challenges, thus serving as a critical barrier protecting the fruit tissues against (a) uncontrolled water loss/uptake [1], (b) uncontrolled exchanges of respiratory gasses (O_2, CO_2) and the hormone ethylene (C_2H_4) [2], (c) UV-radiation [2,3] and (d) invasion by pathogens [4,5]. In modern horticulture, some of these functions require opposing properties, such as protection against cell content leakage, while at the same time permitting penetration of foliar-applied nutrients, growth regulators or other agrochemicals [6]. To fulfill these functions, the fruit skin must remain intact throughout the period of fruit growth and development. This review deals with the development of a secondary surface (a periderm) on the skins of commercial fruit types that usually retain their shiny, distinctively-colored, primary surfaces through to harvest and consumption.

A plant organ's primary surface comprises a complex of materials. On the outside, there is a polymeric cuticle that overlies a cellular structure usually consisting of a single epidermal cell layer, which itself overlies one to several layers of hypodermal cells. In most fruit crops, the epidermis and hypodermis are responsible for the skin's mechanical properties, while the cuticle is responsible for the skin's barrier properties [7,8]. It is also the primary fruit skin that determines the appearance and attractiveness of the fruit to end consumers, as well as to seed-dispersing animals. After all, the wild types of most commercial fruitcrop species evolved to attract animals as their agents of seed dispersal. Thus, the epicuticular waxes on the cuticle are responsible for the skin's gloss, and the pigments in the cuticle and subtending cell layers for the skin's distinctive color [9,10].

However, the skins of a significant number of commercial fruit types are partially or wholly covered by areas of a secondary surface. Horticulturists refer to this as russeting [11,12]. The proportion of the surface of a mature fruit that is primary vs. secondary is genetically determined. Thus, in apple, some cultivars rarely exhibit areas of russeting (Royal Gala); in some, russeting is a cultivar characteristic (Cox's Orange Pippin); while in others, the whole fruit surface is usually russeted (Egremont Russet). Russeting is seen as a market defect (market value is reduced) only in the first case or in the second if the russeted area is excessive.

A secondary surface forms when the primary surface fails. Failure may occur for various reasons. Potential reasons include the normal internal processes of ontogeny (e.g., growth strain) or external factors such as mechanical or chemical damage or harsh environmental conditions such as freezing [7]. A periderm forms to (partially) restore the impaired barrier properties of the damaged primary fruit skin. The proportion of the fruit-skin affected by russeting ranges from small patches in particular regions of the fruit surface to a uniform layer that covers the entire fruit.

From a horticultural point of view, the dull, reddish-brown appearance of russeting is usually unattractive to the consumer. Russeting is therefore considered to be a fruit surface disorder in many fruitcrop species and in all 'smooth-skinned' cultivars. In many russet-susceptible cultivars, russeting is readily accepted as being 'normal'. Thus, the entire fruit skin is russeted in most kiwifruit cultivars/species. Similarly, russeting is considered normal and acceptable in the 'Reinette' apple cultivars and in pear cultivars, such as Bosc, Conference and Gold La France, the latter being a russeted sport of the non-russeted cultivar La France [13]. Similarly, in Asian pear, smooth-skinned cultivars, as well as entirely russeted cultivars, are known. Melons form a notable exception. Here, the 'netting' pattern of russeting of the fruit skin is seen as a positive indicator of fruit quality and, so, is considered highly desirable [14].

Russeting is not a new phenomenon. The first research publications date back nearly two centuries [12,15–22]. Most of the literature on russeting relates to pome fruit, and especially to apple. Fewer studies relate to pear, kiwifruit, mango, tomato, bell pepper and others (Table 1). Occasionally, russeting has been reported for plums and grapes. Sweet and sour cherries, peaches, apricots and most 'berryfruit' crops, including currants, blueberries, raspberries, blackberries and strawberries, are essentially free of russet. The published information on russeting is scattered and often not conclusive. The objective of this paper is to review the literature on the practical aspects of russeting, including its occurrence, triggers, mechanical bases and management strategies adopted to reduce russeting under orchard conditions by cultivation and breeding. For a comprehensive review of the biochemistry and molecular biology of russet formation, the reader is referred to the excellent recent reviews by Macnee et al. [23] and Wang et al. [24].

2. Occurrence and Symptoms of Russet

Russeting occurs in a large number of fruitcrop species (Table 1). Often, russet-susceptible and non-susceptible cultivars are known within a species. In apple, some highly russet-susceptible cultivars are identified by the cultivar name. Examples include Red Russet, Golden Russet, Roxbury Russet [22] or Egremont Russet [25], as well as the Reinette-type cultivars [26].

Table 1. Occurrence, symptoms, causes and management of russeting. Results are compiled from literature sources.

