Evaluation of Tuber-Bearing *Solanum* Species for Nitrogen Use Efficiency and Biomass Partitioning

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ABSTRACT

Modern potato cultivars (Solanum tuberosum L.) require high rates of fertilizer nitrogen (N). This practice is costly and can pose a serious threat to surface and groundwater. Previous evaluation of wild potato germplasm demonstrated the existence of species capable of producing high total biomass under low N conditions, with the ability to make maximum use of added N. Therefore, a two-year field experiment was conducted in 1994 and 1995 to investigate the response of selected wild potato accessions and their hybrids with the haploid USW551 (USW) to low and high N environments. The haploid USW and cultivars Russet Burbank, Red Norland, and Russet Norkotah were also included in the study. Uniform propagules and seedlings from the various Solanum species were transplanted to a Hubbard loamy sand (Udic Haploboroll) at Becker, Minn. and were subjected to two N treatments: 0 and 225 kg N ha⁻¹. At harvest, total dry biomass of wild and hybrid potato germplasm was equal to or higher than that of the cultivars. However, cultivar biomass partitioning was 1% to roots, 15% to shoots, 0% to fruits, and 84% to tubers, whereas wild potato species partitioned 18% to roots plus nontuberized stolons, 52% to shoots, 23% to fruits, and only 7% to tubers. Hybrids were intermediate, allocating 9% of their biomass to roots plus nontuberized stolons, 39% to shoots, 14% to fruits, and 38% to tubers. Nitrogen use efficiencies for many of the species and crosses were comparable to that for Russet Burbank and greater than those for Red Norland and Russet Norkotah. Of the wild species tested, S. chacoense accessions had the highest biomass accumulation and N uptake efficiencies and may be the best source of germplasm for improving NUE in a potato breeding program.

INTRODUCTION

The potato (*Solanum tuberosum* L) is the fourth most important world food crop, after rice, wheat, and maize (Spooner and Bamberg, 1994). However, compared to these crops, cultivated forms of potato require higher inputs of pesticides and nitrogen (N) fertilizer. High N applications are costly and can pose a serious threat of nitrate accumulation in surface and groundwater (Vitosh and Jacobs, 1990; Errebhi *et al.*, 1998a).

According to Simmonds (1962), modern potato cultivars have been bred from a relatively narrow base. He reported that only a few stocks from the cultivated forms were introduced from South America into Europe. Despite their heterozygosity, the genetic base was reduced further in Europe by the selection of "short-day" forms, and still further limited by the blight epidemics in the 1840's. Moreover, exposure to high fertilizer rates in potato breeding and cultivar development programs resulted in cultivars that are more responsive to N and less capable of producing high yields under minimum or insufficient N (Rowe, 1969; Hawkes, 1990). The genetic base of cultivated potatoes narrowed, possibly limiting progress in crop selection. Thus, for potato improvement, there is a need to assess the resources available in the wild species.

Many breeding programs have been able to capitalize on the diversity of tuber-bearing *Solanum* species for potato improvement (Hawkes, 1977). However, there are no known reports of the use of wild potato germplasm for improvement of N use efficiency (NUE) in the development of cultivars.

Genotype differences in N uptake and utilization have been found in wheat (*Triticum aestivum* L.) (Cox *et al.*, 1985; Rooney and Leigh, 1993), corn (*Zea mays* L.) (Chevalier and Schrader, 1977), sorghum (*Sorghum bicolor* (L.) Moench) (Gardner *et al.*, 1994), potato (Kleinkopf *et al.*, 1981), and dry bean (*Phaseolus vulgaris* L.) (Haag *et al.*, 1978). Our previous work documented that some wild *Solanum* species with poor yield at low N were greatly improved at high N, while some were not (Errebhi *et al.*, 1998b). Other species with high biomass, even at low N, did

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not improve in the high N environment, while others showed a significant improvement. The latter ones were capable of producing high yields under low N conditions, with the ability to make maximum use of added N by producing even higher yields. Efficient, inefficient, and intermediate species were identified. The present research is an extension of concepts and calculations of nitrogen use efficiency (NUE) components reported by Errebhi *et al.* (1998b). In the present study, we also include a modified approach of N use efficiency developed by Siddiqi and Glass (1981) who suggested that for genotypic variability studies, the yield component should have a greater weighting in the calculation of efficiency of nutrient utilization.

This work represents the first step in the effort to use wild genetic resources to improve NUE in potato. Breeding selected wild accessions with the cultivated forms of potato may have the potential of improving N uptake or reducing crop N requirement, thus minimizing the potential for nitrate leaching and accumulation in groundwater, while maintaining acceptable yields. The primary objective of this research was to evaluate selected wild potato accessions and their hybrids from crosses with a *tuberosum* line for biomass production and partitioning, and for N use characteristics under low and high N.

