

Biomass Partitioning and Nitrogen Use Efficiency of ‘Superior’ Potato Following Genetic Transformation for Resistance to Colorado Potato Beetle

Francis Zvomuya and Carl J. Rosen¹

Department of Soil, Water, and Climate, University of Minnesota, 1991 Upper Buford Circle, St. Paul, MN 55108

ADDITIONAL INDEX WORDS. *Solanum tuberosum*, ‘NewLeaf Superior,’ transgenic potato

ABSTRACT. Current techniques used in genetic transformation can result in variation of numerous traits in addition to the transformed trait. Backcrossing to the standard genotype can eliminate this variation, but because of the heterozygous nature of potatoes (*Solanum tuberosum* L.), backcrossing is not effective. Therefore, the chances of obtaining altered performance in transformed potato are high. ‘Superior’ potato plants were recently genetically modified to resist attack and damage by the Colorado potato beetle [*Leptinotarsa decemlineata* (Say)]. The transformed clone, ‘NewLeaf Superior’ (‘NewLeaf’), has been shown in previous field trials to be more vigorous than the standard clone. The objective of this 2-year study was to evaluate the performance of ‘NewLeaf’ relative to that of the standard clone at various fertilizer nitrogen (N) levels. The two clones were randomly assigned as subplots to main plots consisting of four N levels (28, 112, 224, or 336 kg·ha⁻¹). Based on regression analysis, total yield was higher for ‘NewLeaf’ than for ‘Superior’ at N rates below 92 kg·ha⁻¹ in 1997. At higher rates, however, ‘Superior’ had higher yields than the transgenic clone. In 1998, the clone × N rate interaction was significant, but there was no consistent trend to the response of the two clones to N application. At the 112 kg·ha⁻¹ N rate, total yield was higher for ‘NewLeaf’ than for ‘Superior’, but yields were similar for the two clones at other N rates investigated. Nitrogen and biomass accumulation in vines increased more for ‘NewLeaf’ than for ‘Superior’ as N rate was increased from 28 to 336 kg·ha⁻¹. At equivalent N rates, these traits were higher for the transformed than for the standard clone within the range of N rates investigated. However, harvest index at equivalent N rates was higher for the standard clone than for ‘NewLeaf’. ‘Superior’ and ‘NewLeaf’ produced similar tuber dry weight yields per unit of N supplied and per unit of N absorbed by the plant. Nitrogen uptake efficiency (NUE) was 16% higher for ‘NewLeaf’ than for the standard clone at the low N rate (112 kg·ha⁻¹), whereas at higher N rates NUE was either lower for ‘NewLeaf’ or similar for the two clones. This observation, together with the finding that yield for ‘NewLeaf’ was maximized at lower N levels than the standard clone, suggests that ‘NewLeaf’ may require lower N input than the standard clone. Results from the study indicate that the greater efficiency of ‘NewLeaf’ at lower N levels was associated with acquisition of N from the soil rather than utilization of absorbed N in metabolism.

Recent advances in plant transformation technology have facilitated the development of insect-resistant potato (*Solanum tuberosum* L.) strains (Perlak et al., 1993). ‘Superior’ potato plants were recently genetically modified by Monsanto Co. (St. Louis, Mo.) to resist attack and damage by the Colorado potato beetle. The transformation, which entailed insertion of the *cryIIIA* gene encoding for the insecticidal crystal proteins of *Bacillus thuringiensis* var. *tenebrionis*, resulted in development of the strain, ‘NewLeaf Superior’ (hereafter ‘NewLeaf’). ‘NewLeaf’ is completely protected from Colorado potato beetle and produces vines that are more vigorous and tend to stay green longer than the standard clone (Stephens, 1998).

Variability resulting in altered performance in transgenic potato plants has been attributed to somaclonal variation (Dale and McPartlan, 1992), T-DNA insertional mutagenesis (Feldman, 1991), and effects deriving from the expression of the introduced genes (Rietveld et al., 1991). Plant tissue culture can introduce genetic and epigenetic (i.e., not linked to changes in the DNA sequence) changes in cultured cells, which result in the production of plants that differ in one or more characters from the parent cultivar (Larkin and Scowcroft, 1981). Jones (1987) indicated that when potato cells pass through a callus phase, the plants subsequently regenerated might

well exhibit differences from the original genotype.

