Critical Nitrogen Curve and Nitrogen Nutrition Index for Potato in Eastern Canada

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ABSTRACT

Plant diagnostic methods of N deficiency should be based on the definition of a critical N concentration, that is the minimal N concentration required to achieve maximum growth. The critical N concentration (N_c) of potato was determined from six on-farm field trials in which two cultivars (Russet Burbank and Shepody) were grown under three or four N rates with and without irrigation. Dry matter yield and N concentration of shoots and tubers were determined approximately weekly during the growing season. The N_c was determined by selecting data points for which the highest total biomass comprised of shoots and tubers was obtained, and by expressing N concentration (N) as a function of total biomass (W). The N nutrition index (NNI), calculated as the ratio between measured N concentration and predicted N_c during the growing season, was then related to the relative yield measured at harvest. Under non-limiting water conditions, the allometric relationship between N_c and total biomass for Russet Burbank ($N_c = 4.57W^{-0.42}$) was different from that of Shepody ($N_c = 5.04W^{-0.42}$), indicating that Shepody had a greater N concentration than Russet Burbank. The N concentration of Shepody was also greater than that of Russet Burbank under limiting water conditions. These results suggest that there is intra-specific variability in potato for the relationship between N concentration and biomass. The NNI ranged from 0.50 to 1.4. The relationship between relative yield and NNI expressed by a quadratic function accounted for a greater proportion of the variability with irrigation (71% for Russet Burbank and 82% for Shepody) than without irrigation (65% for Russet Burbank and 32% for Shepody). Our results suggest that the NNI could be a reliable indicator of the level of N stress during the growing season, particularly under non-deficient water conditions.

RESUMEN

Los métodos de fitodiagnóstico de deficiencia de N deben basarse en la definición de una concentración crítica de N, es decir, la concentración mínima requerida para alcanzar el crecimiento máximo. La concentración crítica de N (N_c) en la papa fue determinada en seis campos experimentales de agricultores, en los cuales crecieron dos cultivares (Russet Burbank y Shepody) bajo tres o cuatro niveles de N con y sin irrigación. Los rendimientos en materia seca y la concentración de N en las yemas y tubérculos se determinaron aproximadamente cada semana durante la temporada de crecimiento. La N_c se determinó seleccionando los datos por los cuales se obtuvo la biomasa total más alta, que incluía yemas y tubérculos, y expresando la concentración de N (N) como una función de la biomasa total (W). El índice de nutrición de N (NNI, en inglés) calculado como la relación entre la concentración medida de N y la N_c pronosticada durante la temporada de crecimiento, se relacionó entonces con el rendimiento relativo medido y cosechado. Bajo condiciones de abundancia de agua, la relación alométrica entre N_c y la biomasa total para Russet Burbank ($N_c = 4.57W^{-0.42}$) fue diferente que para Shepody ($N_c = 5.04W^{-0.42}$), indicativo de que Shepody tiene una mayor

concentración de N que Russet Burbank. La concentración de N de Shepody fue también mayor que la de Russet Burbank bajo condiciones limitadas de agua. Estos resultados sugieren que hay una variabilidad intraespecífica en la papa en la relación entre la concentración de N y la biomasa. El índice de nutrición de N (NNI) osciló entre 0.50 a 1.4. La relación entre el rendimiento relativo y el NNI, se expresó por una función cuadrática contabilizada por una mayor proporción de la variabilidad con irrigación (71% para Russet Burbank y 82% para Shepody) que sin irrigación (65% para Russet Burbank y 32% para Shepody). Nuestros resultados sugieren que el NNI podría ser un indicador confiable del nivel de estrés de N durante la temporada de crecimiento, particularmente bajo condiciones no deficientes de agua.

INTRODUCTION

Plant-based diagnostic methods of N deficiency can be used to improve the efficiency of N utilization and reduce the risks of N losses to the environment. These diagnostic methods should be based on the definition of a critical N concentration, that is the minimal N concentration required to achieve maximum crop growth. The concept of a critical N concentration based on whole plants was first developed by Lemaire and Salette (1984) for tall fescue (*Festuca arundinacea* Schreb.), and was later tested for winter wheat (*Triticum aestivum* ssp. *Vulgare*) (Justes *et al.* 1994), winter rape (*Brassica napus* L.) (Colnenne *et al.* 1998) and potato *(Solanum tuberosum* L.) (Greenwood *et al.* 1990; Duchenne *et al.* 1997).

The critical N concentration (N_c) is represented by an allometric function:

$$N_c = aW^{-b} \quad (1)$$

where W is the shoot biomass expressed in t DM ha^{-1}, N_c is the total N concentration in shoots, and a and b are parameters to be estimated (Bélanger and Gastal, 2000). The parameter a represents the N concentration with 1 t DM ha^{-1}, and the parameter b represents the coefficient of dilution which describes the pattern of decrease of N concentration with increasing shoot biomass. In potato, the values of the parameters a and b are estimated using the combined biomass of shoots and tubers, and the N concentration of this combined biomass. Greenwood *et al.* (1990) using data from Scotland and the Netherlands reported values of a = 5.36 and b = 0.46 whereas Duchenne *et al.* (1997) in France obtained values of a = 5.21 and b = 0.56. The

coefficient of dilution reported in those two European studies differ by more than 15%. Furthermore, the parameters were obtained under pedo-climatic conditions and with cultivars different from those in eastern Canada.

Our objective was to determine the critical N curve for potato under the growing conditions and with cultivars widely grown in eastern Canada, and to assess the possibility of using this critical N curve based on whole plants to estimate the level of N nutrition of potato grown under different N rates.