MATERIALS AND METHODS

A two-year field experiment was conducted in 1994 and 1995 to investigate the response of selected wild potato accessions and their hybrids of crosses with USW551 (USW) to two N environments, 0 and 225 kg N ha⁻¹. USW is a haploid of the *S. tuberosum* cultivar Chippewa. The species and crosses used are presented in Table 1. The species selected were based on a an initial N use efficiency screening study by Errebhi *et al.*, (1998b). All hybrids were produced at the Potato Introduction Station at Sturgeon Bay, Wis. using standard protocols (Peloquin and Hougas, 1959). Also included in the study were the cultivars Russet Burbank, Red Norland and Russet Norkotah. In 1995, additional accessions within the same species were used to evaluate the variability in biomass accumulation within species.

Cultural Practices, Experimental Design, and Data Collection

In 1994, seedlings from the wild and hybrid species and propagules from USW and the cultivars were grown under greenhouse conditions. Forty-day old seedlings and propagules were transplanted to a loamy sand (Udic Haploboroll) at

| TABLE 1.—Wild | Solanum accessions, hybrids, and clonal geno- |
|---------------|---|
| types | evaluated in 1994 and 1995 for response to |
| fertil | izer N at Becker, Minnesota. |

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| 1994 | | 1995 | | | |
|--------------------------|--------------------------------|------------------------------|--------------------------------|--|--|
| Genotype | Plant Intro- duction # (PI) | Genotype | Plant Intro- duction # (PI) | | |
| chacoense(chc) | 197760 | chacoense(chc) | 197760 | | |
| chacoense(chc) | 320293 | chacoense(chc) | 320293 | | |
| fendleri(fen) | 498004 | chacoense(chc) | 275139 | | |
| microdontum(mcd) | 500041 | commersonii(cmm) | 243503 | | |
| megistacrolobum (mga) | 265873 | fendleri(fen) | 498004 | | |
| phureja(phu) | 225665 | fendleri(fen) | 275156 | | |
| phureja(phu) | 225679 | fendleri(fen) | 497998 | | |
| stoloniferum(sto) | 498057 | microdontum(mce) | 500041 | | |
| tarijense(tar) | 195206 | microdontum(mcd) | 218225 | | |
| USW x phureja | USW x 225679 | microdontum(mcd) | 473171 | | |
| USW x chacoense | USW x 197760 | megistacrolobum(mga) | 265873 | | |
| USW x chacoense | USW x 320293 | phureja(phu) | 225665 | | |
| USW x microdontum | nUSW x 500041 | phureja(phu) | 225679 | | |
| USW x phureja | USW x 225665 | stoloniferum(sto) | 498057 | | |
| USW 551 ^z | | tarijense(tar) | 195206 | | |
| Russet Burbank | | USW x phureja | USW x 225679 | | |
| Red Norland | | USW x chacoense | USW x 197760 | | |
| Russet Norkotah | | USW x chacoense | USW x 320293 | | |
| | | USW x microdontum | USW x 500041 | | |
| | | USW x phureja | $USW \ge 225665$ | | |
| | | USW x commersonii USW 551 | USW x 243503 | | |
| | | Russet Burbank | | | |
| | | Red Norland | | | |
| | | Russet Norkotah | | | |

²USW 551 (USW) is a haploid of the *S. tuberosum* cultivar Chippewa.

Becker, Minn. Transplants were placed on hills of rows that had a banded application of 253 kg ha⁻¹ of 0-6-35. All entries were subjected to two N treatments, 0 and 225 kg N ha⁻¹, replicated four times in a split-plot design, with N rates as the main plots and the species randomly assigned to the subplots. Residual soil nitrate-N (0-60 cm) ranged from 22 to 29 kg N ha⁻¹. Each single-row subplot consisted of 6 transplants spaced 30 cm apart, and bordered by Red Norland seed potato at each end. Red Norland subplot row ends were bordered by a Russet Burbank seed potato since the two cultivars have different tuber colors. Subplot rows were 91 cm apart.

Nitrogen, as ammonium nitrate, was applied on three occasions according to the following rates and schedule: plots received on 26, 32, and 40 days after transplanting (DAT) 69, 78, and 78 kg N ha⁻¹, respectively. Fertilizer N was surface applied to both sides of the hill, by use of a hand-

pushed N fertilizer applicator, and irrigated in. Roots, tubers, shoots, and fruits were harvested separately 105 DAT.

