# Susceptibility to Potato Leafroll Virus in Potato: Effects of Cultivar, Plant Age at Inoculation, and Inoculation Pressure on Tuber Infection

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**ABSTRACT**

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Three potato (*Solanum tuberosum*) cultivars differing in susceptibility to potato leafroll virus (PLRV)—Russet Burbank (highly susceptible), Kennebec (moderately resistant), and Cascade (resistant)—showed increasing resistance to PLRV in the field as plants aged. As inoculation age (measured in days after plant emergence) increased, percent tuber infection decreased significantly ($P < 0.05$) in each cultivar. As inoculation pressure (measured by viruliferous aphid-days) increased, percent tuber infection per plant increased significantly for Russet Burbank and Cascade. The percentage of PLRV-infected tubers for any inoculation age and aphid-day treatment combination was always less for Kennebec and Cascade than for Russet Burbank. In each cultivar, there was no significant difference in percent PLRV infection among four size categories of tubers. A greenhouse bioassay classified potato cultivars into PLRV resistance categories corresponding to previously reported field resistance. However, Cascade was not as resistant in the greenhouse bioassay as it was in field trials.

Potato leafroll virus (PLRV) is a phloem-limited, aphid-vectored virus that occurs worldwide where potato (*Solanum tuberosum* L.) is grown. Early-season infection reduces yield and in some cultivars causes tuber net necrosis. Seed potatoes are rejected for certification if PLRV incidence exceeds established thresholds, which in the limited generation program in Minnesota are 0.1–0.4% (15). To meet these phytosanitary standards, it is important to reduce virus inoculum levels and aphid vector populations. The most efficient PLRV vector is the green peach aphid (*Myzus persicae* (Sulzer)) (19). In most seed potato-growing areas, control of green peach aphid is necessary to meet certification standards. However, green peach aphid has acquired resistance to all but a few of the insecticides registered for use on potato.

Calendar-based spray schedules hasten development of resistance. Recently, action thresholds based on green peach aphid apterae per 100 leaves have been proposed for PLRV control in Russet Burbank (12). Russet Burbank is highly susceptible to PLRV, but many cultivars have some inherent resistance to PLRV infection (1). In resistant cultivars, field spread of PLRV is reduced (1,5) and action thresholds for the green peach aphid can be elevated (10). Adjusting thresholds to reflect these inherent differences in cultivar susceptibility could, for PLRV-resistant cultivars, provide satisfactory control with fewer insecticide applications.

Most potato cultivars, even those highly susceptible to PLRV, exhibit mature plant resistance to PLRV (11,14). There is less PLRV spread in fields inoculated later in the growing season, and plants initially infected at a mature stage tend to have fewer PLRV-infected tubers (2,7,13,14,18). Presumably, green peach aphid action thresholds for control of PLRV should be dynamic, increasing as plants mature to reflect increasing resistance to PLRV infection. Previous studies of mature plant resistance have not considered effects of varying PLRV inoculation pressure (a first step toward modifying action thresholds), although there is evidence that increasing inoculation pressure increases the chance of infection (2,4). One objective of the present study was to determine if mature plant resistance could be quantified by using known inoculum pressure in cultivars differing in PLRV resistance.

If action thresholds for green peach aphid could be modified to reflect differences in cultivar resistance to PLRV, there is a need to classify cultivars into PLRV resistance categories. The usual procedure to assess cultivar resistance is to conduct several years of field trials (1,16). Therefore, another objective of this study was to develop a simple greenhouse assay to replace lengthy field trials to categorize potato cultivars into both cultivar and mature plant resistance categories.

Most state and provincial seed potato certification programs require seed growers to submit samples of B-sized tubers for virus indexing in winter trials. However, Knutson and Bishop (14) reported that in Russet Burbank, small tubers were less likely to be PLRV-infected than were large tubers from the same plant. This could have important implications for seed certification, so we examined three cultivars differing widely in resistance to PLRV to determine if infection rates were equivalent among four sizes of tubers.