Karp et al. (1989) suggested that variation in the regenerated plants could be triggered by the cocktail of hormones and other components that constitute the tissue culture medium to which the plant cells are subjected during the tissue culture cycle. Phenotypic variation reported in potato plants regenerated from tissue culture includes differences in traits such as height, canopy, leaf size and shape, and size and yield of tubers (Bajaj, 1987). Secor and Shepard (1981) reported differences in vine morphology, tuber yield and composition, maturity, and flowering for protoclones derived from ‘Russet Burbank’, and they noted that some of the variability found was an improvement over normal traits found in the normal cultivar. In a study by Belknap et al. (1994), maintenance of key agronomic and quality properties of parental ‘Russet Burbank’ and ‘Lehmi Russet’ potato material was observed in only four of an original population of 57 transgenic lines in tissue culture. Many of the transformed clones in that study showed inferior yield, shape, and size of tubers.

Phenotypic variation in traits such as vine vigor, canopy size and longevity, and tuber size and yield may result in different N requirements and use efficiency for the transformed plant. It is important that any unanticipated and subtle agronomic effects resulting from genes introduced during transformation are determined so that appropriate agronomic practices can be adopted. We hypothesize that increased vine vigor may alter N requirements and N use efficiency. The objective of this study was to evaluate the performance of ‘NewLeaf’ at various fertilizer N levels relative to that of the standard untransformed clone.

Received for publication 16 Oct. 2001. Accepted for publication 20 Mar. 2002. This research was supported by the Univ. of Minnesota Agricultural Experiment Station. Additional support was provided by Monsanto Co., St. Louis, Mo. We thank Steven Eskelsen, Monsanto, for helpful comments during manuscript preparation.

¹Corresponding author; e-mail crosen@soils.umn.edu.

Materials and Methods

Field studies were conducted in 1997 and 1998 on a Hubbard loamy sand (sandy, mixed, frigid Entic Hapludoll) in central Minnesota. The previous crop each year was winter rye grown without N fertilizer to help reduce soil N availability. Routine soil tests performed as described by Rosen and Eliason (1996) before treatment establishment averaged: pH, 6.4; organic matter, 1.6%; Bray P1, 42 mg·kg⁻¹; and ammonium acetate K, 135 mg·kg⁻¹ for the two seasons. Preplant NO₃⁻-N in the 0-60 cm soil layer was 20 kg·ha⁻¹ in 1997 and 9 kg·ha⁻¹ in 1998. Before planting, potassium chloride (185 kg·ha⁻¹ K) was broadcast and incorporated. Monoammonium phosphate, potassium magnesium sulfate, and additional potassium chloride were applied at furrow opening (mid-April) in a double band 8 cm to the side and 5 cm below the seed piece to supply 28 kg·ha⁻¹ N, 60 kg·ha⁻¹ P, 185 kg·ha⁻¹ K, 22 kg·ha⁻¹ Mg, and 38 kg·ha⁻¹ S.

A randomized complete-block design in a split-plot arrangement with four replications was used each year. Main plot

treatments consisted of four fertilizer N levels of 28, 112, 224, and 336 kg·ha⁻¹, 28 kg·ha⁻¹ of which was applied preplant as described above, with the remainder applied as granular ammonium nitrate in two equal splits at emergence (second week in May) and hilling (fourth week in May). Two clones consisting of standard 'Superior' and 'NewLeaf' were randomly assigned as the subplots in three rows that were 4.6 m long and 0.91 m apart, with the middle row being the harvest row.

Certified generation 3 (G3) hand-cut potato seed pieces (≈60 g) were planted the week of 20 Apr. each year at a spacing of 0.25 m in the row, to give a population of 43,000 plants/ha. Seeds for both clones were obtained from the same farm. Weeds, pests, and diseases were controlled according to standard practice (Hutchison, 1996). Colorado potato beetles were controlled using Admire (imidacloprid; Bayer Corp., Kansas City, Mo.), which was applied to both genotypes to eliminate any effect due to the chemical or differences in beetle populations. The beetle was effectively controlled in both clones. Irrigation water requirements to supplement rainfall were scheduled according to the checkbook method (Wright

Table 1. Effect of N application on the yield and quality of 'Superior' and 'NewLeaf' potatoes in 1997 and 1998.