Cultivar	Symptoms	Causes	Management
Apple	Russet as rough and brown skin [17,28], often in stem [29] and calyx cavities [30], some cultivars with entire surface russeted [31], high susceptibility during early fruit development [12,29,32–34]	Moisture [35–38] or high humidity [17,35], damage by pesticides, growth regulators, surfactants and other substances [19,39–61], frost [27,34], fungi [62–66], viruses [67–69], insects [70,71]	Spray application of growth regulators [30,32,33,56,58,72–81], CaCl$_2$ [82], prohexadione-calcium [72], organic/mineral bio-stimulators [83], chlorogenic acid [84], coatings [82], insecticides to prevent insect damage [71], shading nets [85], rain shelters [48], bagging [17,48,82,86]
Pear	Russet as dull-brownish skin patches, more in calyx and cheek than in neck [87], some cultivars completely russeted [23], high susceptibility during early development [87]	Surface moisture [88–90], high humidity [90], growth stress [87], fungicides, thinners and growth regulators [89–93], insects [94–96], bacteria [97], fungi [98,99]	Bagging [100–104], spray application of GA$_{4+7}$ [105], mancozeb + sulfur [105] or kaolin ± mancozeb [106]
Citrus	Russet as rough texture, brownish-black, greyish discoloration [107].	(Rust) mites, thrips and other sucking insects [107–109], mechanical damage by wind, hail, contact with branches [110,111]	Zineb against citrus mites [108,109,112]
Prune	On immature fruit: longitudinal stripes at stylar end [113], mature: rough, brown, dried surface [113]	Copper spray [113], mechanical damage by wind, abrasion by leaves, shoots, adjacent fruits [113,114], exposure to surface wetness or free water, high humidity [113,114], scab [115]	Captafol, ziram for scab control [113]
Loquat	Deep brown stripes, approx. 1 mm wide [116,117]	Growth stress [116,117], microclimate (high temperature) [116], very high light intensities [116]	Shading using nets to decrease growth rate during cell division phase [116,118]
Tomato	Russet as rough corky discolored surface [119], also referred to as 'shoulder check' [119] or 'cuticle cracking' [120]	Rust mites [71,121], growth stress [120,122,123], surface moisture [119]	Non-susceptible cultivars [123], moderate thinning [123], spray application of Ca+B [119,124]
Melon	Rind netting common in some cultivars [14], russet as dry, white to brownish ridges [14]	Growth stress [125,126], surface moisture [125], wounding [14]	Rind netting desirable, countermeasures not needed
Grape berry	Brown patches of russet [127]	Surfactants [128], fungicides [129], insects [71,130], surface moisture [131]	Spray applications of GA$_3$, GA$_3$ + CPPU [132], insecticides [71], Ca [133]
Mango	Rough brownish irregular patches of russet [134], beginning at lenticels [134]	Surface moisture, cold nights [134]	Bagging [135]
Pomegranate	Corky surface [136]	High humidity [136,137], heat waves [138], temperature fluctuation during maturation [136], pomegranate mite [139]	Spray applications of GA$_3$, CPPU [137,140], acetylsalicylic acid [136], sulfur dust against pomegranate mites [139]

The symptoms of russet are similar between different fruitcrop species. A rough, reddish-brown and corky appearance is characteristic of a russeted surface (Table 1 and Figure 1). The region of the fruit surface affected by russet can differ. In apples, the spatial distribution of russeting differs depending on the cause. Russet induced by growth strain or by exposure to high humidity or dew occurs in large, uniform patches and may cover the entire fruit surface. Russeting limited to the stem cavity is more likely the result of long wetness durations and high growth strains. Russeting in response to mechanical wounding (e.g., scratching or abrasion from contact with a neighboring fruit or leaf or stem) is typically well defined spatially, being strictly limited to the region of direct physical contact. Russeting caused by spray chemicals occurs in regions of the fruit surface where spray droplets collect and later concentrate excessively during drying. Small fruitlets that come into contact with spray solutions during the particularly russet-susceptible early stages of fruit development may be entirely russeted [27]. A net-like pattern of russeting on apple is characteristic of infection with powdery mildew. Russeting caused by the feeding of pests (thrips, stink bugs, mites, etc.) is limited to the site of the puncture wound and the immediately surrounding cells. Forms of russeting caused by frost are typically in rings. These are induced by freezing temperatures when only part of the flower or fruitlet is damaged (Table 1).

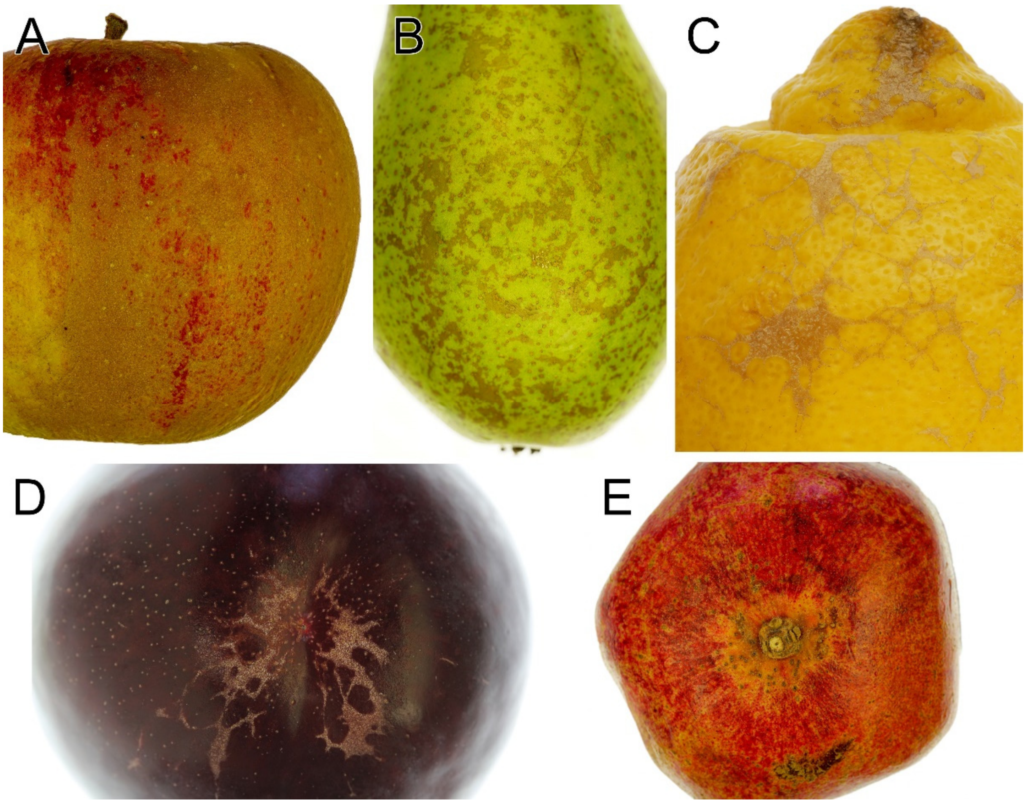

Figure 1. Russeting in different fruit crops. (**A**) Apple; (**B**) pear; (**C**) citrus; (**D**) plum; (**E**) pomegranate. Images: (**A**,**C**) Andreas Winkler, (**B**,**D**,**E**) Martin Brüggenwirth.

3. Some Fruit Skin Disorders Not Related to Periderm Formation

There are some fruit skin disorders that can be confused with russeting. These include skin spots and scarf skin in apple and maturity bronzing (sometimes also called maturity stain) in banana (Table 2). These disorders can bear a visual similarity to russeting. However, they differ from russeting in that a periderm does not develop.

