1,4-Dimethylnaphthalene Treatment of Seed Potatoes Affects Tuber Size Distribution

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ABSTRACT

1,4-DMN is a relatively new sprout inhibitor for use on maincrop and seed potatoes. Despite its registration as a "dormancy enhancer" for seed, relatively little is known about its effects on plant establishment and productivity. The main objective of this study was to evaluate the effects of 1,4-DMN on the productivity of seed potatoes. 'Umatilla Russet' (UR), 'Ranger Russet' (RR), and 'Russet Burbank' (RB) seed tubers were stored at 4, 7, and 9 C over three seasons to create 80-, 554- and 642-degree-day seed, and 1,4-DMN was applied to maintain dormancy several times during each season. 1,4-DMN residue levels at the end of storage were lower in seed aged at higher temperatures. Multiple applications of 1,4-DMN at higher-than-label rates were necessary to effectively inhibit sprouting of seed of all cultivars stored above 4 C. In field trials, depending on cultivar and year, 1,4-DMN either delayed plant emergence slightly or had no effect. 1,4-DMN increased stem numbers from RB and UR seed, but not from RR seed. 1,4-DMN reduced total tuber yields by 3.2 to 5.6 t ha^{-1} (5% to 9%), and U.S. No. 1 tuber yields by 4.8 to 7.8 t ha^{-1} (8% to 15%) in all cultivars, regardless of seed tuber age. 1,4-DMN also reduced the average tuber weight for all three cultivars and shifted the size distribution from larger (>284 g) to smaller tubers. 1,4-DMN reduced the respective yields of >397-g, 340- to 397-g, and 284- to 340-g tubers by 43%, 19%, and 18% for RR seed, 31%, 14%, and 11% for RB seed, and 40%, 47%, and 27% for UR seed. Conversely, depending on cultivar, yields of smaller tubers (≤170 g) were 11% to 38% higher from 1,4-DMN-treated seed. The shift in tuber size distribution for RR was accompanied by a 1,4-DMN-induced increase in tuber number per plant and per hectare. However, no such effects on tuber set occurred in RB and UR. Moreover, in most cases, the 1,4-DMN effects on yield and tuber size distribution were independent of seed age. Since the 1,4-DMN-induced shifts in tuber size distribution were greater than the reductions in total and U.S. No. 1 yields, 1,4-DMN may be a suitable treatment to reduce average tuber size and increase yield and uniformity of specific size classes of tubers to more closely match market requirements.

RESUMEN

El 1,4-DMN (Dimetil naftaleno) es un inhibidor de brotes de papa relativamente nuevo que se usa tanto para cultivos comerciales como para cultivos de semilla. A pesar de su registro como estimulante de dormancia de semilla, se sabe muy poco sobre sus efectos en el establecimiento del plantel y su productividad. El objetivo principal de este estudio fue de evaluar los efectos del 1,4-DMN sobre la productividad de los tubérculos semilla. Tubérculos de 'Umatilla Russet' (UR), 'Ranger Russet' (RR) y 'Russet Burbano' (RB) se almacenaron a 4, 7 y 9 C durante tres campañas agrícolas para producir 80-, 554- y 642-grados-día de semilla y se aplicó 1,4-DMN varias veces durante cada campaña para mantener la dormancia de la semilla. Los niveles de residuo del

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ABBREVIATIONS: 1,4-DMN, 1,4-dimethylnaphthalene; RB, Russet Burbank; RR, Ranger Russet; UR, Umatilla Russet

1,4-DMN al final del período de almacenamiento fueron más bajos en las semillas envejecidas a temperaturas mayores. A temperaturas de almacenamiento por encima de los 4 C se necesitan niveles mayores a los recomendados y aplicaciones múltiplas de 1,4- DMN para inhibir efectivamente el brotamiento de las semillas en todos los cultivares. En pruebas de campo, dependiendo del cultivar y del año, el 1,4-DMN, retardó ligeramente o no tuvo efecto en la emergencia de la planta, aumentó el número de tallos por semilla de RB y UR, pero no en RR. El 1,4-DMN redujo los rendimientos de 3.2 a 5.6 t/ha^{-1} (5 a 9%) en todos los cultivares, sin tener en cuenta la edad del tubérculo semilla. El 1,4-DMN también redujo los rendimientos en el peso promedio del tubérculo en los tres cultivares y cambió la distribución de tamaño de los tubérculos grandes (284 g) a tubérculos más pequeños. Redujo los respectivos rendimientos de tubérculos > 397 g, 340 – 397 g y tubérculos de 284 – 340 g por 43%, 19% y 18% para la semilla de RR, 31%, 14% y 11% para la semilla de RB y 40% 47% y 27% para la semilla UR. Contrariamente, dependiendo del cultivar, los rendimientos de tubérculos más pequeños (170 g) fueron de 11 a 38% mayores que en la semilla tratada con 1,4-DMN. El cambio en la distribución de tamaño en RR aumentó el número de tubérculos por planta y por hectárea inducida por el 1,4-DMN. Sin embargo, no sucedió lo mismo en RB y UR. Más aún en la mayoría de los casos, los efectos del 1,4-DMN sobre el rendimiento y distribución del tamaño del tubérculo fueron independientes de la edad de la semilla. Desde que los cambio inducidos por el 1,4-DMN en la distribución del tamaño del tubérculo fueron mayores que la reducción en el total de tubérculos US-1, el 1,4-DMN puede ser un tratamiento adecuado para reducir el promedio del tamaño del tubérculo y puede aumentar el rendimiento y la uniformidad en el tamaño específico de las clases de tubérculos para que estén de acuerdo con los requerimientos del mercado.

INTRODUCTION

Methyl-substituted naphthalenes occur naturally in potato tubers (Buttery et al. 1970). Some of these compounds and their structurally related analogs, such as diisopropylnaphthalene, exhibit sprout inhibitory activity (Meigh et al. 1973; Lewis et al. 1997). The volatile compound dimethylnaphthalene (1,4-DMN) is naturally produced by tubers and contributes to the flavor and aroma produced by baked potatoes (Coleman et al. 1981). Beveridge et al. (1981a) examined 20 naturally produced volatile chemicals for sprout suppressant activity and concluded that one of the isomers of dimethylnaphthalene, 1,4-DMN, was as effective as tecnazene (a previously registered sprout inhibitor used on seed in the UK, the registration of which was recently withdrawn). Commercial-scale experiments were conducted for both seed and ware potatoes, and 1,4-DMN was found to be effective for sprout control on seed potatoes (at an unspecified storage temperature), but not for ware potatoes stored at 7 to 8 C (Beveridge et al. 1981b).