## MATERIALS AND METHODS

**Field experiments.** Certified seed potatoes were planted at the Agricultural Experiment Station, Rosemount, Minnesota. Cultivars used varied in PLRV resistance. Russet Burbank (highly susceptible) was planted in 1990, and Russet Burbank, Kennebec (moderately resistant), and Cascade (resistant) (1) were planted in 1991. These were the same cultivars used in previous experiments to establish cultivar-specific green peach aphid action thresholds for PLRV control (10,12). Plants were serologically tested at emergence to confirm freedom from PLRV infection. Plants were sprayed with mancozeb (1.1 kg/ha) weekly from mid-July to September to control early blight caused by *Alternaria solani* Sorauer and with methamidophos (0.84 kg a.i./ha) as needed to control potato leafhopper (*Empoasca fabae* (Harris)).

Plants were inoculated with PLRV at 25 (vegetative), 50 (early tuber bulking), 75 (late tuber bulking), or 100 (early senescence) days after plant emergence in 1990 and at 30 (vegetative) or 60 (tuber bulking) days after plant emergence in 1991. On each date, groups of 10 (1990) or five (1991) plants were exposed to 20, 50, 100, or 200 viruliferous aphid-days per plant. A viruliferous aphid-day was defined as the product of the number of viruliferous green peach aphids used to inoculate a plant and the number of days they remained on the plant. Viruliferous aphids were obtained by rearing green peach aphids on PLRV-infected Russet Burbank potatoes. Plants were inoculated by clip-caging 10–50 aphids per plant, two to five aphids per clip-cage, each stem having at least one clip-cage. Every stem was inoculated to avoid the possibility of mixed progenies (9), i.e., both infected and healthy tubers on the same plant, resulting simply from inoculating only one stem of a multiple-stemmed plant. If mixed infections occurred, they would be the result of host

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or mature plant resistance. Clip-cages were removed after 2 or 4 days, depending on the desired number of aphid-days. For example, 200 aphid-days were generated by using 10 clip-cages of five aphids each, held in place for 4 days. When clip-cages were removed, all aphids were destroyed and the systemic insecticide aldicarb was incorporated at the base of plants to prevent subsequent recolonization.

In both years, all tubers from every plant were harvested. In 1990, plants were harvested 2 wk after the last inoculation date and the tubers were stored at 4 C. In December, tubers were removed from cold storage, individually weighed, and planted in a greenhouse. In 1991, plants were harvested 5 wk after the last inoculation date and the tubers were individually weighed, treated with gibberellic acid (15 ppm), and planted immediately in a greenhouse. When plants were 10–15 cm tall, upper leaflets were collected and tested for PLRV by enzyme-linked immunosorbent assay (ELISA) (6), using antisera purchased from Boehringer-Mannheim (Indianapolis, IN). A plant was considered infected if the absorbance ($A_{405}$) of the *p*-nitrophenol product was three standard deviations above the mean $A_{405}$ of 10 healthy controls run on the same ELISA plate.

Each year the percentage of PLRV-infected tubers per inoculated plant was determined. Analysis of variance (17) was used to measure the significance of cultivar, plant age at inoculation, and PLRV inoculation pressure on mean percent tuber infection. Ryan's *Q* test (8) was used to separate treatment means. To examine PLRV infection as a function of tuber size, tubers from each plant were placed before ELISA testing into one of four categories based on tuber weight: <40 g, 40–120 g (B-sized), 121–300 g (A-sized), and >300 g. Analysis of variance (17) was used to determine if plant age at inoculation or PLRV inoculation pressure affected incidence of PLRV infection among tuber size categories.