In 1995, protocols similar to those of 1994 were followed, except that Admire (imidacloprid, 1-[(6-chloro-3pyridimyl)methyl]-nitro-2-imidazolidinimine), a newly released insecticide, was used successfully for Colorado Potato Beetle (CPB) control. Also, main plots were replicated three times compared to four times in 1994. Main plots received 56, 78, and 91 kg N ha⁻¹ on 14, 28, and 42 DAT, respectively. Shoots, fruits, roots, and tubers were harvested 97 DAT. For both experiments, total dry weight was obtained by addition of the dry weights for the various plant parts.

Tissue Analyses and Calculation of the Various N Use Efficiency Indices

Plant parts were rinsed in water, oven dried at 70 C to a constant weight, and weighed for partial and total biomass production. Subsamples were ground for N analysis and N uptake determination. Plant tissue N concentration was determined by the conductimetric procedure of Carlson *et al.* (1990), following salicylic Kjeldahl nitrogen digestion (Assoc. Official Anal. Chemists, 1970).

For fertilized plots, nitrogen uptake efficiency was calculated as the ratio of PN/SN (plant N/soil N, where soil N was taken as applied fertilizer N), and N utilization efficiency was calculated as TDW/PN (total dry weight/plant N). The overall NUE, was designated as the product of uptake efficiency and utilization efficiency after Bock (1984). The overall equation is:

NUE = (PN/SN) x (TDW/PN) = (TDW/SN) or (Yield Efficiency) = (Uptake Efficiency) x (Utilization Efficiency).

An additional approach reported by Siddiqi and Glass (1981) was also used. They suggested that the efficiency of nutrient utilization be redefined so that the yield component has a greater weight than nutrient uptake. For nitrogen, the proposed efficiency of utilization, E, is redefined as the product of utilization efficiency (TDW/PN) and TDW, with the overall equation:

$E = (TDW/PN) \times TDW = TDW^2/PN$

where: E is efficiency of utilization, TDW is total dry weight, and PN is plant N content.

The advantage of the Siddiqi and Glass approach is that a ranking for E can be attained for nonfertilized control plots as well as N fertilized plots. For the other NUE approaches knowledge of soil applied N is required. For nonfertilized plots, uptake efficiency (PN/SN), and consequently NUE (PN/SN x TDW/PN) cannot be mathematically determined since soil applied N (SN) is equal to zero. Therefore, only utilization efficiency (TDW/PN) and Siddiqi & Glass's index E (TDW 2 /PN) are reported for the nonfertilized controls in this study.

Percent nitrogen recovery for the fertilized plots was estimated by the difference between N content of fertilized plants and N content of control plants, divided by the amount of N applied to the soil (Bock, 1984; May *et al.*, 1991).

Data Analyses

The general linear model procedure was used to evaluate genotype, nitrogen, and interaction effects. Means were separated using the LSD test set at 5%.

RESULTS AND DISCUSSION

Biomass Accumulation Partitioning for the Various Genotypes

In 1994, despite the use of repeated preventative measures, an uncontrollable outbreak of CPB occurred. The combined stress of 0 N fertilizer coupled with CPB damage was very severe on the cultivars and on USW. These entries yielded 133 to 406 g less (P<0.05) than the hybrids USW x 320293(chc), USW x 500041(mcd), USW x 225665(phu), and USW x 197760(chc) (Table 2). The wild parents PI 197760(chc) and 320293(chc) were particularly superior, surpassing the modern cultivars by as much as 11 times total biomass production. Addition of 225 kg N ha⁻¹ did not significantly alleviate the CPB severity, and the four hybrids produced more (P<0.05) total biomass than any of the cultivars. Total dry weight for USW was similar to those of the 3 cultivars at 0 N, but lower (P<0.05) than for Russet Norkotah at 225 kg N ha⁻¹.

The poor performance by the cultivars and USW could be attributed to their greater susceptibility to insect damage that significantly limited their growth, which in turn reduced yield, even though insects and diseases were treated by standard methods (Hutchison, 1991).

During 1995, when the more effective and recently released pesticide, Admire, was used to reduce insect pressure, differences in total yield under both N conditions show that Russet Burbank is clearly superior to some wild and hybrid genotypes. However, at 0 N, dry weights for PI 320293 (chc) and USW x 320293(chc) were not different from that of Russet Burbank (Table 4). At 225 kg N ha⁻¹, dry weight for USW x 320293(chc), PI 275139(chc), USW x 197760(chc), and USW x 243503(cmm) were not different (P<0.05) from Russet R

| TABLE 2.—Tuber and total dry weight for wild Solanum |
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| accessions, hybrids, and clonal genotypes under |
| low and high fertilizer N conditions at Becker, |
| Minnesota, 1994. |

