Shoot- and tuber-based critical nitrogen dilution curves for the prediction of the N status in potato

C.M. Giletto[a,*], N.I. Reussi Calvo[a,b,c], P. Sandaña[d], H.E. Echeverría[a], G. Bélanger[e]

[a] *Unidad Integrada Balcarce, Facultad de Ciencias Agrarias (UNMdP)-INTA Balcarce, Ruta 226 km 73,5 (7620) Balcarce, Buenos Aires, Argentina*
[b] *Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina*
[c] *Laboratorio de suelos FERTILAB, Moreno 4524, (7600) Mar del Plata, Buenos Aires, Argentina*
[d] *Institute of Plant Production and Protection, Universidad Austral de Chile, Campus Isla Teja, Valdivia, Chile*
[e] *Honorary Research Scientist, Science and Technology Branch, Agriculture and Agri-Food Canada, Québec City, Canada*

ARTICLE INFO

ABSTRACT

Critical nitrogen (N) dilution curves describe the critical N concentration in plant tissues during crop growth and they are used to estimate the N nutrition status of whole plants in potato. Little is known, however, about the critical N dilution curves in specific plant parts such as shoots and tubers. Our objectives were (i) to determine critical shoot and tuber N dilution curves; (ii) to compare these curves with critical N dilution curves determined on whole plants (shoot + tubers); and (iii) to assess the possibility of using the critical shoot and tuber N dilution curves to estimate the N nutrition status of potato and tuber quality. Seven potato cultivars were assessed under different N supplies and environmental conditions in Canada and Argentina. Shoot biomass (leaves + stems) and tuber biomass along with their N concentrations were measured at regular intervals during the growing season. Tuber yield, dry matter concentration, and nitrate ($N-NO_3^-$) concentration were measured at harvest. We determined the coefficients of the critical N dilution curves expressed as $N = a \times W^{-b}$ with N as the N concentration in shoot or tuber biomass, and W their respective biomass. Among cultivars, coefficients a and b for shoot biomass ranged from 5.08 to 5.68 and from 0.18 to 0.28, respectively, while coefficients a and b for tubers ranged from 1.54 to 1.87 and from 0.17 to 0.21, respectively. The shoot (NNI_{sh}) and tuber (NNI_t) N nutrition indices were both highly related to the N nutrition index in whole plants ($R^2 = 0.88$; $R^2 = 0.98$; $P < 0.05$; respectively) and to relative tuber yields ($R^2 = 0.61$; $R^2 = 0.53$; $P < 0.05$; respectively). For a NNI_{sh} or $NNI_t \geq 1.00$, the relative yield was near 95 %, while it decreased with decreasing NNI_{sh} or NNI_t below 1.00. The tuber N nutrition index at harvest was related to tuber dry matter concentration and tuber $N-NO_3^-$ concentration ($R^2 = 0.30$; $R^2 = 0.53$; $P < 0.05$; respectively). Our results demonstrate that shoot and tuber N nutrition indices identified adequately the N status in potato cultivars and tuber quality and, therefore, they have potential as plant diagnostic tools to estimate the N status of potato crops across different cultivars and environmental conditions.

1. Introduction

Nitrogen (N) is often considered the most important limiting factor for biomass production. Nitrogen fertilization is usually required to provide a sufficient N supply for achieving the potential yield allowed by the climatic conditions (Lemaire et al., 2008). Nitrogen management is especially important for potato (*Solanum tuberosum* L.). An insufficient N supply can result in a reduced tuber yield, while excessive N can result in reduced tuber yield and quality, and N losses to the environment (Gianquinto and Bona, 2000; Bélanger et al., 2002, 2003;

Vos, 2009). Tuber specific gravity, an important quality parameter for potato processing, decreases with increasing fertilizer N rate, particularly when N fertilization exceeds crop requirements (Bélanger et al., 2002). Tuber nitrate (N-NO$_3^-$) concentrations generally increase with increasing fertilizer N rates, with the highest tuber N-NO$_3^-$ concentrations occurring when relative yield is at or close to 1.0 (Bélanger et al., 2002; Zebarth et al., 2012). Consequently, the challenge for modern potato production systems is to minimize N fertilization without affecting negatively the yield progress, which implies that N fertilization practices of potato crops must be improved. Therefore, new plant-based diagnostic methods need to be developed to optimize the management of N fertilization for tuber yield and quality, while minimizing the risk of N losses to the environment (Goffart et al., 2008; Ziadi et al., 2012).

Plant-based diagnostic tests that assess potato N sufficiency can be used to guide in-season N fertilizer management. The diagnosis of the plant N status during the growing season consists in the early detection of plant N deficiencies in order to determine the necessity of additional N fertilizer applications. Plant-based diagnostic methods of N deficiency can be based on critical N dilution curves (Lemaire et al., 2008; Goffart et al., 2008; Ziadi et al., 2012). Critical N dilution curves have been described empirically by a negative power function (Lemaire and Salette, 1984) relating plant N concentration to the shoot biomass (leaves + stems). Under situations when a mínimum N supply results in a maximum crop growth rate during the vegetative growth period, it is possible to define the critical N dilution curve:

$$N_C = a_c \times W^{-b} \tag{1}$$

where W is the shoot biomass expressed in Mg DM ha^{-1}, N$_C$ is the critical N concentration in the shoot biomass expressed in g 100 g^{-1} DM, and a_c and b are fitted parameters. The coefficient a_c represents the critical plant N concentration for W = 1 Mg DM ha^{-1}, and it depends on the rate of steady state N supply and may also be affected by species (Greenwood et al., 1990). The coefficient b is dimensionless and represents the ratio between the relative decline in plant N concentration and the relative crop growth rate (Gastal et al., 2015). Critical N dilution curves have been characterized in different crops, such winter wheat (*Triticum aestivum* L.) (Justes et al., 1994; Yue et al., 2012), rice (*Oryza sativa* L.) (Sheehy et al., 1998), winter rapeseed (*Brassica napus* L.) (Colnenne et al., 1998), corn (*Zea mays* L.) (Ziadi et al., 2008), grain sorghum (*Sorghum bicolor* L.) (Van Oosterom et al., 2001), tomato (*Lycopersicon esculentum* Mill.) (Tei et al., 2002), spring wheat (*Triticum aestivum* L.) (Ziadi et al., 2010), and potato (Bélanger et al., 2001; Giletto and Echeverría, 2012, 2015). The N concentration in individual plants within a dense canopy declines as the plants grow, even when there is an ample N supply. This phenomenon has been interpreted as a resulting from gradual changes in the proportion of N-rich metabolic and N-poor structural tissues as plant size increases (Lemaire et al., 2008).

In potato, critical N dilution curves have been defined on a whole plant basis (shoot biomass + tuber biomass). This aproximation was first studied by Greenwood et al. (1990), following the initial work of Lemaire and Salette (1984) on forage grasses. Thereafter, several authors determined values for the coefficients a_c and b of Eq. (1) for potato. The reported values ranged from 5.04 to 5.53 for coefficient a_c and from 0.25 to 0.56 for coefficient b (Greenwood et al., 1990; Duchenne et al., 1997; Bélanger et al., 2001; Giletto and Echeverría, 2015) in different potato cultivars grown in different regions. Studies conducted in Canada and Argentina both confirmed cultivar differences in the critical N dilution curves (Bélanger et al., 2001; Giletto and Echeverría, 2015).

To account for the empirical observations of N dilution in crops, Greenwood et al. (1990) and Lemaire and Gastal (1997) developed a theory based on the work of Caloin and Yu (1984). Plant mass (W) is composed of two compartments: (1) W$_m$, the metabolic tissues directly involved in growth processes such as photosynthesis and meristematic activity with a high N concentration (%N$_m$); and (2) W$_s$, the structural tissues necessary for plant architecture with a low N concentration (%N$_s$). Then:

$$W = W_m + W_s \tag{2}$$

and the plant N concentration (%) is:

$$\%N = 1/W \times (\%N_m \times W_m + \%N_s \times W_s) \tag{3}$$

The N dilution process is determined by the allometry between W$_s$ and W$_m$ as plant size increases. During plant growth, W$_s$ increases at a relatively higher relative rate than W$_m$, leading then to an ontogenetic decline of the metabolic component that can be expressed as follows:

$$W_m = k \times W^\alpha \tag{4}$$

Eqs. (3) and (4) can be combined:

$$\%N = k \times (\%N_m - \%N_s) \times W^{\alpha-1} + \%N_s \tag{5}$$

This equation is close to Eq. (1) if we consider that N$_s$ is small as shown by Lemaire and Gastal (1997).