The EPA registered (Reg. Number 67727-1) a synthetic formulation of 1,4-DMN as a reduced-risk pesticide for use as a growth regulator on stored potatoes in 1995 (Borolo 1995; Bennett 1998). A study published in 1997 found that 1,4-DMN applied as a thermal aerosol fog at 300 mg active ingredient (a.i.) kg^{-1} fresh weight was effective as a sprout inhibitor on a short-term basis, but was not as effective as CIPC at 22 mg a.i. kg^{-1} fresh weight (Lewis et al. 1997). A more recent study compared the sprout-suppressant activity of 1,4-DMN with CIPC, ethylene and carvone (Kalt et al. 1999). At the end of a 25-wk storage period at 9 C, sprout suppression was greatest with CIPC, followed by carvone, ethylene, 1,4-DMN, and air, in that order. The mode of action of substituted naphthalenes is unknown, but is likely hormonally based (Meigh et al. 1973; Kleinkopf et al. 2003). In contrast, CIPC inhibits cell division, thereby inhibiting sprout growth. Different modes of action no doubt contribute to the relative differences in efficacies of these chemicals as inhibitors of sprout growth. At rates specified on the label, multiple applications of 1,4-DMN are necessary to maintain sprout control during long-term storage (Lewis et al. 1997).

1,4-DMN is currently marketed under the trade names 1,4-Seed™ and 1,4-Sight™, for use as a dormancy enhancer on seed and maincrop potatoes, respectively. In contrast to the relatively permanent sprout-inhibiting properties of CIPC, the temporary sprout-suppressing ability of 1,4-DMN is requisite for the chemical to have any potential use in the seed industry. However, except for early work with different isomers of dimethylnaphthalene on seed of fresh market European cultivars in Scotland (Beveridge et al. 1981a, 1981b), little is known about the effects of this chemical on plant establishment and the productive potential of seed tubers. This is surprising in light of the availability of 1,4-DMN to commercial seed growers throughout North America. We therefore initiated a 3-yr study to evaluate the effects of 1,4-DMN on the productivity of seed of long-season russet cultivars important to the fresh market and frozen processing industries in the Pacific Northwest. By manipulating the physiological age of seed tubers during storage, we produced seed with different durations of dormancy and thus sprouting potentials. The effects of seed storage temperature (physiological age) and 1,4-DMN treatments during the storage season on subsequent plant establishment, stem number and tuber yield and grade were evaluated.

MATERIALS AND METHODS

Aging of Seed Tubers

Studies were conducted over a 3-yr period from 2001 to 2003. 'Russet Burbank,' 'Ranger Russet,' and 'Umatilla Russet' certified seed tubers (G-3) were obtained directly from seed growers in Montana and Washington, within days of harvest (early October). Three physiological ages of seed tubers were then produced by differential heat-unit accumulation during storage. The seed tubers were initially wound healed at 10±0.5 C (95% RH) for 14 days and then stored at 4±0.5 C until further aging treatments were imposed in early November. On 7 November, samples of seed of each cultivar were placed at 7±0.5 C and 9±0.5 C for 159 and 43 days, respectively. The 9 C-stored tubers were placed at 7 C on 20 December, where they remained for the final 116 days of storage. Control tubers were held at 4 C (after wound healing) for the entire storage season. These treatments resulted in seed that had accumulated 80, 554, and 642 storage degree-days (4 C base temperature) over the 200-day storage period for each year of the study.

1,4-DMN Treatments

Seed tubers were treated with 1,4-DMN three times during the storage season (see below). 1,4-DMN was applied as a thermal fog in a 210-L steel barrel that served as a treatment chamber. The chamber was loaded with seed tubers (approximately 37 kg per treatment per cultivar), sealed and 1,4-DMN was vaporized (530 C) into the bottom of the barrel through an inlet port. An outlet port at the top of the barrel was connected to the vapor generator and inlet port at the bottom of the barrel, providing a continuous loop through which circulation of 1,4-DMN vapor was maintained for 24 h with a small air pump (2.7 L min^{-1}). Seed tubers were initially treated on 20 December with 40 mg 1,4-DMN kg^{-1} tubers. A second 1,4-DMN treatment (40 mg kg^{-1}) was applied 25 January, when the 37 kg of 1,4-DMN-treated Ranger Russet and Umatilla Russet seed tubers stored at the highest temperatures were showing visible signs of sprouting (sprouts ≤1 mm in length). A final application of 1,4-DMN (10 mg kg^{-1}) was made on 27 February, when the 1,4-DMN-treated Ranger Russet seed tubers were again showing visible signs of sprouting (sprouts ≤2 mm in length). Non-treated samples of each age of tubers served as controls. There were thus six treatments for each cultivar, three tuber ages (80, 554, and 642 storage degree-days) x two levels of 1,4-DMN (treated or non-treated).

1,4-DMN Residue Analysis

The three ages of Ranger Russet seed tubers were sampled for 1,4-DMN content at planting. A 1.6-cm-diameter core was cut, perpendicular to the longitudinal axis of the tuber, from the apical and basal ends. Tissue samples with periderm attached (1.6 cm diameter, 2 cm long) were trimmed from the ends of these cores. The resulting four samples of tissue, representing apical and basal portions of a tuber, were collectively weighed, frozen in liquid nitrogen and fractured with a Bio-Pulverizer II (BioSpec Products, Inc., Bartlesville, OK, USA). 1,4-DMN was extracted from the pulverized tissue into 10 mL of ethanol:hexane (7:3, v/v) containing 50 µL ethyl naphthalene as internal standard, and the crude extract was incubated for 15 min at 50 C in a water bath. The tissue residue was discarded, and the extract was washed once with 10 mL of 0.2 M NaCl. 1,4-DMN in the hexane layer was quantified via FID-GC. The Hewlett Packard 6890 GC (Agilent Technologies) was equipped with a 60 m x 0.32 µm DB-1 column. The injector and flame ionization detector were both operated at 250 C. Helium carrier gas was split 10:1 at the inlet and held at a constant column flow of 1.5 mL min^{-1}. The oven temperature was programmed to hold 80 C for 1 min, then increased to 200 C at 5 C min^{-1} and held for 5 min. 1,4-DMN residues were analyzed in three replicates of tubers for each age.