In skin spots, cuticular microcracks are causal. These form due to moisture exposure during late-stage fruit development [36]. In this stage, the apple fruit skin is no longer able to form a periderm [36,38]. Here, the impaired barrier properties of the skin are restored to some extent by the deposition of lignin in the cell walls immediately underlying a microcrack. This process hydraulically isolates the portion of the fruit skin underlying a microcrack. The characteristic spot-like appearance is caused by the resulting cell death [141].

Apples with scarf skin symptoms look as if they have a thin and very ‘soft’ periderm. However, periderm formation is not involved in scarf skin. Instead, scarf skin is thought to result from the formation of subepidermal air spaces [142]. The cause of this is not yet known. Surface moisture may be involved since bagging during early fruit development (when russet susceptibility is particularly high) reduces scarf skin [143].

Maturity bronzing in banana is also connected to fractures in the cuticle, which propagate into the epidermis [144]. Maturity bronzing occurs primarily in the tropical wet season when temperatures and humidities are especially high, and the sky is overcast [145]. These conditions result in high rates of growth strain, which may be causal in maturity bronzing [144].

Table 2. Fruit surface disorders that bear some similarity with russet, but where no periderm is involved. Data are compiled from literature sources.

Disorder	Crop Affected	Symptoms	Causes	Management
Skin spots	Apple	Irregular patches of small, round and brown spots, develops in CA-storage, promoted by 1-MCP [141]	Moisture-induced microcracks late in the season [36,141]	Reducing surface wetness duration, for susceptible batches, no storage or cool-storage only [36,141]
Scarf skin	Apple	Whitish lines or stripes [146], whitish or opalescent sheen [147], due to formation of subepidermal air spaces [142]	Unknown	-
Maturity bronzing or maturity stain	Banana	Pre-harvest necrosis of the skin, bronze coloration [144]	Growth stress [148], water stress [144]	Bagging [149], reducing the number of leaves [150]

4. Anatomy of Russeted Fruit Skin

In botanical terms, a russeted fruit skin represents a periderm consisting of phellem, phellogen and phelloderm [7,23]. The phellem is the outermost layer of this composite, the phelloderm the innermost. The phellogen is the interfacing sheet-like meristematic layer. The phellogen is formed in the hypodermal cell layer by dedifferentiation of hypodermal cells [16,151]. Periclinal cell division in the phellogen generates stacks of phellem cells where each cell of a stack originates from the division of a single underlying mother cell of the phellogen [7].

Phellem cells have suberized cell walls. When the stacks of phellem cells reach the surface, they come into contact with the atmosphere. Here, the suberized cell walls turn brown. It is the suberin that is responsible for the dull and reddish/brown color of a russeted fruit surface [152]. Due to the lipophilic character of suberin, suberized cell walls present a significant barrier to water loss [153].

From the above, it is evident that during the early stages of periderm formation, the periderm may still be covered by a cuticle, epidermal cells and some hypodermal cells. The periderm reaches the surface as growth proceeds and as the residues of the primary fruit skin (now hydraulically isolated and desiccated) tear and are sloughed off.

5. Physiology of Russeted Fruit Skin

The physiological properties of the fruit skin change with russeting. For the fruit of a particular apple cultivar, the water vapor permeance of a russeted area of skin is higher than that of a non-russeted area [11,134]. Furthermore, a non-russeted area of the primary surface of a russet-susceptible apple cultivar has a higher water vapor permeance than a non-russeted area of a non-russet-susceptible cultivar [38]. This latter finding is likely due to a higher incidence of microcracking of the cuticles of the russet-susceptible cultivars. Compared to non-russet-susceptible cultivars, the higher water vapor permeance results in greater water loss during storage, and thus, a higher mass loss and (possibly) more shrivel. In this way, russeted fruit have reduced cool-storage potential and shorter supermarket shelf-lives compared to non-russeted fruit. We are unaware of studies that measure the fruit skin permeances to O_2, CO_2 or ethylene of russeted fruit.

The mechanical properties of fruit skins differ slightly between russeted and non-russeted fruit surfaces. The maximum stress and maximum strain that the fruit skin can withstand without failure are of similar magnitude for non-russeted and russeted skins [18]. Enzymatically isolated periderms of apple and pear are more plastic than isolated cuticles as indexed by a higher strain at maximum stress and a lower modulus of elasticity [18]. The higher plasticity renders the periderm a very suitable ‘repair patch’ for an overly-strained fruit surface. It allows the periderm to cope with ongoing area expansion during growth without excessive increases in stress build up [18,154].

6. Factors in Russet Formation

Russeting has been related to a number of factors. Growth strains are considered causal in russet formation in apple [18], pear [87], loquat [116,117], tomato [120,122,123] and melon [125,126]. During growth, the skin of developing fruit is subject to considerable tangential strain [7], arising from the increase in fruit volume and hence in fruit surface (area strain). Support for the idea that excessive growth strain lies behind the formation of russet comes from the following observations. First, susceptibility to russet is highest during early fruit development [12,29,32–34,155]. During early development, the relative surface area growth rate is at a maximum, resulting in maximum rates of strain [156]. The relative surface area growth rate equals the increase in surface area per unit time (cm^2 d^{-1}) divided by the surface area (cm^2) at that time. Relative surface area growth rate, thus, has the units d^{-1}. Second, the calyx and cheek regions of pear are more russeted than the neck [87]. Both these regions have higher relative surface area growth rates than the neck [87]. Third, the stem cavity of apple fruit is often russeted. Here, stress concentration is at maximum due to the small radius of curvature of the fruit surface [154].

Extended periods of exposure of fruit surfaces to moisture, either as liquid water or as high water-vapor concentration (high relative humidity), has been identified as causal in russeting. Typical examples include russet in apple, pear, prune, tomato, melon, grape and mango (Table 1). Surface moisture is particularly critical during the early stages of fruit development when susceptibility to russeting is high [38]. The following observations support a role for moisture in russeting: First, the development of fruit under cool, rainy and high-humidity conditions stimulates russet formation in apple [156,157] and pear [88–90]. Second, experimental exposure of fruit surfaces to water, by immersion [73], by mounting a test tube filled with water on the fruit surface [38] or by overhead sprinkling [36], results in enhanced russeting. Indeed, these techniques are often used experimentally to induce russeting [37,158].

