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Quantifying critical N dilution curves across G × E × M effects for potato using a partially-pooled Bayesian hierarchical method
--Manuscript Draft--

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Abstract:	Multiple critical N dilution curves [CNDCs] have been previously developed for potato; however, attempts to directly compare differences in CNDCs across genotype [G], environment [E], and management [M] interactions have been confounded by non-uniform statistical methods, biased experimental data, and lack of proper quantification of uncertainty in the critical N concentration [%N _c]. This study implements a partially-pooled Bayesian hierarchical method to develop CNDCs for previously published and newly reported experimental data, systematically evaluates the difference in %N _c [$\Delta\%$ N _c] across G × E × M effects, and directly compare CNDCs from the Bayesian framework to CNDCs from conventional statistical methods. The partially-pooled Bayesian hierarchical method implemented in this study has the advantage of being less susceptible to inferential bias at the level of individual G × E × M interactions compared to alternative statistical methods that result from insufficient quantity and quality of experimental datasets (e.g., unbalanced distribution of N limiting and non-N limiting observations). This method also allows for a direct statistical comparison of differences in %N _c across levels of the G × E × M interactions. Where found to be significant, $\Delta\%$ N _c was hypothesized to be related to variation in the timing of tuber initiation (e.g., maturity class) and the relative rate of tuber bulking (e.g., planting density) across G × E × M interactions. In addition to using the median value for %N _c (i.e., CNDC), the lower and upper boundary values for the credible region (i.e., CNDC _{lo} and CNDC _{up}) derived using the Bayesian framework should be used in calculation of N nutrition index (and other calculations) to account for uncertainty in %N _c . Overall, this study provides additional evidence that %N _c is dependent upon G × E × M interactions; therefore, evaluation of crop N status or N use efficiency must account for variation in %N _c across G × E × M interactions.
Suggested Reviewers:	Ignacio Ciampitti ciampitti@ksu.edu Dr. Ciampitti has authored a number of studies on similar topics to this manuscript and would be an excellent reviewer/editor.

	<p>Gilles Lemaire gilles.lemaire.inra@gmail.com Dr. Lemaire has authored a number of studies on similar topics to this manuscript and would be an excellent reviewer.</p>
	<p>David Makowski makowski@grignon.inra.fr Dr. Makowski has authored a number of studies on similar topics to this manuscript and would be an excellent reviewer.</p>
	<p>Javier Fernández jafernandez@ksu.edu Dr. Fernández has authored a number of studies on similar topics to this manuscript and would be an excellent reviewer.</p>
	<p>Victor Sadras victor.sadras@sa.gov.au Dr. Sadras has authored a number of studies on similar topics to this manuscript and would be an excellent reviewer.</p>

23 November 2022

To the Reviewers:

We would like to thank the two reviewers of this manuscript for their careful consideration of our work and helpful suggestions for improvement. In the revised manuscript we are resubmitting, we have addressed every reviewer comment in the manner specified below. Note that all of our references to manuscript line number in this letter refer to the original manuscript submission.

Reviewers' comments:

Reviewer #1:

This paper presents and discuss a new method for estimating Critical Nitrogen Dilution Curve for potatoes. Authors have pooled a large data set from different countries, Argentina, Canada and Belgium with different cultivars, and by using a Bayesian statistical approach they analysed the uncertainty of CNDC parameter determination and tried to infer on variation across Genotype-Environment-Management conditions. The manuscript is very well written and very well organized. As said by authors the use of Bayesian method for CNDC uncertainty analysis is not fully original, but they used this method very accurately and they proposed a new approach of partial pooling for a better analysis of G-E-M effects. So this manuscript is a very original and relevant contribution to crop N diagnosis problem. As I am not an expert in statistics, I cannot provide any comments on this part of the work. I guess that reviewing this manuscript by an expert in statistics and more particularly in Bayesian approach would be important. So our reviewing focus on agronomic and physiological interpretation.

The problem of "N dilution" process in crop having a strong "reserve" compartment as grain or tuber has been perfectly identified and discussed in introduction by authors. The "N dilution" model, originally developed on forage crop... only concern with plants in vegetative growth: producing only leaves and stems.... It was the reason why CNDC were limited in theory to flowering stage or just to early reproductive development when "grain biomass" was not too high... For taking into account grain or tuber growth... it should be necessary to have a two step N dilution (i) during vegetative growth ... with a given allometry coefficient "b1" reflecting the biomass allocation to "metabolic" and "structural" compartment...; and (ii) during grain or tuber filling reflecting C-N remobilisation from vegetative part and filling grain and tuber...with a more or less different value of allometry "b2" depending on the C-N ratio of grain or tuber accumulated. So "b2" being >> "b1" for grain and tuber accumulating preferentially starch (as for potatoes) or more or less = o r< b1 for grain accumulating preferentially proteins such as grain legumes... So it is clear that representing a single CNDC with a constant allometry "b"... while there is in fact a "break" in dilution process from "b1" to "b2".... is a problem... This problem is not so important statistically if b1 and b2 are not very differents... but becomes very

important when they are very different as for potatoes. So the best way for showing this "break" in CNDC and to determine when this break occurs would be to represent CNDC in Log-Log term... So I suggest authors to illustrate that and to determine at which extent variation in the "break time" on the "crop biomass axis... would depend on G-E-M ? I think Giletto et al. (see their paper in EJA) have already well analysed this problem in Argentina? So it should be easy to this group of authors to deep this question. They can also refers to analogous work made on maize and wheat (ZHAO, B., ATA UL KARIM, S., T., LEMAIRE G.. DUAN, A., LIU, Z., GUO, Y., QIN, A., NING, D., LIU, Z., 2021. Exploring the source-sink relationship to quantify ear nitrogen accumulation in summer maize and winter wheat using critical nitrogen dilution curve. Field Crop Research, 274. <https://doi.org/10.1016/j.fcr.2021.108332>). By this way their comparison with "other crops" should be more complete because in their manuscript they compare CNDC of potatoes including tuber filling process with other crops where CNDC was limited to "vegetative period"!!! So for potatoes, if G-E-M interaction has an impact on the onset of the change from b1 to b2 (as the start of tuber development)...as a consequence it should have an impact on the "average" CNDC fitted with a constant "b"!!! So it should be important to verify this hypothesis: has G-E-M an effect of both b1 or b2 separately...? or has G-E-M has only an effect of the onset of change from b1 to b2 ? That would be a more fundamental question?

So my conclusion is that this excellent manuscript should be accepted for publication... But I suggest authors to improve its scientific value by adding some informations on "b1" and b2" for being able to discuss more strongly the hypothesis above.

- We agree that the proposed approach suggestion by Reviewer 1 is an extremely valuable and a key question for future research to consider; however, we find that this analysis would fall outside the scope of this manuscript. Given the suggestion from Reviewer 2 to focus and reduce the length of this manuscript, we have limited our discussion of this suggestion from Reviewer 1 to a paragraph in a new Section 4.1.4. We look forward to addressing this research question in a subsequent publication.

Details:

- Line 67: *No, NNI is very sensible to any fertilization management...as it detect any effect on plant N nutrition status....*
 - Change made here as suggested to clarify and correct statement.
- Line 76: *No, b is the ration between relative rate of %N decline $(d\%N)/(\%N)dt$ and the relative rate of biomass accumulation dW/Wdt that is different of the rate of %N decline $(d(\%N)/dt$*
 - Change made here as suggested to clarify and correct statement.
- Line 92: *add "Acceleration" of dilution....*

- Change made here as suggested to clarify and correct statement.
- *Line 189: "reduce" is repeated two time....*
 - Change made here as suggested to clarify and correct statement.

Reviewer #2:

This study advances on the use of Bayesian hierarchical frameworks to develop critical N dilution curves introducing a partial pooling approach through random components. This could represent a useful alternative for comparing CNDCs across G × E × M conditions. Moreover, it could be further extended for developing critical N dilution curves of potato but also potentially of other crops. I found it interesting to read and review, which makes me think it would be very relevant for EJA journal.

I also found the paper excessively (and unnecessary) long in several sections, so my first main suggestion is to reduce the length of the manuscript reorganizing paragraphs and ideas. I identified below several sections and paragraphs where this could be done. Similarly, I would suggest reducing the number of figures considering the complexity of the methodology and number of panels. I believe the paper will have more impact if ideas (including figures) are more succinct.

- We have addressed this main comment as described in the specific comments below.

My second main suggestion is on one of the methodologies used and (at some point) recommended to evaluate uncertainty in the CNDC. This should be addressed before publication. See below specific comments related to this in LI423 & LI524.

- We have addressed this main comment as described in the specific comments below.

Specific comments:

- *LI28: "was attributed to variation" is a statement that cannot be confirmed with this analysis due to the lack of factorial combinations of the G (maturity classes) × M (plant density) at each site (i.e., E). It would be better to claim "was hypothesized".*
 - Change made here as suggested to clarify and correct statement.
- *LI59-62: no need to go back to the rate-response approach as the paper is not about it, could be removed.*
 - Change made here as suggested to remove this reference.

- *L182-114: I think this section can be largely summarized in a single paragraph. This paper is more about the methodology of fitting and quantifying uncertainty in CNDC, so only a brief overview of the dilution theory + use in potato is needed.*
 - This paper is focused both on the methodology of fitting and quantifying uncertainty in CNDC as well as understanding the particular mechanisms of N dilution for potato across G x E x M factors. The comments by Reviewer 1 highlight the need for this key background information in the Introduction section, with respect to understanding the mechanism of dilution across G x E x M factors. Therefore, we have not made this change as suggested by Reviewer 2.
- *L117-118: this is a good example of the type of "expensive" writing used along the paper that makes it hard to read... "Previous development of CNDCs for potato has been conducted using a non-uniform set of statistical methods and with limited quantification of uncertainty in either the range of plausible %Nc values or the fitted parameter values themselves" can be rephrased with the same meaning by "Previous CNDCs for potato have been developed with different statistical methods and limited quantification of their uncertainty." Simplifying sentences would not only reduce the length of the paper but also increase the impact of each message. I would recommend considering this point when re-organizing ideas.*
 - Change made here as suggested to simplify this statement.
- *L126-127 & 133-134: These three paragraphs can be combined into one, no need for break lines*
 - Change made here as suggested to consolidate paragraphs.
- *L141: "linear plateau was designed to discriminate against" Not clear. In the paragraph above, it was claimed that the linear plateau cannot address these exact two points?*
 - Change made here as suggested to delete this phrase to clarify and correct statement.
- *L166-192: Should be combined into a single paragraph.*
 - Change made here as suggested to consolidate paragraphs.
- *Tables 2, 3 and 4 can be combined into one. Table 1 can be combined within Table 2-3-4 and Table 5. Will then need only two tables.*

- Change made here to combine Tables 2, 3, and 4 into a new Table 2. Thank you for the excellent suggestion for simplification! It is not clear, however, how further combining Table 1, Table 2-3-4, and Table 5 can be done to simplify data presentation; therefore, we have kept three tables, instead of two as suggested.
- *L1273: Is confusing referring here as "experimental" data, considering the first set of sites were classified as "Experimental" vs "Prev. published". Can consider the use of terms here.*
 - Change made here as suggested to clarify and correct statement.
- *Section 2.1.2. I suggest using the Tables to report detailed information of these experiments, considering detailed information has been already reported in previous publications. Can use text to report only data that is not in Table, such as location site.*
 - Changes have been made to Section 2.1.2. and Table 5 as suggested. Another excellent suggestion by the reviewer for simplification!
- *L1336-347: Is this paragraph needed? Most of this has been mentioned in the introduction. Same with figure 1, I think it is not a critical figure of the manuscript and could be removed?*
 - Changes have been made as suggested to remove this paragraph and Figure 1.
- *L1391: What about replicates? How they were treated in the model?*
 - Changes have been made to clarify that models were fit using treatment-level means and replicates were not included in model hierarchical structure. Data at replicate level was not available for all experimental trials.
- *L1395: Convergence checks? I assume they were conducted, please add.*
 - Change made here to clarify and describe methods used.
- *L1397: "biologically or physically impossible predictions" not sure what that means.*
 - Change made here as suggested to clarify and explain statement.
- *L1401: What about priors for the random effects variances? it looks to me that the priors from Table 6 are very informative and could constrain parameters to a short range of variation, but according to the results, there seems less restriction on priors for the random effects? This can be tested through a sensitivity analysis with less informative prior distributions.*

- Change made here as suggested to clarify and explain the need for informative priors for random effect variances, specifically related to ensuring joint prior predictive distribution was biologically and physically plausible as well due to propagation of variance in joint prior predictive distribution in hierarchical models.
- *LI405: This is great addition and authors should be congratulated for this.*
 - We thank the reviewer for their recognition of this!
- *LI423: I am not sure I understood this, but this might not be correct. Did you fit a new model (and frequentist?) to the data estimated by the parameters of the 90% credible limits of the Bayesian curves? There is circularity in this approach, and not sure why it was done.*
 - The reviewer's interpretation of our method as described above is correct. This step was done to create parameterized estimates of the 90% credible region. While the 90% credible region as determined from the posterior distribution of the fitted Bayesian hierarchical model is most appropriate to use, it is very difficult to communicate the 90% credible region in this manner (i.e., non-parameterized, requires very large model object). Without parameterized estimates of the upper and lower boundary of the 90% credible region, then it is very difficult to propagate uncertainty in %Nc to derivative computations (i.e., calculating NNI). This is discussed in Section 4.3. of the original manuscript. Additional description of the methods has been added to this section.
- *LI436: The definition of delta%Nc is not clear. This is a very complex and long sentence, but critical to understand the paper. What is "the difference between the 0.50 quantile for %Nc and the various methods to quantify uncertainty (i.e., 90% credible region for %Nc, CND_{Cup} & CND_{clo}, and estimates of credible region for %Nc using 90% credible interval for parameters a and b)"?*
 - Changes were made here to clarify the definition of Δ%Nc in Sections 2.3.2., 2.3.3., and 2.3.4.
- *LI448-455: Another case of "expensive" writing.*
 - Change made here as suggested to simply this statement.
- *LI479: Figure 1 again? Check numbering of all figures.*
 - It appears that numbering of figures was affected by an error in the manuscript upload process. This has been corrected for the revised manuscript, and numbering

of all figures and tables has been checked as well as updated based on consolidation and removal of tables and figures as suggested by the reviewer.