For potato, along with the metabolic and structual compartments, a third compartment involved in reserve storage must also be considered. Potato growing can be simplified into two main phases: (1) the pre-flowering phase, when plants develop only foliage and roots, and when young leaves and roots behave as sinks; and (2) the post-flowering phase, when senescing leaves are sources of carbohydrates and reduced N for developing the tubers, a storage compartment. In many cultivars, flowering coincides with the stage of initiation of tuberization. Nitrogen taken up by the plants is allocated to leaves and stems during the vegetative growth stage and to leaves, stems, and tubers during the tuber bulking stage (Kleinkopf et al., 1981; Vos, 2009). The N dilution process during the tuber bulking stage can also be attributed to the translocation of N from the shoot biomass to the tubers (Kleinkopf et al., 1981; Vos, 2009). Tubers are composed of storage tissues with mainly starch and a low N concentration. As tubers develop, the whole plant N dilution (shoots + tubers) is therefore affected by this third compartment for reserve storage.

So far, all determinations of the critical N dilution curves of potato have been based on whole plants that included both shoots and tubers (Greenwood et al., 1990; Duchenne et al., 1997; Bélanger et al., 2001; Goffart et al., 2008; Giletto and Echeverría, 2015; Stanislav Magnitskiy and Rodríguez, 2019). Nitrogen deficiencies can change the allocation of biomass to different plant parts and, therefore, the shape of the dilution curves may change depending on which plant parts are included. The concept of critical N dilution curves specific to plant parts (e.g., leaves and stems) is similar to that on whole plant basis. The crop critical N dilution theory has also been used to develop critical N dilution curves on plant index bases (leaf, stem, and spike) in rice (Yao et al., 2014a; Ata-Ul-Karim et al., 2017), wheat (Yao et al., 2014b; Zhao, 2014; Zhao et al., 2016), and rapeseed (Weymann et al., 2016). These findings offer an opportunity to develop less expensive and time-consuming procedures to obtain N nutrition indexes (one organ vs. whole plant), which is the main limitation for applying whole plant critical N nutrition curves to assess the N status of crops (Lemaire et al., 2008). Critical N dilution curves for specific plant organs (e.g. leaves, stems, and tubers) have not yet been determined in potato and these could be useful for assessing the potato N nutrition status. Therefore, our general objective was to evaluate the N dilution in both shoots and tubers of different potato cultivars grown in Canada and Argentina. Our specific objectives were: (i) to determine critical shoot N dilution curves and critical tuber N dilution curves; (ii) to compare these curves with critical N dilution curves determined on a whole plant basis; and (iii) to assess the possibility of using the critical shoot and tuber N dilution curves to estimate the N nutrition status of potato and tuber quality.

2. Materials and methods

2.1. Field experiments

Field experiments were conducted in both Canada and Argentina. In Canada, a field experiment was conducted in the province of New Brunswick at two locations in 1995 and two locations in 1997 (Bélanger et al., 2000). From planting to harvest (May-October), the average temperature across the four locations ranged from 14 to 19 °C, while the cumulative rainfall ranged from 186 to 243 mm and the potential evapotranspiration ranged from 344 to 442 mm. In Argentina, a field experiment was conducted from 2003 to 2006 in Balcarce in the province of Buenos Aires (Giletto and Echeverría, 2015). From planting to harvest (October-March), the average temperature ranged from 17 to 19 °C, the cumulative rainfall ranged from 385 to 587 mm, and the potential evapotranspiration ranged from 594 to 743 mm.

2.2. Sampling and measurements

2.2.1. Canadian experiment

Two potato cultivars (Shepody and Russet Burbank) were grown under varying N fertilization rates (0, 50, 100, and 250 kg N ha^{-1}) and non-limiting water conditions (Bélanger et al., 2001). Shoot (leaves + stems) and tuber biomass were measured on ten sampling dates at approximately weekly intervals starting around 40 days after planting (DAP) until early September. The data used came from sampling between 2 July and 20 September. Two plants per plot were sampled on the first two sampling dates, and one plant per plot was sampled on the last eight sampling dates. The plants were sampled on the outside rows with one plant left between two sampling dates. Shoot and tubers were dried at 70 °C for determination of dry matter (DM) concentration. The N concentration in shoots and tubers was determined by dry combustion using a LECO CNS analyzer (LECO, St. Joseph, MI, USA). At harvest, the middle two rows of each plot were harvested to determine total tuber yield in fresh weight. A tuber subsample was dried to constant weight and the N-NO$_3$- concentration (mg kg^{-1} DM) was determined colorimetrically using Cd-reduction (Bélanger et al., 2002).

2.2.2. Argentinian experiment

Five cultivars with different morphological and agronomic characteristics (Innovator, Gem Russet, Umatilla Russet, Bannock Russet, and Markies Russet) were grown under different N fertilization rates (0, 80, 150, and 250 kg N ha^{-1}) and non-limiting water conditions (Giletto and Echeverría, 2015). Shoot (leaves + stems) and tuber biomass were measured at different times during each growing season, starting around 40 DAP until senescence, by harvesting plants from 1 m of one row in each plot. Sampling dates were selected in order to have information from different stages of the crop cycle: vegetative growth (from emergence until 50 DAP), tuber initiation (50–60 DAP), and tuber bulking (60 DAP until physiological maturity) (Westermann, 1993). Shoot and tuber biomass were weighed fresh and a subsample of around 200 g was collected for determination of DM concentration and laboratory analyses. Subsamples were dried at 60 °C in a forced air draft oven for 7 d, ground to pass through a 1-mm sieve in a Wiley mill, and stored at room temperature before laboratory analyses. The N concentration in shoot and tuber biomass was determined using a TruSpec CN analyzer (LECO, St. Joseph, MI, USA). At harvest, 1 m of the two central rows of each plot was harvested by hand to assess total tuber yield in fresh weight. A sample of tubers of around 5 kg was selected and the DM concentration was determined by measuring the specific gravity. A subsample of around 200 g was dried in an oven at 60 °C to constant weight and was used to determine the N-NO$_3$- concentration (mg kg^{-1} DM) by the fenoldisulfonic acid method (Keeney and Nelson, 1982).

2.3. Data analysis

2.3.1. Critical N dilution curve

Curves of the critical shoot N concentration and critical tuber N concentration for each cultivar were determined using Eq. (1), following the procedure proposed by Greenwood et al. (1990) and Bélanger et al. (2001). Because there were less than five rates of N fertilization in both Canadian and Argentinian experiments, the data could not be separated into two populations by regression lines as proposed by Justes et al. (1994). The critical shoot N dilution curve is expressed as follows:

$$N_{shC} = a_{sh} \times W_{sh}^{-bsh} \tag{6}$$

where N_{shC} is the critical shoot N concentration, W_{sh} is the shoot biomass (Mg DM ha^{-1}), a_{sh} is the shoot N concentration when $W_{sh} = 1$ Mg DM ha^{-1}, and b_{sh} is a dimensionless coefficient that corresponds to the ratio of the relative rate of decline of N_{shC} to the relative rate of W_{sh} accumulation. The upper limit of W_{sh} in the critical shoot N dilution curve depended on the cultivar and was reached before the onset of leaf senescence.

The critical tuber N dilution curve is expressed as follows:

$$N_{tC} = a_t \times W_t^{-bt} \tag{7}$$

where N_{tC} is the critical tuber N concentration, W_t is the tuber biomass (Mg DM ha^{-1}), a_t is the tuber N concentration when $W_t = 1$ Mg DM ha^{-1}, and b_t corresponds to the ratio of the relative rate of decline of N_{tC} to the relative rate of W_t accumulation.

The determination of the critical shoot and tuber N dilution curves requires the identification of critical data points for which N does not limit shoot or tuber biomass growth or is not in excess. Shoot and tuber biomass and N concentration for each cultivar, year/location, and sampling date were subjected to analyses of variance (ANOVA) using the PROC GLM procedure (SAS Institute, 2002). Sampling dates were not used in determining the critical shoot and tuber N dilution curves if the analysis of variance indicated no significant ($P < 0.05$) differences among N rates. For the remaining sampling dates, the N fertilizer treatments were classified using the Fisher's protected least significant difference (LSD) test. The highest shoot and tuber biomass obtained with any rate of N fertilizer and the corresponding N concentration for each year/location and each sampling date were included in the database. When the highest shoot and tuber biomass was obtained with two or more rates of N fertilization, data obtained with the lowest rate were selected (Greenwood et al., 1990; Bélanger et al., 2001). These critical N data points were pooled across years, locations, and samplig dates and they were used to determine the relationship between N concentration and either shoot or tuber biomass for each cultivar using an allometric function (Eqs. (6) and (7)). When shoot and tuber biomass were below 1 Mg DM ha^{-1}, we assumed that N_{shC} and N_{tC} took a constant value. The estimated paramenters of the critical shoot and tuber dilution curves (Eqs. (6) and (7)) for each cultivar were obtained using the NLIN procedure (SAS Institute, 2002).