Mechanical damage of the fruit surface is also a trigger for russeting. Mechanical damage may be caused by a combination of wind and contact of fruit with a neighboring branch, shoot, leaf or fruit. Hail also damages fruit skin and causes russeting [110,111,113,114].

Pests and diseases may cause russeting in several fruitcrops. Examples of such pests include the citrus rust mite [107–109] and the tomato rust mite [71,121]. Similarly, fungi, such as powdery mildew in apple or epiphytic yeast species in apple and pear, have been reported to be causal in russeting (Table 1).

Exposure of fruit to freezing temperatures may result in formation of russet. Characteristic shapes of russet due to frost in apple are “periderm tongues” that run from the stem cavity downwards to the equatorial plane along one side of the fruit or rings of russeting that completely surround the fruit [27,34]. Why these characteristic shapes arise is unknown.

Application of agrochemicals may increase, not affect or decrease russeting. Compounds known to induce russeting include lime sulfur, copper hydroxide and thinners such as ammonium thiosulfate or ethephon (Table 3). Surfactants such as Tween 20 or Citowett that are often used in agrochemical formulations are reported to induce russeting in some fruitcrops (Table 3). An important factor would seem to be the developmental stage at the time of agrochemical application. Applications made during periods of high susceptibility to russet (e.g., during early fruit development) are more likely to induce russet. Meanwhile, the same chemical compounds may have no effect on russet formation when applied at a later stage when susceptibility is lower. In addition, environmental conditions, such as high temperatures, that favor the rapid uptake of agrochemicals are more likely to induce russeting. Rapid uptake may result in overloading of the contacted cells and thus a phytotoxic reaction. This occurs particularly in regions of the fruit surface where spray droplets collect; the droplets coalesce, and highly-concentrated chemical deposits form as the droplets dry. Then, when the critical concentration is exceeded, the cells collapse.

Reduced incidence of russeting has been found following the application of fungicides, such as mancozeb. This effect is accounted for by a reduction in the population of fungal species that induce russet.

Table 3. Effect of fungicides, surfactants and foliar fertilizers on russet. Results are compiled from literature sources.

Chemical	**Category**	**Crop**	**Cultivar**	**Time of Application**	**Effect on Russet**	**Reference**
Di-l-p-methene (2.5%)	Antitranspirant	Apple	Golden Delicious	4, 13, 21 and 27 DAFB	Increased	[48]
B (300 mg L^{-1}) B (300 mg L^{-1}) + Ca (2 g L^{-1})	Foliar fertilizer	Tomato	Mountain Spring	Weekly	Decreased	[119]
Dithane (4 kg ha^{-1}) Packhard (0.5% Ca)	Foliar fertilizer	Apple	Golden Delicious Spur	Flowering, PF and FS	Increased	[39]
Zn (100 g ha^{-1})	Foliar fertilizer	Apple	Elstar	Green and pink stage and at bloom beginning	Increased	[40]
Captafol (1.8 g a.i. L^{-1})	Fungicide	Plum	French	60–90% FB	Decreased	[113]
Chlorothalonil (3.37 kg ha^{-1})	Fungicide	Grape berry	Concord	10 DAFB	Increased	[129]
Kocide (Copper hydroxide) (0.32 g L^{-1})	Fungicide	Apple	Braeburn	Weekly starting at pink tip stage	Increased	[41]
Kocide (Copper hydroxide) (1.5 g L^{-1})	Fungicide	Apple	Golden Delicious	3 to 9 weeks after FB	Increased	[42]
Kocide (Copper hydroxide) (16 or 63 g L^{-1})	Fungicide	Apple	Granny Smith	Pink bud, FB and PF	Increased	[43]
Copper hydroxide (50%) (2.5 kg ha^{-1}) + amino acids (10%) (2 L ha^{-1})	Fungicide	Pear	Conference	PF and 1 week after PF	Increased	[89]
Copper hydroxide (0.3 g L^{-1})	Fungicide	Pear	Beurré Bosc	PF, 7, 14 and 21 DAPF	Increased	[91]
Copper hydroxide	Fungicide	Pear	Bosc	PF	Increased	[90]
Copper hydroxide Copper oxychloride	Fungicide	Apple	Idared	FB	Increased	[44]
Copper oxychloride (4 g L^{-1})	Fungicide	Apple	Red Fuji	Green tip stage	Increased	[19]
Lime sulfur (6 g L^{-1})	Fungicide	Apple	Fuji More	90% FB	Increased	[45]
Lime sulfur (2%)	Fungicide	Apple	Honeycrisp	Fruitlet stage	Increased	[46]
Lime sulfur (2%) + winter oil Fish emulsion (3%) + 2% fish oil Fish emulsion (3%) + Tween 20 (0.125%)	Fungicide	Apple	Gala	20% and 80% FB	Increased	[47]
Mancozeb (2 g L^{-1}) + Sulfur (2 g L^{-1})	Fungicide	Pear	Packham's Triumph	80% FB	Decreased	[105]
Wettable sulfur (17 kg ha^{-1})	Fungicide	Apple	Golden Delicious Spur	FB, PF and FS	Decreased	[39]
Ziram (2.4 g a.i. L^{-1})	Fungicide	Plum	French	60–90% FB	Decreased	[113]
Diazinon (0.08%)	Insecticide	Apple	Golden Delicious	18 DAFB	Increased	[48]
Rape oil (10 or 30 g L^{-1}), Sunflower oil (30 g L^{-1}), Soya oil (30 g L^{-1})	Oil	Apple	Golden Delicious	FB	Increased	[49]
Superior oil (0.5%)	Oil	Apple	Golden Delicious	18 DAFB	Increased	[48]
Citowett (>1%) Tween 20 (≥1%)	Surfactant	Apple	Golden Delicious	FB, PF and 10 weeks after FB	Increased	[50]
Ortho X-77 (1.0%)	Surfactant	Apple	Suntan	3 weeks after FB	Increased	[51]