- *L1525: Figure 4: why 15 individual draws are represented in red? Please clarify this analysis.*
 - Change has been made here to remove Figure 4b and references to this figure, for the purpose of conciseness and clarity.
- *L1542: Why is quite uninformative? I do not agree with this analysis of comparing methods to measure uncertainty of the CNDC because there are basically different things being compared. If there is interest in quantifying uncertainty of the %Nc, credible intervals for the %Nc should be analysed. If there is interest in quantifying uncertainty in the parameters of the CNDC, credible intervals for a and b parameters. This is the advantage of the Bayesian framework through the obtained posterior distributions.*
 - Change made to clarify the approach used and conclusion of findings of this approach, following from changes made in Sections 2.3.2. and 2.3.3.
- *L1612: If there were significant differences, wasn't it also biased? Can claim that was less biased.*
 - Change made here as suggested to clarify and correct statement.

- Critical N dilution curves [CNDCs] for potato are subject to G x E x M effects
- Bayesian methods can quantify uncertainty in critical N concentration [%N_c]
- Partial pooling Bayesian method enables direct comparison of G x E x M effects
- Variation in %N_c for potato due to tuber initiation timing and tuber bulking rate
- N use efficiency and N nutrition index depend on %N_c variability and uncertainty

Notes detailing specific revisions can be found in the Covering Letter submitted with this Revised Manuscript.

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v1.docx

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v1.xlsx

Brian J. Bohman: Writing - Original Draft, Formal Analysis, Data Curation, Visualization, Investigation, Conceptualization, Methodology, Software

Michael J. Culshaw-Maurer: Writing - Original Draft, Methodology, Software, Formal Analysis, Visualization

Feriel Ben Abdallah: Writing - Review & Editing, Investigation, Data Curation

Claudia Giletto: Writing - Review & Editing, Investigation, Data Curation

Gilles Bélanger: Writing - Review & Editing, Investigation, Data Curation

Fabián G. Fernández: Writing - Review & Editing, Supervision

Yuxin Miao: Writing - Review & Editing, Supervision

David J. Mulla: Writing - Review & Editing, Supervision

Carl J. Rosen: Writing - Review & Editing, Project Administration, Funding Acquisition, Supervision, Investigation, Methodology, Data Curation, Resources

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Carl J. Rosen reports financial support was provided by Minnesota Area II Potato Growers Research and Promotion Council.

1 1 **Quantifying critical N dilution curves across G × E × M effects for potato using a partially-**
2 2 **pooled Bayesian hierarchical method**

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4 **Abstract:** Multiple critical N dilution curves [CNDCs] have been previously developed for potato;
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6 however, attempts to directly compare differences in CNDCs across genotype [G], environment
7 [E], and management [M] interactions have been confounded by non-uniform statistical methods,
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9 biased experimental data, and lack of proper quantification of uncertainty in the critical N
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11 concentration [%N_c]. This study implements a partially-pooled Bayesian hierarchical method to
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13 develop CNDCs for previously published and newly reported experimental data, systematically
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15 evaluates the difference in %N_c [$\Delta\%N_c$] across G × E × M effects, and directly compare CNDCs
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17 from the Bayesian framework to CNDCs from conventional statistical methods. The partially-
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19 pooled Bayesian hierarchical method implemented in this study has the advantage of being less
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21 susceptible to inferential bias at the level of individual G × E × M interactions compared to
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23 alternative statistical methods that result from insufficient quantity and quality of experimental
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25 datasets (e.g., unbalanced distribution of N limiting and non-N limiting observations). This method
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27 also allows for a direct statistical comparison of differences in %N_c across levels of the G × E ×
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29 M interactions. Where found to be significant, $\Delta\%N_c$ was hypothesized to be related to variation
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31 in the timing of tuber initiation (e.g., maturity class) and the relative rate of tuber bulking (e.g.,
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33 planting density) across G × E × M interactions. In addition to using the median value for %N_c
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35 (i.e., CNDC), the lower and upper boundary values for the credible region (i.e., CNDC_{lo} and
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37 CNDC_{up}) derived using the Bayesian framework should be used in calculation of N nutrition index
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39 (and other calculations) to account for uncertainty in %N_c. Overall, this study provides additional
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41 evidence that %N_c is dependent upon G × E × M interactions; therefore, evaluation of crop N status
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43 or N use efficiency must account for variation in %N_c across G × E × M interactions.

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4 36 **Keywords:** critical N concentration; critical nitrogen dilution curve; nitrogen nutrition index;
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6 37 nitrogen use efficiency; potato; Bayesian; genotype-by-environment-by-management interactions
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14 39 **Abbreviations:** NUE, nitrogen use efficiency; NUpE, nitrogen uptake efficiency; NUtE, nitrogen
15 utilization efficiency; NNI, nitrogen nutrition index; CNDC, critical nitrogen dilution curve;
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17 41 CNUC, critical nitrogen uptake curve; CNUtEC, critical nitrogen utilization efficiency curve; W,
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19 42 total dry weight plant biomass; N_{Plant} , plant nitrogen content, $\%N_{Plant}$, plant nitrogen concentration;
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21 43 $\%N_c$, critical plant nitrogen concentration; NUtE_c, critical nitrogen utilization efficiency; $\Delta\%N_c$,
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24 44 difference in critical nitrogen concentration; $\%N_{c,up}$, upper bounds of credible interval for critical
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26 45 nitrogen concentration; $\%N_{c,lo}$, lower bounds of credible interval for critical nitrogen
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28 46 concentration; NNI_{up}, upper bound of credible interval for nitrogen nutrition index value; NNI_{lo},
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31 47 lower bound of credible interval for nitrogen nutrition index value; CNDC_{lo}, lower boundary of
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33 48 credible region for critical nitrogen dilution curve; CNDC_{up}, upper boundary of credible region for
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35 49 critical nitrogen dilution curve; G, genotype; E, environment; M, management; EONR,
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4 52 **1. Introduction**
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8 53 Identifying optimal crop nitrogen [N] status to maximize growth and yield production is an elusive
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10 54 goal. Traditionally, either the yield-goal approach or rate-response curves have been used to
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12 55 identify optimal N fertilizer application rate (Morris et al., 2018). The N nutrition index [NNI] is
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14 56 an alternative approach to the current paradigm and comprises a well-developed framework to
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16 57 determine optimal crop N status (Lemaire et al., 2019). Typically, NNI is used to determine crop
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18 58 N status using whole plant analysis and to direct adaptive N management within a growing season
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20 59 (Houlès et al., 2007; Morier et al., 2015). The NNI framework has conventionally been considered
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22 60 generalizable across E × M effects (e.g., year-to-year, geographic, or cultural practices variability)
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24 61 and can be defined for any particular G effect (e.g., crop species or cultivar). In this manner, NNI
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26 62 reflects intrinsic physiological properties and reflects absolute crop N status across variation in
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28 63 environmental conditions (e.g., net soil N supply) or management practices (e.g., rate, source,
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30 64 timing, and placement of N fertilizer) (Sadras & Lemaire, 2014).

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38 65 The NNI approach is defined based on the allometric relationship of declining plant N
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40 66 concentration [%N_{Plant}] with increasing plant biomass, referred to as the critical N dilution curve
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42 67 [CNDC], which defines the critical N concentration [%N_c] below which relative growth rate is
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44 68 reduced (Gastal et al., 2015):

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46 69 %N_c = a W^{-b} [1]
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52 70 where W represents dry weight plant biomass, and a and b are empirically fitted parameters.
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54 71 Parameter a is numerically equivalent to %N_c expressed in units of g N 100 g⁻¹ when W is equal
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56 72 to 1 Mg ha⁻¹, and parameter b represents the ratio of the relative rate of decline in %N_c to the
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4 73 relative rate of increase in W. Using the CNDC, NNI values are then calculated as ratio of %N_{Plant}
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6 74 and %N_c:

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10 75 $NNI = \%N_{Plant} / \%N_c$ [2]
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14 76 When NNI is greater than 1.0, crop N status is said to be in excess, and crop growth is not limited
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16 77 by N, while when NNI is less than 1.0, crop N status is deficient, and crop growth is limited by N.
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18 78 At NNI equal to 1.0, crop N status is optimal (Lemaire & Gastal, 1997).

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22 79 A robust theoretical framework has been developed to explain decline in N concentration as
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24 80 biomass increases, but the application of this theory is most commonly restricted to the vegetative
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26 period where only metabolic and structural tissues are present (Greenwood et al., 1990; Justes et
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28 81 al., 1994; Sadras & Lemaire, 2014). Dilution of N in vegetative tissue occurs in relationship to an
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30 82 increasing proportion of structural biomass, with low N concentration, relative to metabolic (i.e.,
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32 83 photosynthetic) biomass, with high N concentration (Lemaire & Gastal, 1997; Gastal et al., 2015).