Field Studies

Field studies to assess the effects of 1,4-DMN on the productive potentials of the different ages of seed tubers were conducted at the Washington State University Research and Extension Unit, Othello, WA (46° 47.277' N. lat., 119° 2.680' W. long.). 1,4-DMN and age treatments were factorially arranged in randomized complete block designs (separate experiments for each cultivar) in field plots with five blocks. Approximately 4 days prior to planting, 1,4-DMN-treated and non-treated seed tubers of each age were sorted for size (150-200 g each) and hand cut into 50- to 64-g seedpieces. The field plots were blocked for seed tuber size, number of cut surfaces on the seedpieces, and seedpiece portion (i.e., seedpieces derived from apical or basal ends of seed tubers). Cut seedpieces were held at 9±0.5 C (95% RH) for 2 to 5 days prior to planting, which occurred on or about 15 April of each year.

Seedpieces were planted 20 cm deep in a Shano silt loam soil with a custom built two-row assist-feed planter. Individual treatment plots consisted of 24 hills. Seedpieces were planted 25 cm apart within a row; rows were spaced 86 cm apart, and a 1.3-m alley was left between plots. Guard seedpieces (cv Dark Red Norland) were planted at the beginning and end of each plot to minimize variation in interplant competition for plants at the ends of plots, and to facilitate the separation of individual plots during mechanical harvesting in the fall. Plots were located under a linear move irrigation system. Soil moisture was maintained at a minimum of 65% of field capacity with the aid of soil moisture probes positioned throughout the field. Pre-plant and in-season fertilizer applications were based on soil tests and petiole analyses, respectively, following standard practices for long-season russet potatoes in the Columbia Basin. Herbicides, insecticides and fungicides were also applied as needed, according to standard practices.

Plant emergence was assessed at 2- to 5-day intervals from 27 to 55 days after planting in 2002 and 2003 only. Aboveground mainstem numbers were recorded 55 to 60 days after planting, just prior to row closure, in all years. Vines were killed with a flail-type mower approximately 150 days after planting and tubers were harvested with a single-row mechanical harvester 7 to 10 days later. Tubers were washed, weighed, counted, and sorted into the following categories: under 113 g, 113-170 g, 170-284 g, 284-340 g, 340-397 g, over 397 g, and cull tubers. Total yield included the combined weights of all categories, while U.S. No. 1 yield was equal to the sum of all categories except cull and undersize (<113 g) tubers.

Data Analysis

The effects of 1,4-DMN and seed age on stem number per plant, tuber number per hectare, average tuber weight, and yields of tuber size classes were evaluated. Data were subjected to analysis of variance and sums of squares were partitioned into single degree-of-freedom contrasts for main effects (1,4-DMN and age) and interactions, as appropriate.

RESULTS

The sprouting potential of seed potatoes varied between cultivars and increased with increasing storage degree-days (data not shown), necessitating the use of multiple applications of 1,4-DMN to inhibit sprouting during storage. Interestingly, the onset of sprouting was fairly consistent during each year of the study, occurring first in the 642-degree-day Ranger Russet seed in mid-January. Observations on the final degree of sprout development from seed tubers were noted annually, at the end of each 200-day storage period. As expected, the greatest extent of sprout development was observed in the oldest (642-degree-day) seed tubers of each cultivar, which were subjected to the most temperature fluctuation during aging in storage. By the end of storage, the non-1,4-DMN-treated aged tubers of Ranger Russet showed the greatest degree of sprouting, with sprout lengths as long as 5 cm in about 28% of the tubers. In contrast, the longest sprouts for the non-1,4-DMN-treated aged Russet Burbank and Umatilla Russet seed tubers were 2.5 and 2 cm, respectively, in about 23% and 80% of the tubers, respectively. These results are consistent with previously established differences in the lengths of dormancy for these cultivars (RR<UR<RB) (Knowles et al. 2004a). Sprouts on 1,4-DMN-treated tubers of all cultivars were ≤5 mm in length, confirming the sprout suppressing effect of 1,4-DMN.

Residue concentrations were assessed in the 1,4-DMN-treated Ranger Russet tubers at the end of the 2000/01-storage season. 1,4-DMN levels were highest in the 80-degree-day seed tubers and decreased linearly ($R^2 = 0.99$, $P \leq 0.01$) with increasing storage degree-days (Table 1). 1,4-DMN levels in non-treated tubers were less than 0.3 mg kg^{-1} periderm.

Table 1—1,4-DMN residues in Ranger Russet seed tubers at the end of a 200-day storage period. Residues in non-treated tubers were <0.3 mg kg^{-1} periderm.

Storage Deg. Days	1,4-DMN Residue (mg kg–1 periderm)
80	5.1±0.9
554	2.0±0.2
642	1.5±0.1
DD_{Lin}	**