Table 3. *Cont.*

Chemical	**Category**	**Crop**	**Cultivar**	**Time of Application**	**Effect on Russet**	**Reference**
Polysorbate 20 (0.5%), Polysorbate 60 (0.5%), Polysorbate 80 (0.5%), Lecithin (0.5%)	Surfactant	Apple	Golden Delicious	At 12.5 + 18 or 18 + 20 mm diameter	Increased	[52]
Polysorbate 20 (0.5%), Polysorbate 60 (0.5%)	Surfactant	Apple	Fuji	At 12.5 + 18 mm diameter	Increased	[52]
Potassium soap (500 mg L^{-1})	Surfactant	Apple	Golden Delicious Smoothee	FB and 2 DAFB	Increased	[53]
Ammonium thiosulphate (4%)	Thinner	Apple	Golden Delicious	20% FB	Increased	[55]
Ammonium thiosulphate (1.2%)	Thinner	Pear	Conference	20% or 50% FB	Increased	[92]
Endothal (0.8–1.2 mL L^{-1}) + CyLex (150 mg L^{-1})	Thinner	Apple	Oregon Spur Red Delicious	80% FB	Increased	[54]
Apasil (silicon dioxide) (2.5%)	Other	Apple	Golden Delicious	1 to 4 applications between 4–25 DAFB	Decreased	[48]
PEG 20000 (2.5%)	Other	Apple	Golden Delicious	4, 13, 21 and 27 DAFB	Increased	[48]

PEG = polyethylene glycol; FB: full bloom; PF: petal fall; FS: fruit set; DAFB: days after full bloom; DAPF: days after petal fall; Dithane: ethylene-bis dithy-ocarbamate manganese 62%, Mn 16%, Zn 2%; Packard: 8% Ca, 6% carboxylic acids, 0.5% B, pH < 3.0.

7. The Mechanism of Russeting—A Central Role for Cuticular Microcracks

Microscopic cracks in the cuticle, so-called microcracks, play a key role in russet formation [12,159]. Microcracks are invisible, or barely visible, to the naked eye. They are limited to the thickness of the cuticle and do not propagate deeper into the underlying cell layers [160]. Importantly, the formation of microcracks provides a unifying explanation for a diverse list of factors found to trigger russeting.

7.1. Temporal and Spatial Heterogeneity

High growth strains represent the critical factor for microcracking of the cuticle. The skin of a developing fruit is subject to ongoing tangential strain as the fruit volume and, hence, the fruit surface area increases during growth [7]. In the epidermal and hypodermal cell layers, the increase in skin surface area is accommodated by a combination of cell division (more cells) and cell extension (larger cells). Furthermore, some epidermal cells change their shape from 'portrait' to 'landscape' (in anticlinal view) as they increase in periclinal area and decrease in anticlinal height, but without significant change in (anticlinal) perimeter [16,151,161,162]. The change in cell shape implies that areas of previously anticlinal cell walls de-bond and change their orientation to form part of the expanding periclinal cell wall [162]. Such a re-orientation of cell wall material will focus the associated cuticular strain on the narrow region immediately above the anticlinal cell walls. Because the cuticle is a non-living polymer, it cannot divide but instead is dragged along (stretched) as the underlying surface expands. The strain concentration above the anticlinal cell wall (see just above) makes the cuticle particularly vulnerable to microcracking in this region. This explains the characteristic pattern of microcracks above the anticlinal cell walls as seen in a number of fruit crops, including in apple [162,163]. It also explains why fruits of many species are particularly susceptible to microcracking and russet formation during early-stage development [73]. In early-stage fruit development, the relative surface area growth rate is maximal.

Whether the microcracks propagate more deeply to traverse the entire cuticle or instead remain shallow and limited to the outer (older) volume of the cuticle depends on the relativity between the rate of deposition of new cuticular material (on the inside, adjacent to the cell wall) and the rate of fruit area growth. As mimicked in a uniaxial tensile test of a portion of fruit skin, a high surface area growth rate, in the absence of an appropriately high cuticle deposition, causes the cuticle to thin and thus fail. This occurs before the cellular components fail [164]. Correspondingly, a high rate of cuticle deposition in the absence of an appropriate surface area occurs and results in an increase in cuticle thickness. In apple fruit skin, the rate of cutin and wax deposition usually exceeds that required to match the increase in fruit surface area. Hence, cuticle thickness increases during development [165].

As previously noted, the deposition of cutin occurs on the inner surface of the cuticle (i.e., adjacent to the cell wall) [166]. Thus, the outer cuticle layers are older and, thus, have a longer history of being stretched and are more strained than the younger, inner layers [167]. This results in a radial gradient in strain across the cuticle. The gradient also accounts for the occurrence of shallow microcracks in the outer layers of the apple fruit cuticle that do not extend through to the inner layers [12,168,169]. Because cuticular microcracks differ in depth, the extent of impairment of the cuticle's barrier properties differ. These factors explain why shallow microcracks occur on fruit surfaces without triggering periderm formation, whereas deep ones do trigger it.

Temporal and spatial heterogeneity in fruit expansion during growth is another factor in strain concentration and thus microcracking of the cuticle. The heterogeneity may be due to irregular and variable cell sizes in the epidermis [151,161,170]. Moreover, structures in the epidermis may vary cuticle stiffness—structures such as stomata [171], lenticels [172] and trichomes. Thus, cuticular microcracks may be associated with trichomes and lenticels [173]. Furthermore, cellular heterogeneity may also arise from damage caused by browsing pests, diseases, agrochemical phytotoxicity or freezing injury. Again, periods of high rates of surface area growth result in high susceptibility to microcracking.

Moisture induces microcracking and subsequent russeting—occurring either as liquid-phase water on the fruit surface or as high concentrations of vapor-phase water close by (high humidity). While these trigger effects are well documented for a number of fruitcrop species, including apple, grape and sweet cherry [27,37,62,158], the mechanistic bases for these effects are not known. A possible explanation for moisture-induced microcracking is a higher state of hydration of the cuticle. Cuticular hydration decreases its modulus of elasticity, stiffness and fracture force, whereas its fracture strain increases [8,73]. All these changes increase the likelihood of cuticular microcracking. Other possible explanations include a weakening of cell-to-cell adhesion due to the swelling of cell walls [174].