N rate		Tuber yield (M·ha ⁻¹)				Tubers/	Specific
Genotype	(kg·ha ⁻¹)	<5.1 cm	5.1–7.5 cm	>7.5 cm	Total	plant	gravity
1997							
Superior	28	11.0	25.1	7.0	43.1	8.1	1.069
	112	9.6	28.1	10.3	47.9	8.4	1.069
	224	9.2	25.6	14.2	49.0	8.4	1.070
	336	6.5	24.9	18.9	50.2	7.6	1.071
NewLeaf	28	7.6	27.0	11.4	46.0	7.8	1.077
	112	6.0	23.0	18.0	46.9	7.6	1.078
	224	5.2	23.7	14.4	43.3	6.8	1.078
	336	7.4	21.8	9.0	38.2	7.0	1.071
ANOVA		<i>P</i> > <i>F</i>					
N rate (N)		NS	*	**	NS	NS	**
Linear (N _{lin})		*	**	**	NS	NS	**
Quadratic (N _{quad})		NS	NS	*	NS	NS	**
Clone		**	*	NS	**	**	**
Clone × N		**	NS	**	**	NS	NS
Clone × N _{lin}		**	NS	**	**	NS	*
Clone × N _{quad}		*	NS	NS	NS	NS	NS
1998							
Superior	28	2.8	36.5	4.4	43.7	8.0	1.078
	112	2.1	33.5	16.0	51.6	7.3	1.075
	224	2.4	37.9	22.3	62.6	8.8	1.072
	336	1.6	36.3	20.7	58.5	8.2	1.069
NewLeaf	28	3.0	33.2	7.5	43.6	7.2	1.074
	112	1.8	41.4	17.1	60.3	8.4	1.076
	224	1.9	30.8	28.9	61.5	7.6	1.076
	336	2.7	23.0	30.2	56.0	7.1	1.072
ANOVA		<i>P</i> > <i>F</i>					
N rate (N)		NS	NS	**	**	NS	*
Linear (N _{lin})		NS	NS	**	**	NS	**
Quadratic (N _{quad})		NS	NS	**	**	NS	NS
Clone		NS	*	**	NS	*	NS
Clone × N		NS	**	NS	*	**	**
Clone × N _{lin}		NS	**	NS	NS	NS	**
Clone × N _{quad}		NS	NS	NS	NS	NS	*

NS, *, ** Nonsignificant or significant at *P* = 0.05 or 0.01, respectively.

and Bergsrud, 1991) to maintain a soil moisture deficit of 25 mm or less during the vegetative growth stage and 14 mm or less during tuber bulking. Rainfall and air temperature data were collected from a weather station located near the experimental plots.

Following natural senescence, vines were harvested from the entire middle row about one week before final tuber harvest for determination of biomass and N content. Potato tubers were harvested from the same rows the third week in August each year using a tractor-drawn potato digger. Tubers from each plot were counted and graded by hand into four categories based on diameter: <5.1 cm, 5.1 to 6.4 cm, 6.4 to 7.5 cm, and >7.5 cm. Tuber weights were recorded for each category and summed to give total yield. The average number of tubers per plant was calculated from the total number of tubers per plot and the number of plants in each plot. A sample consisting of 25 marketable tubers was taken from each subplot for determination of specific gravity by the hydrometer method (Snack Food Association, 1995), dry weight (DW), and N content. Subsamples were diced and dried at 60°C for determination of biomass and N concentration.

Dry vine and tuber samples were weighed and ground to pass through a 1-mm screen. Concentration of N in vines and tubers was determined conductimetrically (Carlson, 1978) following digestion of ground tissue samples using a modified Kjeldahl method in which NO_3^- -N was reduced by salicylic acid (Bremner, 1996).