MATERIALS AND METHODS

The measurements used to estimate the critical N curve and the N nutrition index (NNI) were taken at two sites in each of three years as part of a larger study conducted at four on-farm sites in each of three years, 1995 to 1997, in the upper St-John River Valley of New Brunswick, Canada. The sites for the larger study are referred to as S1 to S4 in 1995, S5 to S8 in 1996, and S9 to S12 in 1997 (Bélanger *et al.* 2000). At each site, the experiment consisted of two large blocks (irrigated and non-irrigated). Within each block, a split plot arrangement of the experimental treatments was used with cultivars as main plots and N fertilization rates as sub-plots with four replications. Two potato *(Solanum tuberosum* L.) cultivars were used with a row spacing of 0.75 m and in-row spacings of 0.30 m for Shepody and 0.46 m for Russet Burbank. Nitrogen as ammonium nitrate was placed in a band 2 cm to the side and 2 cm below the seedpiece at planting with a modified Wintersteiger plot planter adapted for potato at 0, 50, 100, 150, 200, and 250 kg N ha^{-1}. Individual plots consisted of six rows each 7.6 m in length. There were 1.5 m between plots within a block and 24.3 m between the irrigated and non-irrigated blocks. Phosphorus (165 kg P_2O_5 ha^{-1}) and potassium (165 kg K_2O ha^{-1}) were surface broadcast prior to planting as a 0-15-15 blend.

Irrigation applications were scheduled using the Wisdom© computer software program (IPM Software, Madison, WI). The program utilizes a water budget approach to schedule irrigation (Curwen and Massie 1984). Water was applied when soil moisture reserves were reduced to 65% of the soil water holding capacity. Water was applied at a rate of 0.68 cm h^{-1} with a portable overhead irrigation system. The seasonal water balance ranged from 0 to -218 mm (Bélanger *et al.* 2000). The experimental sites and other experimental procedures were described by Bélanger *et al.* (2000).

At two of the sites in each of three years (S1 and S2 in 1995; S5 and S7 in 1996; S11 and S12 in 1997), the biomass of shoots

(excluding stolons) and tubers was measured on ten sampling dates at approximately weekly intervals starting around 30 days after planting until early September. Two plants per plot were sampled on the first two sampling dates, and one plant per plot was harvested on the last eight sampling dates. The plants were sampled on the outside rows with one plant left between two sampling dates. In 1995, sampling was done on plots having received 0, 50, and 250 kg N ha^{-1}. In 1996 and 1997, the sampling was conducted on plots having received 0, 50, 100, and 250 kg N ha^{-1}. The shoots were dried at 70 C for determination of dry matter (DM) concentration. We assumed a tuber DM concentration of 20% (MacKerron and Waister 1985). The average specific gravity at harvest (4 October to 19 October) was 1.087. Total biomass was calculated by adding shoot and tuber dry weight. Tubers were sliced in small pieces and dried at 70 C. The dried samples of shoots and tubers were ground to pass a 1-mm screen and stored prior to laboratory analyses. The N concentration in shoots and tubers was determined by dry combustion using a LECO CNS 1000 analyser (LECO Corporation, St. Joseph, MI, USA). The total biomass N concentration was calculated by adding the N contents of shoots and tubers and dividing by total biomass.

The critical N concentration, the minimum N concentration required to achieve maximum growth, was defined as a function of the total biomass using an allometric function described in equation (1). The data used to establish the model of critical N concentration were selected using the approach described by Greenwood et al. (1990). For each site, irrigation treatment and cultivar, the highest total biomass obtained with any rate of fertilizer at each sampling date, and the corresponding N concentration were identified and included. Where the highest biomass was obtained with each of two or more rates of fertilizer, the data obtained with the lower rate were selected. Only data with biomass ranging from 1 to 6 t DM ha^{-1} were selected because N concentration is assumed constant for total biomass less than 1 t DM ha^{-1} (Lemaire and Gastal 1997) and to avoid including measurements with senescence towards the end of the growth cycle. The data used came from sampling between 28 July and 14 August at S1, 17 July and 10 August at S2, 23 July and 6 August at S5, 23 July and 7 August at S7, 28 July and 20 August at S11, and 23 July and 11 August at S12. Since there was no effect of irrigation in 1996 (Bélanger et al. 2000), the data obtained without irrigation were combined with those obtained with irrigation. The fitted parameters a and b were estimated by the FIT routine of GENSTAT 5 (Genstat 5 Committee 1993) after a logarithmic transformation of the data.

A linear parallel curve analysis with grouped data was used on the transformed data to determine if the response curves (N concentration, N uptake) to an explanatory variable (total biomass) differed among cultivars. Using the FIT routine of Genstat 5 (Genstat 5 Committee 1993), the response curves were described by the following model:

$$Y = k + lX \quad (2)$$

where Y is the response variable, X is the explanatory variable, and l and k are estimated variables. The procedure initially calculated one equation (for the two cultivars) to describe the average response to the explanatory variable. On the next step, separate k parameters were estimated for each cultivar to determine the vertical separation between parallel lines (i.e., response curves). The next step estimated separate linear parameters l for the slope (i.e., the linear portion of the cultivars by the explanatory variable interaction). At each step, the statistical significance was calculated for the change in the sum of squares explained by the addition of another parameter to the model.

The NNI at each sampling date was calculated as the ratio between measured N concentration and predicted N_c, an approach previously used on potato (Duchenne et al. 1997) and other crops (Bélanger et al. 1992; Justes et al. 1997a; Colnenne et al. 1998). The predicted N_c was calculated with equation (1) using the fitted parameters for Shepody and Russet Burbank. The relative yield was calculated as the ratio of the final harvest tuber yield obtained at a given rate of N application and the highest tuber yield among the six N rates. Final harvest tuber yields were presented in a previous paper (Bélanger et al. 2000). The relative yield was then expressed as a function of NNI (Bélanger et al. 1992; Duchenne et al. 1997), and quadratic functions were estimated by the least squares method (SigmaPlot 4.0, SPSS Inc., Chicago, IL).