7.2. Trigger and Signal Transmission

The question remains, how does cuticular microcracking trigger periderm formation? Microcracking occurs in the cuticle, but periderm formation occurs in the hypodermis, several cell layers below. This implies that some signals are transmitted across several cell layers that connect the two processes.

We know that microcracks impair the barrier properties of the cuticle and that this seems to trigger periderm formation. We hypothesize that these two are related, with the reduction in barrier properties somehow triggering the initiation of the periderm. What support is there for this hypothesis? First, when periderm formation is induced experimentally in apple fruit by exposing the fruit surface to moisture, the periderm begins to form only after the surface moisture is removed [37,158]. Apparently, although surface moisture has induced the cuticular microcracking, the periderm formation has been induced by the re-exposure of the (now) microcracked cuticle to the atmosphere. This conclusion is based on histological evidence [37] and gene expression analysis [158]. Second, in another experiment with apple, the formation of a wound periderm was markedly delayed when the periderm-inducing wound was sealed by silicone rubber (Chen, unpublished data). Both these experimental results indicate that the trigger is related to the impaired barrier function. Potential candidate triggers are (1) a decrease in the tissue water potential (more negative) as a result of an increase in transpiration through the microcrack and/or (2) an increase in internal O_2 concentration and/or a decrease in internal CO_2 concentration [37,158]. Based on the literature, an increase in the internal O_2 concentration is the more likely trigger. Thus, in kiwifruit, O_2 is essential for wound-induced suberization [175]; in grape, the O_2 concentrations just below the cuticle is lower than in the ambient atmosphere and decreases with increasing distance from the surface [176]; in apple, similar results have been reported [177] and, in potato, periderm and suberin formation are inhibited by a low O_2 concentration and a high CO_2 concentration [178,179].

8. Management

Various approaches have been investigated to reduce or eliminate russeting: (1) Spray applications of gibberellins and other plant growth regulators (PGRs), (2) applications of foliar fertilizers and other compounds, (3) the exclusion of moisture using bagging and (4) selective breeding.

8.1. Application of PGRs

The gibberellins A_3 (GA_3) and A_{4+7} (GA_{4+7}) are used to improve peel finish and reduce russet in russet-susceptible cultivars of apple, pear, grape and pomegranate (Table 1). Typically, four sprays of 10 mg L^{-1} gibberellic acid (GA) at 10 d intervals starting from petal fall are applied. Russet is reduced significantly (Table 4). The modes of action of GA in decreasing russet formation are several-fold. First, GA results in more uniform and smaller epidermal cells [30]. Skins comprising smaller epidermal cells are likely to be mechanically stiffer. Furthermore, the structural support of the cuticle provided by smaller cells is more uniform. This decreases stress concentrations, a critical factor in microcracking. Second, GA decreases moisture-induced microcracking in russet-susceptible 'Golden Delicious' apple [73]. Applications of GA have no effect on cuticle mass, wax content or mechanical strength of the isolated apple fruit cuticle [73].

Often, GA is combined with the cytokinin benzyladenine (BA). In this combination, BA is thought to offset certain adverse effects that GA may have on flowering [58,80]. Further, GA_{4+7} plus BA (known commercially as 'Promalin') increases fruit size and alters fruit shape. The length to width ratio of the fruit increases, particularly in the calyx region, with the result that fruit have more extended calyx lobes [80,180]. If BA is applied alone, it increases russeting [58,93]. The reason for this negative effect is unknown. The combination GA_{4+7} plus BA decreases russet only to the same extent as GA_{4+7} (Table 4).

In grapes, GA_3 plus the cytokinin *N*-(2-chloro-4-pyridyl)-N′-phenylurea (CPPU) reduces russeting, but GA_3 alone has little effect on russeting [181]. It is thought that CPPU stimulates cell division with the result that fruit have larger numbers of smaller cells [182,183]. Whether these effects also apply for the epidermis and whether microcracking of the cuticle is decreased, as observed in apple, is unknown. We suggest that such an effect would not be unlikely, and it would also account for reduced russeting following CPPU application.

8.2. Foliar Sprays of Fertilizers and Other Compounds

Insufficient supplies of boron (B) cause a number of fruit disorders, including russeting [184]. In mango, sprays of B plus Ca result in thicker cell walls and smaller intercellular spaces. As a consequence, cells are more densely packed, thereby providing greater mechanical stiffness and thus better support for the cuticle [185]. The potential roles of B in russeting also include effects on cell wall synthesis, lignification and cell wall structure, for example, by cross-linking cell wall constituents, such as pectins [186]. It is thought that B also helps maintain cell wall extensibility. In B-deficient plants, cell walls become less elastic and more rigid [184]. This causes cell walls to crack more easily and/or cells to separate from one another under tension along their middle lamellae. A separation of epidermal and/or hypodermal cells weakens the cellular support substrate for the cuticle and is therefore likely to increase cuticular microcracking. There were no effects on russeting following applications of B in pomegranate [137]. However, B applied alone or in combination with Ca did reduce russeting in tomato [119,124]. Several studies have reported decreased microcracking of fruit following applications of B, with or without Ca [187–190]. Since the initial steps in fruit cracking (macrocracking) and russeting would seem to be the same, in that both processes first require cuticular microcracking [191], it would not seem unlikely that applications of B will also decrease microcracking and russeting.

A small number of studies have reported on the effects of 'exotic' compounds on russeting. Thus, chlorogenic acid applied during early development reduced russet formation in 'Golden Delicious' apples. The authors suggest inhibition of lignin synthesis is the underlying mechanism [84]. In other studies, calmodulin and various fruit coatings have been applied, and these are reported to reduce russeting [82]. While the mode of action of calmodulin in inhibiting russeting is unknown, fruit coatings are likely to cover and thus help seal cuticular microcracks and thereby may help restore the impaired barrier functions of a microcracked cuticle. Unfortunately, direct evidence for the effect is lacking. For such an effect, the permeance of the 'exotic' coating to O_2, CO_2 and ethylene should be similar to that of an intact cuticle. Ideally, the coating should be waterproof if it is to be rain-fast. Lastly, the stomatal conductance of the leaves must not be compromised by these exotic coatings, or photosynthesis will be adversely affected—note that it is commercially impracticable to apply these coatings to the fruit without also applying them to the leaves.