Nitrogen uptake by vines and tubers was calculated by multiplying the respective dry weights by the corresponding N concentrations. Total N accumulation in the whole plant was estimated by summing the vine and tuber N contents. Since a zero N control was not included among the treatments, indices of N use efficiency were calculated relative to plots receiving 28 $\text{kg}\cdot\text{ha}^{-1}$ N preplant. All indices were based on N accumulation as measured at harvest. Nitrogen use efficiency indices were computed as follows:

$$\text{NUE} = (\text{TN}_p - \text{TN}_{p28}) / (\text{N}_F - \text{N}_{F28}) \quad [1]$$

$$\text{AUE} = (\text{TDM} - \text{TDM}_{28}) / (\text{N}_F - \text{N}_{F28}) \quad [2]$$

$$\text{PUE} = (\text{TDM} - \text{TDM}_{28}) / (\text{TN}_p - \text{TN}_{p28}) \quad [3]$$

$$\text{NHI} = (\text{tuber N} - \text{tuber N}_{p28}) / (\text{TN}_p - \text{TN}_{p28}) \quad [4]$$

where NUE is N uptake efficiency, AUE and PUE are agronomic

and physiological use efficiency, respectively; NHI is the N harvest index, which is the proportion of total plant N that is partitioned to potato tubers; N_F , TDM, tuber N, and TN_p are, respectively, fertilizer N applied, total (vine plus tuber) DM, total N uptake by tubers, and total N uptake by tubers plus vines. The subscript 28 on these parameters refers to the 28 $\text{kg}\cdot\text{ha}^{-1}$ N treatment.

Data were analyzed using the GLM procedure of SAS (SAS Institute, Inc., 1990). Percentage and count data were analyzed after square-root transformation when the data failed analysis of variance assumptions. Years and replicates were considered random effects in the analyses. The data sets for the two years (1997 and 1998) were combined and tested to determine if a pooled analysis across years was justified. Probability level for significance was set at 0.05. Rate main effects and interactions were partitioned into linear and quadratic components. Where the polynomial orthogonal contrasts were significant, appropriate regression equations were fitted to the response data (Gomez and Gomez, 1984).

Results and discussion

Total rainfall amounts from April through September in 1997 (514 mm) and 1998 (462 mm) were 36 and 88 mm, respectively, below the long-term average for the area. Supplementary irrigation brought the totals to 783 and 773 mm in 1997 and 1998, respectively.

Initial analysis of the data indicated that the year \times clone \times N rate interaction was significant for all yield categories except the <5.1 cm tuber grade. The data were therefore analyzed separately for each year. A pooled analysis across the years, however, was performed on data for efficiency indices and biomass and N accumulation in the plant parts, because the three-way interactions were generally not significant at the 5% probability level.

TUBER YIELD AND QUALITY. The clone \times N rate interaction was significant for all but the 5.1–7.5 cm yield grade in 1997 and the <5.1 cm and >7.5 cm tuber categories in 1998 (Table 1). Regression analysis indicated that total tuber yield in 1997 increased 0.021 $\text{Mg}\cdot\text{kg}^{-1}$ N for standard ‘Superior’ but decreased 0.027 $\text{Mg}\cdot\text{kg}^{-1}$ N for ‘NewLeaf’ as N rate increased from 28 to 336 $\text{kg}\cdot\text{ha}^{-1}$ (Fig. 1). In 1997, ‘NewLeaf’ had higher total yield than ‘Superior’ at N rates

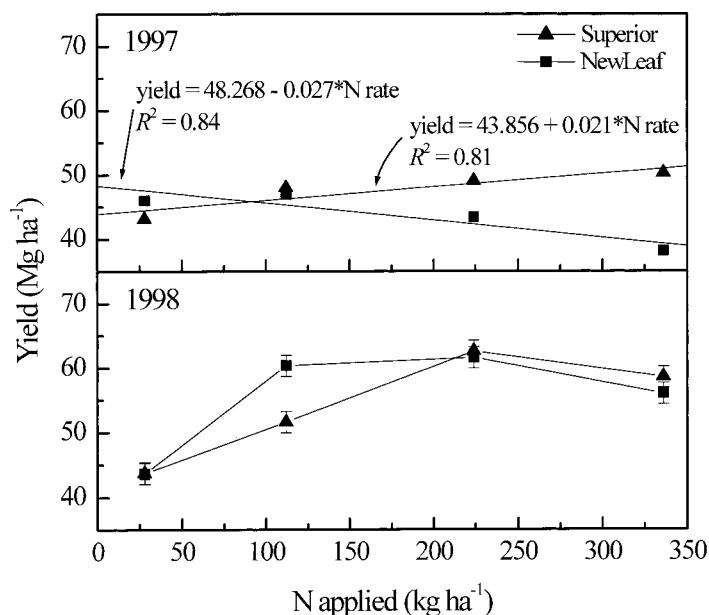


Fig. 1. Effect of N rate on total tuber yield of ‘Superior’ (▲) and ‘NewLeaf’ (■) in 1997 and 1998. Vertical bars = SE values of the mean.