RESULTS AND DISCUSSION

Determination of Critical N Concentration

Total biomass N concentration decreased with increases in biomass under non-limiting water conditions obtained with irrigation in 1995 and 1997, and with and without irrigation in 1996 (Figure 1) and under limiting water conditions obtained without irrigation in 1995 and 1997 (Figure 2). The decline in N concentration with increasing biomass is attributed to a decrease in the fraction of the total amount of N in plant which is associated with photosynthesis and a concomitant increase in the N fraction in structural tissue and storage constituents (Caloin and Yu
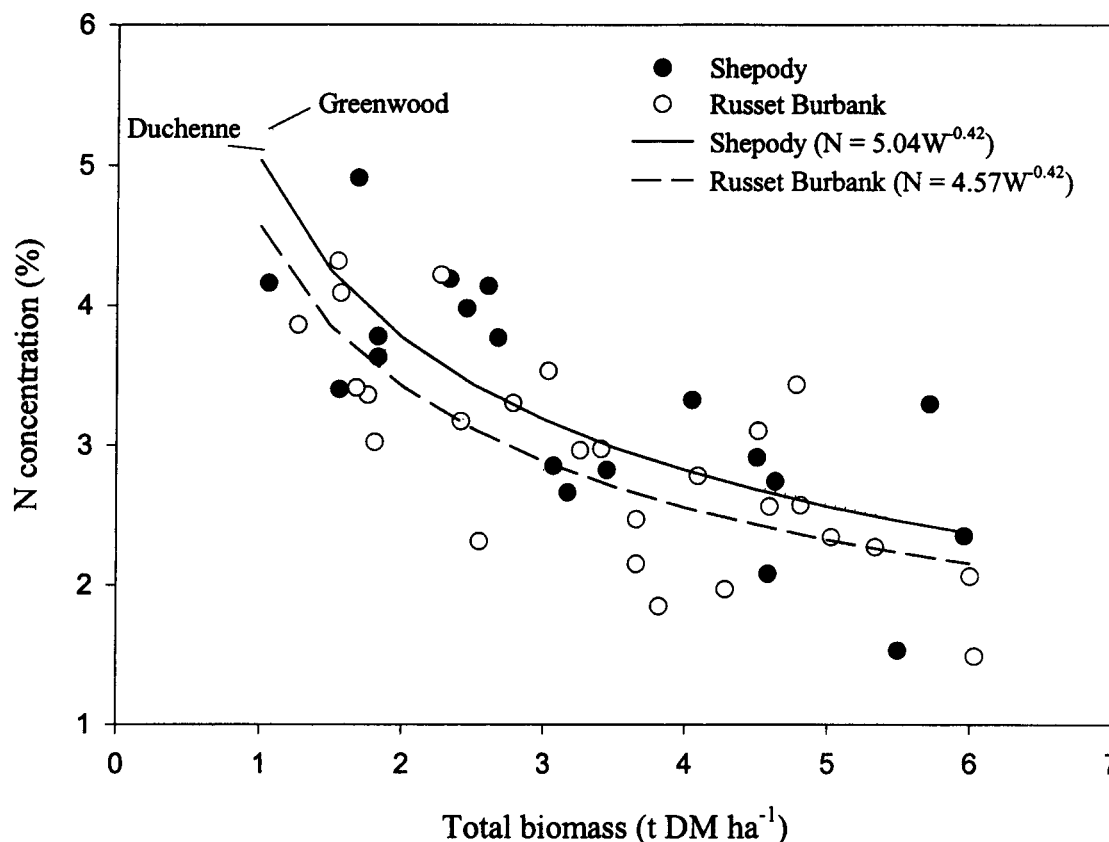
FIGURE 1.

Nitrogen concentration (N) as a function of total biomass (W) for two cultivars under non-limiting water conditions. Data points correspond to maximum total biomass for each site and cultivar. The models of Duchenne (1997) (N = 5.21W$^{-0.56}$) and Greenwood et al. (1990) (N = 5.36W$^{-0.46}$) are presented by dotted lines.

1984; Lemaire and Gastal 1997; Bélanger and Gastal 2000).

The self-thinning rule (Hardwick 1987) based on the principle that there is a strong link between N in plant and its metabolic activities suggests that the coefficient of dilution (b) should have a value of 0.34 (Greenwood et al. 1990). When considering only the potato data, Greenwood et al. (1990) found that the coefficient of dilution (b = 0.46) was significantly greater than the theoretical value of 0.34; whereas those of tall fescue, alfalfa (*Medicago sativa* L.) and wheat were similar to the theoretical value. Our coefficient of dilution for the two cultivars (b = 0.42) is close to that proposed by Greenwood et al. (1990), and confirms that the coefficient of dilution of potato is greater than the theoretical value of 0.34. Greenwood et al. (1990) explained this difference by the presence in potato of significant quantities of N in tubers.

Under non-limiting water conditions, the cultivar difference in the relationship between N concentration and total biomass was near significance (P = 0.10) as indicated by the linear paral-

lel curve analysis (Table 1). The value of parameter a was greater for Shepody (a = 5.07) than for Russet Burbank (a = 4.57). Hence, for a given level of biomass, the N concentration of Shepody was greater than that of Russet Burbank (Figure 1). The non-significant yield by cultivar linear interaction (Table 1) indicated that both cultivars had similar coefficients of dilution (b = 0.42).