| | | Dry w | veight (g/6 plants) | | | |
|------------------|---------|-------|---------------------------|--------|-------|--|
| C | kg N ha | -1 | 225 kg N ha ⁻¹ | | | |
| Genotype | Tuber | Total | Genotype | Tubers | Total | |
| 197760(chc) | 0 | 489 | 197760(chc) | 11 | 1021 | |
| USW x 320293 | 246 | 452 | USW x 320293 | 491 | 974 | |
| $USW \ge 500041$ | 189 | 376 | USW x 197760 | 170 | 777 | |
| USW x 225665 | 264 | 362 | $USW \ge 500041$ | 253 | 747 | |
| 320293(chc) | 0 | 359 | USW x 225679 | 405 | 721 | |
| 195206(tar) | 84 | 350 | 195206(tar) | 224 | 701 | |
| USW x 197760 | 95 | 328 | 320293(chc) | 2 | 659 | |
| USW x 225679 | 208 | 269 | USW x 225665 | 307 | 619 | |
| 498057(sto) | 0 | 264 | 500041(mcd) | 0 | 524 | |
| 500041(mcd) | 0 | 249 | Russet Norkotah | 374 | 419 | |
| Russet Norkotah | 182 | 195 | 498057(sto) | 7 | 390 | |
| 225679(phu) | 62 | 160 | Red Norland | 236 | 277 | |
| Red Norland | 136 | 157 | 498004(fen) | 0 | 196 | |
| 498004(fen) | 0 | 150 | 225679(phu) | 45 | 189 | |
| 225665(phu) | 63 | 120 | USW551(USW) | 136 | 165 | |
| USW551(USW) | 84 | 96 | 225665(phu) | 23 | 146 | |
| 265873(mga) | 0 | 94 | Russet Burbank | 97 | 127 | |
| Russet Burbank | 39 | 46 | 265873(mga) | 0 | 86 | |
| LSD(0.05) | 91 | 118 | LSD(0.05) | 158 | 250 | |

set Burbank. These PIs and hybrids had total biomass accumulation greater than that of Red Norland and Russet Norkotah. At both N regimes, dry weight for the haploid parent USW551 was similar to that of Red Norland and Russet Norkotah, but lower than that of Russet Burbank.

Of the species tested, accessions of *S. chacoense* and their hybrids consistently ranked highest in biomass production in this study as well as in the initial screening study (Errebhi *et al.*, 1998b). Other species such as *S. microdontum*, which ranked high in the initial screening study, were only moderate performers in the present study. Differences in climatic conditions among the years and CPB in 1994 may have played a role in the performance of *S. microdontum* accessions.

Averaged over the two growing seasons and across the both N rates, dry weight partitioning was closely associated with the level of domestication of the potato species (Figure 1). The cultivars partitioned dry weight production as follows: 84% to tubers, 1% to roots and nontuberized stolons, 15% to shoots, and < 0.1% to fruits, whereas wild potato species partitioned 18% to roots and nontuberized stolons,

52% to shoots, 23% to fruits, and only 7% to tubers. Hybrids were intermediate, allocating 9% of their biomass to roots and nontuberized stolons, 38% to tubers, 39% to shoots, and 14% to fruits. Caution should be used in interpretation of these results. While wild species and hybrids continued to accumulate biomass and N in the haulm, haulm growth of the cultivars stopped and partitioning of carbohydrates to tubers occurred. At harvest, most of cultivar roots had disintegrated. This difference in maturity was less advantageous for tuber production by the wild and hybrid species. Some of this difference is due to photoperiod adaptation. Poor tuber production by wild types is due to the fact that in their original habitat tuber initiation and growth is induced by short days and long nights; this is clearly the opposite of the present experimental conditions. Under these circumstances, breeding should be focused on selecting lines that can partition more carbohydrates to tubers.

Errebhi *et al.* (1998b) reported total biomass partitioning levels very close to these results, within +1% for cultivars and +3% for wild germplasm. Oparka *et al.* (1987) found that when the potato cultivar "Maris Piper" received 240 kg N ha⁻¹, it partitioned 70% of total dry weight to tubers and 30% to shoots; root weight was not determined. Millard *et al.* (1989) found that "Maris Piper", fertilized at the rate of 200 kg N ha⁻¹ partitioned 80% and 20% of dry weight to tubers and shoots, respectively.