2.3.2. Nitrogen nutrition index

The shoot N nutrition index (NNI$_{sh}$) and tuber N nutrition index (NNI$_t$) were calculated at each sampling date and for each cultivar as follows:

$$NNI_{sh} = N_{sh}/N_{shC} \tag{8}$$

$$NNI_t = N_t/N_{tC} \tag{9}$$

where N_{sh} is the actual shoot N concentration and N_t is the actual tuber N concentration. For both shoots and tubers, values of NNI < 1 indicate that biomass growth was limited by the N supply, while a value of NNI = 1 indicates that biomass growth was not limited by the N supply and values of NNI > 1 indicate luxury N consumption. The N nutrition index (NNI) of the whole plants (shoots + tubers) at each
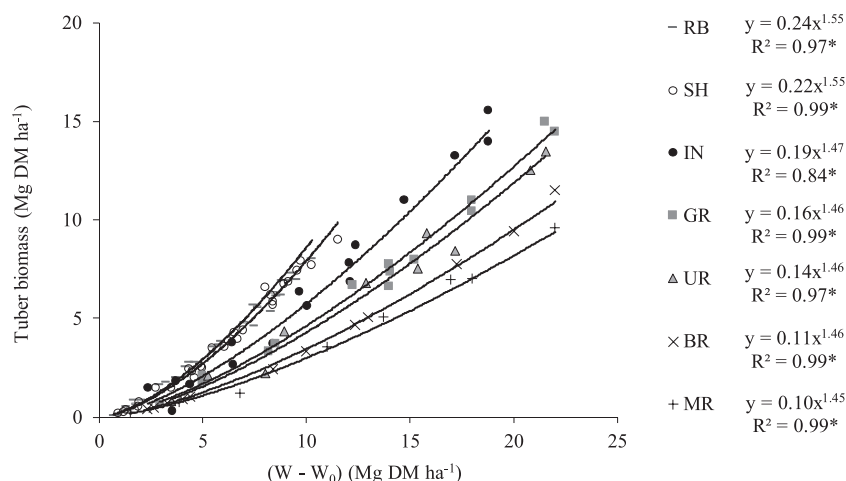
Fig. 1. Relationship between tuber biomass and normalized total biomass (W - W_0) for each cultivar where W_0 is the total biomass at tuber initiation under nonlimiting water conditions for all cultivars from the Canadian and Argentinian experiments. RB: Russet Burbank; SH: Shepody; IN: Innovator; GR: Gem Russet; UR: Umatilla Russet; BR: Bannock Russet; MR: Markies Russet. R^2 is the coefficient of determination and * indicates a significant allometric function (Eq. (10)) at $P <$ 0.05.

sampling date was determined by dividing the actual N concentration of the total biomass by Nc from Eq. (1) (Bélanger et al., 2001; Giletto and Echeverría, 2015) (data not shown).

2.3.3. Statistical analysis

The effects of the N fertilization rates on shoot and tuber biomass, shoot and tuber N concentrations, and NNI_{sh} and NNI_t for each sampling date, location/year, and cultivar were assessed by an analysis of variance (ANOVA) with the PROC MIXED procedure (SAS Institute, 2002). The N rate was considered a fixed effect and replications were considered a random effect. Normality of factors was tested using the Shapiro–Wilks test and the homogeneity of variances was evaluated and confirmed with the Levene-test ($P > 0.05$) (R Core Team, 2014). The effects of N fertilization were considered significant with $P < 0.05$.

Cultivar differences in biomass partitioning to tubers during the growing season were evaluated with the relationship of tuber biomass (W_t) to the total biomass (W) using an allometric function (Lemaire et al., 2019):

$$W_t = k \times (W - W_0)^c \tag{10}$$

where W - W_0 is the normalized total biomass, W_0 is the total biomass at tuber initiation, k is the tuber biomass when the normalized total biomass is 1 Mg DM ha^{-1}, and c is a scaling coefficient equal to the ratio between relative tuber growth rate [$1/W_t \times d(W_t)/dT$] and relative plant growth rate [$1/W \times d(W)/dT$]. Total and tuber biomass were log-transformed to estimate the parameters of the allometric function and to estimate W_0 using a linear regression. The slopes and intercepts of these linear regressions for the different cultivars were analyzed using dummy variables (Littell et al., 1991). The relationship between the dilution coefficients (b, b_{sh}, b_t) and k was determined using linear regression analyses.

To quantify the yield response to N rates and to reduce the variation in yield associated with different locations and years, Schroder et al. (2000) recommended transforming absolute yields into relative yields. The relative tuber yield was calculated as the ratio between the tuber yield obtained at a given N rate and the highest tuber yield among all N application rates for each cultivar and location/year. The relative yield was then expressed as a function of the NNI_{sh} or NNI_t during tuber bulking (60–90 DAP). This period of the growing season was selected to use NNI_{sh} or NNI_t as diagnostic tools because it corresponds to the highest daily tuber growth rate (Horneck and Rosen, 2008). The critical values NNI_{sh} or NNI_t were calculated following the Arcsine–Logarithm Calibration Curve (ALCC) described by Dyson and Conyers (2013) and modified by Correndo et al. (2017). Critical values were determined for 95 % of the relative yield (Dow and Roberts, 1982; Ulrich, 1996). The relationship of NNI_{sh} or NNI_t across sampling dates with the N nutrition index (NNI) of whole plants was determined using regression analyses

with the PROC REG procedure (SAS Institute, 2002). Relationships of the tuber N nutrition index at harvest (NNI_{tH}) with the tuber DM concentration and the tuber N-NO_3^- concentration were determined using regression analyses with the PROC REG procedure (SAS Institute, 2002).

3. Results

3.1. Biomass production and N concentration

Across locations/years, cultivars, N rates, and sampling dates, total biomass ranged from 0.26 to 24.15 Mg DM ha^{-1} (data not shown), while shoot biomass ranged from 0.14 to 19.30 Mg DM ha^{-1} and tuber biomass from 0.02 to 19.04 Mg DM ha^{-1} (Appendix A and B). The variation in shoot biomass among N fertilization rates tended be greater during tuber bulking (70–114 DAP) than during vegetative growth stage (40–60 DAP). Shoot biomass was less with the cultivars Shepody and Russet Burbank at the Canadian locations (0.14–6.60 Mg DM ha^{-1}) than with the cultivars at the Argentinian location (0.46–19.30 Mg DM ha^{-1}). These differences between the Canadian and Argentinian locations are probably due to a combination of climatic conditions and cultivars (Appendix A and B). Average temperature, potential evapotranspiration, and cumulative rainfall during the growing season were less at the Canadian locations than at the Argentinian location. The growing season was also shorter at the Canadian locations (130 vs. 140 days).

The cultivars differed in their biomass partitioning to the tubers. The allometric function (Eq. (10)) between W_t and the normalized total biomass (W - W_0) throughout the crop cycle was different for each cultivar (Fig. 1) according to the parallelism and coincidence test (SAS Institute, 2002). The total biomass at tuber initiation (W_0) was 1.64, 1.78, 1.20, 1.02, 0.99, 0.29, and 0.30 Mg DM ha^{-1} for the cultivars Innovator, Gem Russet, Umatilla Russet, Bannock Russet, Markies Russet, Russet Burbank, and Shepody, respectively. The lower total biomass at tuber initiation of the two cultivars at the Canadian locations (Russet Burbank and Shepody) indicate that they started producing tubers at a much lower shoot biomass than the cultivars at the Argentinian location. The tuber biomass when the normalized total biomass was 1 Mg DM ha^{-1} (coefficient k) ranged from 0.10 to 0.24 and the values were greater for the cultivars at the Canadian locations than for the cultivars at the Argentinian location (Fig. 1). Values of the coefficient c ranged from 1.45 to 1.55 and they were greater for the two cultivars at the Canadian locations than for the cultivars at the Argentinian location. Greater values of this coefficient indicate a greater ratio between the relative tuber growth rate and the relative plant growth rate and, therefore, a greater biomass partitioning to the tubers of the two Canadian cultivars.
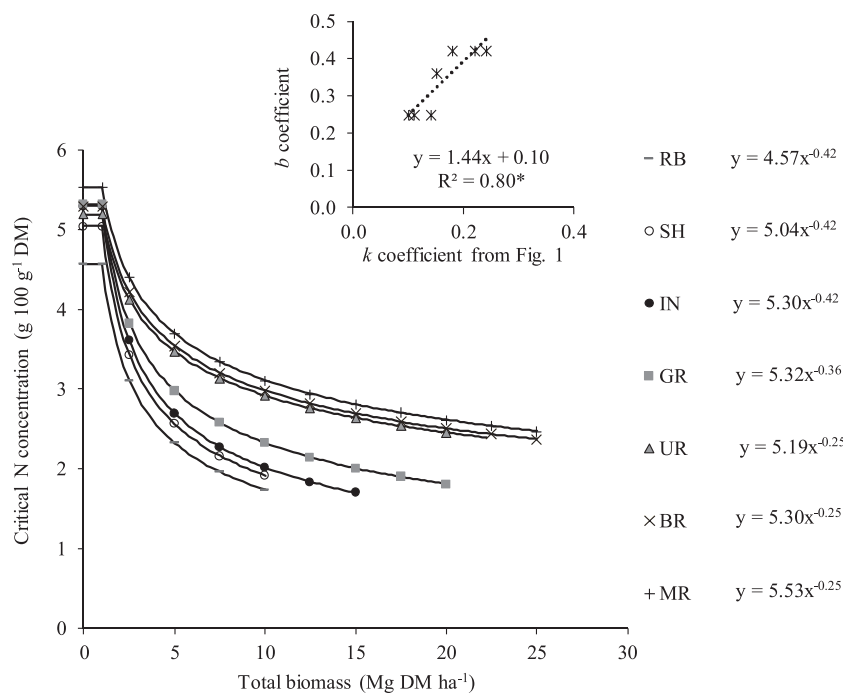
Fig. 2. Relationship between critical N concentration and total biomass (shoots + tubers) under nonlimiting N and water conditions for all cultivars from the Canadian and Argentinian experiments. RB: Russet Burbank; SH: Shepody; IN: Innovator; GR: Gem Russet; UR: Umatilla Russet; BR: Bannock Russet; MR: Markies Russet. Critical N dilution curves in the total biomass of whole plants were adapted from Bélanger et al. (2001) and Giletto and Echeverría (2015). R^2 is the coefficient of determination. * indicates a significant allometric function at $P < 0.05$. Insert represents the relationship between values of the k (Eq. (10)) and b (Eq. (1)) coefficients.