The N concentration of Shepody was also greater than that of Russet Burbank under water deficient conditions (Figure 2). The cultivar difference in the relationship between N concentration and total biomass was significant (P = 0.002) as indicated by the linear parallel curve analysis (Table 1). Our results suggest that there is intra-specific variability in potato for the relationship between N concentration and biomass. It could be argued that the cultivar difference in parameter a is an artifact of the greater plant density of Shepody (4.4 plants m^{-2}) compared to that of Russet Burbank (2.9 plants m^{-2}), which resulted in smaller plants of Shepody (data not shown); this might have affected N
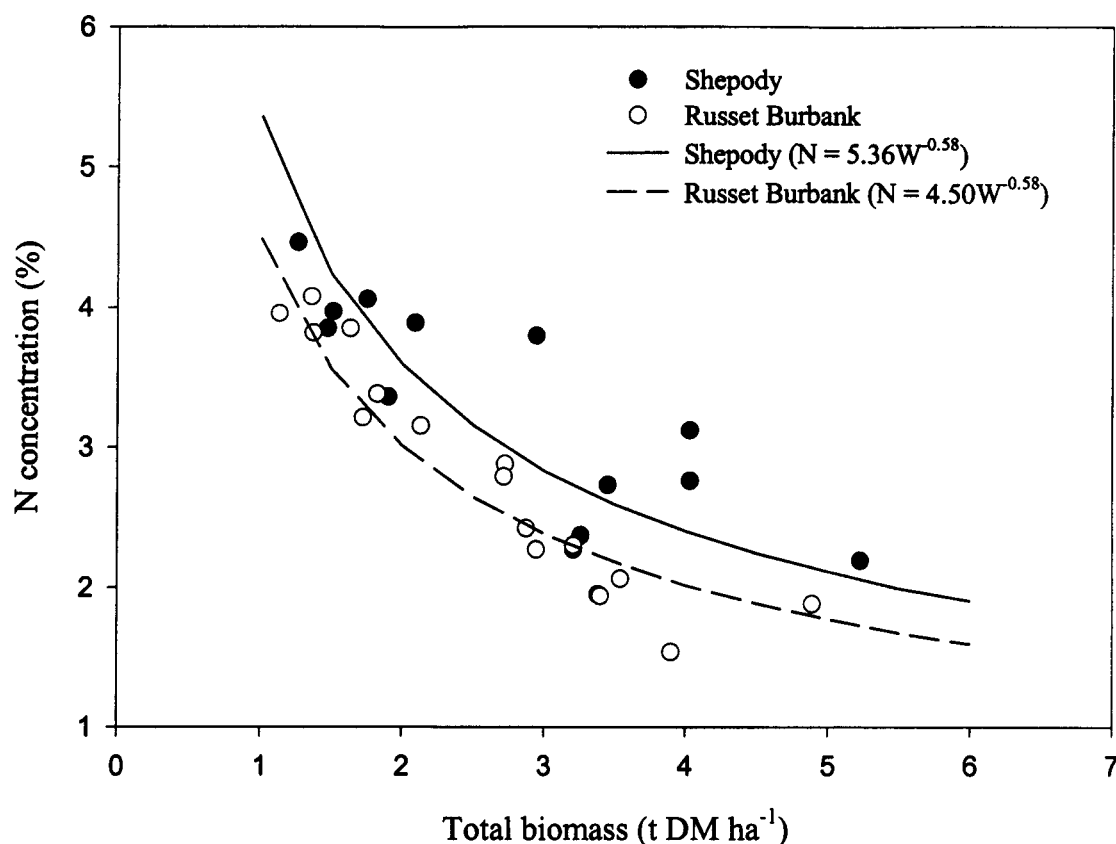
FIGURE 2.

Nitrogen concentration (N) as a function of total biomass (W) for two cultivars under limiting water conditions. Data points correspond to maximum total biomass for each site and cultivar.

TABLE 1—*Linear parallel curve analysis of the response curves of N concentration and N uptake as a function of total biomass for two cultivars.*

| Estimated parameters | d.f. | Mean square | | N uptake |
| | | N concentration | | |
		Irrigated	Non-irrigated	
Yield	1	1.8063 (<0.001)[1,2]	1.6793 (<0.001)	83.315 (<0.001)
Cultivars	1	0.1030 (0.10)	0.2232 (0.002)	0.495 (0.003)
Yield x cultivar linear interaction	1	0.0004 (0.92)	0.0421 (0.15)	0.001 (0.91)
Residual	41,27,119[3]	0.0373	0.4897	0.052
R^2		0.52	0.78	0.93

[1]Probability values are presented in parentheses.

[2] Statistical significance of the additional mean square contributed to the model $Y = k + lX$ as individual parameter k and l for each cultivar is estimated in steps.

[3] Degrees of freedom for N concentration (irrigated), N concentration (non-irrigated) and N uptake, respectively.

concentration because N concentration usually decreases as plants grow larger. However, the results on N dilution in isolated plants of sorghum (*Sorghum bicolor* L.) (Lemaire and Gastal 1997) and potato (Duchenne *et al.* 1997) suggest that the difference in individual plant weight between Shepody (22.7 g plant[1]) and Russet Burbank (34.5 g plant[1]) for a same total biomass of 1 t DM ha[1] would have a minimal impact on N concentration.