Variability in Biomass Accumulation Among Accessions within Species

In 1995 a number of accessions within the same species were evaluated. For some Solanum species, differences among PIs in plant total dry weight depended on the level of soil N, while for others soil N fertility did not affect the significance of the difference (Table 3). At 0 kg N ha⁻¹, PI 320293(chc) produced more (P<0.05) biomass than PI 275139(chc). However, when accessions received fertilizer N at the rate of 225 kg N ha⁻¹, there was no difference (P>0.05) between biomass accumulated by these 2 PIs. For S. fendleri, PI 497998(fen) had significantly greater total dry weight than that of PI 498004(fen) at both N environments. Accession PI 275156(fen) had greater dry weight than PI 498004(fen) only when plots were supplied with N. For S. microdontum and S. phujera significant differences among accessions within each species for dry weight were not found at either N rate. The importance of variability among accessions within species is that it offers added

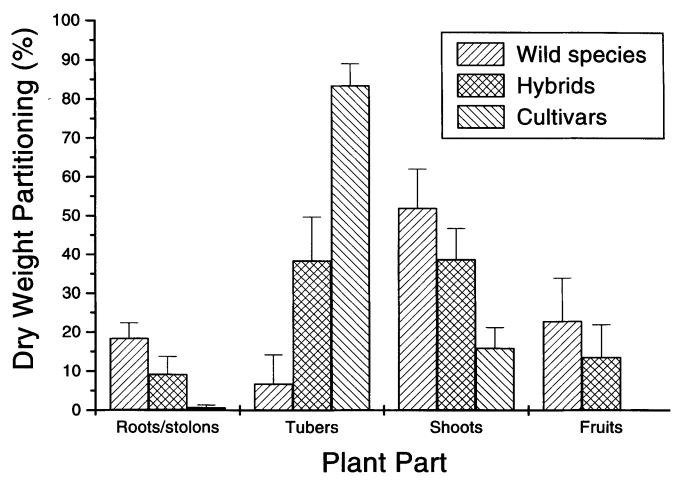


FIGURE 1.

Biomass partitioning among plant parts for potato cultivars, hybrids, and wild species averaged over nitrogen treatments and years. Vertical bars are standard error of the mean.

diversity to a plant breeding program. Among the three species studied, *S. fendleri* seems to be the most variable for total biomass accumulation; although overall biomass accumulation was significantly lower than accessions of *S. chacoense*.

N Uptake, Utilization, and Recovery Efficiencies

In 1994, at 0 N applied, N utilization efficiency did not differ (P>0.05) for USW x 320293(chc), USW x 500041(mcd), USW x 225679(phu), 195206 (tar), USW x 225665(phu), Russet Norkotah, and Red Norland (Table 4). However, when total dry weight was given due weight to obtain the index E = TDW 2 /PN as suggested by Siddiqi and Glass (1981), only 1997760(chc), USW x 320293(chc), and USW x 225665(phu)

made up the top group with E being statistically the same for all of them.

With N applied at the rate of 225 kg N ha⁻¹, all 5 hybrids as well as the 4 wild accessions 197760(chc), 195206(tar), 320293(chc), and 500041(mcd) had significantly greater N uptake efficiency than that of Russet Burbank and Red Norland. The hybrids USW x 320293(chc), USW x 197760(chc), USW x 225679(phu), the wild accessions PI 197760(chc), and PI 320293(chc) were statistically more efficient at N uptake than Russet Norkotah. These results may have been confounded with the effect of CPB to which there were different degrees of susceptibility among the genotypes. Utilization efficiency of N, a measure of the amount of dry matter produced per unit N absorbed, was not linearly related to uptake efficiency. For example, USW and Norland were significantly

TABLE 3.—Tuber and total dry weight for wild Solanum accessions, hybrids, and clonal genotypes under low and high fertilizer N conditions at Becker, Minnesota, 1995.