**Significant at $P \leq 0.01$. DD, storage degree days above 4 C; Lin., linear.

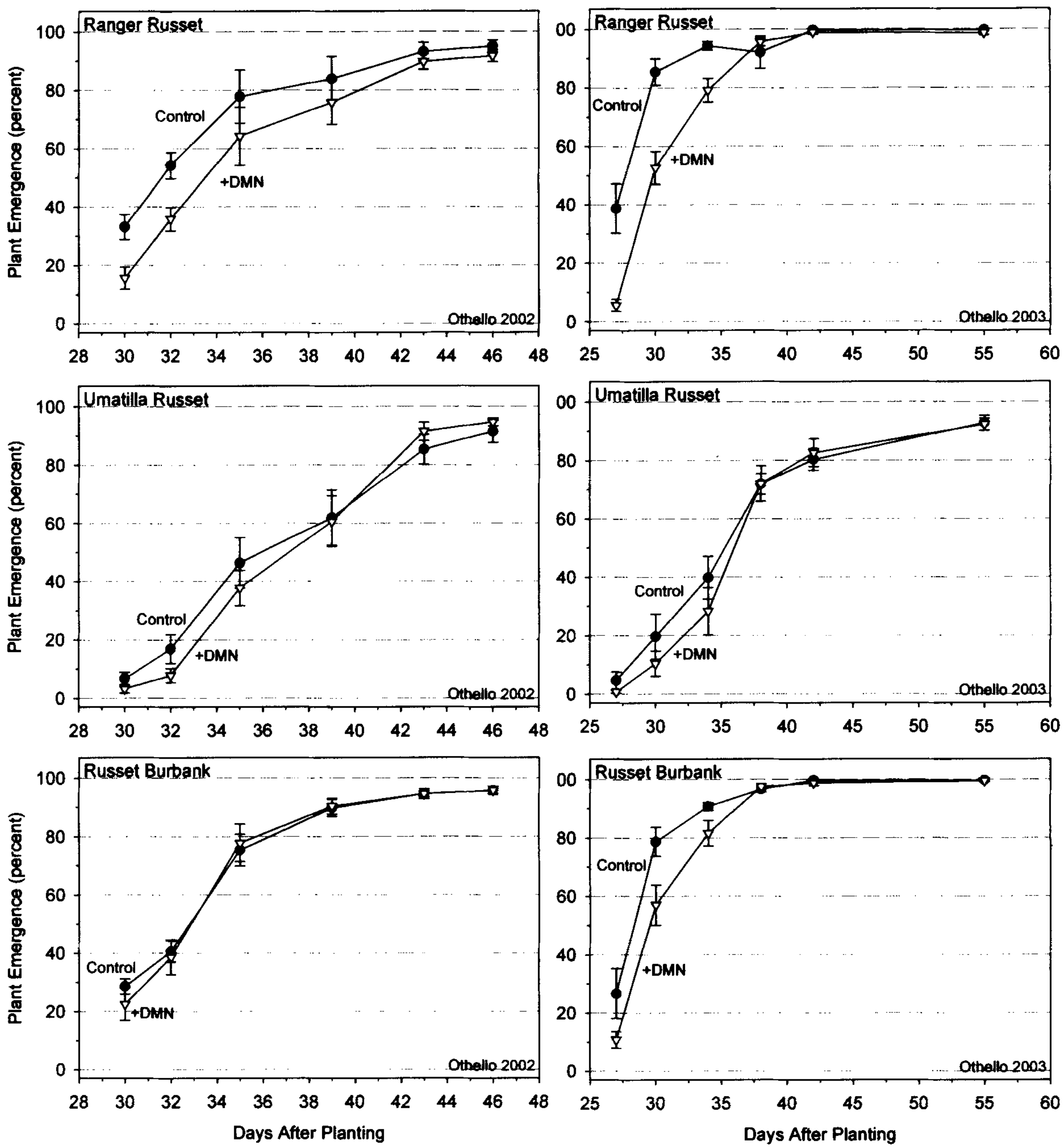

FIGURE 1.

Plant emergence responses from 1,4-DMN-treated Ranger Russet, Umatilla Russet, and Russet Burbank seed tubers during 2002 and 2003 at Othello, WA. Data are averaged over the 80-, 554- and 642-degree-day seed to reveal the significant effects of 1,4-DMN on Ranger Russet ($P \le 0.01$) in 2002 and 2003, and Umatilla Russet ($P \le 0.05$) and Russet Burbank in 2003 ($P \le 0.01$). Bars indicate SE.

Plant emergence over time was profiled during the 2002 and 2003 growing seasons. Averaged over years, accumulated storage degree-days had no consistent effects on plant emergence and stand establishment (data not shown). Conversely, 1,4-DMN delayed plant emergence ($P \le 0.01$) for Ranger Russet in 2002 and 2003, and Umatilla Russet ($P \le 0.05$) and Russet Burbank ($P \le 0.01$) in 2003 (Figure 1). Despite these slight delays, final plant stand was unaffected by 1,4-DMN treatment. Stand establishment was quickest for Ranger Russet, followed by Russet Burbank and Umatilla Russet.

TABLE 2—*Effects of 1,4-DMN on stem numbers and productivity of Ranger Russet seed tubers. After an initial wound healing period at 10 C, seed tubers were stored at 4, 7, and 9 C to accumulate 80, 554, and 642 degree-days (4 C base temperature) during each 200-day storage season. 1,4-DMN was applied (thermal fog) at 40 mg kg^{-1} on 20 December, and again on 25 January. A final treatment (10 mg 1,4-DMN kg^{-1}) was applied on 27 February. Seed was cut and planted into replicated plots at Othello, WA, on or about 15 April. Data are averaged over three years.*

Storage		Stems	Ranger Russet Tuber Grades									Tuber No.	F. Wt.
Deg. Days	DMN	No./plant	Total	U.S.#1	<113g	113-170g	170-284g	284-340g	340-397g	>397g	Cull	(x10^3 ha^{-1})	(g/tuber)
			t ha^{-1}										
80	-	2.9	68.2	62.4	4.51	8.06	18.9	7.84	6.77	20.7	1.32	283	245
	+	2.8	65.5	57.1	6.50	9.90	22.5	6.71	5.67	12.3	1.84	314	208
554	-	2.6	61.7	54.4	4.92	6.88	14.8	7.83	5.86	19.1	2.37	259	245
	+	2.6	60.2	51.0	6.39	10.2	19.6	7.12	4.83	9.33	2.78	299	199
642	-	2.6	62.9	56.1	4.20	6.84	17.5	9.33	6.18	16.3	2.59	257	244
	+	2.5	57.3	47.6	6.49	9.32	16.7	6.57	4.68	10.3	3.19	280	199
	DMN	ns	*	**	**	**	**	**	**	**	ns	**	**
	DD_{Lin}	**	**	**	ns	**	**	ns	ns	*	**	**	ns
	DD_{dev}	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	DMN x DD_{LT}	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	DMN x DD_{dev}	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns

*,** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively. ns, not significant; DD, degree day; Lin., linear; dev., deviations from linearity.

Stem Number and Yield Responses of Ranger Russet

A slight reduction (10%) in the number of aboveground stems from Ranger Russet seed tubers occurred with increasing storage degree-days over the 3-yr study period (Table 2). This effect of seed tuber age was consistent during each year of the study. However, regardless of seed tuber age, 1,4-DMN had no effect on the number of stems per plant. Averaged over 1,4-DMN treatments, total and U.S. No. 1 yields declined significantly by 10% (6.8 t ha^{-1}) and 13% (8.0 t ha^{-1}), respectively, as seed tuber age increased to 642 degree-days. Total and U.S. No. 1 tuber yields from 1,4-DMN-treated seed tubers were reduced marginally, by 5% (3.3 t ha^{-1}) and 10% (5.7 t ha^{-1}) respectively, for all ages of seed tubers.