Shoot N concentrations were higher than tuber N concentrations and both generally increased with increasing N rates and declined gradually with time (Appendix A and B). Across locations/years, cultivars, N rates, and sampling dates, shoot N concentrations (N_{sh}) ranged from 1.41 to 7.11 g $100\,g^{-1}$ DM and tuber N concentrations (N_t) ranged from 0.66 to 3.13 g $100\,g^{-1}$ DM.

3.2. Critical N dilution curves

Critical N dilution curves for whole plants (shoots + tubers) were previously published by Bélanger et al. (2001), for the cultivars of the Canadian experiment, and by Giletto and Echeverría (2015), for the cultivars of the Argentinian experiment, and they are shown in Fig. 2. The coefficient a ranged from 4.57 to 5.53, while the coefficient b ranged from 0.25 to 0.42. The values of the coefficient b were positively related ($R^2 = 0.80$; $P < 0.05$) to the values of the coefficient k (Eq. (10)) (insert in Fig. 2). Thus, the large values of the coefficient k, reflecting a greater biomass partitioning to the tubers, are associated with greater whole plant N dilution.

Critical N dilution curves for shoot biomass and tubers were determined with selected data points (Appendix A and B). Among those selected data points, W_{sh} ranged from 1.00–12.50 Mg DM ha^{-1}, while N_{sh} ranged from 3.00–5.20 g $100\,g^{-1}$ DM. The N_{sh} declined with increasing W_{sh} in all cultivars (Fig. 3a). The coefficient a_{sh} ranged from 5.08 to 5.68, while the coefficient b_{sh} ranged from 0.18 to 0.28. Cultivars differed in both coefficients according to the parallelism and coincidence test (SAS Institute, 2002), which indicates a different pattern of decrease in N_{sh} with increasing shoot biomass. More interestingly, the values of the coefficient b_{sh} were positively related ($R^2 = 0.90$; $P < 0.05$) to the values of the coefficient k (Eq. (10)) (insert in Fig. 3a), showing the link between the partitioning of biomass to tubers and the coefficient b_{sh}.

Among the selected data points, W_t ranged from 1.00 to 15.90 Mg DM ha^{-1} and N_t ranged from 0.80 to 2.00 g $100\,g^{-1}$ DM. The N_t declined with increasing W_t in all cultivars (Fig. 3b). The coefficient a_t ranged from 1.59 to 1.95 and the coefficient b_t ranged from 0.17 to 0.21. The cultivars had different values of the coefficient a_t but similar values of the coefficient b_t according to the parallelism and coincidence test (SAS Institute, 2002). The positive relationship between

coefficients b_t and k was significant but not as strong as that for shoot biomass ($R^2 = 0.60$; $P < 0.05$) (Eq. 10) (insert in Fig. 3b).

3.3. Nitrogen nutrition status

The N nutrition indices based on whole plants (NNI) ranged from 0.34 to 1.70 (Fig. 4). Across locations/years, cultivars, N rates, and sampling dates, the NNI_{sh} ranged from 0.30 to 1.67 (Appendix A and B). The NNI and NNI_{sh} increased with N fertilization and decreased during the growing season. The maximun NNI_{sh} was observed at vegetative and tuber initiation stages (40–60 DAP), while the minimum NNI_{sh} was observed at the tuber bulking stage (70–114 DAP). The NNI_{sh} generally decreased at the tuber bulking stage (Appendix A and B). The NNI_{sh} was < 1.0 in the treatments that received the least N fertilizer, because N deficiency caused early senescence in shoot biomass at the bulking tuber stage. The NNI_{sh} was highly related ($R^2 = 0.88$; $P < 0.05$) to the NNI measured during the growing season (Fig. 4a). For NNI < 1.0, the NNI_{sh} was proportional to NNI with almost all values around the y = x line but for NNI > 1.0, the NNI_{sh} underestimated NNI. The NNI_{sh} is therefore a useful tool to identify and quantify a N deficiency, but it may underestimate slightly the luxury N consumption. Furthermore, the non-linear relationship between NNI_{sh} and NNI suggests a $N\text{-}NO_3^-$ accumulation in shoots and possibly tubers when the NNI is greater than 1.0. The NNI_t ranged from 0.55 to 1.90 during the growing season (Appendix A and B). The NNI_t also increased with increasing N fertilization and was linearly related ($R^2 = 0.98$; $P < 0.05$) to the NNI during the growing season with values close to the the y = x line (Fig. 4b).

Average fresh tuber yields ranged from 25.3–59.6 Mg ha^{-1} in the Canadian experiment (Bélanger et al., 2000) and from 40.5 to 66.8 Mg ha^{-1} in the Argentinian experiment (Giletto and Echeverría, 2015). The ALCC equations describing the relationship between the relative tuber yield and NNI_{sh} or NNI_t were significant ($R^2 = 0.61$; $R^2 = 0.53$; $P < 0.05$; respectively). For a NNI_{sh} or NNI_t greater than 1.0, the relative tuber yield was near 95 % but the relative tuber yield decreased with decreasing NNI_{sh} or NNI_t below 1.0 (Fig. 5). Nitrogen nutrition indices determined in shoots and tubers therefore provide valuable information for the diagnosis of the crop N status of potato.

Across locations/years, cultivars, and N rates, the tuber N nutrition index at harvest (NNI_{tH}) ranged from 0.69 to 1.96 (Fig. 6). The NNI_{tH}
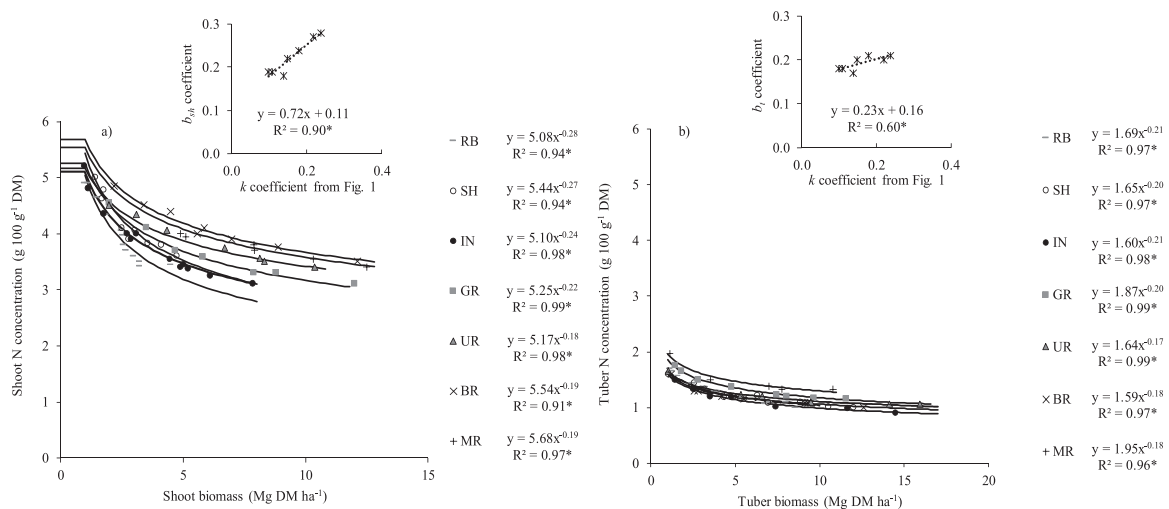
Fig. 3. Relationship between critical shoot N concentration and shoot biomass (a) and between critical tuber N concentration and tuber biomass (b) under non-limiting N and water conditions for all cultivars from the Canadian and Argentinian experiments. RB: Russet Burbank; SH: Shepody; IN: Innovator; GR: Gem Russet; UR: Umatilla Russet; BR: Bannock Russet; MR: Markies Russet. R^2 is the coefficient of determination. * indicate a significant function at $P < 0.05$. Inserts represent the relationship between values of the b_{sh} (Eq. (6)) and k (Eq. (10)) coefficients (3a) and between values of the b_t (Eq. (7)) and k (Eq. (10)) coefficients (3b).