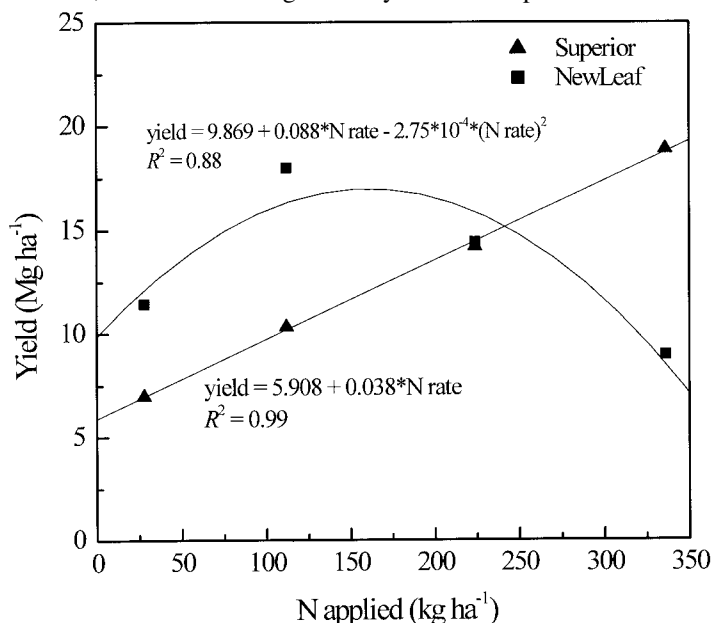


Fig. 2. Effect of N rate on large (>7.5 cm) tuber yield of ‘Superior’ (▲) and ‘NewLeaf’ (■) in 1997.

Table 2. Effect of N rate on biomass accumulation and partitioning in 'Superior' and 'NewLeaf' potatoes in 1997 and 1998.

Variable	Dry wt (Mg·ha ⁻¹)			Harvest index†
	Vine	Tuber	Total	
Year				
1997	2.3	8.5	10.8	0.79
1998	1.2	9.7	10.9	0.90
N rate (kg·ha ⁻¹)				
28	0.9	8.2	9.1	0.90
112	1.4	9.4	10.8	0.87
224	2.0	9.7	11.7	0.83
336	2.6	9.0	11.6	0.78
Clone				
Superior	1.1	8.9	10.0	0.89
NewLeaf	2.3	9.2	11.5	0.80
ANOVA	<i>P</i> > <i>F</i>			
Year	**	NS	NS	NS
N rate (N)	**	NS	NS	*
Linear (N _{lin})	**	NS	*	**
Quadratic (N _{quad})	NS	NS	NS	NS
Clone	*	NS	NS	**
Clone × N	*	NS	NS	NS
Clone × N _{lin}	**	NS	NS	*
Clone × N _{quad}	NS	NS	NS	NS
Year × N	NS	NS	NS	NS
Year × clone	NS	NS	NS	NS
Year × clone × N	NS	NS	NS	NS

†Harvest index = tuber dry weight/total dry weight

NS, *, ** Nonsignificant or significant at *P* = 0.05 or 0.01, respectively.

below 90 kg·ha⁻¹ but lower yield at higher rates of N. In 1998, the clone × N rate interaction was significant, but there was no consistent trend to the response of the two clones to N application. At the 112 kg·ha⁻¹ N rate, total yield was higher for 'NewLeaf' than for 'Superior' but yields were similar for the two clones at other N rates investigated.

Averaged across clones, the yield of large tubers (>7.5 cm), which are used mainly for chipping, was a quadratic function of N rate in both years. In 1997, however, there was a significant clone × N rate interaction for this yield category, with 'Superior' showing a linear and 'NewLeaf' a quadratic response to N application (Fig. 2). In 1997, yield in this category was higher for 'NewLeaf' than for 'Superior' at N rates below 242 kg·ha⁻¹ but higher with the standard clone at higher N rates. While the yield of large tubers was maximized at 160 kg·ha⁻¹ for the transgenic clone (maximum yield = 16.9 Mg·kg⁻¹) in 1997, that for 'Superior' did not reach a maximum within the range of N rates investigated. In 1998, mean large tuber yield was higher for 'NewLeaf' than for 'Superior' at equivalent N rates.