**Greenhouse experiments.** In 1990 and 1991, greenhouse experiments were conducted with five cultivars of varying PLRV resistance (1): Russet Burbank, highly susceptible; Red Pontiac, susceptible; Kennebec, moderately resistant; Abnaki, resistant; and Cascade, resistant. Twenty-five plants of each cultivar, grown from certified seed, were inoculated at 10 (early vegetative), 23 (vegetative), 46 (early tuber bulking), or 64 (late tuber bulking) days after plant emergence. Green peach aphids used to inoculate test plants were reared on PLRV-infected Russet Burbank plants. Five viruliferous green peach aphids were clip-caged to an upper leaflet on two different stems and removed 1 wk later (= 70 aphid-days). Test plants were grown to maturity and three tubers were harvested per plant and stored at 4 C. After 3 mo of cold storage, tubers were planted in a greenhouse. When foliage was 10–15 cm tall, upper leaflets were assayed for PLRV by ELISA using reagents purchased from Agdia Inc. (Elkhart, IN). Plants were considered infected when $A_{405}$ exceeded the mean absorbance of healthy controls plus three standard deviations.

## RESULTS AND DISCUSSION

**Field experiment.** Russet Burbank was highly susceptible to PLRV infection in both 1990 and 1991. Approximately 95% of inoculated Russet Burbank plants were infected, having produced at least one PLRV-infected tuber (Table 1). With Kennebec, all plants inoculated 30 days after emergence produced infected tubers, whereas only 55% produced infected tubers when inoculated 60 days after emergence. Cascade was resistant to PLRV throughout the season, as only 55% (30 days after emergence) and 25% (60 days after emergence) of PLRV-inoculated plants produced infected tubers.

When data were combined across inoculation pressures, a significantly ($P < 0.05$) greater percentage of tubers were infected in 1990 from Russet Burbank plants inoculated 25 days after emergence (94.7%) than from plants inoculated 50 or more days after emergence (51.1–78.1%) (Table 1). In 1991, a significantly greater percentage of tubers were infected from plants inoculated 30 rather than 60 days after emergence for Russet Burbank (97.6 vs. 65.1%), Kennebec (88.2 vs. 40.2%), and Cascade (34.9 vs. 7.4%) (Table 1). When data were combined across inoculation dates, Russet Burbank plants inoculated in 1990 with 20 viruliferous aphid-days produced significantly fewer PLRV-infected tubers (58.0%) than plants inoculated with 50, 100, or 200 aphid-days (70.6–81.3%) (Table 2). In 1991, the trend was similar but not significant in Russet Burbank and Kennebec. The effect of inoculation pressure was most apparent in Cascade, where plants inoculated with either 20 or 50 aphid-days had significantly fewer PLRV-infected tubers (4.5 and 3.7%, respectively) than plants inoculated with 100 or 200 aphid-days (36.1 and 40.3%, respectively) (Table 2).

The interacting effects of plant age and inoculation pressure in viruliferous aphid-days were most pronounced on the last inoculation date (Figs. 1 and 2). However, the interacting effects were significant only for Russet Burbank inoculated on day 100 (Fig. 1), where plants exposed to 20 aphid-days had fewer infected tubers, and for Cascade inoculated on day 30 (Fig. 2), where plants exposed to 20 and 50 aphid-days

**Table 1.** Effect of plant age at inoculation on percent PLRV-infected plants and percent PLRV-infected tubers per plant in three potato cultivars, Rosemount, Minnesota, 1990 and 1991[y]

| | Plant age at inoculation in days after plant emergence | | | | | |
|---|---|---|---|---|---|---|
| **Cultivar, year** | **25** | **30** | **50** | **60** | **75** | **100** |
| Russet Burbank, 1990 | | | | | | |
| Percent infected plants | 100 | ... | 87 | ... | 90 | 100 |
| Percent infected tubers/plant | 94.7 a | | 59.1 c | | 78.1 b | 51.1 c |
| Russet Burbank, 1991 | | | | | | |
| Percent infected plants | ... | 100 | ... | 95 | ... | ... |
| Percent infected tubers/plant | | 97.6 a | | 65.1 b | | |
| Kennebec, 1991 | | | | | | |
| Percent infected plants | ... | 100 | ... | 55[z] | ... | ... |
| Percent infected tubers/plant | | 88.2 a | | 40.2 b | | |
| Cascade, 1991 | | | | | | |
| Percent infected plants | ... | 55 | ... | 25 | ... | ... |
| Percent infected tubers/plant | | 34.9 a | | 7.4 b | | |

[y] Numbers in rows followed by the same letter are not significantly different ($P = 0.05$).
[z] Based on incomplete data, generally only one to three tubers tested per plant; 268 tubers harvested, 69 tubers tested, 26 tubers PLRV-infected.