| | | Dry w | veight (g/6 plants) | | | |
|------------------|--------------|-------|---------------------|---------------------------|--------------|--|
| 0 | kg N ha | -1 | 22 | 225 kg N ha ⁻¹ | | |
| Genotype | <u>Tuber</u> | Total | <u>Genotype</u> | Tubers | <u>Total</u> | |
| Russet Burbank | 475 | 640 | Russet Burbank | 769 | 1151 | |
| 320293(chc) | 0 | 569 | USW x 320293 | 365 | 1137 | |
| USW x 320293 | 160 | 569 | 275139(chc) | 0 | 970 | |
| USW x 243503 | 40 | 464 | USW x 197760 | 142 | 938 | |
| 197760(chc) | 12 | 464 | USW x 243503 | 111 | 935 | |
| USW x 197760 | 120 | 442 | 197760(chc) | 3 | 901 | |
| 275139(chc) | 15 | 415 | 320293(chc) | 0 | 894 | |
| 498057(sto) | 9 | 383 | USW x 500041 | 45 | 590 | |
| Russet Norkotah | 306 | 333 | 195206(tar) | 109 | 586 | |
| $USW \ge 500041$ | 121 | 323 | 218225(mcd) | 8 | 562 | |
| 497998(fen) | 0 | 317 | 498057(sto) | 7 | 545 | |
| USW551(USW) | 234 | 315 | USW x 225665 | 163 | 533 | |
| 243503(cmm) | 19 | 292 | 275156(fen) | 0 | 487 | |
| USW x 225665 | 141 | 290 | USW551(USW) | 295 | 475 | |
| 195206(tar) | 0 | 284 | 243503(cmm) | 15 | 473 | |
| Red Norland | 238 | 271 | Russet Norkotah | 423 | 450 | |
| 218225(mcd) | 0 | 257 | 500041(mcd) | 4 | 432 | |
| 473171(mcd) | 5 | 240 | 497998(fen) | 3 | 424 | |
| 275156(fen) | 0 | 226 | USW x 225679 | 228 | 416 | |
| USW x 225679 | 97 | 207 | 473171(mcd) | 14 | 405 | |
| 500041(mcd) | 0 | 162 | Red Norland | 303 | 318 | |
| 498004(fen) | 0 | 159 | 498004(fen) | 0 | 171 | |
| 225665(phu) | 42 | 88 | 225679(phu) | 7 | 102 | |
| 225679(phu) | 8 | 67 | 265873(mga) | 5 | 88 | |
| 265873(mga) | 0 | 65 | 225665(phu) | 14 | 84 | |
| LSD(0.05) | 63 | 112 | LSD(0.05) | 94 | 232 | |

less efficient than PI 320293(chc) in N uptake but were more efficient in N utilization. These observations argue against the singular use of either uptake efficiency or utilization efficiency of N to distinguish genotypes. Moll et al. (1982) and Siddiqi and Glass (1981) recommended the development of genotypes with both high N uptake and utilization efficiency. Based on the index E of Siddiqi and Glass (1981), the genotypes 197760 (chc) and USW x 320293(chc) had the highest performance, followed by, but significantly different from USW x 500041(mcd), USW x 197760(chc), and 195206 (tar). NUE combines the effect of N uptake and utilization, but does not provide information about plant N content, since PN is mathematically omitted from the equation. In this study the ranking of genotypes using NUE was similar to that using E. However, E is more useful when evaluating efficiencies when fertilizer N is not applied.

Nitrogen recovery was relatively high for most wild and hybrid genotypes, but low for the cultivars and for USW. The overall recoveries are relatively low compared to published data (Millard *et al.*, 1989), and may be due in part to the CPB damage.

In 1995, insect feeding was effectively suppressed. At 0 N applied, 195206 (tar) had the highest N utilization efficiency (P<0.05), followed by Russet Burbank, USW x 243503(cmm), Russet Norkotah, and Red Norland. When utilization efficiency was multiplied by TDW (total dry weight) to obtain E, genotype ranking changed with Russet Burbank being at the top, preceding USW x 320293(chc), 320293 (chc), and USW x 243503(cmm). The E indices for these genotypes were higher than those for 195206(tar), Russet Norkotah, and Red Norland.

At 225 kg N ha⁻¹, there was no difference (P>0.05) for N uptake efficiency between Russet Burbank and the hybrids USW x 320293(chc), USW x 197760(chc), and USW x 500041(mcd) (Table 6). Russet Norkotah and Red Norland, however had lower N uptake efficiency compared to the same hybrids. Uptake or utilization efficiency alone cannot be used to separate potato genotypes. As an example, N uptake efficiencies for Norland and Norkotah were significantly lower than those of PI 218225(mcd) and USW x 500041(mcd), yet comparative N utilization efficiencies were reversed. An important point worth noting is that a high utilization efficiency is not sufficient if N uptake is very low. There is a genetic limit to how much biomass a plant can produce if N absorbed is low. The E suggested by Siddigi and Glass (1981) overcomes this problem by giving a higher weight to biomass production.

Russet Burbank, all 3 accessions of *S. chacoense*, USW x 320293(chc), USW x 197760(chc), USW x 243503(cmm), USW x 500041(mcd), and USW x 225665(phu) had higher NUE values than USW, Russet Norkotah, USW x 225679(phu), and Red Norland. As with biomass accumulation, *S. chacoense* hybrids were consistently most efficient in NUE. The fact that some wild and hybrid genotypes, are comparable to Russet Burbank in NUE is important since they may be useful in breeding programs for improving NUE in the cultivars. It may be worth the effort to develop and improve them since they have higher NUE values than Red Norland and Russet Norkotah.