The relatively modest decline (10%) in tuber number per hectare with increasing storage degree-days had no effect on average tuber weight (Table 2). However, 1,4-DMN increased the number of tubers per hectare by 12% (31,000 tubers) and reduced the average tuber fresh weight by 18% (43 g/tuber, $P \leq 0.01$) for all ages of seed tubers. This drop in average tuber fresh weight was a consequence of the relatively substantial effects of 1,4-DMN on the size distribution of Ranger Russet tubers (Table 2). 1,4-DMN treatment of seed reduced the yields of >397-g, 340- to 397-g, and 284- to 340-g tubers by 18% to 43% on average, and increased the yields of <113-g, 113- to 170-g, and 170- to 284-g tubers by 15% to 43% on average (Figure 2). When averaged across storage degree-days, the 1,4-DMN-induced decrease in yield of larger (>284-g) tubers was 10.8 t ha^{-1}, compared with a 7.1 t ha^{-1} increase in yield of smaller (<284-g) tubers. On a percentage basis, the 1,4-DMN-induced shift in tuber size distribution is clearly evident in Figure 2, and this trend was consistent over the 3-year study period.

Stem Number and Yield Responses of Russet Burbank

In contrast to Ranger Russet, 1,4-DMN treatment of Russet Burbank seed tubers increased the number of aboveground stems (Table 3). This increase was greatest in older seed tubers, mostly because of a slight decline in stem numbers in the non-1,4-DMN-treated seed with advancing seed tuber age (storage degree-days). 1,4-DMN decreased the total and U.S. no. 1 yields by 4.4 t ha^{-1} (6%) and 4.8 t ha^{-1} (8%), respectively, regardless of tuber age. Total and U.S. No. 1 yields also fell modestly (6.4% on average) as seed tuber age increased.

The 1,4-DMN- and age-related declines in yield of Russet Burbank were not attended by changes in tuber number per plant or per hectare (Table 3). Therefore, average tuber weight fell 4.4% and 7% with increasing seed tuber age and 1,4-DMN treatments, respectively. The slight drop in average tuber fresh weight from 1,4-DMN-treated seed reflected a significant 1,4-

TABLE 3—*Effects of 1,4-DMN on stem numbers and productivity of Russet Burbank seed tubers. After an initial wound healing period at 10 C, seed tubers were stored at 4, 7, and 9 C to accumulate 80, 554, and 642 degree-days (4 C base temperature) during each 200-day storage season. 1,4-DMN was applied (thermal fog) at 40 mg kg^{-1} on 20 December, and again on 25 January. A final treatment (10 mg 1,4-DMN kg^{-1}) was applied on 27 February. Seed was cut and planted into replicated plots at Othello, WA, on or about 15 April. Data are averaged over three years.*

Storage		Stems	Russet Burbank Tuber Grades									Tuber No.	F. Wt.
Deg. Days	DMN	No./plant	Total	U.S.#1	<113g	113-170g	170-284g	284-340g	340-397g	>397g	Cull	(x10^3 ha^{-1})	(g/tuber)
			t ha^{-1}										
80	-	3.0	78.0	62.6	9.18	14.5	24.5	8.54	4.42	10.6	6.29	396	184
	+	3.2	73.3	58.4	10.3	14.7	23.2	6.80	4.46	9.24	4.59	396	177
554	-	2.9	74.9	60.1	10.0	13.5	24.1	7.38	5.20	9.82	4.97	393	182
	+	3.5	70.6	55.2	11.5	15.9	23.9	6.51	3.65	5.29	3.50	416	164
642	-	2.7	72.7	59.3	9.61	14.7	24.6	6.65	5.03	8.25	4.03	394	178
	+	3.2	68.6	54.1	11.0	15.7	22.2	6.53	4.32	5.35	3.55	399	167
	DMN	**	**	**	**	*	ns	*	*	**	**	ns	**
	DD_{Lin}	ns	*	*	ns	ns	ns	ns	ns	**	*	ns	**
	DD_{dev}	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	DMN x DD_{LT}	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
	DMN x DD_{dev}	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

*,** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively. ns, not significant; DD, degree day; Lin., linear; dev., deviations from linearity.

DMN-induced shift in tuber size distribution, similar to that observed for Ranger Russet. Yields of >397-g, 340- to 397-g, and 284- to 340-g tubers were reduced by 31%, 14%, and 11%, respectively (Table 3, Figure 2). Conversely, yields of <113-g and 113- to 170-g tubers increased by 14% and 8%, respectively. When averaged across storage degree-days, the 1,4-DMN-induced decrease in yield of tubers greater than 284 g was 4.6 t ha^{-1}, compared with a 2.5 t ha^{-1} increase in tubers less than or equal to 170 g. Hence, 1,4-DMN treatment of Russet Burbank seed shifted the tuber size distribution similar to that characterized for Ranger Russet seed; however, the magnitude of the response was less for Russet Burbank than for Ranger Russet (Figure 2).

Stem Number and Yield Responses of Umatilla Russet

On average, the number of aboveground mainstems from the 554- and 642-degree-day Umatilla Russet seed tubers was 10% lower than that from the 80-degree-day seed (Table 4). Regardless of age, 1,4-DMN-treated seed tubers produced more stems than non-treated seed tubers. Total and U.S. No. 1 yields fell approximately 7.2 t ha^{-1} (10%) and 8.6 t ha^{-1} (16%), respectively, as storage degree-days increased. Moreover, 1,4-DMN treatment of seed reduced the total yield by 5.6 t ha^{-1} (8.5%), and the U.S. No. 1 yield by 7.8 t ha^{-1} (15%) for all ages of seed tubers.