**Table 2.** Effect of PLRV inoculation pressure on percent infected tubers per plant in three potato cultivars, Rosemount, Minnesota, 1990 and 1991[y]

| | PLRV inoculation pressure in viruliferous aphid-days | | | |
|---|---|---|---|---|
| **Cultivar, year** | **20** | **50** | **100** | **200** |
| Russet Burbank, 1990 | 58.0 a[z] | 73.7 bc | 70.6 b | 81.3 c |
| Russet Burbank, 1991 | 70.4 a | 89.8 a | 83.5 a | 81.7 a |
| Kennebec, 1991 | 73.5 a | 92.1 a | 93.5 a | 91.6 a |
| Cascade, 1991 | 4.5 a | 3.7 a | 36.1 b | 40.3 b |

[y] Numbers in rows followed by the same letter are not significantly different ($P = 0.05$).
[z] Data for Kennebec are from plants inoculated 30 days after plant emergence, whereas data for Russet Burbank and Cascade are means of plants inoculated at both 30 and 60 days after plant emergence.

had fewer infected tubers. Cascade was particularly interesting because inoculation at 30 days after emergence with 20 aphid-days resulted in no infected tubers and with 50 aphid-days, only one plant with infected tubers. However, when inoculation pressure was increased, all Cascade plants became infected, although only 54% (100 aphid-days) and 81% (200 aphid-days) of the tubers from these plants were PLRV-infected (Fig. 2). By 60 days after emergence, few Cascade plants and fewer tubers became infected, so differences among inoculation pressures were not significant ($P > 0.05$.). DiFonzo (10) demonstrated that green peach aphid growth, longevity, and reproduction were not diminished on Cascade, suggesting that this cultivar is resistant to PLRV because of a plant-virus interaction, not because Cascade is an inferior green peach aphid host.

Regardless of plant age at inoculation, Russet Burbank was most susceptible to PLRV, Kennebec was intermediate, and Cascade was most resistant, confirming the resistance categories of Bagnall and Tai (1). In 1990, the reduction in the percentage of infected tubers per plant from the earliest inoculation to inoculations later in the season was 33.7% for Russet Burbank (94.7% on day 25 and 62.8% later in the season, the mean of days 50, 75, and 100) (Table 1). In 1991, the reduction in the number of infected tubers per plant between day 30 and day 60 was least in Russet Burbank (33.3%), intermediate in Kennebec (57.3%), and greatest in Cascade (78.8%).

**PLRV infection and tuber size.** Within each cultivar, percent PLRV infection was similar among the four size categories of tubers (Table 3). Further analysis of these data by plant age at inoculation and PLRV inoculation pressure showed the overall effect of tuber size was not significant ($F = 0.04 - 1.38$, $P = 0.30 - 0.99$). This suggests