Table 4. Effect of the plant growth regulators (PGR) benzyladenine (BA), 4-(2,2-Dimethylhydrazin-1-yl)-4-oxobutanoic acid (daminozide), ethephon, gibberellin A_{4+7} (GA_{4+7}), gibberellic acid (GA_3) acid (GA), *N*-(2-chloro-4-pyridyl)-N′-phenylurea (CPPU), (2RS, 3RS)-1-(4-chlorophenyl)-4,4-dimethyl-2-(lH1,2,4-triazol-1-yl) pentan-3-ol (Paclobutrazol) on russeting. Results are compiled from literature sources.

PGR	**Crop**	**Cultivar**	**Concentration (mg L^{-1})**	**Time and Frequency of Application**	**Effect on Russet**	**Reference**
BA	Apple	Golden Delicious, Jonathan	50 or 150	80% PF and once after 7–10 d	Increased	[56]
BA	Apple	Elstar	200 or 300	At 10–12 mm fruit diameter	Increased	[57]
BA	Apple	Golden Delicious	50	0, 4, 12, 26, 42, 57 DAFB	Increased	[58]
BA	Pear	Bartlett	150	PF and 10 mm stage	Increased	[93]
Daminozide	Apple	Golden Delicious	2000	3 DAFB	Increased	[48]
Ethephon	Apple	Fuji	400	FB	Increased	[59]
GA_4, GA_7 and GA_{4+7}	Apple	Golden Delicious, Karmijn de Sonnaville	10	4 applications in 10 d intervals beginning at PF	Decreased	[32]
GA_{4+7}	Apple	Golden Delicious	200	4 applications in 7 d intervals beginning at PF	Decreased	[75]
GA_{4+7}	Apple	Golden Delicious	62.5, 125 or 250	8–15 DAFB	Decreased	[76]
GA_{4+7}	Apple	Golden Delicious	25	0, 4, 12, 26, 42, 57 DAFB	Decreased	[58]
GA_{4+7}	Apple	Golden Delicious	10	4 applications in 10 d intervals beginning at PF	Decreased	[73]
GA_{4+7}	Apple	Golden Delicious	10	4 applications in 10 d intervals beginning at PF	Decreased	[77]
GA_{4+7}	Apple	Golden Delicious	10	PF	Decreased	[33]
GA_{4+7}	Apple	Golden Delicious	15 or 30	5 applications in 7 to 10 d intervals beginning at PF	Decreased	[30]
GA_{4+7}	Apple	Golden Delicious	10	5 applications in 7 d intervals beginning at FB	Decreased	[78]
GA_{4+7}	Apple	Golden Delicious	20	3 applications in 10 d intervals beginning at PF	Decreased	[72]
GA_{4+7}	Apple	Golden Delicious, Jonathan	25–200	80% PF and once after 7–10 d	Decreased	[56]
GA_{4+7}	Apple	Golden Delicious	5, 10	4 applications in 7 d intervals beginning at PF	Decreased	[79]
GA_{4+7}	Pear	Packham's Triumph	5, 10, 20	80% PF and 0 to 3 additional sprays at 10 or 15 d intervals	Decreased	[105]
GA_{4+7} GA_{4+7} + BA	Apple	Golden Delicious	6, 12, 24, 50	Beginning of bloom and 3 additional sprays at 7 d intervals	Decreased	[80]
GA_{4+7} + BA	Apple	Scarlet Spur II	1, 2.5 or 5	3 to 4 applications in 10 d intervals beginning at PF	Decreased	[81]
GA_3	Apple	Karmijn de Sonnaville	10	4 applications in 10 d intervals beginning at PF	Decreased	[32]
GA_3	Apple	Golden Delicious	100 or 200	PF	Decreased	[33]
GA_3	Apple	Golden Delicious	100	PF	Increased	[60]
GA_3	Pomegranate	G-137	50	Mid May–Mid June	Decreased	[137]
CPPU	Apple	Scarlet Spur II	2, 5 or 10	3 to 4 applications in 10 d intervals beginning at PF	Decreased	[81]
CPPU	Apple	Golden Delicious	20	PF	Increased	[60]
CPPU	Pomegranate	Kandhari	5 or 10	Mid May	Decreased	[140]
CPPU	Pomegranate	G-137	5	Mid May–Mid June	Decreased	[137]

Table 4. *Cont.*

PGR	Crop	Cultivar	Concentration (mg L^{-1})	Time and Frequency of Application	Effect on Russet	Reference
CPPU+GA_3	Grapes	Shine Muscat	10 CPPU + 25 GA_3	FB	Decreased	[132]
CPPU+GA_3, CPPU+GA_4	Apple	Golden Delicious	20 CPPU + 100 GA_3/GA_4	PF	Increased	[60]
Paclobutrazol	Apple	Suntan	120 or 240	3 weeks after FB	Increased	[51]
Paclobutrazol	Apple	Smoothee Golden Delicious	250	Between early bloom and PF	Increased	[61]

FB: full bloom; PF: petal fall; DAFB: days after full bloom.

Where russeting is induced primarily by insect pests or fungi, spray applications of suitable agrochemicals will likely be successful in decreasing russeting. Examples reported include applications of zineb for citrus mites [108,109,112] or captafol or ziram for scab in prune [113]. However, the right dose and timing must be chosen, or the product may itself cause russeting.

8.3. Bagging

Fruit bagging is reported to be a successful countermeasure to inhibit russeting in several fruitcrop species (Table 5). Bagging prevents russeting by keeping the fruit surface dry. However, selecting a suitable material for the bag is critical as the bag material must prevent contact of the fruit surface with liquid water and, at the same time, avoid an elevated humidity in the microclimate of the enclosed fruit. A high-humidity environment inside the bag severely increases russeting [17], probably by increasing cuticular microcracking [73].