Storage degree-days reduced the number of tubers produced per hectare equally for the 1,4-DMN-treated and non-treated Umatilla Russet seed (Table 4). The average tuber weight produced by the non-1,4-DMN-treated seed tubers was not affected by seed tuber age. However, average tuber weight from 1,4-DMN-treated tubers fell by 9 g (5.4%), 26 g (15%), and 31 g (18%) per tuber as seed age advanced from 80- to 554- to 642-degree-days, respectively. As with the other cultivars, these changes in average tuber weight of Umatilla Russet were the result of substantial shifts in tuber size distribution in response to 1,4-DMN treatments. 1,4-DMN decreased the yields of 170- to 284-g tubers by 2.7 t ha^{-1} (13%), 284- to 340-g tubers by 1.8 t ha^{-1} (27%), and >397-g tubers by 2.6 t ha^{-1} (40%) (Figure 2). Yield of 340- to 397-g tubers decreased from 10% to 77% (0.4-4.1 t ha^{-1}) as tuber age progressed from 80- to 642-degree-days (Table 4, Figure 2). Therefore, the yield reduction of tubers weighing more than 170 g from 1,4-DMN-treated seed tubers ranged from 7.5 to 11.2 t ha^{-1}, depending on the number of accumulated degree-days during storage. On the other hand, seed treated with 1,4-DMN produced 2.3 t ha^{-1} (21%) more undersize (<113-g) tubers than non-treated seed, regardless of seed tuber age. Umatilla Russet was thus the most sensitive cultivar for shift in tuber size distribution and overall yield reduction in response to 1,4-DMN treatments.

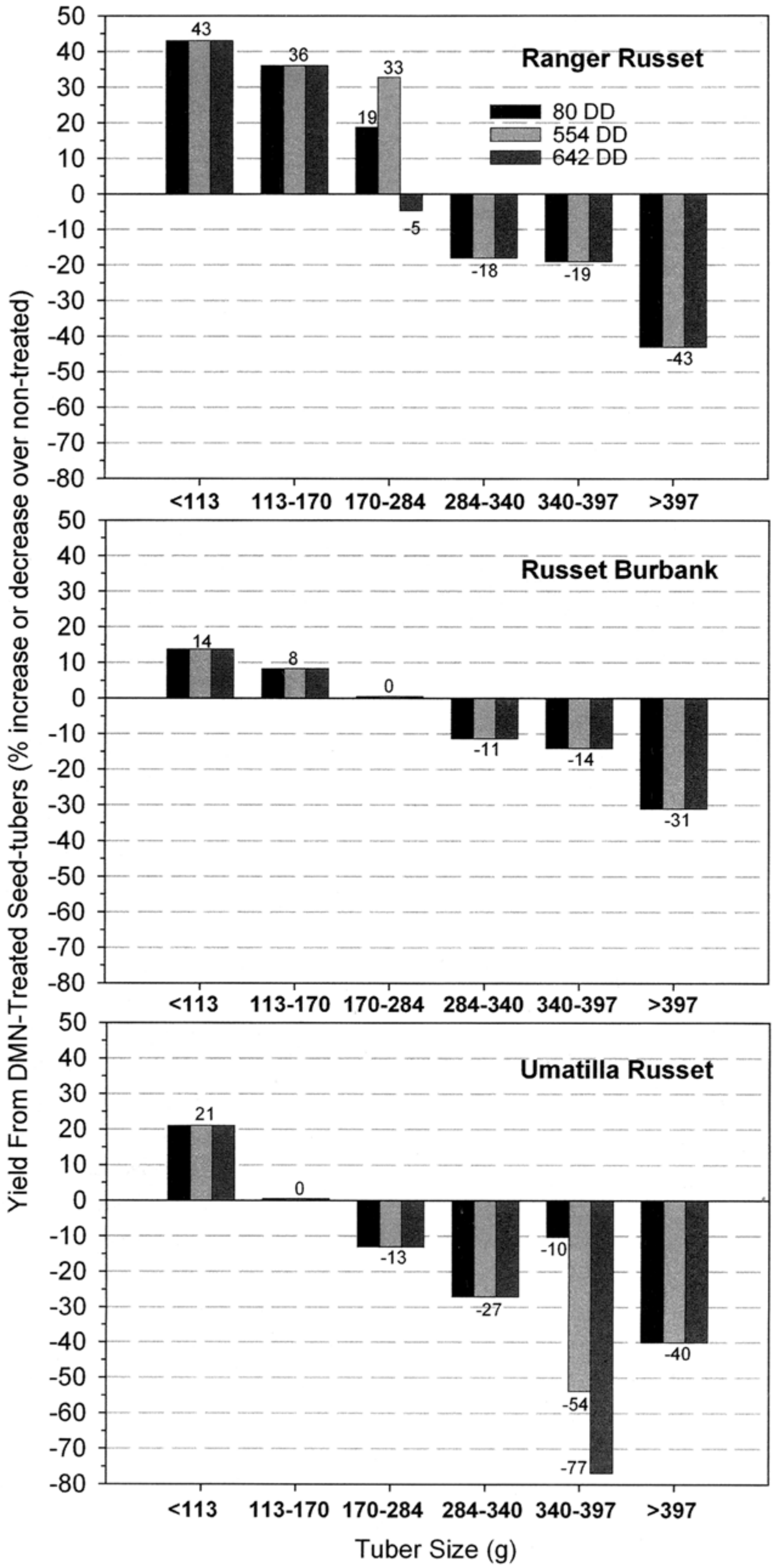

FIGURE 2.

1,4-DMN-induced changes in the size distribution of tubers produced by aged Ranger Russet, Russet Burbank, and Umatilla Russet seed tubers planted in field plots at Othello, WA. Seed age (degree-day) and 1,4-DMN treatments were applied during storage of the seed, as described in Table 2. Yields of each tuber size class are expressed as a percent increase or decrease over non-1,4-DMN-treated seed. In the absence of age x 1,4-DMN interactions, the 1,4-DMN-induced changes in yield are best represented by the average across storage degree-days, as indicated by equal changes in percent yield for the three seed tuber ages for particular tuber size classes. The actual percent changes for the effects of tuber age on yield of a particular size class are shown in cases where the 1,4-DMN x age interaction was significant. The levels of significance appear in Tables 2-4. Data are averaged over three years.