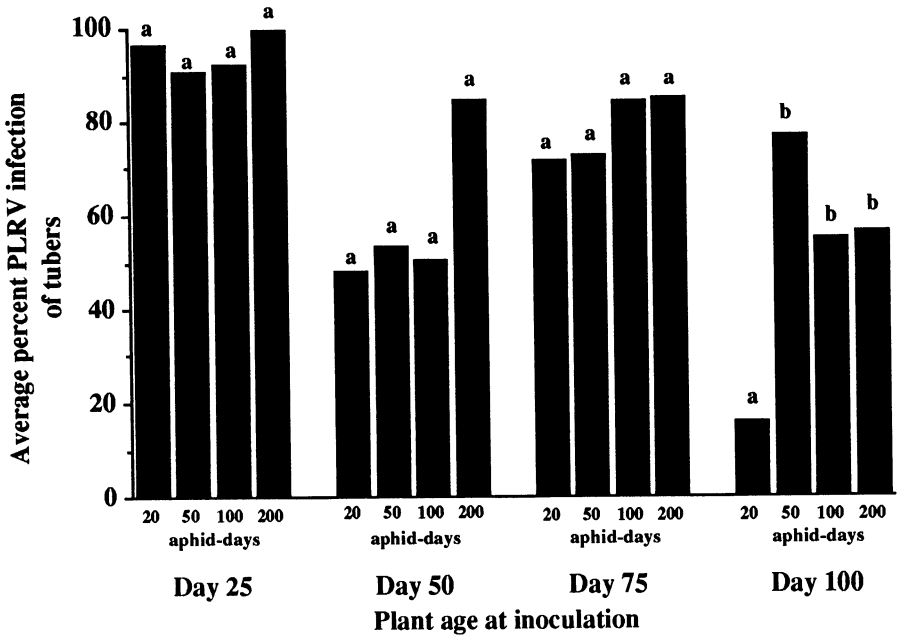


**Fig. 1.** Average percent PLRV-infected tubers per plant in potato cv. Russet Burbank, 1990. Treatments were combinations of four PLRV inoculation pressures measured in viruliferous aphid-days and four plant ages at inoculation measured in days after emergence. Within plant ages at inoculation, aphid-day bars with the same letter are not significantly different according to Ryan's $Q$ test ($P = 0.05$).