Based on the index E, Russet Burbank, USW x 243503(cmm), and USW x 320293(chc) form a distinguished cluster that is superior to the remaining genotypes. USW, Russet Norkotah, and Red Norland performed relatively

| Genotype | 0 kg N ha ⁻¹ | | 225 kg N ha ⁻¹ | | | | | |
|-----------------|--|-------------------------------------|-------------------------------------|--|---|---------------------------------------|-----------------------------------|--|
| | N Utilization Efficiency ² | E ⁵ Siddiqi and Glass | N Uptake Efficiency ¹ | N Utilization Efficiency ² | N Use Efficiency ³ (NUE) | E ⁵ , Siddiqi and Glass | Nitrogen Recovery ⁴ | |
| | g g ⁻¹ | g | % | g g-1 | g g-1 | g | | |
| 197760(chc) | 71 | 35 | 35 | 72 | 25 | 73 | 18 | |
| USW x 320293 | 91 | 41 | 33 | 72 | 24 | 71 | 21 | |
| USW x 197760 | 79 | 24 | 28 | 68 | 19 | 52 | 17 | |
| USW x 500041 | 83 | 31 | 25 | 75 | 18 | 56 | 13 | |
| USW x 225679 | 82 | 22 | 27 | 67 | 18 | 48 | 19 | |
| 195206(tar) | 85 | 28 | 23 | 75 | 17 | 52 | 13 | |
| 320293(chc) | 61 | 22 | 29 | 57 | 16 | 37 | 14 | |
| USW x 225665 | 89 | 32 | 22 | 69 | 15 | 43 | 12 | |
| 500041(mcd) | 70 | 18 | 20 | 65 | 13 | 34 | 11 | |
| Russet Norkotah | 83 | 16 | 17 | 62 | 10 | 26 | 11 | |
| 498057(sto) | 64 | 17 | 18 | 54 | 10 | 21 | 8 | |
| Red Norland | 86 | 14 | 10 | 70 | 7 | 19 | 5 | |
| 498004(fen) | 62 | 9 | 10 | 50 | 5 | 10 | 4 | |
| 225679(phu) | 72 | 12 | 8 | 63 | 5 | 12 | 2 | |
| USW551(USW) | 70 | 7 | 6 | 71 | 4 | 12 | 2 | |
| 225665(phu) | 61 | 7 | 6 | 56 | 4 | 8 | 2 | |
| Russet Burbank | 74 | 3 | 4 | 72 | 3 | 9 | 3 | |
| 265873(mga) | 46 | 4 | 6 | 37 | 2 | 3 | 1 | |
| LSD (0.05) | 10 | 9 | 9 | 12 | 1 | 10 | 5 | |

TABLE 4.—Various indexes of N use efficiency estimates for wild Solanum accessions, hybrids, and clonal genotypes under low and high fertilizer N conditions at Becker, Minnesota, 1994[&].

&Ranking of species was based on Nitrogen Use Efficiency (NUE).

¹N Uptake Efficiency is the ratio of "total plant N/soil applied N".

²N Utilization Efficiency is the ratio of "total dry weight/ total plant N.

 3 N Use Efficiency (NUE) is the product of "uptake efficiency x utilization efficiency"; it reduces to total dry weight/soil applied N.

⁴Nitrogen Recovery in percent is estimated by the difference between total plant N content of fertilized and control plots divided by the amount of N applied to the soil.

⁵E, after Siddiqi and Glass (1981); E = TDW²/PN (total dry weight x total dry weight/total plant N).

poorly and fell below many wild and hybrid species. With few exceptions, NUE and E gave similar rankings of the genotypes. Either would be useful as a screening tool for N use characteristics in a breeding program when fertilizer N is applied.

In general, N recovery values found in 1995 were slightly higher than those for 1994, but were still lower than values reported in the literature (Errebhi *et al.*, 1998a and b; Millard *et al.*, 1989). The reason for the apparent low recoveries could in part be due to the late planting date (June), early harvest date (105 days after transplanting) and greater uptake of N by nonfertilized plants in this study.

CONCLUSIONS

The evaluation of accessions within species showed that for several *Solanum* species there is some significant vari-

ability for total biomass accumulation under low and high N regimes. Thus, it may be advantageous to screen collections of accessions for degree of diversity. Generally, the modern cultivars partitioned about 1 % of their biomass to roots, 84% to tubers, and 15% to shoots, whereas the wild accessions allocated 20% to roots, plus nontuberized stolons only 5% to tubers, 49% to shoots, and 26% to fruits. Hybrids partitioned 10% to roots, plus nontuberized stolons 38% to tubers, 37% to shoots, and 15% to fruits. Under a stress environment (i.e. insect pressure), the cultivated potatoes had very poor biomass production as opposed to the wild and hybrid species. Under normal environmental conditions, tuber production of the hybrids was lower than in modern cultivars. However, total biomass produced by the hybrids was similar, and in some instances was higher, compared to the cultivars tested. If backcrossing can improve tuber yield by resulting in the partitioning of more carbohydrates to tubers, the hybrids