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37 85 Multiple previous studies have extended and empirically validated the CNDC relationships beyond
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39 its typical applications to describe declining N concentration over the entire crop growth cycle,
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41 including periods of reproductive growth, by including consideration of storage tissues in addition
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43 87 to structural and metabolic tissues (Greenwood et al., 1986; Duchenne et al., 1997; Plénet &
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45 88 Lemaire, 2000; Herrmann & Taube, 2004). Acceleration of N dilution beyond the vegetative
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47 period primarily occurs as low N biomass (i.e., starch) accumulates in storage tissues such as grain
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49 90 or tubers where the rate of decline is determined by the relative N concentration in storage biomass
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51 compared to vegetative biomass (Duchenne et al., 1997; Plénet & Lemaire, 2000). Duchenne et al.
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53 92 (1997) observed that as an increasing proportion of biomass accumulates in tubers, the rate of
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55 93 decline in N concentration increases with increasing biomass. Certain crops, such as potato,
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4 95 exclusively use a CNDC based on whole plant biomass due to the complex relationship between
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6 96 vine growth and tuber production (Duchenne et al., 1997; Bélanger et al., 2001a; Giletto &
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8 97 Echeverría, 2015; Ben Abdallah et al., 2016). Despite the validity of this approach, interpreting
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10 98 variation in CNDC observed between cultivars and geographies has been challenging.
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15 99 However, recent work by Giletto et al. (2020) identified a mechanistic relationship underpinning
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17 100 the observed empirical relationships in N dilution for potato. The CNDC based on whole plant
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19 101 biomass reflects dilution in both the tuber and vine biomass, individually, and the increasing
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21 102 proportion of biomass allocated to low concentrations of N in biomass (i.e., tubers) as whole plant
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23 103 biomass increases. Giletto et al. (2020) also observed that varieties and locations with a greater
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25 104 proportion of biomass allocated to tubers have a greater value for parameter b of the CNDC, where
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27 105 parameter b of the CNDC represents the relative rate of decline in $\%N_c$ as biomass increases.
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33 106 Based on this framework developed by Giletto et al. (2020), it is reasonable to expect that variation
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35 107 in CNDC for potato would occur due to variation in total biomass and harvest index (i.e., timing
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37 108 of tuber initiation, relative rate of tuber bulking) across $G \times E \times M$ gradients. Understanding the
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39 109 effects of $G \times E \times M$ interactions on crop N requirements and status is critical to improving
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41 110 agronomic outcomes and N use efficiency [NUE] within cropping systems (Lemaire & Ciampitti,
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43 111 2020).
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49 112 Previous CNDCs for potato have been developed with different statistical methods and limited
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51 113 quantification of their uncertainty (Duchenne et al., 1997; Bélanger et al., 2001a; Giletto &
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53 114 Echeverría, 2015; Ben Abdallah et al., 2016). This makes it difficult to ascertain whether observed
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55 115 differences in CNDCs result from underlying $G \times E \times M$ effects, are confounded by the limitations
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4 116 of the statistical approach, or biased due to insufficient quantity or quality of experimental data
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6 117 (e.g., unbalanced distribution of N limiting and non-N limiting observations).
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10 118 The conventional approach to fit a CNDC consists of a two-step process: first, the critical points
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12 119 from the relationship of %N_{Plant} as a function of biomass are selected using statistical criteria;
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14 120 second, a negative exponential curve is fit to the subset of critical points using non-linear
15 regression. There are two commonly used statistical approaches to identify critical points: (1)
16 linear-plateau curve fit and (2) ANOVA and protected multiple comparison. Using a linear-plateau
17 curve to derive critical points was originally suggested by Justes et al. (1994). This approach is
18 rigorous and requires sufficient empirical data such that a linear-plateau curve can be identified
19
20 122 (i.e., at least one N limiting and at least two non-N limiting data points) for each observation date.
21
22 123 Therefore, this approach can be difficult or impossible to implement due to potential limitations
23 of the experimental data used such as insufficient levels of N treatments (i.e., fewer than three
24 treatment levels) or interactions between management practices and environmental conditions (i.e.,
25 all observations are either N limiting or non-N limiting). In contrast, many studies use methods
26 similar to Ben Abdallah et al. (2016) where critical points are determined using a simplified
27 statistical method. In this approach, ANOVA is first used to identify experimental dates where
28 variation in biomass is statistically significant. Subsequently, a protected multiple comparisons
29 analysis is used to identify which experimental treatments had the highest level of biomass – the
30 treatment level with the significantly greatest level of biomass is then defined as the critical point.
31
32 130 While this statistical method is more flexible to implement, it cannot resolve deficiencies in the
33 underlying empirical data (e.g., insufficient level of N treatments, interactions with environmental
34 conditions). Therefore, the critical points selected using the simplified method may be biased due
35 to inherent deficiencies of the underlying experimental data used.
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4 139 Novel statistical methods developed first by Makowski et al. (2020) provide a framework which
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6 140 allows for standardization in statistical approach and quantification of uncertainty for deriving in
7
8 141 CNDCs which enables comparison of %N_c across G × E × M interactions. In short, this framework
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10 142 implements a hierarchical Bayesian model which simultaneously identifies critical points using
11
12 143 the linear-plateau method (e.g., Justes et al. (1994)) while fitting the negative exponential curve
13
14 144 which defines %N_c. The advantage of this method is that it fits the CNDC from the entire set of
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16 145 experimental data for a given G × E × M interaction level and removes the arbitrary intermediate
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18 146 step of separately identifying critical points. This approach has already been successfully used by
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20 147 Ciampitti et al. (2021), Yao et al. (2021), and Fernández et al. (2021) to evaluate differences in
21
22 148 CNDCs across G × E × M interactions for maize, wheat, and tall fescue cropping systems,
23
24 149 respectively. Through this single-step process, the Bayesian hierarchical method both eliminates
25
26 150 the need to separately identify critical points and implements the theoretically preferred method
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28 151 (e.g., linear-plateau curve fit) to select critical points.
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37 152 The Bayesian hierarchical method, however, remains subject to inferential bias due to both limited
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39 153 quantity and quality of experimental data (Fernández et al., 2021; Fernandez et al., 2022). With
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41 154 respect to quantity, having an insufficient number of observations from a limited number of
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43 155 experimental trials to derive an individual CNDC will result in increased bias in %N_c. With respect
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45 156 to quality, using experimental data that does not reflect a full range of biomass values or does not
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47 157 sufficiently represent both limiting and non-limiting N conditions will result in increased bias in
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49 158 %N_c. Datasets used to derive the CNDC using the Bayesian hierarchical method should contain at
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51 159 least eight experimental trials containing at least three N treatments and at least three sampling
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53 160 dates (Fernández et al., 2022).

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4 161 However, there are multiple approaches to pooling across $G \times E \times M$ interactions within the
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6 162 Bayesian hierarchical method to address this bias due to experimental data limitations: no pooling,
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8 163 full pooling, and partial pooling. The no pooling approach treats each experimental data level
9 independently where experimental data from one level is not used in inference for any other level
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11 164 (McElreath, 2020). The no pooling approach was used by Makowski et al. (2020), Ciampitti et al.
12
13 165 (2021), Yao et al. (2021), and Fernández et al. (2021) to develop independent models for each G
14
15 166 $\times E \times M$ interaction. For the Bayesian hierarchical method, the no pooling approach is directly
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17 167 limited by the quantity and quality of experimental data for each $G \times E \times M$ interaction level. The
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19 168 full pooling approach, in contrast, treats each experimental data level in an equivalent manner
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21 169 where the experimental data from all levels are used simultaneously for inference (McElreath,
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23 170 2020). The full pooling approach was used by Fernández et al. (2021) to develop a single model
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25 171 across $G \times E \times M$ interaction levels. While this approach was found by Fernández et al. (2021) to
26
27 172 potentially reduce inferential bias from the Bayesian hierarchical method (i.e., by increasing the
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29 173 combined quantity and quality of data used to fit a given CNDC), the fully pooled approach has
30
31 174 the explicit tradeoff that inference at individual levels of $G \times E \times M$ interactions is not possible.
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33 175 The partial pooling approach balances the tradeoffs between fitting a single population-level model
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35 176 (i.e., full pooling) and fitting multiple independent group-level models (i.e., no pooling) by using
36
37 177 the entire set of experimental data to fit a single model with where the data from all other levels of
38
39 178 an effect influence the inference for a particular level and reduce inferential bias (McElreath,
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41 179 2020). In this manner, individual effect levels are said to be “borrowing strength” through the
42
43 180 process of “shrinkage”, where more extreme values are pulled toward the average (Lindstrom &
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45 181 Bates, 1990; Bates, 2010). Therefore, using a partially-pooled Bayesian hierarchical method
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47 182 should reduce the inferential bias for a given $G \times E \times M$ interaction level where the quantity and
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49 183 should reduce the inferential bias for a given $G \times E \times M$ interaction level where the quantity and
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51 184 should reduce the inferential bias for a given $G \times E \times M$ interaction level where the quantity and
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53 185 should reduce the inferential bias for a given $G \times E \times M$ interaction level where the quantity and
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65 191 should reduce the inferential bias for a given $G \times E \times M$ interaction level where the quantity and

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4 184 quality of experimental data are not otherwise sufficient and enable inference for each individual
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6 185 $G \times E \times M$ interaction level. However, the partial pooling approach has not yet been implemented
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8 186 within in the Bayesian hierarchical method to derive CNDCs.
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13 187 Building upon previous work, the objectives of this study are to 1) develop CNDCs using the
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15 188 hierarchical Bayesian framework for potato varieties in Minnesota (from both previously
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17 189 published and unpublished experimental data) and for potato varieties in Argentina (Giletto &
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19 190 Echeverría, 2015), Canada (Bélanger et al., 2001a), and Belgium (Ben Abdallah et al., 2016) (from
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21 191 previously published experimental data), 2) extend the implementation of the hierarchical
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23 192 Bayesian framework using a partial pooling approach to compare CNDCs across $G \times E \times M$
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25 193 interactions based on the uncertainty in $\%N_c$ and curve parameters a and b , 3) identify the optimal
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27 194 methods to determine uncertainty in $\%N_c$ for use in calculating NNI and other derivative metrics,
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29 195 and 4) compare CNDCs developed with the hierarchical Bayesian framework methods to
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31 196 previously published CNDCs for the same data with different statistical methods.
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39 197 **2. Materials and Methods**
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42 198 *2.1. Experimental Data*
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46 199 This study combines experimental data from both newly reported and previously published sources
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48 200 (Ben Abdallah et al., 2016; Giletto et al., 2020). The data used for analysis in this study are
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50 201 summarized in Table 1 and the relevant methods related to the experimental trials are reported
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52 202 below. All individual experimental observations used in this study are presented in the
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54 203 Supplemental Materials (Table S1).
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5 **Table 1.** Summary of experimental data used in this study.

Study	Location	Variety	Site-Years	Sampling Dates	Samples
Present Study	Minnesota	Clearwater	2	10	30
		Dakota Russet	2	14	70
		Easton	2	14	70
		Russet Burbank	9	52	328
		Umatilla Russet	2	10	30
Giletto et al. (2020)	Argentina	Bannock Russet	3	13	52
		Gem Russet	4	18	72
		Innovator	4	18	72
		Markies Russet	2	9	36
		Umatilla Russet	3	14	56
Ben Abdallah et al. (2016)	Canada	Russet Burbank	4	30	104
		Shepody	4	30	105
Belgium		Bintje	17	49	238
		Charlotte	7	24	114

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205 2.1.1. Newly Reported Data – Minnesota

206 Six individual plot-scale field experiments were conducted over a total of eight years (MN-1:
207 1991–1992; MN-2: 2014-2015, MN-3: 2016, MN-4: 2018-2019, MN-5: 2019, MN-6: 2020) at the
208 Sand Plain Research Farm [SPRF] in Becker, MN ($45^{\circ} 23' N$, $93^{\circ} 53' W$). A summary of the
209 treatments and sampling design for each experiment is presented in Table 2, and a summary of key
210 experimental factors across G, E, and M effects are presented in Table 3.
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212 A randomized complete block design with three or four replicates was used in each field
213 experiment. All experiments evaluated at least three N rates ($0 - 400 \text{ kg N ha}^{-1}$) for Russet Burbank
214 potato [*Solanum tuberosum* (L.)], with some studies evaluating additional potato varieties (Table
215 2). Nitrogen fertilizer was applied using various source and timing regimes including polymer
216 coated urea applied at planting and/or emergence, split-applied urea and urea-ammonium nitrate
217 at emergence and/or post-emergence, ammonium nitrate at planting, emergence, and/or post-
218 emergence. Experiments that evaluated multiple varieties had either a factorial design, or split-plot
219 design with variety treatment as the whole-plot and N treatment as the split-plot. Plots in these
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 4 219 studies were between 5.4 – 6.4 m wide (6 or 7 × 0.9 m rows) and 6.1 – 9.1 m long. Experiments
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 6 220 were planted each year in late-April to early-May and were mechanically harvested in mid-
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 8 221 September with vines terminated one to two weeks prior to harvest. Apart from experimental N
 9
 10 222 and variety treatments, all management and cultural practices were managed by the staff at the
 11
 12 223 SPRF in accordance with common practices for the region (Egel, 2017). Nutrients were applied
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 14 224 based on soil samples and University recommendations (Franzen et al., 2018; Rosen, 2018), and
 15
 16 225 supplemental irrigation was applied based on the University recommended checkbook method
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 18 226 (Wright, 2002; Steele et al., 2010). Additional details on experimental procedures for these studies
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 20 227 have been previously reported (Table 2).
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Table 2. Summary of newly reported experimental small-plot trials in Minnesota, USA

Experiment	Year	N trts. [†]	N rates [kg ha ⁻¹]	Varieties	Sampling Dates	Reference
MN-1	1991	10	0, 135,	Russet Burbank	12 June, 24 June, 2 July,	Rosen et al. (1992); Rosen et al. (1993); Errebbi et al. (1998)
			180, 225,		16 July, 30 July, 13 Aug.,	
			270		10 Sept.	
	1992	10	0, 135, 180, 225, 270	Russet Burbank	10 June, 25 June, 17 July, 5 Aug., 26 Aug., 15 Sept.	
MN-2	2014	5	135, 200, 270, 335,	Russet Burbank, Dakota Russet,	30 June, 15 July, 24 July,	Sun (2017); Sun et al. (2019); Sun et al. (2020)
			400	Easton	11 Aug., 26 Aug., 8 Sept., 15 Sept.	
			135, 200, 270, 335,	Russet Burbank, Dakota Russet,	23 June, 7 July, 21 July, 4 Aug., 17 Aug., 1 Sept., 16 Sept.	
MN-3	2015	5	400	Easton		
MN-4	2016	4	45, 180, 245, 335	Russet Burbank	28 June, 13 July, 26 July, 3 Aug., 10 Aug., 13 Sept.	Crants et al. (2017)
			135, 270, 400	Russet Burbank, Clearwater, Umatilla Russet	26 June, 10 July, 18 July, 1 Aug., 13 Sept.	Gupta and Rosen (2019); Gupta et al. (2020); Li et al. (2021)
	2018	3	400	Russet Burbank, Clearwater, Umatilla Russet	26 June, 11 July, 24 July, 7 Aug., 16 Sept.	
	2019	3	135, 270, 400			
MN-5	2019	8	45, 155, 245, 290, 335	Russet Burbank	25 June, 9 July, 23 July, 6 Aug., 21 Aug., 16 Sept	Bohman et al. (2020)
MN-6	2020	8	55, 155, 245, 270, 290, 335	Russet Burbank	24 June, 7 July, 22 July, 4 Aug., 16 Sept.	Rosen et al. (2021)