TABLE 4—*Effects of 1,4-DMN on stem numbers and productivity of Umatilla Russet seed tubers. After an initial wound healing period at 10 C, seed tubers were stored at 4, 7, and 9 C to accumulate 80, 554, and 642 degree-days (4 C base temperature) during each 200-day storage season. 1,4-DMN was applied (thermal fog) at 40 mg kg^{-1} on 20 December, and again on 25 January. A final treatment (10 mg 1,4-DMN kg^{-1}) was applied on 27 February. Seed was cut and planted into replicated plots at Othello, WA, on or about 15 April. Data are averaged over three years.*

Storage Deg. Days	DMN	Stems No./plant	Umatilla Russet Tuber Grades Total	U.S.#1	<113g	113-170g	170-284g	284-340g	340-397g	>397g	Cull	Tuber No. ($x10^3$ ha^{-1})	F. Wt. (g/tuber)
			t ha^{-1}										
80	-	3.3	71.0	56.8	12.0	16.0	23.5	7.46	3.81	5.94	1.81	424	167
	+	3.5	64.8	50.9	12.7	15.2	21.6	5.83	3.42	4.89	1.17	414	158
554	-	2.9	62.8	48.8	10.8	11.8	20.7	5.62	4.05	6.88	2.74	366	171
	+	3.1	58.7	41.4	13.6	13.6	17.6	4.37	1.88	3.74	3.92	385	145
642	-	2.9	64.7	51.7	10.8	12.8	20.9	6.23	5.31	6.47	2.02	378	170
	+	3.3	58.2	41.5	14.3	15.7	17.8	3.86	1.23	2.87	2.75	405	139
	DMN	**	**	**	**	ns	**	**	**	**	*	ns	**
	DD_{Lin}	**	**	**	ns	*	**	**	ns	ns	**	*	ns
	DD_{dev}	*	ns	ns	ns	ns	ns	ns	ns	ns	**	ns	ns
	DMN x DD_{LT}	ns	ns	ns	ns	ns	ns	ns	**	ns	**	ns	*
	DMN x DD_{dev}	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

*,** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively. ns, not significant; DD, degree day; Lin., linear; dev., deviations from linearity.

DISCUSSION

Since 1,4-DMN is registered as a "dormancy enhancer," it is reasonable to expect that effects of 1,4-DMN on yield may depend on the physiological status or age of seed tubers at planting. 1,4-DMN is marketed specifically to control sprouting of seed during storage and transit, and commercial seed lots differ physiologically, partly as a consequence of differential heat-unit accumulation during handling and storage (Knowles et al. 2003, 2004b). In essence, we created the need for sprout inhibition in our seed tubers by aging them at different temperatures for various periods to produce a range of sprouting potentials.

The frequency (three times during the storage season) and timing of 1,4-DMN applications to inhibit sprouting of the seed was dictated by the degree of sprout development exhibited by tubers stored at the highest temperatures (7-9 C, 642-degree-day seed). As expected, these tubers (all cultivars) emerged from dormancy prior to those stored at lower temperatures, requiring the application of 1,4-DMN to inhibit further sprout development. The efficacy of 1,4-DMN as a dormancy enhancer was not long lasting, as evidenced by the need for multiple applications at monthly intervals starting in late December. The first two applications of 1,4-DMN were at rates (40 mg kg^{-1}) that were twice that of label specifications, further reflecting the low potency and temporary ability of this chemical to delay sprouting of seed stored at slightly higher than normal temperatures (i.e., seed in the process of accumulating a modest amount of heat units above 4 C). Over the storage season, the total amount of 1,4-DMN applied to seed stored under each temperature regime was 90 mg kg^{-1}, 10 mg kg^{-1} over the maximum amount specified in the label for a storage season. The final application of 1,4-DMN (10 mg kg^{-1}) was made 47 days before planting. The reversible sprout-suppressing ability of 1,4-DMN is an essential characteristic for use on seed potatoes. Our observations indicate that monthly applications of 1,4-DMN are needed to effectively suppress sprouting of seed stored at higher temperatures.

1,4-DMN-treated tubers stored at the higher temperatures contained significantly lower residues of 1,4-DMN at the end of storage than those held at 4 C (Table 1), but the lowest residue was well in excess of natural levels (<0.3 mg kg^{-1} periderm) of 1,4-DMN in the non-treated tubers. Despite the differences in residue levels in the differentially aged tubers, residues were sufficiently high to effectively inhibit sprouting through the 200-day storage season (see Results). From a practical standpoint, the decline in 1,4-DMN residue levels with advancing degree-days indicates that seed stored at higher temperatures may require higher concentrations and/or more frequent applications of 1,4-DMN to effectively control sprouting, and underscores the importance of monitoring heat-unit accumulation