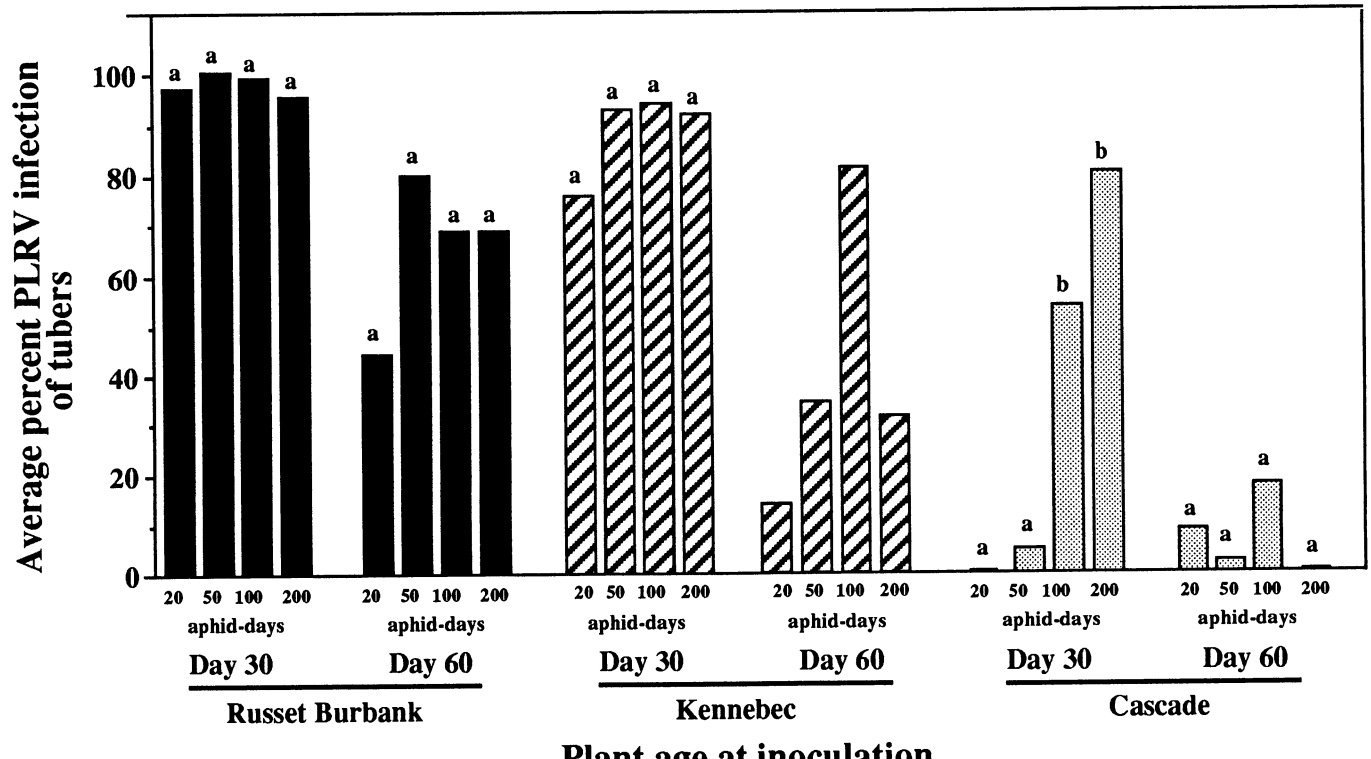


**Fig. 2.** Average percent PLRV-infected tubers per plant in three potato cultivars, 1991: Russet Burbank (PLRV-susceptible), Kennebec (moderately PLRV-resistant), and Cascade (PLRV-resistant). Treatments were combinations of four PLRV inoculation pressures measured in viruliferous aphid-days and two plant ages at inoculation measured in days after emergence. Within plant ages at inoculation, aphid-day bars with the same letter are not significantly different according to Ryan's $Q$ test ($P = 0.05$). Data from Kennebec inoculated 60 days after emergence were insufficient for mean separation.

that for Russet Burbank, Kennebec, and Cascade, tuber size does not bias PLRV indexing results. This is reassuring, since the conventional practice of most seed certification programs is to test only B-size seed in their winter virus indexing programs. It is, however, contrary to findings of Knutson and Bishop (14), who reported 18% more infection in the largest tubers from hills having three to seven tubers. These dissimilar findings may be explained by the differences in experimental methods between the two studies. Knutson and Bishop (14) graft-inoculated single-stemmed plants, visually determined secondary PLRV infection, and analyzed infection data for only the two largest and two smallest tubers per hill. We aphid-inoculated each stem, used ELISA to detect PLRV infection in progeny foliage, and considered all tubers in our data analysis.

**Greenhouse experiment.** Abnaki was the most resistant cultivar to PLRV infection, followed by Kennebec, Cascade, Red Pontiac, and Russet Burbank (Table 4). Cascade showed significant ($P < 0.05$) levels of mature plant resistance, while Red Pontiac and Russet Burbank were equally susceptible at all four growth stages. Abnaki was highly resistant at all growth stages, so the difference between infections at inoculation at day 10 (9.6%) and day 64 (0.0%) was small and weakly significant at $P = 0.10$. Kennebec was tested only in 1991, so these data were not included in the overall analysis. However, Kennebec plants did show moderate mature plant resistance.

In Cascade, PLRV infection declined progressively with increasing plant age at inoculation. Across the 2 yr of the study, Cascade plants inoculated 46 days after emergence had significantly ($P < 0.10$) less PLRV infection (52.2%) than did plants inoculated 10 days after emergence (82.6%), and plants inoculated 64 days after emergence had significantly ($P < 0.10$) less infection (45.7%) than did plants inoculated 23 days after emergence (77.0%). Using multiple-year field trials, Bagnall and Tai (1) grouped Cascade with Abnaki as being highly resistant, while our greenhouse bioassay placed Cascade in an intermediate category with respect to PLRV resistance. In field trials to establish action thresholds for green peach aphid apterae to control PLRV spread (10), Cascade demonstrated a high level of PLRV resistance and was significantly more resistant than Kennebec.

Russet Burbank, Red Pontiac, and Cascade test plants inoculated in the early vegetative stage (10 days after plant emergence) expressed typical symptoms of primary infection with PLRV, but such symptoms were not expressed in Abnaki and Kennebec test plants. This observation is similar to reduced early to mid-season symptom expression in the cultivar Canus, as compared with other European cultivars (7). Further, Abnaki and Kennebec appeared to have a lower virus titer than the other cultivars. Mean ELISA $A_{405}$ values for secondarily infected plants were 0.426 in Abnaki, 1.079 in Kennebec, 1.625 in Cascade, 1.696 in Pontiac, and 1.727 in Russet Burbank. Lower virus multiplication of PLRV in resistant potato genotypes was reported by Barker and Harrison (3). However, resistance of Cascade to PLRV does not appear to be directly related to virus replication or virus antigen titer, as measured by ELISA. In the greenhouse, Cascade was only moderately more resistant to PLRV than the susceptible cultivars Russet Burbank and Pontiac and had a similar virus titer. The factor or factors that confer resistance to PLRV in the field are apparently not due to inherent resistance to replication once the plant becomes infected. Thus, the field resistance of Cascade to PLRV appears to be more complex than could be assessed in the greenhouse study alone.