[†] Including N source, timing, and placement combinations occurring at an equivalent N rate

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4 228 Samples of vine biomass were harvested immediately prior to mechanical termination for
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6 229 determination of fresh weight vine yield. Harvested tubers were mechanically sorted into weight
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8 230 classes and graded (USDA, 1997), and fresh weight tuber yield was determined as the sum of all
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10 231 weight classes and tuber grades. Harvested biomass was oven dried at 60°C to determine dry matter
11
12 232 content of vines and tubers. Dry weight tuber and vine biomass was calculated as the product of
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14 233 fresh weight and dry matter content for each tissue respectively. Total N concentration of vines
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16 234 and tubers was determined from subsamples of plant tissues with either combustion analysis
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18 235 (Elementar Vario EL III, Elementar Americas Inc., Mt. Laurel, NJ) using standard methods
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20 236 (Horneck & Miller, 1998), or with the salicylic Kjeldahl method (Horwitz et al., 1970). Total N
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22 237 content of vines and tubers was calculated as the product of N concentration and dry weight
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24 238 biomass for each tissue respectively. Total plant N content [N_{Plant}] (kg N ha^{-1}) was calculated from
25
26 239 the sum of tuber and vine N content. Total plant dry weight biomass [W] ($\text{Mg dry wt. ha}^{-1}$) was
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28 240 calculated from the sum of vine and tuber dry weight biomass. Plant N concentration [% N_{Plant}] (g
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30 241 N 100 g^{-1} dry wt.) was calculated as the ratio of N_{Plant} to W.
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39 242 Whole-plant samples were also regularly collected during the period of late-May to early-
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41 243 September (Table 2). Two to three plants were harvested from each plot on four to six dates each
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43 244 year with vines, roots, and tubers each measured separately. Dry weight biomass, N concentration,
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45 245 and N content for vines and tubers were determined for these in-season plant tissue samples using
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47 246 the methods described above. Calculations for W, N_{Plant} , and % N_{Plant} were the same as methods
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49 247 previously described above.
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55 248 2.1.2. Previously Published Data – Belgium, Argentina, and Canada
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4 249 Data reported in two previous studies, Giletto et al. (2020) and Ben Abdallah et al. (2016), were
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6 250 included in the analysis conducted for the present study. The data from Giletto et al. (2020)
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8 251 comprises two separate experimental data sets from small-plot experiments conducted in Balcarce
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10 252 in the province of Buenos Aires, Argentina ($37^{\circ} 45' S$; $58^{\circ} 18' W$) (Giletto & Echeverría, 2015)
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12 253 and in the upper St. John River Valley of New Brunswick, Canada ($47^{\circ} 03' N$; $67^{\circ} 45' W$)
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14 254 (Bélanger et al., 2000, 2001a, 2001b). All data from the Giletto et al. (2020) study used in the
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16 255 present analysis was included in this previous publication.
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22 256 The data from Ben Abdallah et al. (2016) represents multiple experimental data set from small-
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24 257 plot experiments were conducted in Gembloux, Belgium ($50^{\circ} 33' N$; $4^{\circ} 43' E$). Only a portion of
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26 258 the data from the Ben Abdallah et al. (2016) study used in the present analysis was included in this
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28 259 previous publication – while the dry weight biomass data were previously reported, the N
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30 260 concentration data from the Ben Abdallah et al. (2016) experiment is reported for the first time in
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32 261 this work.
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38 262 A summary of experimental data from each trial used in the present study is presented in Table 1,
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40 263 and a summary of key experimental factors across G, E, and M effects is presented in Table 3.
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Table 3. Comparison of key experimental factors including for Genotype [G]: variety maturity class [Maturity Class]; Environment [E]: soil texture classification [Soil Texture], dates of typical growing season [Growing Season], soil organic matter content [OM], growing season mean daily temperature [T_{Mean}], growing season cumulative precipitation [Precip.], growing season mean diurnal temperature difference [$\Delta T_{Diurnal}$] calculated as the average of daily diurnal temperature difference (i.e., difference between daily max temperature and daily minimum temperature), growing season cumulative growing degree days [GDD] calculated with base temperature of 7 °C and maximum temperature of 30 °C, growing season mean daily incident solar radiation [Sol. Rad.]; and Management [M]: planting density [Density], N fertilizer application source and timing [N Source & Timing], and use of supplemental irrigation [Irr.].

		G	E								M		
Location	Variety	Maturity Class [†]	Soil Texture [‡]	OM [%]	Growing Season [§]	T_{Mean} [°C]	Precip. [mm]	$\Delta T_{Diurnal}$ [°C]	GDD [°C d]	Sol. Rad. [MJ m ⁻²]	Density [plants ha ⁻¹]	N Source & Timing [¶]	Irr.
Argentina	Bannock Russet	L to VL	L	4.2 – 5.2	1 June – 10 Oct.	18.4	428	13.6	1739	25.5	59,000	Urea @ PL	Yes
	Gem Russet	M to L											
	Innovator	E to M											
	Markies Russet	L to VL											
	Umatilla Russet	ML to L											
Belgium	Bintje	L	SiCL, SiL, L, SL	1.3 – 2.6	10 Oct. – 10 Mar.	15.5	244	8.3	1313	20.0	38,000	AN @ PL	No
	Charlotte	M											
Canada	Russet Burbank	L to VL	CL, L	2.6 – 3.0	20 Apr – 20 Sept.	15.7	371	10.0	1150	19.1	29,000 44,000	AN @ PL	Yes
	Shepody	E to ME											
Minnesota	Clearwater	ML	LS	1.3 – 2.5	1 May – 15 Sept.	18.9	383	11.6	1638	22.7	36,000*	AN, Urea, UAN, and/or PCU @ PL, EM, and/or P-EM	Yes
	Dakota Russet	ML											
	Easton	L											
	Russet Burbank	L to VL											
	Umatilla Russet	ML to L											

[†] Early [E], medium-early [ME], medium [M], medium-late [ML], late [L], very late [VL] as classified by Stark et al. (2020), OSU (2021), Giletto & Echeverría (2015), CFIA (2013), AHDB (2015), Thompson (2013), and Porter (2014)

[‡] Silty clay loam [SiCL], clay loam [CL], silt loam [SiL], loam [L], sandy loam [SL], loamy sand [LS]

[§] Summary weather data based on typical growing season dates and historical climate reconstruction for the period of 1980-2016 (Gelaro et al., 2017; Weather Spark, 2021)

[¶] Ammonium nitrate [AN], urea-ammonium nitrate [UAN], polymer-coated urea [PCU], planting [PL], emergence [EM], post-emergence [P-EM]

* Russet Burbank in MN-1 was planted at a density of 48,000 plants ha⁻¹

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5 269 2.2. Statistical Methods
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9 270 Based on the general approach outlined by Makowski et al. (2020), this study implemented a
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11 271 partially-pooled Bayesian hierarchical framework to infer CNDC parameters for each location and
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13 272 variety within location, assess the uncertainty in model parameters and %N_c, and compare fitted
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15 273 CNDCs across the effects of location and variety.
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20 274 The Bayesian hierarchical framework outlined by Makowski et al. (2020) was extended to
21
22 275 explicitly include the G × E × M interaction levels within the fitted model using a partial pooling
23
24 276 approach. Experimental data were nested according to location and variety within location, where
25
26 277 the linear-plateau curve fitted for each experimental sampling date is nested within a given level
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28 of variety within location (Figure 1). This model structure leverages the advantages of partial
29
30 278 pooling to addresses the limitations identified by Fernández et al. (2021) that a sufficient quantity
31
32 279 and quality of experimental data are required while still enabling direct inference on the individual
33
34 280 G × E × M interaction levels. Using *R* (R Core Team, 2021a), the *brms* package (Bürkner, 2017,
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36 281 2018) was used to implement the statistical framework outlined by Makowski et al. (2020) with
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38 282 the modifications as previously described (Figure 1). The *brms* package, an interface to *Stan*
39
40 283 (Carpenter et al., 2017), was chosen due to the ability to include group-level effects (i.e., random
41
42 284 effects) which allows for the fit of this particular partially-pooled Bayesian hierarchical model.
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44 285 The *brms* package includes a user-friendly modeling language, robust documentation, and a
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46 286 diverse set of tools to analyze and assess models.
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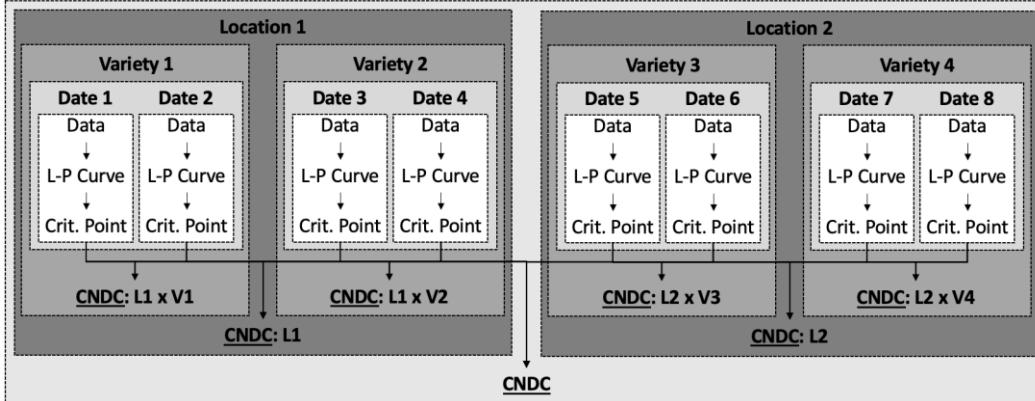


Figure 1. Flowchart showing nested structure used to fit critical N dilution curves [CNDC] using the hierarchical Bayesian method based on Makowski et al. (2020). Linear-plateau (L-P) curves and critical points (i.e., the fitted join point of each linear-plateau curve) are identified at the level of each experimental sampling date and pooled at various levels of location and variety within location to determine the CNDC for that level. This hierarchical model structure simultaneously fits all individual levels of location and variety within location, as well as for the global level of all experimental data, which allows for direct comparison across levels.

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290 A non-linear *brms* model was defined by combining the two separate expressions used by
291 Makowski et al. (2020) to parameterize the Bayesian hierarchical model as previously
32 implemented with *rjags* (Plummer, 2019) and *JAGS* statistical software (Plummer, 2013).

36 293 The first expression from Makowski et al. (2020) represents the linear-plateau component:

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$$W = \min(W_{Max,i} + S_i \cdot (\%N_{Plant} - \%N_c), W_{Max,i}) \quad [3]$$

42 295 where S_i and $W_{Max,i}$ are the slope of the linear-plateau curve and the maximum value of biomass
43 (i.e., plateau) for a given date [i], respectively, \min represents the minima function (i.e., the plateau
46 296 component), and W , $\%N_{Plant}$, and $\%N_c$ have the same meaning as previously defined in this present
47 297 study. This linear-plateau curve is defined with N concentration as the independent variable and
51 298 biomass as the dependent variable and is written in point-slope form where the reference point
53 299 used is the critical point.