| Genotype | 0 kg N ha ⁻¹ | | 225 kg N ha ⁻¹ | | | | | |
|----------------|--|-------------------------------------|-------------------------------------|--|---|---------------------------------------|-----------------------------------|--|
| | N Utilization Efficiency ² | E ⁵ Siddiqi and Glass | N Uptake Efficiency ¹ | N Utilization Efficiency ² | N Use Efficiency ³ (NUE) | E ⁵ , Siddiqi and Glass | Nitrogen Recovery ⁴ | |
| | g g ⁻¹ | g | % | g g ⁻¹ | g g ⁻¹ | g | % | |
| Russet Burbank | 95 | 61 | 34 | 83 | 28 | 95 | 18 | |
| USW x 320293 | 76 | 43 | 37 | 77 | 28 | 87 | 18 | |
| 275139(chc) | 68 | 28 | 34 | 71 | 24 | 69 | 19 | |
| USW x 197760 | 75 | 33 | 33 | 71 | 23 | 66 | 18 | |
| USW x 243503 | 83 | 39 | 24 | 96 | 23 | 90 | 10 | |
| 197760(chc) | 68 | 31 | 34 | 65 | 22 | 58 | 17 | |
| 320293(chc) | 71 | 41 | 32 | 70 | 22 | 63 | 12 | |
| USW x 500041 | 68 | 22 | 27 | 54 | 15 | 32 | 15 | |
| 195206(tar) | 107 | 30 | 24 | 61 | 15 | 36 | 17 | |
| 218225(mcd) | 55 | 14 | 26 | 54 | 14 | 30 | 15 | |
| 498057(sto) | 68 | 26 | 23 | 58 | 13 | 31 | 9 | |
| USW x 225665 | 64 | 19 | 22 | 59 | 13 | 31 | 11 | |
| 275156(fen) | 66 | 15 | 21 | 59 | 12 | 29 | 12 | |
| USW551(USW | 58 | 18 | 20 | 59 | 12 | 28 | 6 | |
| 243503(cmm) | 63 | 18 | 20 | 57 | 12 | 27 | 9 | |
| Russet Nokotah | 82 | 27 | 15 | 75 | 11 | 34 | 5 | |
| 500041(mcd) | 60 | 10 | 20 | 54 | 11 | 23 | 13 | |
| 497998(fen) | 57 | 18 | 21 | 51 | 11 | 22 | 7 | |
| USW x 225679 | 59 | 12 | 19 | 53 | 10 | 22 | 11 | |
| 473171(mcd) | 72 | 17 | 19 | 53 | 10 | 21 | 11 | |
| Red Norland | 80 | 22 | 7 | 73 | 8 | 16 | 4 | |
| 498004(fen) | 51 | 8 | 9 | 47 | 4 | 8 | 1 | |
| 225679(phu) | 54 | 4 | 5 | 53 | 3 | 5 | 2 | |
| 265873(mga) | 35 | 2 | 6 | 39 | 2 | 4 | 1 | |
| 225665(phu) | 50 | 4 | 5 | 47 | 2 | 4 | 0 | |
| LSD (0.05) | 9 | 11 | 10 | 11 | 1 | 13 | 6 | |

TABLE 4.—Various indexes of N use efficiency estimates for wild Solanum accessions, hybrids, and clonal genotypes under low and high fertilizer N conditions at Becker, Minnesota, $1995^{\&}$.

[&]Ranking of species was based on Nitrogen Use Efficiency (NUE).

¹N Uptake Efficiency is the ratio of "total plant N/soil applied N".

 2 N Utilization Efficiency is the ratio of "total dry weight/ total plant N.

³N Use Efficiency (NUE) is the product of "uptake efficiency x utilization efficiency"; it reduces to total dry weight/soil applied N.

⁴Nitrogen Recovery in percent is estimated by the difference between total plant N content of fertilized and control plots divided by the amount of N applied to the soil. ⁵E, after Siddiqi and Glass (1981); E = TDW²/PN (total dry weight x total dry weight/total plant N).

may hold promise, environmentally and economically. For many wild types and their hybrids with USW, N uptake efficiencies were as good as that of Russet Burbank, but significantly above those of Red Norland and Russet Norkotah. Accessions of S. *chacoense* and their hybrids consistently had the highest biomass accumulation and N uptake efficiencies compared to the other species and hybrids tested and may be the best wild species to use in a breeding program for improving NUE. These results show that wild potato germplasm may be valuable for breeding purposes as well as for improving N use efficiency in the potato crop at both low and high N growing conditions.

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