Intra-species differences in the relationship between N concentration and shoot biomass were reported for tall fescue (Gastal *et al.* 1997) and timothy (*Phleum pratense* L.) (Michaud *et al.* 1998). In potato, no differences in the relationship between N concentration and biomass were reported between the cultivars Bintje and Kaptah Vandel grown in France (Duchenne *et al.* 1997). Species differences were reported between rapeseed and winter wheat (Colnenne *et al.* 1998), corn (*Zea mays* L.) and sorghum (*Sorghum bicolor* L.) (Lemaire *et al.* 1996), and tall fescue and orchardgrass (*Dactylis glomerata* L.) (Gastal *et al.* 1997).
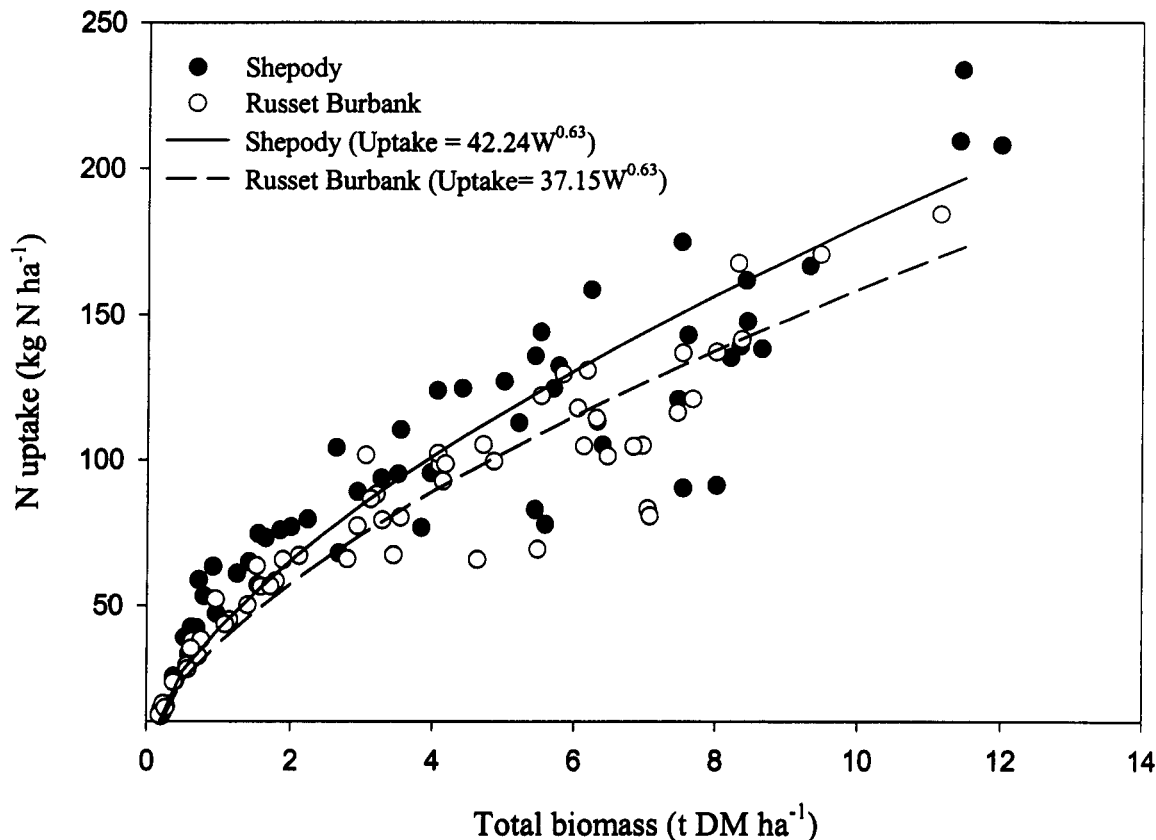
FIGURE 3.

Nitrogen uptake as a function of total biomass (W) for two cultivars. Data are from ten sampling dates and are combined over six sites, irrigation treatments and N rates.

The linear parallel curve analysis also indicated a significant (P = 0.003) cultivar difference in the relationship between N uptake and total biomass under non-limiting and limiting water conditions (Table 1). Hence, more N was taken up by Shepody than Russet Burbank for a similar level of total biomass (Figure 3). Shepody is a shorter season cultivar compared to Russet Burbank and, therefore, our results confirm the hypothesis of Vos (1997) that the relationship between N uptake and DM production should be different for genotypes with a short or a long growing season. Further studies with more cultivars or lines are required to confirm the genetic variability for the relationship between N concentration, N uptake, and biomass, and the possibility of using this variability to improve the N use efficiency of potato. Germplasm differences in N use efficiencies were reported on potato by Errebhi et al. (1999).

The fitted curve for Russet Burbank was relatively closer to the model of Duchenne et al. (1997) than that of Greenwood et al. (1990) (Figure 1). The cultivars studied by Duchenne et al.