Furthermore, the bagged fruit must not overheat [192]. The spectral properties of the bagging material affect the amount and wavelengths of light reaching the fruit surface [193]. In those fruitcrop species and cultivars with colored skins, and where light absorption by the bag impairs pre-harvest fruit coloring, the bag is removed shortly before harvest to induce coloring. With this, there is an increased risk of sunburn, so removal of the bag must be done cautiously, possibly stepwise—for example, by using multi-layer bags [192]. Other benefits of pre-harvest bagging include a decreased incidence of sunburn [194,195], pest infestation and hail damage [196]. However, bagging fruit is laborious, so it requires a high-value product, a high-end market and/or a low labor cost for it to be economic.

Table 5. Effect of bagging fruit on russet and color. Data are compiled from literature sources.

Type of Bag	Crop	Cultivar	Time of Bagging	Effect on Russet	Effect on Color	Reference
Polythene bag (Kordite freeze bags)	Apple	Golden Delicious, Rome Beauty	18 mm diameter	Increased	Greener groundcolor	[17]
Polythene bag with aluminum paper	Pear	Packham's Triumph	Fruit set	Increased	Not determined	[105]
Microperforated polypropylene bags	Pear	Doyenne du Comice	30 DAFB	Decreased	Not determined	[100]
Nylon (polyamide)	Apple	Golden Delicious, Rome Beauty	18 mm diameter	Increased	Decreased red color	[17]
Kraft paper bags	Apple	Golden Delicious, Rome Beauty	18 mm diameter	Decreased	Decreased red color	[17]
Kraft paper bags	Mango	Apple	70 DAFB	Reduced	Decreased red color	[135]
Kraft paper bags	Apple	Golden Delicious	5 DAFB	Reduced	Not determined	[48]
White, yellow and discoloration bags	Apple	Gamhong	20, 30 and 40 DAFB	Reduced	No change	[82]
Light impermeable double layer paper bags	Apple	Golden Delicious	20 DAFB	No russet	Not determined	[86]
Paper bags (single layer)	Pear	Cuiguan	35 DAFB	Decreased	More yellow	[101]
Paper bags (white, single layer)	Pear	Cuiguan	20 DAFB	No russet	No change	[102]
Paper bags (yellow-white, double layer)	Pear	Cuiguan	40 DAFB	No russet	No change	[102]
Papers bags (single layer + double layers)	Pear	Cuiguan	28 DAFB	Decreased	Lighter color	[103]
Paper bags (double layer)	Pear	Cuiguan	20 + 45 DAFB	No russet	Greener groundcolor	[101]
Paper bag (double layered with attached filter)	Pear	Niitaka	30–40 DAFB	Decreased	Lighter color	[104]
Paper bag (triple layer)	Pear	Concorde	After June drop	Increased	Lighter color	[197]

DAFB = days after full bloom.

8.4. Breeding

In the long term, a breeding approach to control russet will likely be the most successful since russet susceptibility is a genetically controlled trait [198–201]. For a review on the molecular biology of russet formation, the reader is referred to the recent reviews by Macnee et al. [23] and Wang et al. [24].

In apple, the anatomies of the skins of russet-susceptible and russet-non-susceptible cultivars have been compared. The cellular layers of the skin differ [151,161]. The russet-susceptible cultivars have larger cells and more variable cell sizes in both the epidermis and hypodermis [161,170]. These result in higher stiffness and lower strain at fracture during early fruit development when russet susceptibility is highest [161]. When subjected to a tangential growth strain, skin cells of irregular size and shape result in greater stress concentrations and increased likelihood of failure. Comparisons of russet-susceptible and russet-non-susceptible cultivars reveal no consistent differences in cuticular properties—such as mass per unit area of the cuticular membrane, the dewaxed cuticular membrane or wax content [31]. Furthermore, there were no significant differences relating to russet susceptibility in cuticular strain or cuticular mechanical properties, as determined in uniaxial tensile tests (i.e., maximum force, strain at maximum force or stiffness of the cuticular membrane) [18]. Genotypes meeting the following criteria are likely to exhibit low susceptibility to russeting: (1) A long period of skin cell division, so the increase in fruit surface area is substantially accounted for by increases in the numbers of cells, rather than by increased cell expansion (which is often associated with changes in epidermal cell aspect ratio). (2) Smaller epidermal and hypodermal cells are also of more uniform size. These are better able to sustain high tensile forces and offer less stress concentration and lower chances of failure. (3) Lack of stress concentration at stomata, lenticels and trichomes. Susceptibility to failure at these sites may be checked by monitoring formation of microcracks following moisture exposure of the fruit surface. Incubating fruit in the fluorescent tracer acridine orange permits localized penetration through microcracks. When viewed using a fluorescence microscope, microcracks are easily identified by the fluorescing 'halo' surrounding sites of preferential uptake.

9. Conclusions

The locally impaired barrier properties of the cuticle due to a microcrack and, probably, increased O_2 diffusion seem to be the primary trigger for periderm formation. Microcracking is likely the integrator of a range of factors that induce russeting. These factors include growth stress, surface moisture and high humidity, but also pests and diseases, mechanical wounds and freezing temperatures. Significant progress has been made in our understanding of molecular biology and of the physiology of russeting.

The classical concepts of reducing russeting by spray applications of gibberellins, with or without cytokinins, or of B and/or of Ca have a sound mechanistic basis and are reported to be effective in a range of fruitcrop species. The identification of impaired barrier properties of the cuticle as the trigger causing periderm formation now provides promising options for russet management that merit further research. These include applications of 'exotic' coatings during critical phases of fruit development, especially when relative surface area growth rates are high. In addition, the prevention of radial extension (i.e., deepening) of microcracks by stimulating the rate of cuticle deposition is not an unrealistic strategy.

Recently, evidence has been presented that feeding oleic acid to the apple fruit surface results in significant incorporation of oleic acid into the cutin fraction [202]. If this treatment could be upscaled in the field to generate gravimetrically detectable increases in cuticle thickness following spray application of a suitable precursor, the increased cutin deposition could hinder cuticle microcracks from propagating so as to fully traverse the cuticle. When applied during phases of high rates of relative surface area growth, the formation of traversing microcracks and, hence, of russet may be prevented or reduced. Several of these aspects merit further study.

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