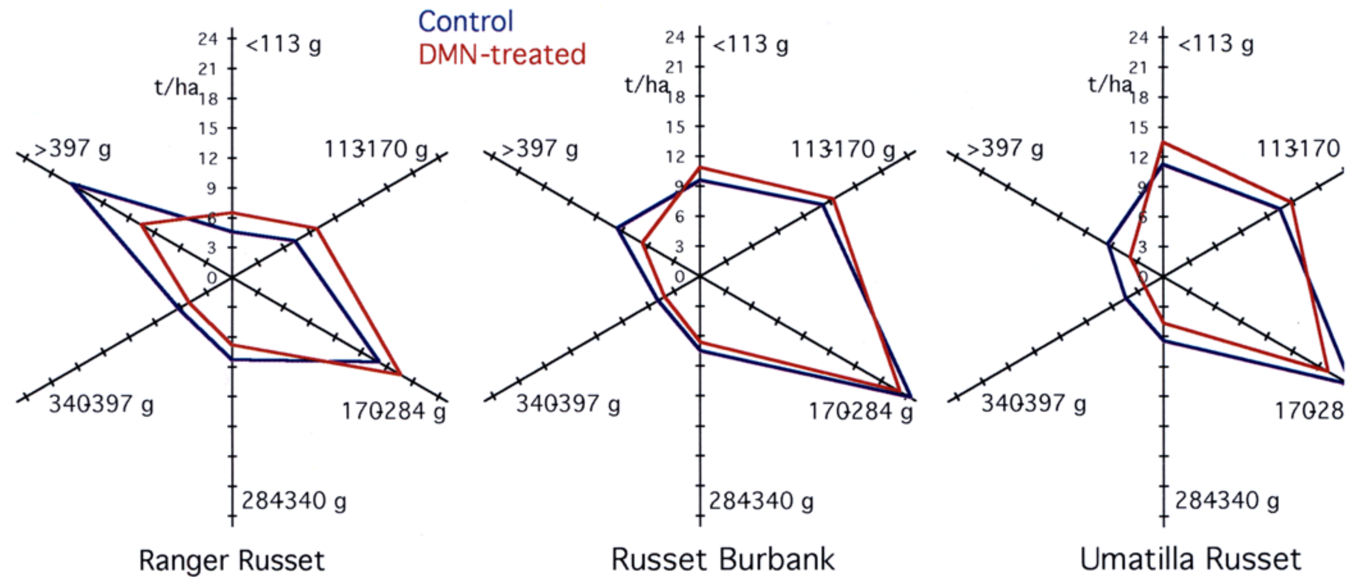

FIGURE 3.
Polygonal diagrams illustrating the shifts in tuber size distribution produced by 1,4-DMN-treated seed tubers. 1,4-DMN treatments were applied to Ranger Russet, Russet Burbank and Umatilla Russet seed tubers during storage, as described in Table 2. Yield axes range from 0 to 24 t ha^{-1} and are equal for the six tuber size classes across cultivars. The area encompassed by each polygon is indicative of total marketable yield. Changes in shape or shifts in position of the polygons characterize an effect of 1,4-DMN on the overall yield profile. Data have been averaged over seed age (storage degree-days) to reveal the main effect of 1,4-DMN for each cultivar. Statistical summaries appear in Tables 2-4. Data are averaged over three years.

during storage and handling in cases where 1,4-DMN is used to control sprouting of seed potatoes. Further research to more precisely establish relationships among storage temperature, degree-days and residue levels is warranted to optimize label recommendations for the commercial use of 1,4-DMN on seed potatoes.

The lower 1,4-DMN residues in 554- and 642-degree-day tubers, along with the shorter dormancy and increased sprouting potential observed from these tubers during storage, suggests that plant establishment from the older 1,4-DMN-treated tubers may be faster than that from tubers stored at 4 C in which 1,4-DMN residues were higher (i.e., a 1,4-DMN x age interaction). However, differences in plant emergence among the three ages of seed tubers were non-existent over the 3-yr study period and 1,4-DMN did not interact with seed tuber age to affect plant emergence and establishment. The slight delay in plant emergence from 1,4-DMN-treated seed had no effect on final plant stand (Figure 1). Hence, the relatively high concentrations of 1,4-DMN used in this study effectively controlled sprouting of Ranger Russet, Russet Burbank, and Umatilla Russet seed tubers during storage at different temperatures with no deleterious effects on subsequent plant establishment. Beveridge et al. (1981a) reported similar results with 100 mg 1,4-DMN kg^{-1} (applied on alumina dust) in preliminary studies with the cvs Redskin and Record.

In general, tuber number per plant increases with increasing stem number (Gillison et al. 1987). This in turn affects plant source-sink relationships, resulting in smaller tubers and, depending on cultivar and the extent of stem number increase, can significantly shift the tuber size distribution and thus grade (Knowles and Knowles 2004b). However, the effects of 1,4-DMN on stem and tuber numbers were not consistent across cultivars and where they did occur (Tables 2-4), were certainly of insufficient magnitude to account for the observed shifts in tuber size distribution according to stem number/tuber set models documented recently for these cultivars in the Columbia Basin (Knowles and Knowles 2004a, 2004b). The 1,4-DMN-induced shifts in yield profiles for the cultivars are illustrated in the polygonal plots of Figure 3. To achieve such shifts in tuber size distribution through changes in aboveground stem numbers alone, would require 1,4-DMN-treated seed to produce from 0.8-1.2 additional stems, depending on the cultivar (Knowles and

Knowles 2004b). 1,4-DMN either had no effect on stem numbers (Ranger Russet) or increased stems by only 0.3 (Umatilla Russet) or 0.4 (Russet Burbank) with no effect on tuber numbers in the latter two cultivars. The shifts in tuber size profiles are also difficult to explain on the basis of the rather innocuous effects of 1,4-DMN on plant emergence and establishment. Hence, the mechanism(s) by which 1,4-DMN affected tuber size distribution was likely not through effects on stand establishment or stem number/tuber set relationships and remains to be discovered.

Since the effect of 1,4-DMN on total and U.S. no. 1 tuber yields was, in most cases, minor relative to the impact on tuber grade, 1,4-DMN may provide an effective treatment for shifting tuber size profiles to more closely match the needs of specific markets. This would only be true in situations where the economic incentives for a particular tuber size profile more than compensate for potential losses due to the slight reductions in total and U.S. No. 1 yields that may result from 1,4-DMN treatment. The yield reductions from 1,4-DMN treatment of seed appear to be concentration-dependent. For example, a single application of 6 mg 1,4-DMN kg^{-1} tubers stored at 4 C did not affect stem number, average tuber weight, tuber number per plant, or tuber size distribution in preliminary studies on Russet Burbank grown in Tasmania (Brown et al. 2000). Such low concentrations, however, would have limited efficacy at controlling sprout growth at higher storage temperatures (Beveridge et al. 1981a, 1981b). Beveridge et al. (1981a) was the first to suggest from preliminary studies that 1,4-DMN at higher concentrations (100 mg kg^{-1}) may have a minor effect on tuber size distribution.

Our results clearly show that multiple applications of 1,4-DMN not only inhibit sprouting of seed tubers stored at higher than normal (4 C) temperatures, but can modify tuber yield and size distribution to obtain a greater number of tubers of smaller average size, which may be desirable for particular segments of the fresh, processing, and seed potato industries. For example, more uniform, smaller size tubers are desirable in retail markets and the restaurant trade for sale as boiling potatoes to be served whole. Processors of potatoes for the whole canning industry also seek smaller size tubers. For the U.S. fresh market, 1,4-DMN could potentially be used to shift the yield profile to more closely match a desired carton count. In the seed-potato industry, smaller size seed tubers result in less waste during the cutting operation and produce a better stand in the field because of a significant reduction in "blind" seedpieces. 1,4-DMN treatments could also be used to increase the proportion of single-drop seed tubers. Hence, when applied to stored seed potatoes, 1,4-DMN can effectively modulate the subsequent productivity and tuber size distribution. The commercial feasibility and potential advantages of using 1,4-DMN to alter tuber size distribution for various markets will depend on the outcome of comprehensive economic analyses, relating 1,4-DMN-induced changes in yield profiles to the specific needs of fresh, processing and seed potato markets.

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