57 301 The second expression from Makowski et al. (2020) represents the CNDC component:

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4 302 $\%N_c = a W_{Max,i}^{-b}$ [4]
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8 303 where a and b are the parameters that define the negative exponential curve and $\%N_c$ and $W_{Max,i}$
9
10 304 have the same meanings as defined above.
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14 305 Using algebraic substitution (i.e., for $\%N_c$), these two expressions (Eq. [3] and Eq. [4]) were
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16 306 combined to produce following non-linear *brms* model formula:
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20 307 $W \sim min(W_{Max,i} + S_i (\%N_{Plant} - (a W_{Max,i}^{-b})), W_{Max,i})$ [5]
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23 308 Two group-level (i.e., random) effects were specified for this *brms* model to parameterize the
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25 309 nested structure (Figure 1). First, the parameters S and W_{Max} included group-level effects to fit a
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27 310 linear-plateau curve to each experimental sampling date:
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31 311 $W_{Max} + S \sim 1 + (1 | index)$ [6]
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35 312 where *index* represents the unique level of each experimental sampling date, nested within a given
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37 313 level of variety within location. Second, the parameters a and b included group-level effects to fit
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39 314 the CNDC:
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43 315 $a + b \sim 1 + (1 | location) + (1 | location:variety)$ [7]
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47 316 where *location* and *location:variety* represents the unique effect level for location and variety
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49 317 within location, respectively. Models were fit using treatment-level means (i.e., an effect of
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51 318 *replicate* was not included in the model).
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55 319 The *brms* model was fitted using 4 chains and 10000 iterations with 3000 warmups per chain.
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58 320 Model convergence was verified by determining that all parameters had satisfactory R-hat values
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60 321 of less than 1.01 with bulk-ESS and tail-ESS values of at least 100 samples per chain (Vehtari et
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4 322 al., 2021). The priors for this model were chosen based on expert knowledge (i.e., previously
 5 reported values), empirical observations (i.e., summary values from the data set), and inspection
 6 of the joint prior predictive distribution. Evaluating the joint prior predictive distribution is
 7 particularly important for hyperparameters dealing with the standard deviation between groups in
 8 a hierarchical model due to the propagation of variance throughout model levels. If a set of
 9 relatively uninformative priors led to biologically or physically impossible predictions which
 10 prevented model convergence, the prior ranges were narrowed (Schad et al., 2021). In particular,
 11 325 a positive value for S is required to represent the positive physiological relationship between W
 12 and $\%N_{Plant}$ (i.e., linear-plateau curve where W increases as $\%N_{Plant}$ up to W_{max} at $\%N_c$). Similarly,
 13 having non-positive value for W_{max} is physically impossible. A summary of the prior values used
 14 326 in this model is given below (Table 4).

Table 4. Priors used in fitting the hierarchical Bayesian model with *brms*.

Parameter	Distribution	Bounds	
		Lower	Upper
a	Normal (5.3, 0.1)	0	∞
$\sigma(a_{location})$	Normal (0.10, 0.02)	$-\infty$	∞
$\sigma(a_{location:variety})$	Normal (0.05, 0.01)	$-\infty$	∞
b	Normal (0.40, 0.01)	0	1
$\sigma(b_{location})$	Normal (0.05, 0.02)	$-\infty$	∞
$\sigma(b_{location:variety})$	Normal (0.02, 0.01)	$-\infty$	∞
W_{max}	Normal (8.0, 0.1)	1	∞
$\sigma(W_{max,index})$	Normal (7.0, 1.0)	$-\infty$	∞
S	Normal (6.0, 0.1)	0	∞
$\sigma(S_{index})$	Normal (1.0, 0.1)	$-\infty$	∞
σ	Student's t (3, 1.0, 0.1)	$-\infty$	∞

47 333 The entire statistical and data workflow used to generate this analysis is reproducible and available
 48
 49 334 via GitHub repository (<https://github.com/bohm0072/bayesian-cndc-potato>). The *renv* package
 50
 51 335 (Ushey, 2021) was used to document the computing environment utilized while conducting this
 52
 53 336 analysis to ensure code portability and reproducibility.

60 338 2.3. Evaluating Uncertainty

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4 339 2.3.1. Critical N Dilution Curve Parameter Uncertainty
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8 340 After the statistical model was successfully fit to the data (n=28,000 draws), values for parameters
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10 341 a and b of the CNDC were reported at the 0.05, 0.50 (i.e., median) and 0.95 quantiles for the effect
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12 342 levels of *location* and *location:variety* to determine the 90% credible interval for each parameter.
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15 343 The correlation between values for parameters a and b was determined for each effect level of
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17 344 *location:variety* using the fitted parameter values at the level of the individual draws.
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21 345 2.3.2. Critical N Concentration Uncertainty
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24 346 Uncertainty in %N_c was characterized using three methods: (1) directly modeled 0.05 and 0.95
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26 347 quantile value of posterior distribution of %N_c; (2) parameterized approximation of 0.05 and 0.95
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28 348 quantile value of posterior distribution of %N_c; (3) indirect calculation of %N_c using 0.05 and 0.95
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30 349 quantile values for a and b .
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35 350 For the directly modeled method, %N_c for a set of discrete values of W between 1 Mg dry wt. ha⁻¹
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37 351 ¹ and the maximum observed value of W in the experimental data set was calculated for each
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39 352 individual posterior draw based on the fitted values of parameters a and b for that draw. From the
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41 353 distribution of %N_c values, the 0.05, 0.50 (i.e., median) and 0.95 quantile values were identified
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43 354 for each effect level of *location:variety* to determine the 90% credible region for %N_c. This
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45 355 approach makes maximal use of the jointly estimated parameters contained in the posterior
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47 356 distribution.
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53 357 For the parameterized approximation method, two negative exponential curve of the same form as
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55 358 the CNDC (i.e., $y = a x^{-b}$) were fit using *nls* (R Core Team, 2021b) to the 0.05 and 0.95 quantile
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57 359 values of the posterior distribution of %N_c computed using the directly modeled method described
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above. This approach to derive parameterized approximation of the 90% credible region attempts to simplify the complexity of communicating and propagating uncertainty in $\%N_c$. These parameterized curves approximating the upper and lower boundaries of the credible region for the CNDC are respectively referred to as $CNDC_{up}$ and $CNDC_{lo}$, where parameters a_{up} and b_{up} correspond to $CNDC_{up}$ and parameters a_{lo} and b_{lo} correspond to $CNDC_{lo}$:

$$365 \quad \%N_{c,lo} = a_{lo} W^{-b_{-lo}} \quad [8]$$

$$366 \quad \%N_{c,up} = a_{up} W^{-b_{-up}} \quad [9]$$

For the indirect calculation method, an estimate of the 90% credible region for $\%N_c$ was calculated by using the boundary values of the 90% credible interval of parameters a and b . The estimate for the upper boundary of the credible region for $\%N_c$ was determined from the 0.95 quantile value for parameter a and 0.05 quantile value for parameter b ; the estimate for the lower boundary of the credible region of $\%N_c$ was determined from the 0.05 quantile value for parameter a and 0.95 quantile value for parameter b . This approach does not account for the joint estimation of parameters offered by the Bayesian approach; therefore, the paired combination for parameters a and b (i.e., 0.05 and 0.95 quantiles, respectively) might not actually occur in the posterior distribution.

Difference in critical N concentration [$\Delta\%N_c$] were calculated as the difference between a reference value [$\%N_{c,ref}$] and a comparison value [$\%N_{c,i}$]:

$$378 \quad \Delta\%N_c = \%N_{c,ref} - \%N_{c,i} \quad [10]$$

To compare differences between the various methods used to quantify uncertainty in $\%N_c$, $\Delta\%N_c$ was calculated (Eq. [10]) where $\%N_{c,ref}$ was set as the median value (i.e., 0.50 quantile) of $\%N_c$

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4 381 from the directly modeled method, while $\%N_{c,i}$ was varied and set as the upper and lower values
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6 382 of $\%N_c$ from the directly modeled, parameterized approximation, and indirect calculation methods
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8 383 as described above.
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13 384 2.3.3. Comparing Critical N Concentration across $G \times E \times M$ Effects
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16 385 Using the directly modeled method described above, $\%N_c$ for each posterior draw was calculated.
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18 386 At the effect level of *location:variety*, $\Delta\%N_c$ was calculated (Eq. [10]) where $\%N_{c,ref}$ is the median
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20 387 $\%N_c$ from the posterior distribution for the reference level and $\%N_{c,i}$ was the median $\%N_c$ from
21
22 388 the posterior distribution for each pairwise comparison of all other levels. From this computed set
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24 389 of $\Delta\%N_c$, the 0.05, 0.50 (i.e., median) and 0.95 quantile values were identified for each pairwise
25
26 390 comparison of *location:variety* levels to determine the 90% credible region for $\Delta\%N_c$. The
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28 391 comparison curve was considered to be not significantly different from the reference curve when
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30 392 the 90% credible region for $\Delta\%N_c$ contained zero. This approach allows for the direct evaluation
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32 393 of differences in $\%N_c$ across $G \times E \times M$ effects (i.e., *location:variety* levels).
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39 394 2.3.4. Comparing Critical N Concentration across Statistical Methods
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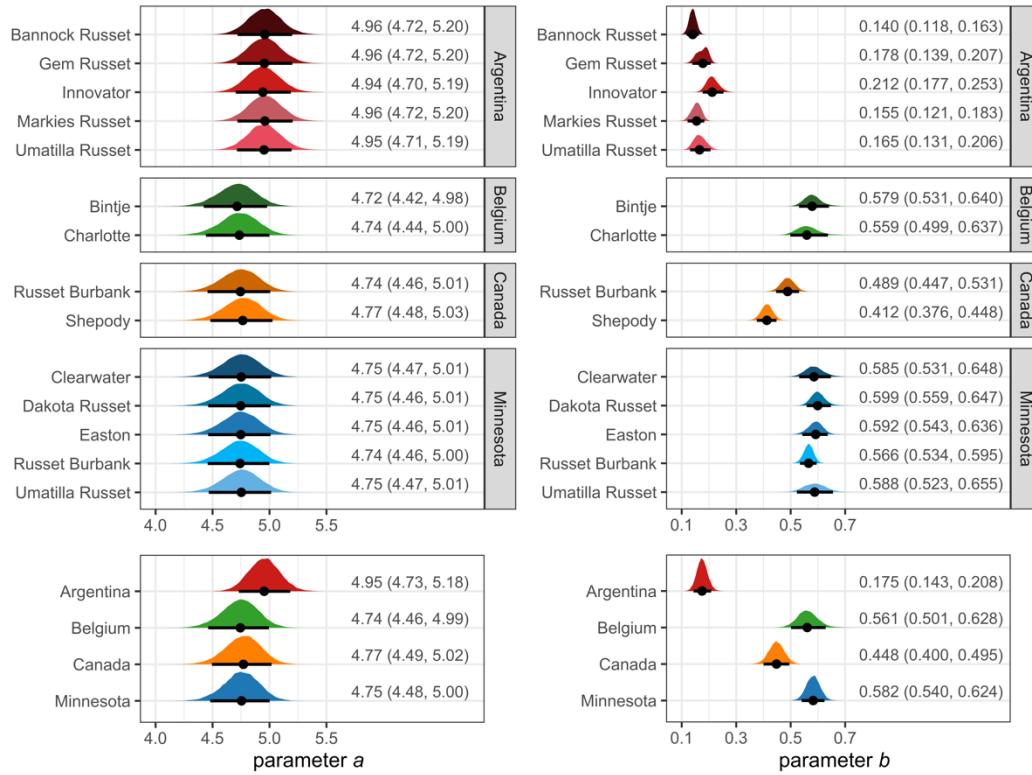
42 395 An analogous method was also used to compare the CNDCs fitted in the present study to the
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44 396 CNDCs published in previous studies (i.e., Ben Abdallah et al. (2016); Giletto et al. (2020)).
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46 397 Specifically, $\Delta\%N_c$ for each level of *location:variety* with previously published CNDC was
47
48 398 calculated (Eq. [10]) using where $\%N_{c,ref}$ was set as the median value (i.e., 0.50 quantile) of $\%N_c$
49
50 399 from the directly modeled method, and $\%N_{c,i}$ was set as the previously published values of $\%N_c$.
51
52 400 If $\Delta\%N_c$ falls outside of the 90% credible region for $\%N_c$ determined from the directly modeled
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54 401 method, then the two curves are determined to be significantly different over the range for which
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56 402 the previous value falls outside of the credible region. This approach allows for direct evaluation
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4 403 of differences in %N_c for CNDCs developed from the same set of data across various statistical
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11 405 **3. Results**
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15 406 *3.1. Fitted Critical N Dilution Curve*
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18 407 The posterior distribution of fitted values for CNDC parameters a and b are presented in Figure 2
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20 408 showing the median value and 90% credible interval (i.e., 0.05 and 0.95 quantile values). For
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22 409 parameter a , there was no significant difference for the effect of location at 90% credible interval
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24 410 threshold (Figure 2a). Although Argentina has a numerically greater value of parameter a (4.95)
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26 411 than the other three locations (4.74 – 4.77), these differences are not significant. Additionally, the
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28 412 variation in parameter a for the variety within location effect is negligible and not statistically
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30 413 significant (Figure 2a).
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(a)