was related with NNI_t measured during the growing season ($R^2 = 0.45$; $P < 0.05$). Across locations/years, cultivars, and N rates, tuber DM concentration ranged from 17.8 to 23.5 g DM 100 g^{-1} fresh matter and was negatively related to NNI_{tH} (Fig. 6a). Tuber N-NO$_3$- concentrations at harvest ranged from 2.2 to 254.7 mg kg^{-1} DM. The relationship between NNI_{tH} and tuber N-NO$_3$- concentration, expressed by an allometric function (Fig. 6b), indicates a significant increase in tuber N-NO$_3$- concentration for NNI_{tH} values above 1.0. For a NNI_{tH} value of 1.0, the estimated tuber DM concentration was 21.0 g DM 100 g^{-1} fresh matter and the estimated tuber N-NO$_3$- concentration was 40.2 mg kg^{-1} DM.

4. Discussion

### 4.1. Critical N dilution curves for shoots and tubers

The gradual decline in shoot N concentration with increasing potato shoot biomass (Fig. 3a) has been widely reported in several crop species including winter wheat, maize, and soybean (Justes et al., 1994; Ziadi et al., 2008; Divito et al., 2016). During the vegetative growth stage of potato, the constant N_{sh} value and the limited N dilution was attributed to the low competition among plants for light and available soil N due to the predominantly isolated growth of plants (Lemaire et al., 2008). The dilution of N with increasing shoot mass in isolated plants is known to be less pronounced than for plants in dense stands (Lemaire et al., 2008). However, the N dilution increases when the potato crop closes

the furrow and leaf shading increases. The shoot N dilution is due to two processes: self-shading of leaves (Lemaire et al., 1991; Lemaire and Chartier, 1992) and change in the leaf to shoot ratio during crop development (Lemaire et al., 1992). Furthermore, the proportion of cell wall constituents (cellulose and lignin) increases in stem tissues during aging and the N concentration simultaneously decreases when compared to that of leaf blades (Lemaire et al., 1992). Finally, senescence of older leaves due to intra and inter-plant competition for light and mineral nutrients is accompanied by N remobilization towards growing organs (Salette and Lemaire, 1981; Justes et al., 1994). The N dilution in potato shoots follows the classical pattern found in other crops (Duchenne et al., 1997; Lemaire and Gastal, 2009; Sadras and Lemaire, 2014) with a dilution coefficient equal to or smaller than that of other crop species that do not have a reserve compartment.

Values of the critical N concentration in shoots with a shoot biomass of 1 Mg DM ha^{-1}, estimated by the coefficient a_{sh} (5.08–5.68), were similar to the values of the coefficient a for the critical N concentration in the total biomass (4.50–5.53) in processing potato cultivars under non-limiting water conditions in Canada (Bélanger et al., 2001) and Argentina (Giletto and Echeverría, 2012, 2015). This similarity is likely due to the predominance of leaves during early growth of potato and the absence of tubers. The dilution coefficient for the shoot biomass (b_{sh}; 0.18 to 0.28), however, was less than the dilution coefficient for the total biomass (0.25 to 0.42) previously reported (Bélanger et al., 2001; Giletto and Echeverría, 2012, 2015). Values of the coefficient b_{sh} for shoot biomass, however, were significantly related to those of the
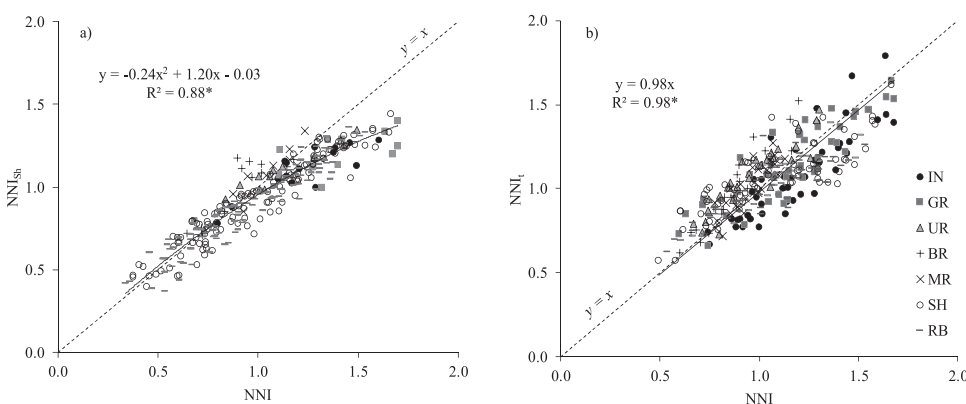
Fig. 4. Relationship of the shoot N nutrition index (NNI_{sh}) (a) and tuber N nutrition index (NNI_t) (b) with the whole plant N nutrition index (NNI) during the growing season (60-90 DAP) for all cultivars from the Canadian and Argentinian experiments. IN: Innovator; GR: Gem Russet; UR: Umatilla Russet; BR: Bannock Russet; MR: Markies Russet; SH; Shepody; RB: Russet Burbank. R^2 is the coefficient of determination. * indicates a significant regression function at $P < 0.05$.
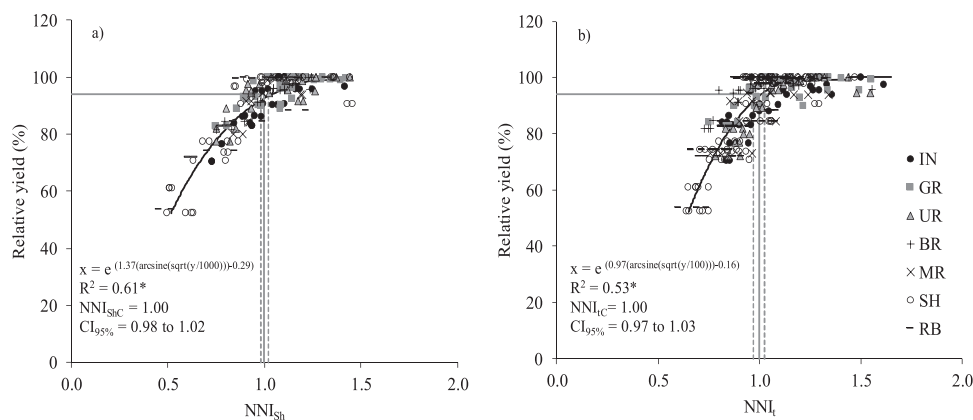
Fig. 5. Relationship of the relative yield with the shoot N nutrition index (NNI_{sh}) (a) and the tuber N nutrition index (NNI_t) determined at 60-90 DAP for all cultivars from the Canadian and Argentinian experiments. IN: Innovator; GR: Gem Russet; UR: Umatilla Russet; BR: Bannock Russet; MR: Markies Russet; SH; Shepody; RB: Russet Burbank. R^2 is the coefficient of determination. * indicates a significant Arcsine–Logarithm Calibration Curve at $P < 0.05$. Gray dotted lines represent 95 % confidence interval (CI95 %) for critical NNI_{sh} (NNI_{shC}) and NNI_t (NNI_{tC}) estimated by the modified arcsine-logarithm method.

coefficient b for the whole plant ($R^2 = 0.88$; $P < 0.05$). This result indicates that the whole plant N dilution is greater than shoot N dilution (Fig. 8). The greater dilution coefficient in whole plants is due to increasing presence of the tubers, a N-poor reserve component. In shoots, the metabolic and structural components and the change in their proportions during growth explain the decrease in N concentration.

The N_t concentration declined gradually with the growth of tuber biomass in all the cultivars (Fig. 3b). The decrease in tuber N concentration with increasing tuber biomass was previously described by Duchenne et al. (1997) but they did not provide a fitted equation to quantify this decrease. Their values ranged from 2.0 to 2.5 g 100 g^{-1} DM at the start of tuber initiation to around 1.0 g 100 g^{-1} DM at harvest, a range of values similar to that oberved in our study. Values of the critical N concentration in tubers with a tuber biomass of 1 Mg DM ha^{-1} (a_t; 1.59–1.95) were much lower than those in whole plants and in the shoot biomass because tuber N concentration is much lower than leaf and stem N concentrations (Kolbe and Beckmann, 1997; Gianquinto and Bona, 2000). Values of the coefficient b_t for tubers (0.17 to 0.21) were significantly related with those of the coefficient b in whole plants ($R^2 = 0.90$; $P < 0.05$) and in the shoot biomass (b_{sh}) ($R^2 = 0.77$; $P < 0.05$). The tuber N concentration decreased as the tuber biomass increased, but these changes were less pronounced than in shoot biomass (Fig. 8). In tubers, there is no strutural component. It is therefore likely that the reserve component increases faster than the metabolic component during growth and this would explain the decrease in tuber N concentration (Kolbe and Beckmann, 1997; Gianquinto and Bona, 2000).