(1997) in France and Greenwood et al. (1990) in Scotland and the Netherlands were different from those used in our study. Furthermore, the pedo-climatic conditions and the length of the growing seasons differed greatly. Contrary to Greenwood et al. (1990) and Duchenne et al. (1997) who based their estimation of the critical N concentration on data with a range up to 12- 15 t DM ha^{-1}, we limited our data set to biomass less than 6 t DM ha^{-1} for which leaf senescence can be assumed to be negligible (Bélanger and Gastal 2000). Despite these differences and the relatively large variability in our data set due to the sampling of only one or two plants per plot on each sampling date, our results indicate that the model parameters developed by Duchenne et al. (1997) in France should apply to the cultivar Russet Burbank under the growing conditions of eastern Canada when water is not limiting growth. This is particularly true for the range of total biomass (1.5 - 3.5 t DM ha^{-1}) for which a meaningful diagnostic interpretation during early season growth could be made. Different parameters, however, are needed for
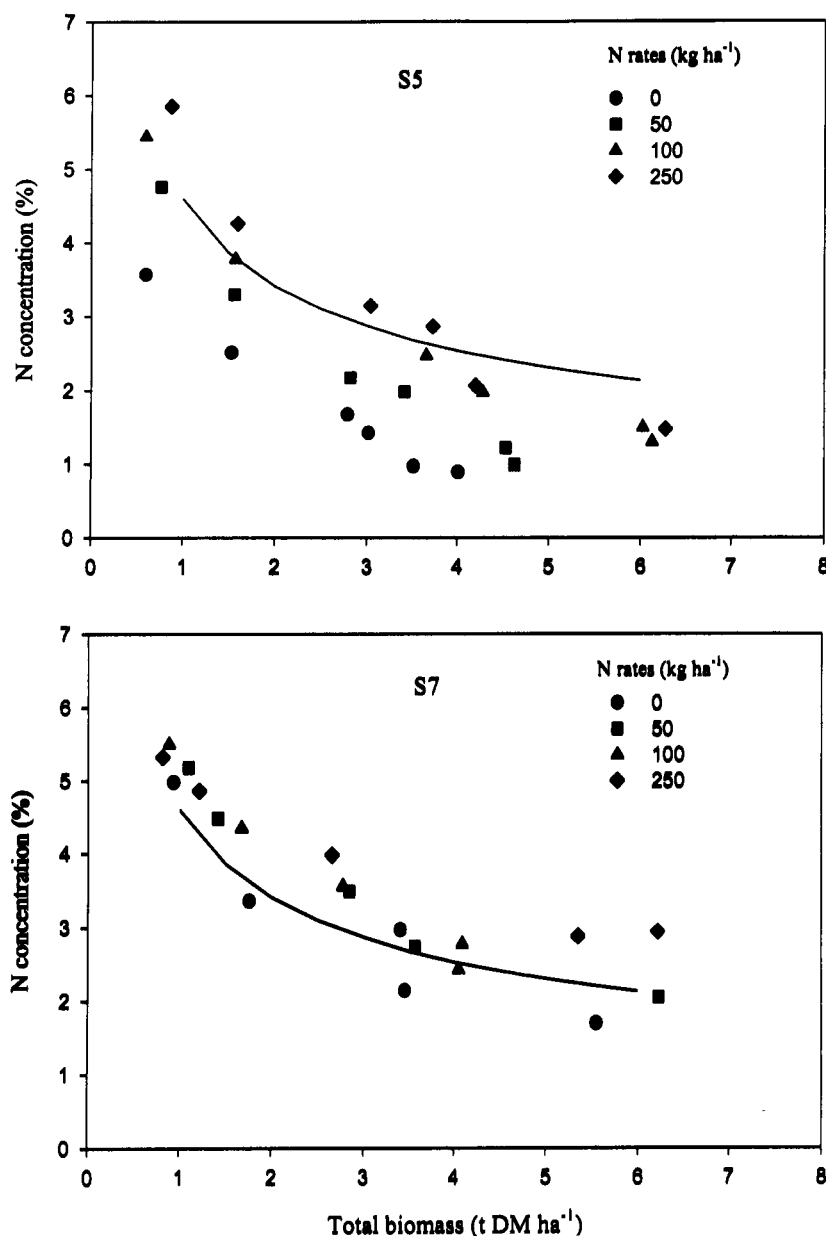
FIGURE 4.

Nitrogen concentration as a function of total biomass for the cultivar Russet Burbank grown under four N rates and with irrigation at two sites in 1996. The solid line represents the critical N curve defined for Russet Burbank ($N = 4.57W^{-0.42}$).

no other reports of the effect of water deficiencies on the relationship between N concentration and biomass in potato.

The DM concentration of tubers was not measured on the different sampling dates. The DM concentration of tubers progressively increases during the growth of the crop (Jefferies *et al.* 1989). By assuming a constant value of 20% for tuber DM concentration, the total biomass was most likely over-estimated for the first sampling dates used for the determination of the critical N concentration. The interval between the first and last sampling dates ranged from 15 to 24 days with an average of 20 days. Assuming a rate of change in tuber DM concentration of 0.015% (C d)$^{-1}$ (Jefferies *et al.* 1989) and an average daily temperature of 18 C, the tuber DM concentration would have increased by 5.4% during the interval between the first and last sampling dates. If we then assume a tuber DM concentration of 15% on the first sampling date rather than the 20% used in our calculations, and we consider that the tuber biomass represented approximately 30% of the total biomass on the first sampling date (Bélanger *et al.* 2001), the total biomass would be reduced by approximately 7.5%. This would probably result in a small decrease in the coefficient of dilution. Greenwood *et al.* (1990) reported a coefficient of dilution of 0.46 based on data for which the tuber DM concentration was measured. The coefficient of dilution in our study is, therefore, unlikely to be much smaller than 0.42.

The DM concentration of tubers is also affected by N fertilization and cultivars (Harris 1992). Tubers represented approximately 30% of the total biomass on the first sampling date and less than 50% on most sampling dates used to establish the critical N curve (Bélanger *et al.* 2001). The critical N curve would therefore be minimally affected by an effect of N fertilization and cultivars on tuber DM concentration.

N Nutrition Index

The critical N curve defined by equation (1) discriminates three different types of N status (Colnenne *et al.* 1998). Data

the cultivar Shepody, and this might be the case for other short-season cultivars.

The N concentration at a given level of total biomass was lower without (Figure 2) than with irrigation (Figure 1), primarily for Russet Burbank. This suggests that the water deficiency decreased N uptake and, therefore, indirectly created conditions of N deficiency. Similar results were reported for grasslands (Duru and Langlet 1994). To our knowledge, however, there are

points below the curve represent situations where N is limiting growth, whereas data points above the curve represent situations of excessive N nutrition. Data points located on or near the curve correspond to situations where N is not limiting growth and the N nutrition is not excessive. For instance, the data points with N rates of 0, 50 and 100 kg N ha^{-1} were below the critical N curve at S5 for Russet Burbank, indicating that N was limiting growth (Figure 4). With 250 kg N ha^{-1}, however, the data points were near the critical N curve, indicating that N was not limiting growth. At S7, only the data points with no applied N were below the critical N curve. With the highest N rate (250 kg N ha^{-1}), the data points were well above the critical N curve, which indicated an excessive N nutrition.