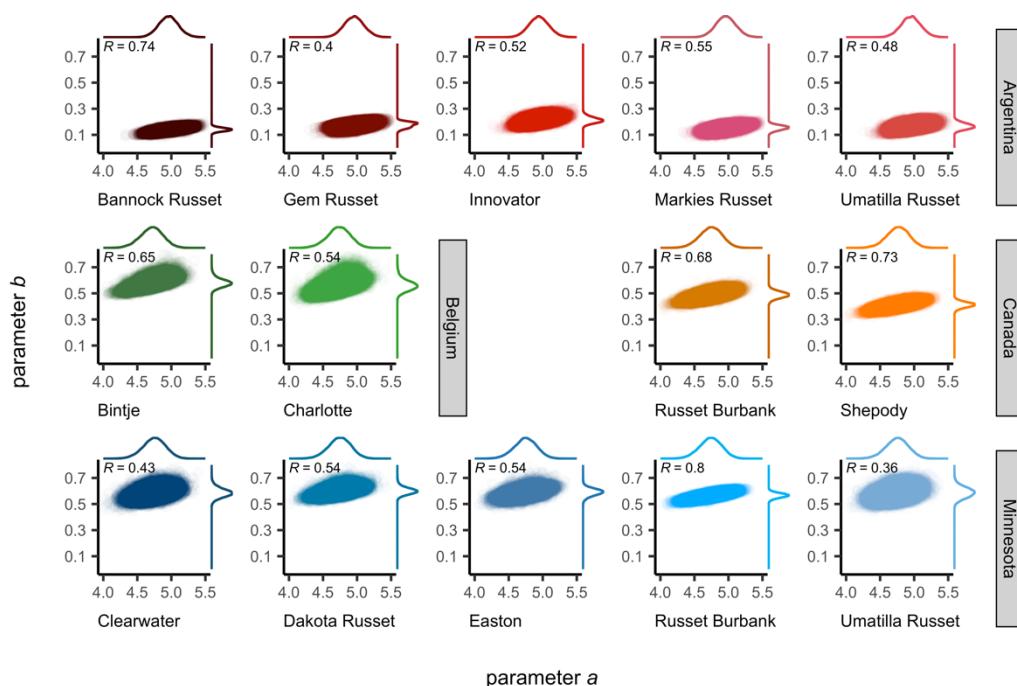
(b)

Figure 2. Posterior distribution of variety and variety within location effects for (a) parameter a ; and (b) parameter b . Points represent median value and line represents 0.05 and 0.95 quantile range. Values displayed with the figures are the median value with the 90% credible interval boundaries (i.e., 0.05 and 0.95 quantiles) displayed within the parentheses.

For parameter b , there were significant differences for both the effect of location and variety within location at a 90% credible interval threshold (Figure 2b). For location, Argentina had the lowest value for parameter b (0.175), while Canada had a greater value for parameter b (0.448) than Argentina but lower than either Belgium (0.561) or Minnesota (0.582). The difference between parameter b for Belgium and Minnesota was not significant. For the variety within location effect, parameter b significantly varied for varieties in Argentina and Canada, while there were no significant differences in parameter b within either Belgium or Minnesota. For Argentina, Innovator had the greatest value for parameter b (0.212), followed by Gem Russet, Umatilla Russet, Markies Russet, and Bannock Russet (0.178, 0.165, 0.155, and 0.140, respectively). The

425 difference between Innovator and Umatilla Russet, Markies Russet, and Bannock Russet was
426 significant, while all other differences between varieties were not significant. For Canada, Russet
427 Burbank had a significantly higher value for parameter b (0.489) than Shepody (0.412).

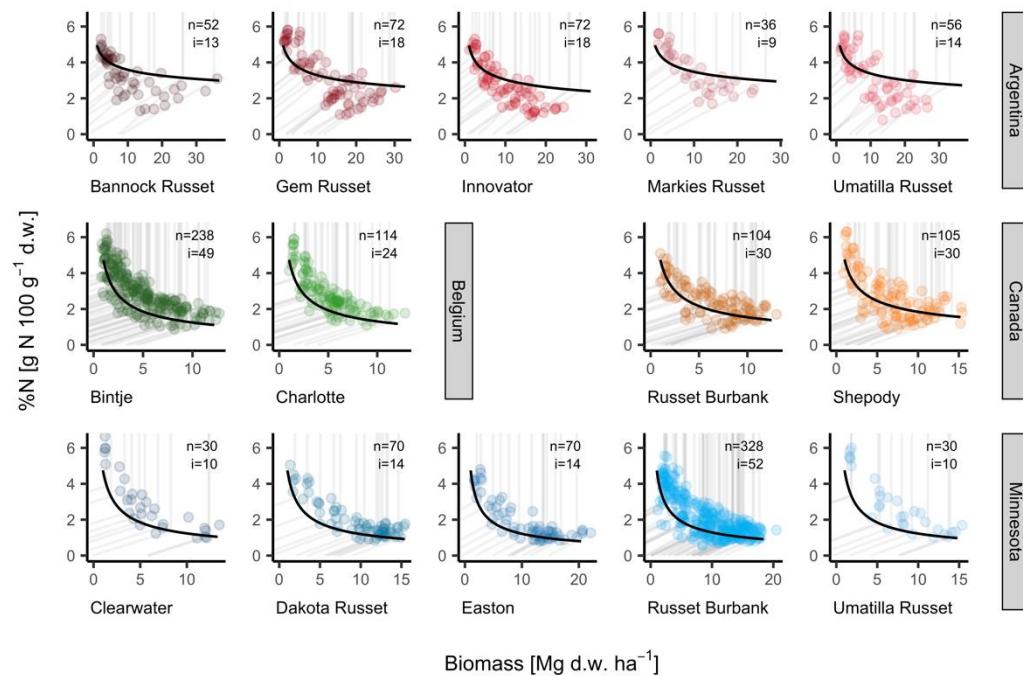
428 There was a positive correlation found between parameters a and b (Figure 3) which indicates that
429 quantifying differences in these parameter values independently (Figure 2) is not appropriate to
430 describe the uncertainty in $\%N_c$ determined by the correlated parameters. Stated alternatively,
431 significant differences for either parameter a or b do not necessarily imply that differences in $\%N_c$
432 are also significant.



50 **Figure 3.** Distribution of posterior values for parameters a and b for each location within variety shown
51 as a scatterplot with marginal density distribution given for each parameter. Pearson correlation coefficient
52 [R] is displayed for the relationship between parameters a and b . Data are shown at the level of individual
53 draws ($n=28,000$).

434
435 Critical N dilution curves for each variety within location and the experimental data, median linear-
436 plateau curve for each experimental sampling date, and median value of $\%N_c$ are presented (Figure

4 437 4). The individual linear-plateau curves fitted for each experimental sampling date nested within
 5 each level of the variety within location effect are presented in the Supplemental Materials (Figure
 6 438 S1).



36 **Figure 4.** Critical N dilution curves (i.e., median value of critical N concentration [$\%N_c$]) fitted from the
 37 hierarchical Bayesian model are shown as a solid black lines for each variety within location. Biomass
 38 and N concentration [%N] data are displayed as points with the median linear-plateau curve for each
 39 sampling date shown as grey line. The number of samples [n] and the number of sampling dates [i] are
 40 displayed on each individual panel.

42 441
 43
 44 442 For the Argentina varieties, more than 60% of the observed data fall below the CNDC (i.e.,
 45 represent N limiting conditions) with over 40% of sampling dates having exclusively N limiting
 46 conditions observed. For both the Belgium and Minnesota varieties, more than 80% of the
 47 443 observed data fall above the CNDC (i.e., represent non-N limiting conditions) with almost 30% of
 48 444 sampling dates having exclusively non-N limiting conditions observed. For the Canada varieties,
 49 445 over 60% of observed data represented non-N limiting conditions but less than 10% of sampling
 50 446 dates had exclusively non-N limiting conditions observed (Figure S1).

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4 449 *3.2. Critical N Concentration Uncertainty*
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8 450 The credible region for %N_c varies across variety within location and across levels of biomass
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10 451 (Figure 5). The symmetry of the credible region distribution varies by variety within location.
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12 452 Some levels of variety within location, such as Argentina × Gem Russet, have a skewed
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14 453 distribution, while other levels, such as Canada × Shepody, have a symmetrical distribution (Figure
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16 454 5a). There are also differences in the range of the credible region, where some varieties within
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18 455 location, such as Argentina × Umatilla Russet, have greater uncertainty in %N_c than others, such
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20 456 as Minnesota × Russet Burbank. The uncertainty in %N_c also varies across the level of biomass
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22 457 for a given CNDC. For example, as the level of biomass increases, Argentina × Umatilla Russet
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24 458 has an increasing credible region range, Minnesota × Russet Burbank has a decreasing credible
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26 459 region range, and Argentina × Bannock Russet has a nearly constant credible region range.
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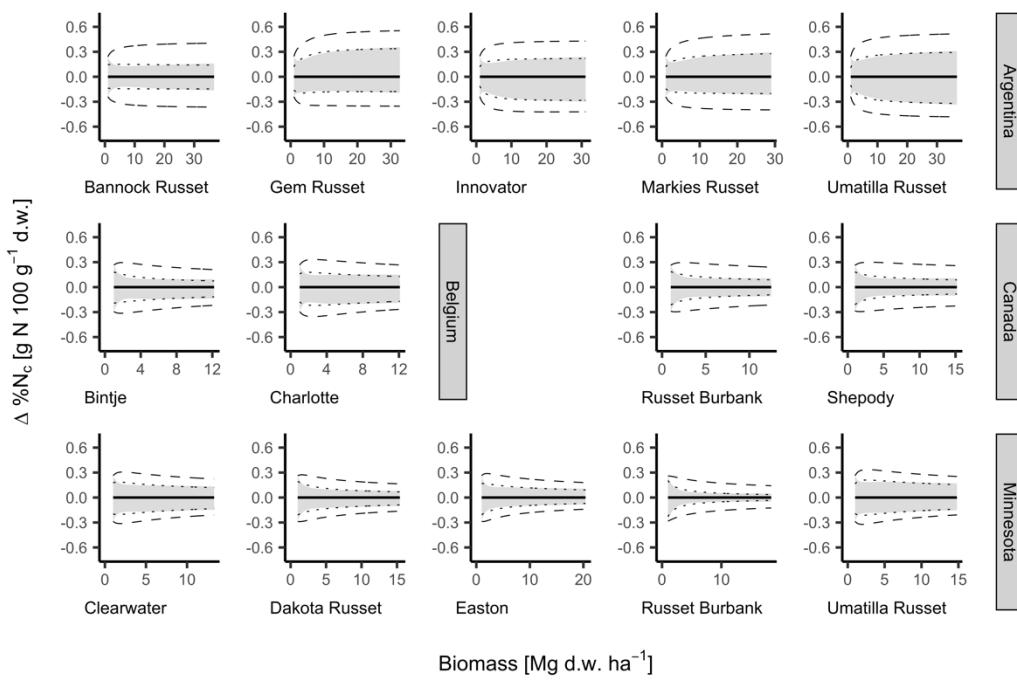


Figure 5. Comparison of the difference in critical N concentration values [$\Delta\%N_c$]. The reference critical N concentration [% $N_{c,\text{ref}}$] is represented as a solid black line at constant $\Delta\%N_c$ value of zero. The grey shaded region represents the 90% credible region of $\%N_c$ from the directly modeled approach (i.e., $\%N_c$ computed from parameter estimates of each posterior draw). The dotted lines represent the estimated upper and lower bounds of $\%N_c$ from the parameterized estimate approach (i.e., $CNDC_{lo}$ and $CNDC_{up}$). The dashed lines represent the approximated lower and upper bounds of $\%N_c$ from the indirect calculation approach (i.e., $\%N_c$ computed based on posterior distribution of parameters a and b). Data are presented for all levels of variety within location.

461

462 Estimation of the upper and lower boundaries of the 90% credible region using the parameterized
 463 estimate approach (i.e., CNDC_{lo} and CNDC_{up}) (Table 5) appears to be reasonable based on
 464 graphical evaluation (Figure 5). However, these fitted CNDC_{lo} and CNDC_{up} curves do not
 465 themselves represent a draw directly from the posterior distribution and do not necessarily
 466 represent the most extreme possible curves. While credible regions with boundaries that are non-
 467 monotonic (e.g., Argentina \times Innovator) have portions of the curve fit approximation that are
 468 poorer performing, the credible regions with monotonic boundaries (e.g., Minnesota \times Dakota
 469 Russet) seem to be satisfactory across the entire range of the curve.
 470

Table 5. Critical N dilution curve parameters for each variety within location, with the median value of the posterior distribution for parameters a and b (CNDC), and the estimates for the credible region lower (CNDC_{lo}) and upper (CNDC_{up}) boundaries using the parameterized estimate approach.