Cultivars differed in their critical N dilution curves for shoots and tubers. Similar differences were observed at at the whole plant level for the same cultivars (Bélanger et al., 2001; Giletto and Echeverría, 2015). Therefore, if either shoots or tubers were to be used for a diagnostic test, critical N curves specific to each cultivar would be necessary.

4.2. Nitrogen nutrition status

Lemaire and Gastal (1997) proposed the use of the N nutrition index to quantify the intensity of both N deficiency and luxury consumption during the growing season. The usefulness of this index is emphasized by the fact that the relationship between the critical N concentration and crop mass does not vary substantially with major environmental factors, other than those affecting the soil N supply (Lemaire et al., 2008). All published critical N dilution curves of potato and the derived N nutrition indices have been based on whole plants that included both shoots and tubers (Greenwood et al., 1990; Duchenne et al., 1997; Bélanger et al., 2001; Goffart et al., 2008; Giletto and Echeverría, 2015; Stanislav Magnitskiy and Rodríguez, 2019). Our results indicate that the N nutrition index based on potato shoots (NNI_{sh}) can also be used to identify and quantify differences in crop N status from 60 to 90 DAP, a period of high daily nutrient absorption (Horneck and Rosen, 2008) when the crop begins to manifest N deficiencies. This result confirms the link between shoot N uptake and potato yield and, thus, the pertinence of NNI_{sh} for forecasting the actual yield (Chambenoit et al., 2004). The determination of NNI_{sh} during the active growth period of potato could help optimize the N application time in order to adjust the N supply to the N demand of the crop. These results provide evidence for monitoring the crop N status with NNI_{sh} because it would be less time consuming and cheaper than using the N nutrition index based on whole plants. Moreover, we also established that NNI_t from 60 to 90 DAP can be used to quantify a N deficiency because of its close relationship to relative tuber yield. Further research should focus on investigating whether the N nutrition index in specific organs (shoots or tubers) can be used to determine threshold values for N sufficiency with other N diagnostic tools (e.g. SPAD, remote sensing, nitrate in petiole, and N in leaf).

Our results also provide the first evidence of the possibility of using the N nutrition index based on potato tubers at harvest (NNI_{tH}) for assessing the risks of poor tuber quality. The relationship between the
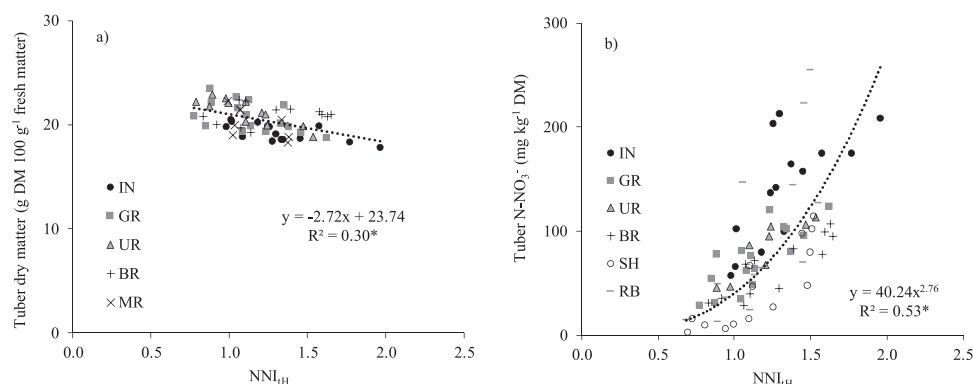
Fig. 6. Relationship of the tuber dry matter concentration (a) and the tuber N-NO_3^- concentration (b) with the tuber N nutrition index at harvest (NNI_{tH}) for all cultivars from the Canadian and Argentinian experiments. IN: Innovator; GR: Gem Russet; UR: Umatilla Russet; BR: Bannock Russet; MR: Markies Russet. R^2 is the coefficient of determination. * indicates a significant regression function at $P < 0.05$. The tuber dry matter concentration was not determined in the Canadian experiment and the tuber N-NO_3^- concentration of the cultivar Markies Russet in the Argentinian experiment was not determined.

tuber N concentration at harvest and two attributes of tuber quality, the specific gravity used as an estimate of tuber DM concentration and tuber nitrate concentration, was previously reported by Bélanger et al. (2002). We went a step further by calculating a N nutrition index for tubers at harvest, which had never been done before. We showed that it was significantly related to the two attributes of tuber quality. The possibility of using the N nutrition index based on potato tubers at harvest for predicting attributes of tuber quality has never been explored. Validation of this approach and its practical use require more research.

4.3. The role of the tubers on N dilution in potatoes

Our results showed that the biomass partitioning to tubers, characterized by the values of the coefficients k and c, differed among cultivars. Both coefficients varied with cultivars but the variation in the coefficient k was proportionnaly greater than that of the coefficient c. Values of coefficient k were significantly related to the dilution coefficients of the whole plant N dilution. The coefficient k represents the intrinsic aptitude of the cultivars to partition biomass to the tubers. Cultivars that partitioned a greater proportion of their biomass to tubers had a greater whole plant dilution. This result on cultivar differences confirms the role of tubers, a reserve compartment, in whole plant N dilution. The role of tubers in whole plant N dilution can also be seen by considering N uptake. From Eq. (1), the relationship between total N uptake (N_{upt}) and total biomass (W) or between shoot N uptake ($N_{sh\text{-}upt}$) and shoots biomass (W_{sh}) can be derived as follows:

$$N_{upt} = a´W^{1-b} \tag{11}$$

$$N_{sh\text{-}upt} = a´´W_{sh}^{1-b} \tag{12}$$

The coefficient $a´$ corresponds to the N_{upt} values for W = 1 Mg DM ha^{-1} and the coefficient $a´´$ corresponds to the $N_{sh\text{-}upt}$ value for W_{sh} = 1 Mg DM ha^{-1}. The allometric coefficient $1\text{-}b$ corresponds to the ratio between the relative N uptake rate and the relative growth rate of the crop.

Relationships between total N uptake and total biomass (shoots + tubes), and between shoot N uptake and shoot biomass were analyzed in ln-scales (Fig. 7) so that linear regressions could be used. The coefficient $1\text{-}b$, corresponding to the slope of this linear relationship, changed with the level of biomass. The period from emergence until tuber initiation (vegetative stage), that is the period when potato plants can be considered as nearly isolated, the coefficient $1\text{-}b$ was 0.92. In that period, the plants grew only in two dimensions, that is in area but not in height or in thickness (Lemaire and Gastal, 2009). During the period from tuber initiation until maturation (bulking tuber stage), the canopy closed the furrow and the coefficient $1\text{-}b$ declined from 0.92 to 0.86 for shoot N uptake with increasing shoot biomass (Fig. 7b), while it declined from 0.92 to 0.66 for N uptake in the total biomass with increasing total biomass (Fig. 7a). When comparing the two stages of
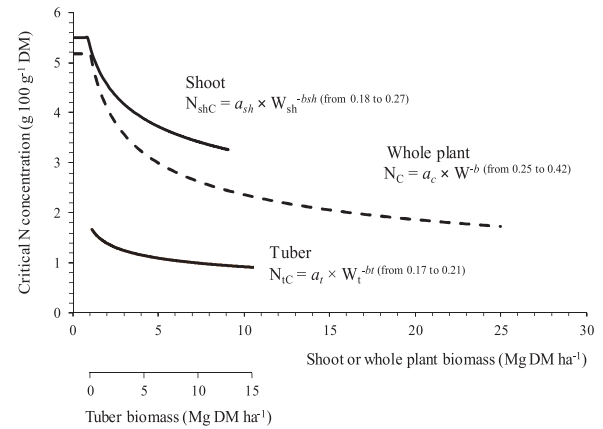

Fig. 8. Schematic representation of critical N dilution curves based on whole plant, shoot, and tuber biomass. The range of values of the coefficient b among cultivars is presented for shoots, tubers, and whole plants.

growth, the variation between the coefficients $1\text{-}b$ was significantly greater for total biomass (0.92 vs. 0.66) that for shoot biomass (0.92 vs 0.86). This result demonstrates that the biomass partitioning to tubers affect the whole plant N dilution.