The yield of medium-sized tubers (5.1 to 7.5 cm), which are desirable for the fresh market, decreased linearly with increasing N rate in 1997 and was higher for 'Superior' than for 'NewLeaf' (Table 1). In 1998, the response differed for 'Superior' and 'NewLeaf', as indicated by the significant clone × N_{lin} rate interaction. Regression analysis, however, indicated no significant trend for either clone. The yields were higher for 'NewLeaf' with N at 112 kg·ha⁻¹, but lower for this clone with N at 224 and 336 kg·ha⁻¹.

The clone × N rate interaction in 1997 was significant for the yield of small tubers (<5.1 cm), but treatment main or interaction effects were not significant for this size category in 1998 (Table

1). In 1997, small tuber yield was a linear function of N rate for 'Superior' but a quadratic function of N rate for 'NewLeaf'.

Potato tuber specific gravity was higher for 'NewLeaf' than for 'Superior' in 1997 (Table 1). In 1998, specific gravity of 'NewLeaf' tubers showed a quadratic response to N rate (specific gravity = $1.073 + 4.77 \times 10^{-5} \times \text{N rate} - 1.45 \times 10^{-7} \times (\text{N rate})^2$, $R^2 = 0.99$) whereas that for 'Superior' showed a linear response (specific gravity = $1.079 - 3.08 \times 10^{-5} \times \text{N rate}$, $R^2 = 0.99$). Based on these regressions, specific gravity was higher for 'Superior' at N rates below 96 kg·ha⁻¹ but higher for 'NewLeaf' at higher rates. Specific gravities found in this study agree closely with those reported for 'Superior' (mean = 1.074) in the north central United States (Rieman, 1962).

The number of tubers per plant at harvest was 11.4% and 6.5% higher for 'Superior' than for 'NewLeaf' in 1997 and 1998, respectively (Table 1). In 1998, however, clonal differences for tuber number varied with N level, as indicated by the significant clone × N rate interaction, with the tuber number being higher for 'Superior' than for 'NewLeaf' at all N rates investigated except 112 kg·ha⁻¹. These results for tuber number do not parallel those for total tuber yield discussed above, and suggest that the differences in yield between the two clones cannot be adequately explained on the basis of the number of tubers per plant. Differences in tuber size appear to be more important than tubers per plant in explaining variation in fresh weight yield.

BIOMASS ACCUMULATION. Vine biomass increased linearly with N rate and was greater for 'NewLeaf' than for the standard clone at equivalent N rates. The linear functions, however, differed for the two clones, as indicated by the significant clone × N_{lin} rate interaction (Table 2). Comparison of regression coefficients for the clones revealed that the increase in vine biomass

Table 3. Effect of N rate on N uptake and N use efficiency in 'Superior' and 'NewLeaf' potatoes in 1997 and 1998.

Variable	N uptake (kg·ha ⁻¹)			Efficiency index			
	Vine	Tuber	Total	NHI ^z (g·g ⁻¹)	NUE ^y (%)	AUE ^x (g·g ⁻¹)	PUE ^w (g·g ⁻¹)
Year							
1997	37	113	150	0.77	42.5	9.5	22.3
1998	26	139	165	0.85	53.4	20.4	40.5
N rate (kg·ha ⁻¹)							
28	14	79	93	0.85	---	---	---
112	23	114	137	0.83	54.0	22.5	47.2
224	35	159	194	0.81	51.7	13.6	25.5
336	53	154	205	0.75	38.2	9.2	22.9
Clone							
Superior	21	135	155	0.87	47.9	11.7	24.4
NewLeaf	42	118	159	0.75	48.0	18.5	39.3
ANOVA				<i>P</i> > <i>F</i>			
Year	NS	NS	NS	NS	NS	NS	NS
N rate	*	NS	**	NS	NS	NS	NS
Linear (N _{lin})	**	*	**	NS	NS	NS	*
Quadratic (N _{quad})	NS	NS	NS	NS	NS	NS	NS
Clone	*	NS	NS	**	NS	NS	NS
N × Clone	*	NS	NS	NS	*	NS	NS
Clone × N _{lin}	**	*	NS	NS	NS	NS	NS
Clone × N _{quad}	NS	NS	NS	NS	*	NS	NS
Year × N	NS	*	NS	NS	NS	NS	NS
Year × clone	NS	NS	NS	NS	NS	NS	NS
Year × clone × rate	NS	NS	NS	**	NS	NS	NS