Location	Variety	<u>CNDC_{lo}</u>		<u>CNDC</u>		<u>CNDC_{up}</u>	
		a_{lo}	b_{lo}	a	b	a_{up}	b_{up}
Argentina	Bannock Russet	4.82	0.146	4.96	0.140	5.10	0.135
	Gem Russet	4.80	0.190	4.96	0.178	5.07	0.152
	Innovator	4.83	0.241	4.94	0.212	5.06	0.193
	Markies Russet	4.82	0.167	4.96	0.155	5.08	0.135
	Umatilla Russet	4.85	0.195	4.95	0.165	5.06	0.143
Belgium	Bintje	4.52	0.606	4.72	0.579	4.90	0.567
	Charlotte	4.56	0.607	4.74	0.559	4.89	0.531
Canada	Russet Burbank	4.53	0.498	4.74	0.489	4.93	0.480
	Shepody	4.55	0.416	4.77	0.412	4.95	0.406
Minnesota	Clearwater	4.56	0.622	4.75	0.585	4.93	0.558
	Dakota Russet	4.54	0.619	4.75	0.599	4.94	0.588
	Easton	4.54	0.608	4.75	0.592	4.91	0.567
	Russet Burbank	4.51	0.562	4.74	0.566	4.95	0.567
	Umatilla Russet	4.56	0.631	4.75	0.588	4.92	0.546

471
 472 However, the approximation of uncertainty in $\%N_c$ based on the indirect calculation method were
 473 found to contain the entire credible region for all varieties within location evaluated (Figure 5).
 474 Therefore, the indirect calculation approach based on uncertainty in CNDC parameters is less
 475 informative than either the directly modeled or parameterized estimate approaches. In the absence
 476 of the credible region defined directly from the fitted hierarchical Bayesian model (i.e., directly

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4 477 modeled approach), using the CNDC_{lo} and CNDC_{up} (Table 5) (i.e., parameterized estimate
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6 478 approach) is a suitable first-order representation of the credible region for %N_c.
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10 479 *3.3. Evaluating Differences between Critical N Concentration*
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13 480 3.3.1. Differences Related to G × E × M Effects
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17 481 While an evaluation of the pairwise differences between all varieties within location was
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19 482 conducted and is presented in the Supplemental Materials (Figure S2), a subset of the results
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21 483 comparing Minnesota × Russet Burbank to all other varieties within location, Argentina ×
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23 484 Innovator to all other varieties within Argentina, Canada × Russet Burbank to all other varieties
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25 485 within Canada, and Belgium × Bintje to all other varieties within Belgium are presented in detail
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27 486 here (Figure 6).
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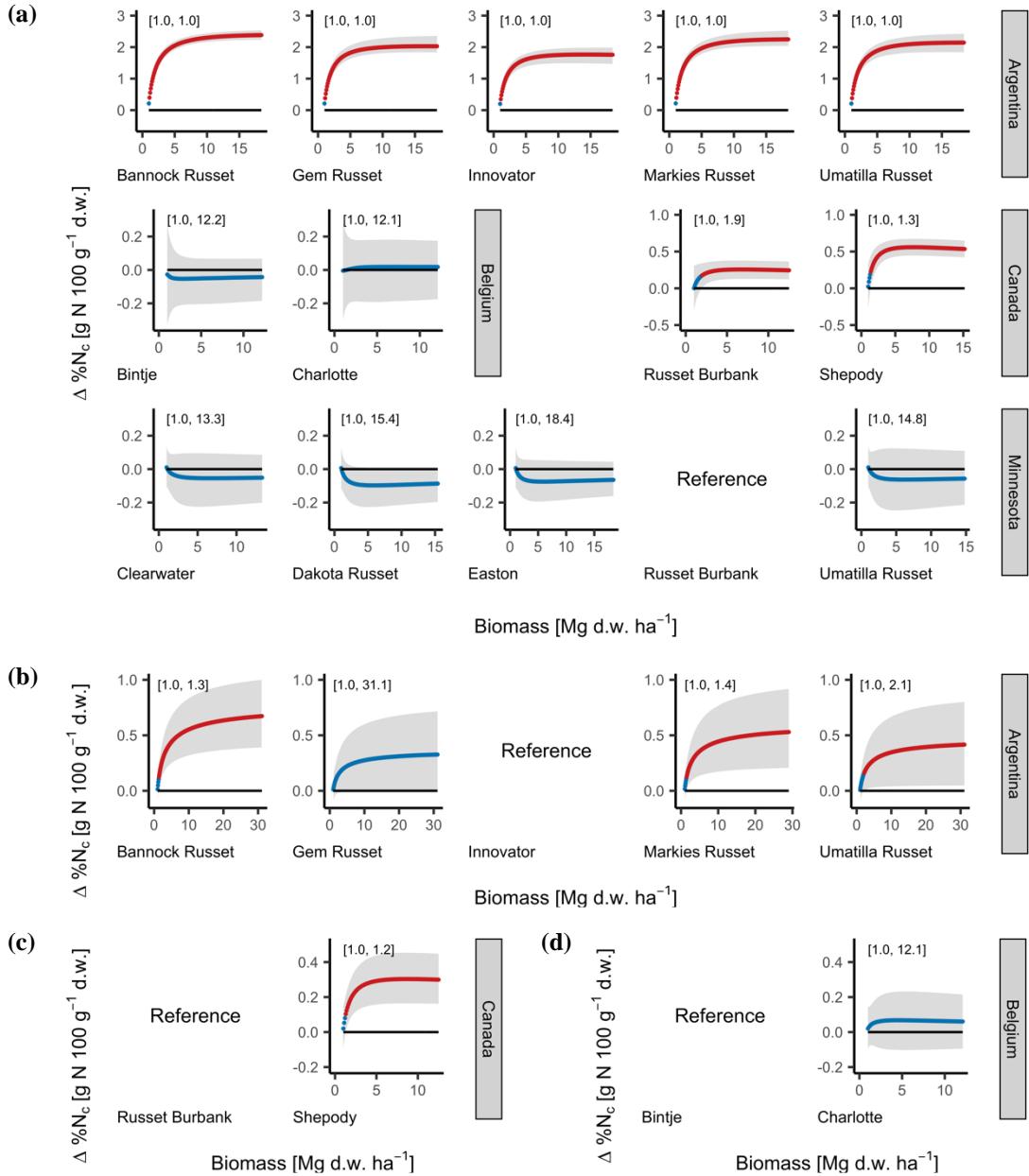


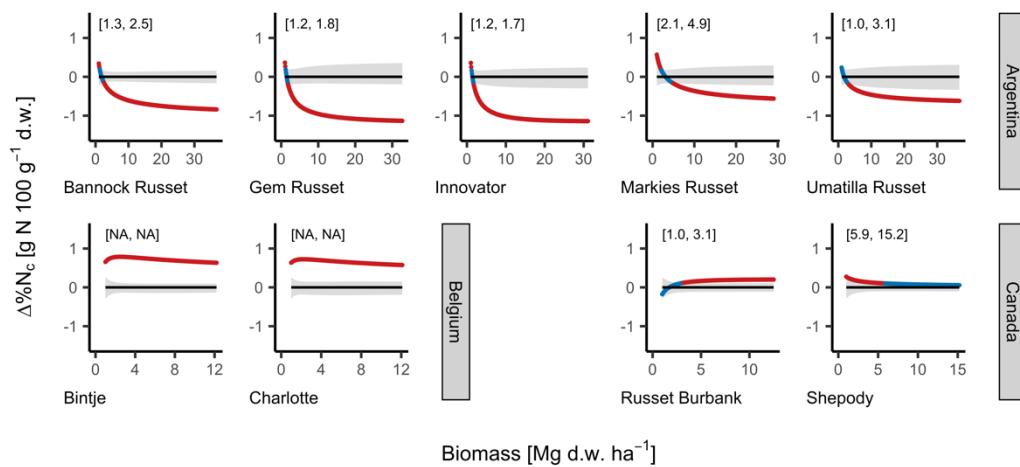
Figure 6. Comparison of the difference in critical N concentration values [$\Delta\%N_c$] between (a) Minnesota \times Russet Burbank and all other varieties within location, (b) Argentina \times Innovator and all other varieties within Argentina, (c) Canada \times Russet Burbank and all other varieties within Canada, and (d) Belgium \times Bintje and all other varieties within Belgium. The grey shaded region represents the 90% credible region for $\Delta\%N_c$. The colored points represent the median value for $\Delta\%N_c$ at a given biomass level where blue or red color respectively indicates that the 90% credible region for $\Delta\%N_c$ does or does not contain zero. The solid black line at constant $\Delta\%N_c$ value of zero represents $\%N_c$ for the reference curve [$\%N_{c,\text{ref}}$] (i.e., Minnesota \times Russet Burbank, Argentina \times Innovator, Canada \times Russet Burbank, and Belgium \times Bintje). The range of biomass values for which $\Delta\%N_c$ is not significantly different (i.e., 90% credible region contains zero) is given in brackets.

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4 489 For Minnesota × Russet Burbank, there were no significant differences in %N_c for any level of W
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6 490 evaluated with any of the other varieties in Minnesota (i.e., Clearwater, Dakota Russet, Easton,
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8 491 and Umatilla Russet) or with the Belgium varieties (i.e., Bintje, and Charlotte) (Figure 6a). The
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10 492 %N_c values for both of the Canadian varieties (i.e., Russet Burbank, and Shepody) were
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12 493 significantly greater than that for Minnesota × Russet Burbank when biomass values were greater
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14 494 than 2 Mg ha⁻¹ dry wt. The %N_c for Canada × Russet Burbank and Canada × Shepody were up to
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16 495 0.3 and 0.6 g N 100 g⁻¹ dry wt. greater than that for Minnesota × Russet Burbank, respectively.
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18 496 The %N_c for the Argentina varieties (i.e., Bannock Russet, Gem Russet, Innovator, Markies
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20 497 Russet, and Umatilla Russet) were significantly greater than for Minnesota × Russet Burbank,
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22 498 except at a biomass value of 1.0 Mg dry wt. ha⁻¹, with a difference in value depending on variety
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24 499 of up to 2.4 g N 100 g⁻¹ dry wt.

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32 500 For Argentina × Innovator, %N_c was significantly lower than for Argentina × Bannock Russet,
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34 501 Argentina × Markies Russet, and Argentina × Umatilla Russet but was not significantly different
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36 502 from Argentina × Gem Russet (Figure 6b). The %N_c values for Argentina × Bannock Russet,
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38 503 Argentina × Markies Russet, and Argentina × Umatilla Russet were up to 0.5 g N 100 g⁻¹ dry wt.
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40 504 greater than that for Argentina × Innovator. For Canada × Russet Burbank, %N_c was significantly
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42 505 lower than for Canada × Shepody (Figure 6c), with a difference in %N_c of up to 0.3 g N 100 g⁻¹
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44 506 dry wt. For Belgium × Bintje, %N_c was not significantly different from Belgium × Charlotte
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46 507 (Figure 6d).