The relationship between tuber biomass and the total biomass in whole plants commonly followed well defined allometric trajectories (Fig. 1) (Weiner, 2004). The tubers used an increasing proportion of C when the amount of C in whole plant increased. Therefore, the allocation of mass between tubers and shoots (tubers to shoot ratio) increases with plant ontogeny. The growing potato tubers influenced the N dilution coefficient because of the great contribution of the tubers to the total weight of the plants. The pattern of N dilution in potato whole plants is caused by the relative increase of the fraction of storage tubers with respect to the total biomass and the simultaneous decline of N concentration in shoots and tubers (Fig. 8).

5. Conclusions

Critical shoot and tuber N dilution curves of potato were determined from data obtained across different environments and cultivars under non-limiting water conditions. Nitrogen dilution occurrred in both shoots and tubers but the estimated parameters of the dilution curves differed for shoots and tubers. The critical shoot and tuber N dilution curves also differed from the critical N dilution curves based on whole plants (shoots + tubers). The N nutrition índices calculated from the critical shoot and tuber N dilution curves, however, were closely related to the N nutrition index calculated from the critical N dilution curves based on whole plants. Indices of N nutrition calculated from the critical shoot (NNI_{sh}) and tuber (NNI_t) N dilution curves identified adequately situations of deficient and non-deficient N nutrition in potato
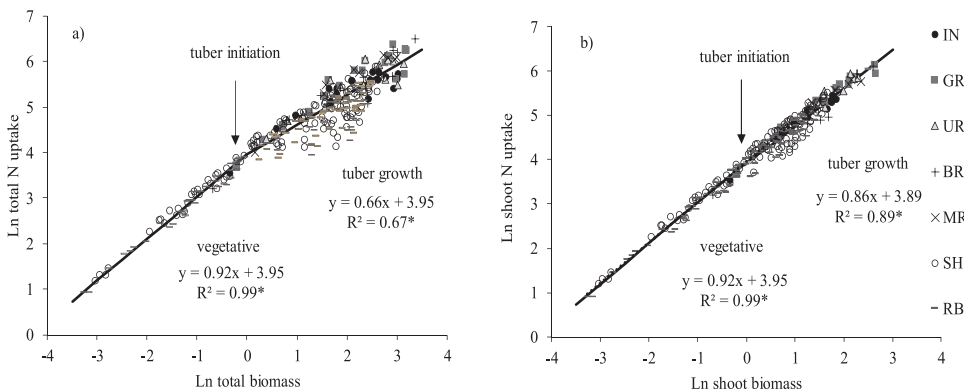

Fig. 7. Relationships between total N uptake and total biomass (a) and between shoot N uptake and shoot biomass (b) in a ln scale. Data were averaged over 40-90 dap sampling dates for all cultivars from the Canadian and Argentinian experiments. IN: Innovator; GR: Gem Russet; UR: Umatilla Russet; BR: Bannock Russet; MR: Markies Russet; SH; Shepody; RB: Russet Burbank. R^2 is the coefficient of determination. * indicates a significant regression function at $P < 0.05$.

cultivars. The tuber N nutrition index at harvest was also closely related to two attributes of potato quality: DM and nitrate concentrations. The role of tubers, a reserve compartment, in whole plant N dilution was also clearly demonstrated. These new findings provide information that will be useful (i) to increase N use efficiency of potato production systems, (ii) to open new opportunities to investigate the relationship between whole plant N nutrition indexes and other N diagnostic tools (SPAD, remote sensing, nitrate in petiole, and N in leaf) under varying sampling times, management practices, and environmental conditions, and iii) to investigate attributes of tuber quality affected by N fertilization.

Declaration of Competing Interest

The authors have no competing interests to declare.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.eja.2020.126114.

References

Ata-Ul-Karim, S.T., Liu, X., Lu, Z., Zheng, H., Cao, W., Zhu, Y., 2017. Estimation of nitrogen fertilizer requirement for rice crop using critical nitrogen dilution curve. Field Crops Res. 201, 32–40. https://doi.org/10.1016/j.fcr.2016.10.009.

Bélanger, G., Walsh, J.R., Richards, J.E., Milburn, P.H., Ziadi, N., 2000. Yield response of two potato cultivars to supplemental irrigation and N fertilization in New Brunswick. Am. J. Potato Res. 77, 11–21. https://doi.org/10.1007/BF02853657.

Bélanger, G., Walsh, J.R., Richards, J.E., Milburn, P.H., Ziadi, N., 2001. Critical nitrogen curve and nitrogen nutrition index for potato in eastern Canada. Am. J. Potato Res. 78, 355–364. https://doi.org/10.1007/BF02884344.

Bélanger, G., Walsh, J.R., Richards, J.E., Milburn, P.H., Ziadi, N., 2002. Nitrogen fertilization and irrigation affects tuber characteristics of two potato cultivars. Am. J. Potato Res. 79, 269–279. https://doi.org/10.1007/BF02986360.

Bélanger, G., Walsh, J.R., Richards, J.E., Milburn, P.H., Ziadi, N., 2003. Residual soil nitrate after potato harvest. J. Environ. Qual. 32, 607–612. https://doi.org/10.2134/jeq2003.6070.

Caloin, M., Yu, O., 1984. Analysis of the time course change in nitrogen content of *Dactylis glomerata* L. using a model of plant growth. Ann. Bot. 54, 69–76. https://doi.org/10.1093/oxfordjournals.aob.a086775.

Chambenoit, C., Laurent, V., Machet, J.M., Boizard, H., 2004. Development of a decision support system for nitrogen management on potatoes. In: Mackerron, D.K.L., Haverkort, A.J. (Eds.), Decision Support Systems in Potato Production, pp. 55–67 The Netherlands, Wageningen.

Colnenne, C., Meynard, J.M., Reau, R., Justes, E., Merrien, A., 1998. Determination of a critical nitrogen dilution curve for winter oilseed rape. Ann. Bot. 81, 311–317. https://doi.org/10.1006/anbo.1997.0557.

Correndo, A.A., Salvagiotti, F., García, F.O., Gutiérrez-Boem, F.H., 2017. A modification of the arcsine–log calibration curve for analyzing soil test value–relative yield relationships. Crop Pasture Sci. 68, 297–304. https://doi.org/10.1071/CP16444.

Divito, G., Echeverría, H.E., Andrade, F.H., Sadras, V.O., 2016. Soybean shows an attenuated nitrogen dilution curve irrespective of maturity group and sowing date. Field Crops Res. 186, 1–9. https://doi.org/10.1016/j.fcr.2015.11.004.

Dow, A.I., Roberts, S., 1982. Proposal: critical nutrients ranges for crops diagnosis. Agron. J. 74, 401–403.

Duchenne, T., Machet, J.M., Martin, M., 1997. Potatoes. In: Lemaire, G. (Ed.), Diagnosis of the Nitrogen Status in Crops. Springer-Verlag, Berlin, Germany, pp. 119–130.

Dyson, C.B., Conyers, M.K., 2013. Methodology for online biometric analysis of soil test–crop response datasets. Crop Pasture Sci. 64 (5), 435–441. https://doi.org/10.1071/CP13009.

Gastal, F., Lemaire, G., Durand, J.L., Louarn, G., 2015. Quantifying crop responses to nitrogen and avenues to improve nitrogen-use efficiency. Chapter 8. Crop Phys. https://doi.org/10.1016/B978-0-12-417104-6.00008-X.

Gianquinto, G., Bona, S., 2000. The significance of trends in concentrations of total nitrogen and nitrogenous compounds. In: Haverkort, A.J., Mackerron, D.K.L. (Eds.), Management of Nitrogen and Water in Potato Production, pp. 35–53 Wageningen, The Netherlands.

Giletto, C.M., Echeverría, H.E., 2012. Critical nitrogen dilution curve for processing potato in Argentinean humid pampas. Am. J. Potato Res. 89, 102–110. https://doi.org/10.1007/s12230-011-9226-z.

Giletto, C.M., Echeverría, H.E., 2015. Critical nitrogen dilution curve in processing potato cultivars. Am. J. Plant Sc. 6 (19), 3144–3156. https://doi.org/10.4236/ajps.2015.619306.

Goffart, J.P., Oliver, M., Frankinet, M., 2008. Potato crop nitrogen status assessment to improve N fertilization management and efficiency: past-present–future. Potato Res. 51, 355–383. https://doi.org/10.1007/s11540-008-9118-x.

Greenwood, D.J., Lemaire, G., Gosse, G., Cruz, P., Draycott, A., Neeteson, J.J., 1990.

Decline in percentage N of C3 and C4 crops with increasing plant mass. Ann. Bot. 66, 425–436. https://doi.org/10.1093/oxfordjournals.aob.a088044.

Horneck, D., Rosen, C., 2008. Measuring nutrient accumulation rates of potatoes – tools for better management. Better Crops Plant Food 92, 4–6.

Justes, E., Mary, B., Meynard, J.M., Machet, J.M., Thelier-Huché, L., 1994. Determination of a critical nitrogen dilution curve for winter wheat crops. Ann. Bot. 74, 397–407. https://doi.org/10.1006/anbo.1994.1133.