The critical N concentration was estimated using our own models described above for Shepody and Russet Burbank. A NNI value above 1.0 indicates that the N concentration was greater than that required to reach maximum growth whereas a value less than 1.0 indicates a N deficiency. As an example, the NNI values over three sampling dates for the cultivar Russet Burbank under irrigated conditions are presented for two contrasted situations at S5 and S7 (Figure 5). As we indicated above for the same examples, N was limiting with all but the highest N rate at S5, and consequently the NNI was smaller than 1.0 when 0, 50, and 100 kg N ha^{-1} were applied. The final harvest tuber yield at S5 was 19.7, 29.4, 35.9, and 35.8 t ha^{-1} with 0, 50, 100, and 250 kg N ha^{-1}, respectively (Bélanger et al. 2000). At S7, N was limiting growth only when no N was applied, which resulted in a NNI less than 1.0 on 56 DAP. The final harvest tuber yield was 44.4, 46.4, 46.1, and 47.0 t ha^{-1} with 0, 50, 100, and 250 kg N ha^{-1}, respectively.

The relative yield was expressed as a function of the average NNI over three sampling dates. For a NNI greater than 1.0, the relative yield was near 1.0 (Figure 6). With decreasing NNI
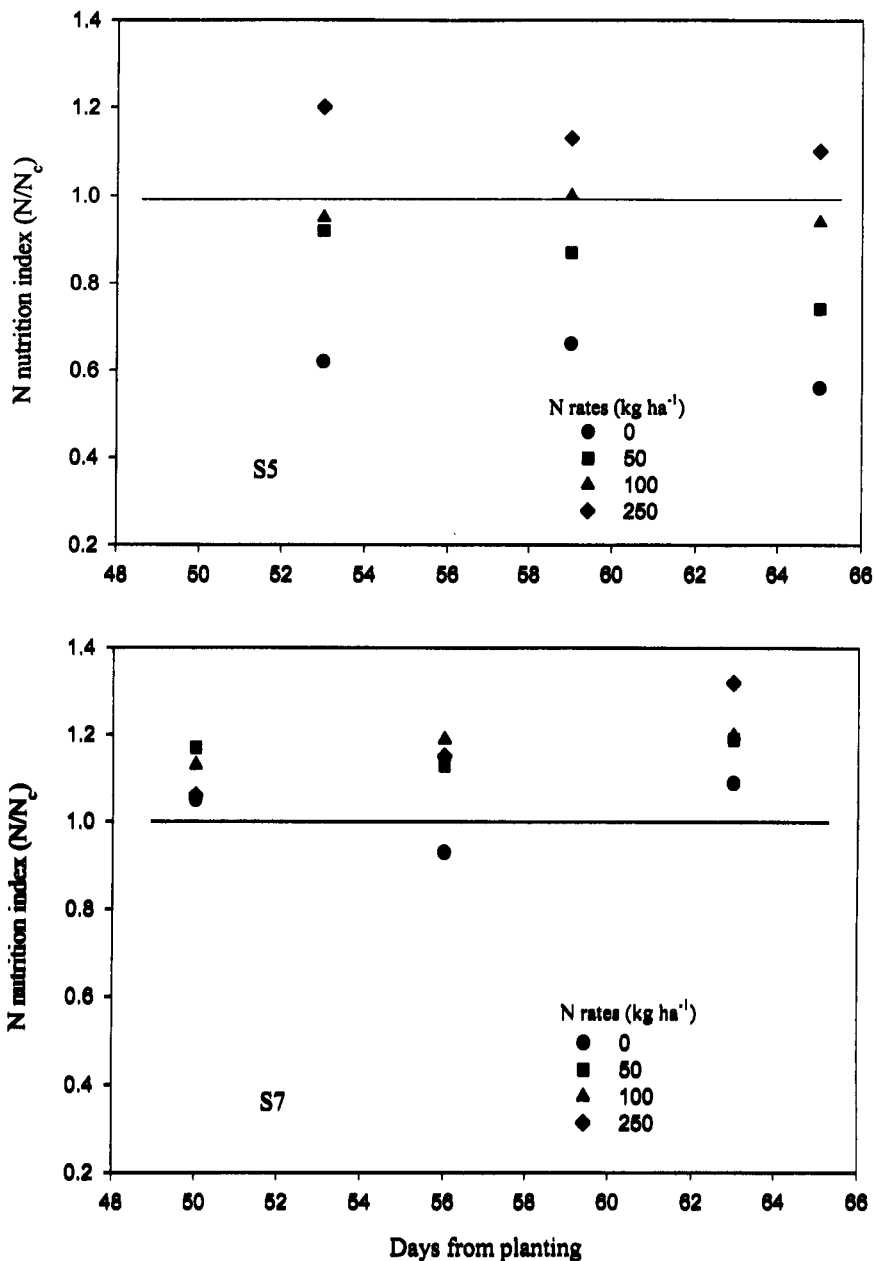
FIGURE 5.
The N nutrition index (NNI) on three sampling dates for the cultivar Russet Burbank grown under four N rates and with irrigation at two sites in 1996. The solid line represents a NNI of 1.0.