It is evident that plant age at inoculation and PLRV inoculation pressure influence the final infection of tuber progeny from individual PLRV-inoculated plants. Tuber size does not appear to affect final infection. This finding is important because most state seed potato certification programs index B-sized tubers. In the field, resistance was evident as early as 50 (1990) and 60 (1991) days after plant emergence. Tuber infection was significantly less in Russet Burbank, Kennebec, and Cascade inoculated later in the season. In the greenhouse, resistance was observed in Abnaki, Cascade, and Kennebec inoculated 46 days after plant emergence. The greenhouse bioassay correctly classified four of the five cultivars into previously reported resistance categories (1). In Cascade, resistance to PLRV was more pronounced in field trials than in the greenhouse bioassay.

In the field, varying inoculation pressure early in the season had little effect on final tuber infection in Russet Burbank or Kennebec. On the last inoculation date, greater inoculation pressure resulted in significantly more tuber infection in Russet Burbank in 1990 and a trend for more tuber infection in Russet Burbank and Kennebec in 1991. In Cascade, varying inoculation pressure significantly affected tuber infection on day 30 but not on day 60 at the inoculation pressures used. Resistance to PLRV increases as the season progresses. With further field research, it may be possible to quantify these changes. Eventually, action thresholds for green peach aphid may be modified accordingly.

**Table 3.** Percent PLRV infection of tubers by tuber size for three potato cultivars and number of tubers tested in each size category[y]

| Cultivar, year | Tuber size (g) | | | |
|---|---|---|---|---|
| | <40 | 40–120 | 121–300 | >300 |
| Russet Burbank, 1990 | 72.9 (768) | 70.7 (608) | 66.1 (319) | 67.3 (49) |
| Russet Burbank, 1991 | 73.2 (228) | 77.7 (231) | 81.3 (244) | 81.3 (47) |
| Kennebec, 1991[z] | 85.7 (63) | 78.6 (98) | 75.9 (116) | 75.0 (60) |
| Cascade, 1991 | 24.9 (213) | 22.7 (277) | 30.1 (316) | 25.7 (101) |

[y]No significant differences in PLRV infection among tuber sizes within each cultivar ($P = 0.30$–$0.99$). Number of tubers tested in parentheses.
[z]Data were available from only 69 of 268 tubers harvested from plants inoculated on day 60.

**Table 4.** Effect of plant age at inoculation on percent PLRV-infected plants of five potato cultivars in the greenhouse, mean of 1990 and 1991 experiments[y]

| Cultivar | Percent infected plants per age at inoculation in days after emergence | | | |
|---|---|---|---|---|
| | 10 | 23 | 46 | 64 |
| Abnaki | 9.6 aA (43) | 8.4 aA (39) | 2.3 aAB (45) | 0.0 aB (38) |
| Kennebec[z] | 70.6 (17) | 81.8 (11) | 20.0 (5) | 25.0 (20) |
| Cascade | 82.6 bA (48) | 77.0 bAB (48) | 52.2 bBC (52) | 45.7 abC (48) |
| Red Pontiac | 91.7 bA (49) | 100.0 cA (41) | 69.5 bA (48) | 80.9 bA (48) |
| Russet Burbank | 100.0 bA (46) | 100.0 cA (41) | 86.5 bA (46) | 80.5 bA (44) |

[y]Differences among cultivars for each growth stage (columns) are given in lowercase letters ($P = 0.05$) and differences among growth stages within each cultivar (rows) are given in uppercase letters using a single factor ANOVA ($P = 0.10$). Number of plants tested in parentheses.
[z]Kennebec tested in 1991 only.


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