Keeney, D.R., Nelson, D.W., et al., 1982. Nitrogen inorganic forms. In: Page, A.L. (Ed.), Methods of Soil Analysis. Part 2. Agron. Monog. 9. ASA and SSSA, Madison, WI, pp. 643–698.

Kleinkopf, G.E., Westermann, D.T., Dwelle, R.B., 1981. Dry matter production and nitrogen utilization by six potato cultivars. Agron. J. 73, 799–802. https://doi.org/10.2134/agronj1981.00021962007300050013x.

Kolbe, H., Beckmann, S.S., 1997. Development, growth and chemical composition of the potato crop (*Solanum tuberosum* L.). II. Tuber and whole plant. Potato Res. 40, 135–153. https://doi.org/10.1007/BF02358240.

Lemaire, G., Chartier, M., 1992. Relationships between growth dynamics and nitrogen uptake for individual sorghum plants growing at different densities. In: Congress, UK. Proceedings of the 2nd ESA 92. pp. 98–99.

Lemaire, G., Gastal, F., 1997. N uptake and distribution in plant canopies. In: Lemaire, G. (Ed.), Diagnosis of the Nitrogen Status in Crops. Springer-Verlag, Berlin, Germany, pp. 3–43.

Lemaire, G., Gastal, F., 2009. Quantifying crop responses to nitrogen deficiency and avenues to improve nitrogen use efficiency. In: Sadras, V.O., Calderini, D.F. (Eds.), Crop Phys. Elsevier, pp. 171–211.

Lemaire, G., Salette, J., 1984. Relationship between growth and nitrogen uptake in a pure grass stand: I, Environmental effects. Agronomie 4, 423–430.

Lemaire, G., Onillon, B., Gosse, G., Chartier, M., Allirand, J.M., 1991. Nitrogen distribution within a lucerne canopy during regrowth: relation with light distribution. Ann. Bot. 68, 483–488. https://doi.org/10.1093/oxfordjournals.aob.a088286.

Lemaire, G., Khaity, M., Onillon, B., Allirand, J.M., Chartier, M., Gosse, G., 1992. Dynamics of accumulation and partitioning of N in leaves, stems, and roots of lucerne (*Medicago sativa*) in a dense canopy. Ann. Bot. 70, 429–435. https://doi.org/10.1093/oxfordjournals.aob.a088499.

Lemaire, G., Jeuffroy, M.H., Gastal, F., 2008. Diagnosis tool for plant and crop N status in vegetative stage. Theory and practices for crop N management. Eur. J. Agric. 28, 614–624. https://doi.org/10.1016/j.eja.2008.01.005.

Lemaire, G., Sinclair, T., Sadras, V., Bélanger, G., 2019. Allometric approach to crop nutrition and implications for crop diagnosis and phenotyping. A review. Agron. Sustain. Dev. 39 (27), 1–17. https://doi.org/10.1007/s13593-019-0570-6.

Littell, R.C., Freund, R.J., Spector, P.C., 1991. SAS System for Linear Models, 3rd edition. SAS Inst., Cary.

R Core Team, 2014. R, a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (Accessed 18 October 2017). http://www.R-project.org.

Sadras, V.O., Lemaire, G., 2014. Quantifying crop nitrogen status for comparisons of agronomic practices and genotypes. Field Crops Res. 164, 54–64. https://doi.org/10.1016/j.fcr.2014.05.006. 0378-4290/ā.

Salette, J., Lemaire, G., 1981. Sur la variation de la teneur en azote des graminées fourragères pendant leur croissance: formulaton d'une loi de dilution. C. R. Séances Acad. Sci. Paris 292, 875–878.

SAS Institute, 2002. The SAS System for Windows. Release Version 9.0. SAS Inst., Cary, NC.

Schroder, J.J., Neeteson, J.J., Oenema, O., Struik, P.C., 2000. Does the crop or soil indicate how to save nitrogen in maize production? Reviewing the state of art. Field Crops Res. 66, 151–164. https://doi.org/10.1016/S0378-4290(00)00072-1.

Sheehy, J.E., Dionora, M.J.A., Mitchell, P.L., Peng, S., Cassman, K.G., Lemaire, G., Williams, R.L., 1998. Critical nitrogen concentrations: implications for high-yielding rice (*Oryza sativa* L.) cultivars in the tropics. Field Crops Res. 59, 31–41. https://doi.org/10.1016/S0378-4290(98)00105-1.

Stanislav Magnitskiy, M.I., Rodríguez, L.E., 2019. Critical dilution curves for nitrogen, phosphorus, and potassium in potato group Andigenum. Agron. J. 111, 419–427. https://doi.org/10.2134/agronj2018.05.0357.

Tei, F., Benincasa, P., Guiducci, M., 2002. Critical nitrogen concentration in processing tomato. Eur. J. Agron. 18, 45–55. https://doi.org/10.1016/S1161-0301(02)00096-5.

Ulrich, A., 1996. Potato. In: Bennett, W.F. (Ed.), Nutrient Deficiencies and Toxicities in Crop Plants. APS Press, Lubbock. Texas, pp. 149–156.

Van Oosterom, E.J., Carberry, P.S., Muchow, R.C., 2001. Critical and minimum N contents for development and growth of grain sorghum. Field Crops Res. 70, 55–73. https://doi.org/10.1016/S0378-4290(00)00152-0.

Vos, J., 2009. Nitrogen responses and nitrogen management in potato. Potato Res. 52, 305–317. https://doi.org/10.1007/s11540-009-9145-2.

Weiner, J., 2004. Allocation, plasticity and allometry in plants. Perspectives in Plant Ecology, Evolution and Systematics. pp. 206–215 6/4.

Westermann, D.T., 1993. Fertility management. In: Rowe, R.C. (Ed.), Potato. Health Management, Minnesota, USA, pp. 77–86.

Weymann, W., Sieling, K., Kage, H., 2016. Organ-specific approaches describing crop growth of winter oilseed rape under optimal and N-limited conditions. Eur. J. Agron. 82, 71–79. https://doi.org/10.1016/j.eja.2016.10.005.

Yao, X., Ata-Ul-Karim, S.T., Zhu, Y., Tian, Y., Liu, X., Cao, W., 2014a. Development of critical nitrogen dilution curve in rice based on leaf dry matter. Eur. J. Agron. 55, 20–28. https://doi.org/10.1016/j.eja.2013.12.004.

Yao, X., Zhao, B., Tian, Y.C., Liu, X.J., Ni, J., Cao, W.X., Zhu, Y., 2014b. Using leaf dry matter to quantify the critical nitrogen dilution curve for winter wheat cultivated in eastern China. Field Crops Res. 159, 33–42. https://doi.org/10.1016/j.fcr.2013.12.007.

Yue, S., Meng, Q., Zhao, R., Li, F., Chen, X., Zhang, F., Cui, Z., 2012. Critical nitrogen dilution curve for optimizing nitrogen management of winter wheat production in the North China Plain. Agron. J. 104, 523–529. https://doi.org/10.2134/agronj2011.0258.

Zebarth, B.J., Bélanger, G., Cambouris, A.N., Ziadi, N., 2012. Nitrogen fertilization strategies in relation to potato tuber yield, quality and crop N recovery. In: Zhonggi, H., Larkin, R., Honeycutt, W. (Eds.), Sustainable Potato Production: Global Case Studies. Springer, USA, pp. 165–186.

Zhao, B., 2014. Determining of a critical dilution curve for plant nitrogen concentration in winter barley. Field Crops Res. 208, 60–68. https://doi.org/10.1016/j.fcr.2014.02.016.

Zhao, B., Ata-UI-Karim, S.T., Yao, X., Tian, Y., Cao, W., Zhu, Y., Liu, X., 2016. A new curve of critical nitrogen concentration based on spike dry matter for winter wheat in Eastern China. PLoS One 11 (10), e0164545. https://doi.org/10.1371/journal.pone.0164545.

Ziadi, N., Brassard, M., Bélanger, G., Cambouris, A.N., Tremblay, N., Nolin, M.C., Claessens, A., Parent, L., 2008. Critical nitrogen curve and nitrogen nutrition index for corn in Eastern Canada. Agron. J. 100, 271–276. https://doi.org/10.2134/2007.0059.

Ziadi, N., Bélanger, G., Claessens, A., Lefebvre, L., Cambouris, A.N., Tremblay, N., Nolin, M.C., Étienne, L., 2010. Determination of a critical nitrogen dilution curve for spring wheat. Agron. J. 102, 241–250. https://doi.org/10.2134/agronj2009.0266.

Ziadi, N., Zebarth, B.J., Belanger, G., Cambouris, A.N., 2012. Soil and plant tests to optimize fertilizer nitrogen management of potato. In: Zhonggi, H., Larkin, R., Honeycutt, W. (Eds.), Sustainable Potato Production: Global Case Studies, pp. 187–207 USA.