^zNitrogen harvest index = tuber N uptake/vines plus tuber N uptake.^yNitrogen uptake efficiency = ((total plant N – total plant N at 28 kg·ha⁻¹ N)/(N rate – 28)) × 100.^xAgronomic use efficiency = (total dry weight – total dry weight at 28 kg·ha⁻¹ N)/(N rate – 28).^wPhysiological use efficiency = (total dry weight – total dry weight at 28 kg·ha⁻¹ N)/(total N uptake – total N uptake at 28 kg·ha⁻¹ N).NS, *, ** Nonsignificant or significant at *P* = 0.05 or 0.01, respectively.

per incremental increase in N rate was significantly greater (*P* < 0.001) for 'NewLeaf' than for 'Superior'. Clone and N rate main effects and interactions were not significant for tuber and total biomass at the 5% probability level (Table 2). These results indicate that differences between the clones for tuber fresh weight were due to differences in moisture content. Average tuber moisture content was 82% for 'Superior' and 81% for 'NewLeaf'.

Harvest index (HI) decreased linearly with increasing N rate and, within the range of N rates applied, was higher for 'Superior' than for 'NewLeaf' at equivalent N rates. These results show that, compared to 'Superior', 'NewLeaf' preferentially partitioned a greater proportion of total dry weight to vines rather than to tubers. The lower HI for 'NewLeaf' may explain its lack of consistent yield advantage over 'Superior' despite its prolonged shoot growth and greater longevity of the canopy for light interception. It is recognized that high biomass production is determined by a leaf canopy that intercepts a high percentage of the incident radiation over a long part of the growing season (Van der Zaag, 1984) and that maximum yields require that the canopy continues to cover the soil late into the season (Ewing, 1997). These factors would favor 'NewLeaf' over 'Superior' with respect to tuber yield across all N rates. Additional leaf area is known to use absorbed energy, which could contribute to tuber growth (Allison et al., 1998). However, Ewing (1997) indicated that if partitioning of biomass to the tubers is too low, the rate of photosynthesis will be sink limited and tuber yield will suffer due to restricted total assimilate production and reduced delivery of

the assimilate to tubers. On the other hand, a high HI may limit leaf growth and hasten maturity.

Harvest indices obtained in this study are within the range of 60% to 90% reported for different potato cultivars in the literature (Wright and Stark, 1990, and references therein). Errebhi et al. (1999) reported a mean HI of 84% for 'Russet Norkotah,' 'Red Norland,' and 'Russet Burbank' potatoes that received 225 kg·ha⁻¹ of N. In separate studies, the cultivar 'Maris Piper' partitioned 70% (Oparka et al., 1987) and 80% (Millard et al., 1989) of total plant biomass to tubers when fertilized with 240 and 200 kg·ha⁻¹ of N, respectively.

NITROGEN ACCUMULATION AND N USE EFFICIENCY INDICES. Nitrogen uptake by vines increased linearly with N application and was greater for 'NewLeaf' than for the standard clone at equivalent N rate within the range investigated (Table 3). However, the clone × N_{lin} rate interaction was significant, indicating that the rate of increase in N accumulation in the vines per increment of N differed for the two clones, being greater for 'NewLeaf' than for the standard 'Superior.' The difference between the two clones with respect to N accumulation in vines reflects their difference in vine biomass response to N application.

Clone and N rate main effects and interactions were not significant for N accumulation in the tubers. Total N uptake did not differ significantly between 'Superior' and 'NewLeaf' but increased linearly and similarly for both clones as N rate increased.

The year × clone × N rate interaction was significant for NHI (Table 3). The effect of N rate on NHI was linear in 1997 but

Table 4. Effect of N rate and genotype on N uptake efficiency in 1997 and 1998.

Rate (kg·ha ⁻¹)	Nitrogen uptake efficiency (%) ^z	
	Superior	NewLeaf
112	49.4 bc ^y	58.5 a
224	56.7 ab	46.7 cd
336	37.7 d	38.7 d

^zNitrogen uptake efficiency = ((total plant N – total plant N at 28 kg·ha⁻¹ N)/(N rate – 28)) × 100.