below 1.0, the relative yield decreased. The relationship between relative yield and NNI expressed by a quadratic function accounted for a greater proportion of the variability with irrigation than without irrigation for both Shepody and Russet Burbank. The relationship between relative yield and NNI appear to be similar for both cultivars. The model of critical N concentration and the resulting NNI, therefore, identified adequately situ-
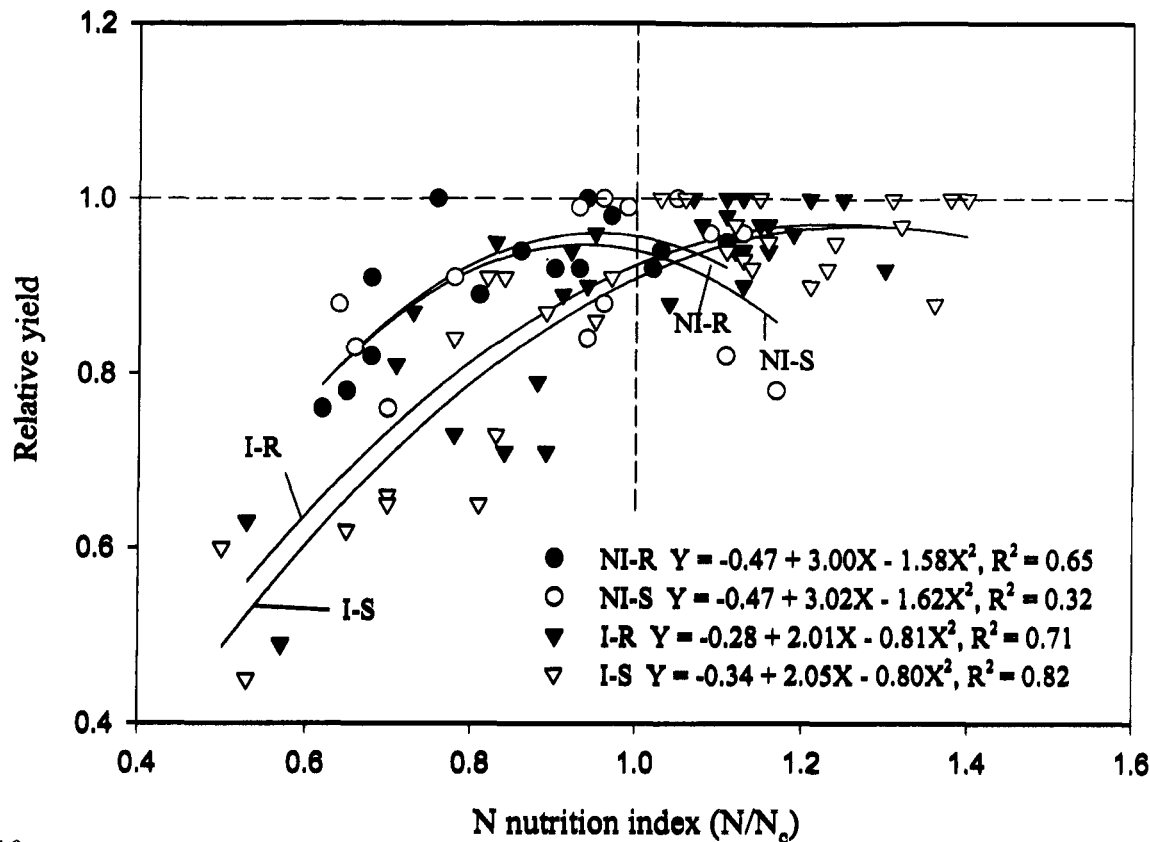
FIGURE 6.

The relationship between relative yield and the N nutrition index (NNI) of two potato cultivars (R: Russet Burbank; S: Shepody) with (I) and without irrigation (NI). Data without irrigation in 1996 were combined to those with irrigation; data of NNI were averaged over three sampling dates.

ations of deficient and non-deficient N nutrition in potato at least under irrigated conditions and make it possible to quantify the level of potato N nutrition. Further research is required to validate this approach under a wider range of conditions, particularly under water-deficient conditions.

The NNI values ranged from 0.50 to 1.4. Justes et al. (1994) concluded that shoot N concentration of heavily fertilized winter wheat could be up to 60% greater than the critical N concentration. In potato, Duchenne et al. (1997) reported values that were up to 40% greater than the critical N concentration. The ability of potato to take up more N than was required to satisfy their immediate requirements for growth was also reported in other studies (Greenwood et al. 1985; Millard and Marshall 1986), and the extra N was predominantly in the form of soluble protein in the leaves and nitrates in the stems (Millard and Marshall 1986). The range of NNI values (0.60 - 0.97; data not shown) with no N applied indicates that the intensity of N stress differed for the different sites.

Critical N curves were determined for two potato cultivars grown in eastern Canada, and they were used to estimate the NNI of potato grown under different N rates with and without irrigation. Our results suggest that the NNI could be used as a reliable indicator of the level of N stress during the growing season, particularly when water is not deficient. The practical utilization and the benefits of NNI in farm situations requires further research. The need to determine the actual crop mass and its N concentration to calculate NNI values represent a major difficulty in using the NNI at the farm level. The NNI could also be used as a reference for simple procedures (e.g,. petiole nitrate concentration) in the diagnosis of crop N status as was done for wheat (Justes et al. 1997b).

The NNI can also be used in crop models to take into account the effect of N on growth and yield as was done for wheat and corn (Brisson et al. 1998; Jeuffroy and Recous 1999). The critical N curve is based on data with total biomass greater than 1.0 t DM ha^{-1} and can only be used in that situation. The crit-

ical N concentration for total biomass less than 1.0 t DM ha⁻¹ was not determined in our study. The relationship between N concentration and biomass also provides a useful framework for the study of genetic variability for N use efficiency.

ACKNOWLEDGMENTS

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