^yNumbers in columns or rows followed by the same letter are not significantly different at $P = 0.05$.

quadratic in 1998 (data not presented). Within the range of N rates investigated, the index was higher in both years for ‘Superior’ than for ‘NewLeaf’ at equivalent N rates. However, there was a significant clone × N_{in} interaction for NHI in 1997, with the index decreasing more ($P < 0.05$) for ‘NewLeaf’ than for ‘Superior’. The lower NHI of ‘NewLeaf’ indicates that this clone retained more N in the foliage late in the growing season, especially at the higher N rates. This is consistent with the observed delayed senescence and more indeterminate growth habit of ‘NewLeaf’. Senescence commenced one to two weeks earlier for ‘Superior’ than for ‘NewLeaf’.

Treatment main effects were not significant for N uptake efficiency (NUE), but there was a significant clone × N rate interaction, suggesting that the difference in NUE between ‘Superior’ and ‘NewLeaf’ differed with N rate (Table 4). Nitrogen uptake efficiency was 16% higher for ‘NewLeaf’ than for ‘Superior’ at the low N rate (112 kg·ha⁻¹). However, the index was 18% higher for ‘Superior’ than for the transgenic clone at 224 kg·ha⁻¹ of N and similar for the clones at 336 kg·ha⁻¹ of N.

The NUE indices obtained in this study are within the range reported for other potato cultivars in previous studies. Joern and Vitosh (1995) reported NUE of 52% for the whole plant of ‘Russet Burbank’ at onset of senescence and 34% for tubers at harvest. Tyler et al. (1983) found NUE of 57% for ‘White Rose’ potato tubers at N rates up to 200 kg·ha⁻¹, but only 39% at N rates of 270 kg·ha⁻¹. Direct comparison between results from these studies and the present study, however, is complicated by the fact that calculations in the present study were based on starter-N treated plots rather than zero N control plots.

Agronomic (AUE) and physiological (PUE) use efficiency indices were not significantly affected by N rate or clone or their interactions, although there was tendency for the two indices to decrease linearly as N rate increased from 112 to 336 kg·ha⁻¹ (Table 3). These results indicate that ‘Superior’ and ‘NewLeaf’ produce similar total dry weight yields per unit of N supplied and per unit of N absorbed.

Vose (1990) identified cultivar or strain differences in plant nutrition in terms of differences in yield response, nutrient uptake, nutrient requirement, and tolerance to toxicities. Differential N uptake was demonstrated in the present study in terms of N recovery efficiency, with greater efficiency for ‘NewLeaf’ compared to ‘Superior’ in fertilizer N uptake at low N rates (<112 kg·ha⁻¹). This observation, together with the finding that yield for ‘NewLeaf’ was maximized at lower N levels in one of the two years, suggests that ‘NewLeaf’ may require lower N input than the standard clone in some years. These results also suggest that the greater efficiency of ‘NewLeaf’ compared to ‘Superior’ at low N rates in 1997 was associated with acquisition of N from the soil rather than utilization of absorbed N in metabolism.

Summary and conclusions

Tuber yields were maximized at lower N rates for ‘NewLeaf’ compared with the standard clone. ‘NewLeaf’ generally produced higher tuber yields at lower N rates, but lower yields at higher N rates compared to ‘Superior’. The transgenic clone always partitioned less dry weight to tubers than did ‘Superior’. The proportion of dry weight allocated to tubers (HI) decreased as N rate increased from 28 to 336 kg·ha⁻¹, but this effect was more pronounced for ‘NewLeaf’ than for ‘Superior’. These factors may explain the lack of consistent yield advantage of ‘NewLeaf’ over the standard clone. Recovery of fertilizer N (NUE) was higher for ‘NewLeaf’ than for ‘Superior’ at lower N rates whereas the production of DM per unit of applied or absorbed N did not differ significantly between the two clones. These results suggest that the better performance of ‘NewLeaf’ at low N levels in 1997 was associated with N acquisition. This work suggests that lower N inputs may be required in some years for ‘NewLeaf’ compared to its parent clone to optimize yield and illustrates the importance of genetic or epigenetic changes that may arise from genetic transformation of plants. Cultural evaluation of transformed potato selections is therefore essential to maximize performance in the field.

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