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53 508 There are two notable findings to point out. First, there were no significant differences between
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55 509 Minnesota × Russet Burbank and any other varieties evaluated in Minnesota or between Belgium
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57 510 × Bintje and Belgium × Charlotte. This finding did not hold true for all varieties within location
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59 511 evaluated, however; Significant differences between varieties were found for both Argentina and

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 4 512 Canada. Second, the comparison between the Minnesota \times Russet Burbank and Canada \times Russet
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 6 513 Burbank curves as well as the comparison between the Minnesota \times Umatilla Russet and Argentina
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 8 514 \times Umatilla (Figure S2) were both significantly different.
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 12 515 3.3.2. Differences Related to Statistical Methods
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 16 516 When comparing the curves fit in the present study with the Bayesian hierarchical method to the
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 18 517 curves fit in the previous studies using conventional statistical methods, there were significant
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 21 518 differences between statistical curve fit methods for all varieties within location evaluated (Figure
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 23 519 7). None of the previous CNDCs fall entirely within the credible region for the respective CNDCs
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 26 520 developed in the present study.
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46
 47 **Figure 7.** Comparison of the difference in critical N concentration values [$\Delta\%N_c$] between the
 48 conventional statistical methods used in previous studies (i.e., Argentina – Giletto and Echeverría (2015);
 49 Belgium – Ben Abdallah et al. (2016); Canada – Bélanger et al. (2001a)) and the hierarchical Bayesian
 50 method used in the present study. The grey shaded region represents the 90% credible region for critical
 51 N concentration [%N_c] using the directly modeled method. The solid black line at a constant $\Delta\%N_c$ value
 52 of zero represents the median value for %N_c using the directly modeled method. Red or blue points
 53 respectively indicate that $\Delta\%N_c$ falls outside of (i.e., is significant) or falls within (i.e., is not significant)
 54 the 90% credible region for %N_c determined by the directly modeled method. The range of biomass values
 55 for which $\Delta\%N_c$ is not significant is given in brackets.
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4 523 The %N_c values from the previously developed CNDCs for the Argentina varieties (Giletto &
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6 Echeverría, 2015) were significantly less than that from the present CNDCs across all varieties for
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8 biomass levels of greater 5 Mg dry wt. ha⁻¹ (Figure 7). The magnitude of this difference was
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10 relatively large, with the Δ%N_c between the previous and present method ranging up to -0.6 to -
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12 1.1 g N 100 g⁻¹ dry wt., depending on variety. Therefore, relative to the statistical method used in
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14 this study it appears that the statistical methods used by Giletto and Echeverría (2015) selected
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16 biased critical points due to an overrepresentation of N limiting observations in the experimental
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18 dataset (Figure 4, Figure S1) leading to a systematic underestimation of %N_c.
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25 531 The %N_c from the previously developed CNDCs for Belgium (Ben Abdallah et al., 2016) were
26
27 significantly greater than that from the CNDCs developed in the present study (Figure 7). For all
28
29 levels of biomass, Δ%N_c between the previous and present methods was significantly different
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31 with a value of 0.7 g N 100 g⁻¹ dry wt. Therefore, relative to the statistical method used in this
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33 study, it appears that the statistical methods used by Ben Abdallah et al. (2016) selected biased
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35 critical points due to overrepresentation of non-N limiting observations in the experimental dataset
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37 leading to a systematic overestimation of the %N_c.
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43 538 The %N_c from the previously developed CNDCs for Canada (Bélanger et al., 2001a) was
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45 significantly greater for both Canada × Russet Burbank and Canada × Shepody than the present
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47 CNDCs for biomass levels of less than 3 Mg dry wt ha⁻¹ and greater than 6 Mg dry wt ha⁻¹,
48
49 respectively (Figure 7). Relative to the other locations, however, the CNDCs for Canada were the
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51 most similar between statistical methods, with a small value for Δ%N_c of only 0.2 g N 100 g⁻¹ dry
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53 wt. Therefore, relative to the statistical method used in this study, it appears that the statistical
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55 method used by Bélanger et al. (2001a) did not select biased critical points likely due to the lesser
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57 bias observed in this experimental dataset.
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4 546 Because a CNDC using the conventional statistical methods has not been previously published for
5 potato in Minnesota, no comparison across statistical methods is made for this experimental
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7 547 dataset. However, the bias observed in the Minnesota experimental dataset is similar to the bias
8 found in the Belgium experimental dataset; therefore, using the conventional statistical methods
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10 549 to derive a CNDC for Minnesota would likely overestimate %N_c relative to the hierarchical
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12 550 Bayesian method.
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21 552 **4. Discussion**
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24 553 *4.1. Mechanisms of Dilution*
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28 554 While the present study presents direct evidence of significant differences between CNDCs for
29 potato across G × E × M effects, previous studies help describe the potential physiological
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31 555 mechanisms for this source of variation. Reviewing previous work on this topic, Lemaire et al.
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33 556 (2019) described a framework with which to consider the variation in relative partitioning of dry
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35 557 matter. First, relative partitioning varies as biomass varies over the growing season indicating that
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37 558 there is an ontogenetic relationship between harvest index and biomass. Second, the allometric
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39 559 trajectory of relative allocation (e.g., harvest index at a given level of biomass) is subject to
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41 560 variation in non-ontogenetic factors (i.e., G × E × M interactions).
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48 562 The findings of Giletto et al. (2020) suggest that the variation in CNDCs for potato are due to non-
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50 563 ontogenetic factors. In general, G × E × M interactions that result in greater and more rapid relative
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52 564 partitioning of biomass from vines (i.e., high N metabolic and structural tissue) to tubers (i.e., low
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54 565 N storage tissues) will result in greater N dilution (i.e., lower %N_c) at the same level of total plant
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56 566 biomass (Lemaire et al., 2019). The two factors described by Giletto et al. (2020) affecting N
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4 567 dilution due to non-ontogenetic factors are total plant biomass at tuber initiation (i.e., timing of
5 tuber initiation) and relative rate of tuber growth to plant growth (i.e., relative rate of tube bulking).
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7 568 These two factors are affected by various physiological mechanisms and G × E × M interactions;
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9 569 however, relatively limited work has been conducted to comprehensively evaluate the combined
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11 570 effect of G × E × M interaction on these two physiological mechanisms for potato.
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17 572 4.1.1. Timing of Tuber Initiation
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21 573 The timing of tuber initiation is affected primarily by variety maturity class (i.e., G). Potato
22 varieties are classified on a spectrum of growth patterns where early maturing varieties are
23 considered to be determinate and later maturing varieties are considered to be indeterminate
24 (Thornton, 2020). Compared to indeterminate varieties, determinate varieties progress more
25 quickly to the tuber initiation growth stage (i.e., at lower total plant biomass) and have a more
26 rapid tuber bulking (i.e., biomass increase) with limited additional canopy and vine biomass
27 growth (i.e., increased harvest index for a given level of biomass) (Kleinkopf et al., 1981).
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37 580 Therefore, it is expected that increasing earliness of maturity for a potato variety would result in
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39 581 an increase in N dilution.
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44 582 In the present study, differences in maturity class between varieties resulted in differences in %N_c.
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46 583 For example, Argentina × Innovator, which has an early to medium maturity class, had
47 significantly lower %N_c than Argentina × Bannock Russet, Argentina × Markies Russet, and
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49 584 Argentina × Umatilla Russet, which have either a medium-late to late or late to very late maturity
50 class; however, Argentina × Gem Russet, which has a medium to late maturity class did not have
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54 587 a significantly different %N_c from Argentina × Innovator (Figure S2). This finding supports the
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4 588 hypothesis that varieties with an earlier maturity class (i.e., earlier tuber initiation) will have lower
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6 589 %N_c (i.e., greater N dilution).
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10 590 Timing of tuber initiation is also subject to G × E × M interactions. Ideal conditions for tuber
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12 591 initiation are moderate to low soil N availability, shorter day length, high light intensity, and cool
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14 592 nighttime temperatures (Ewing & Struik, 1992; Thornton, 2020); when N fertilizer management
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16 593 results in excessively high soil N availability (Kleinkopf et al., 1981), under conditions of reduced
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18 594 solar irradiance (Menzel, 1985), or when nighttime soil temperatures are elevated (Slater, 1968;
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20 595 Kim & Lee, 2019), tuber initiation can be delayed. Therefore, both M effects that result in
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22 596 excessive early-season soil N availability (e.g., all N applied at planting in a soluble form) and E
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24 597 effects that result in increased solar irradiance or reduced nighttime temperatures (i.e., increased
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26 598 diurnal temperature difference) could result in an increase in N dilution.
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33 599 However, due the limitation of the experimental studies (i.e., the effect of M was not systematically
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35 600 varied across a given G × E interaction), it is not possible to directly assess the impact of diurnal
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37 601 temperature difference, solar irradiance, or N fertilizer source and timing (Table 3) on the timing
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39 602 of tuber initiation and N dilution distinct from the combined effect of G × E × M interactions.
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44 603 4.1.2. Rate of Tuber Bulking 45 46

47 604 The rate of tuber bulking and allocation of biomass to tubers is subject to the effects of E.
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49 605 Conventionally, potential biomass production has been considered as the product of total solar
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51 606 radiation and radiation use efficiency (Monteith, 1977; Sinclair & Muchow, 1999) as has been
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53 607 successfully applied to potato (Allen & Scott, 1980). Previous studies have suggested that
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55 608 decreasing diurnal temperature difference results in a reduction in tuber bulking rate (i.e., radiation
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57 609 use efficiency), most likely as a result of increasing utilization of photosynthesis assimilates for
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4 610 maintenance (via increased respiration) as nighttime temperature increases (Benoit et al., 1986;
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6 611 Bennett et al., 1991; Lizana et al., 2017); however, Kim & Lee (2019) did not observe any effect
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8 612 of increasing diurnal temperature difference on tuber bulking rate.
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12 613 Given the limitation of the experimental studies (i.e., the effect of E was not systematically varied
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14 614 across a given G x M interaction), it is not possible to directly assess the impact of diurnal
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16 615 temperature difference and solar radiation (Table 3) on the rate of tuber bulking across G x E x M
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18 616 interactions.
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23 617 Planting density is an important effect of M that may play a key role in determining the relative
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25 618 partitioning of biomass for to tuber. Previous studies investigating this effect have found that as
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27 619 planting density increases, leaf area index increases (Bremner & Taha, 1966; Ifenkwe & Allen,
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29 620 1978; Allen & Scott, 1980), tuber dry weight biomass on a per area basis increases (Bremner &
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31 621 Taha, 1966; Ifenkwe & Allen, 1978), while tuber dry weight biomass on a per plant basis decreases
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33 622 (Bremner & Taha, 1966; Ifenkwe & Allen, 1978). The combination of the effect of increasing
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35 623 planting density could plausibly result in the net effect of an increased relative proportion of
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37 624 biomass allocated to vines (i.e., reduction in harvest index) (Vander Zaag et al., 1990), therefore
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39 625 reducing N dilution and resulting in an increased %N_c.
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43 626 In the present study, variations in %N_c due to variation in planting density were observed. For
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45 627 example, Argentina has the highest planting density of any location (Table 3) which resulted in
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47 628 greater %N_c than all other locations (Figure S2). The relative effect of planting density also appears
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49 629 to be of greater magnitude than other sources of variation (e.g., maturity class). For example,
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51 630 Canada × Russet Burbank, which has a late to very late maturity class and planting density of
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53 631 29,000 plants ha⁻¹, had a lower %N_c than Canada × Shepody, which has an early to medium-early
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4 632 maturity class and planting density of 44,000 plants ha⁻¹ (Table 3, Figure 6c). Therefore, this
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6 633 finding suggests that the effect of planting density (i.e., rate of tuber bulking) may be relatively
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8 634 more important at controlling %N_c than the effect of maturity class (i.e., timing of tuber initiation).
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13 635 Because there was only a single level of M (e.g., planting density) within each level of G × E for
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15 636 the experimental trials considered here, additional experimentation is required to fully consider the
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17 637 independent effects of G, E, and M on critical N dilution. Therefore, future experimental studies
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19 638 explicitly investigating the effect of M (e.g., planting density) on %N_c should be conducted to
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21 639 properly consider the combined effects the G × E × M interaction.
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26 640 4.1.3. Comparison to Other Crops 27 28

29 641 These findings contrast somewhat with the previous studies evaluating G × E × M effects on %N_c.
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31 642 Yao et al. (2021) found a similar magnitude of effect on %N_c for both G and E effects for wheat
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33 643 in China; however, Yao et al. (2021) also reported an E effect where %N_c for wheat in China was
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35 644 significantly different from that reported by Makowski et al. (2020) for wheat in France. Ciampitti
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37 645 et al. (2021) identified variation in %N_c for maize as a result of G × M interactions due to variation
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39 646 in hybrid and planting density. Fernández et al. (2021) found that variation in %N_c for tall fescue
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41 647 across G × E × M effects was negligible. In any case, the magnitude of the difference in %N_c
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43 648 across G × E × M interactions reported by the previous studies for wheat, maize, and tall fescue
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45 649 (Makowski et al., 2020; Ciampitti et al., 2021; Fernández et al., 2021; Yao et al., 2021) is less than
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47 650 that was observed in the present study for potato.
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54 651 Therefore, the impact of G × E × M on %N_c is not only significant for potato, but is also of
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56 652 potentially of much greater relative importance compared to other crops (e.g., wheat, maize, tall
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58 653 fescue). This is because the magnitude of variability in %N_c due to G × E × M interactions found
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4 654 in the present study is relatively greater for potato than other crops; however, further additional
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6 655 experimental data are needed to confirm that this finding is not an artifact of the statistical methods
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8 656 or limitations of experimental data used in the present study.
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13 657 4.1.4. Limitations of Interpretation
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16 658 Previous studies, including that of Giletto et al. (2020) on potatoes, have identified that N dilution
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18 659 follows a two-step process where the rate of N dilution varies between the vegetative period (i.e.,
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20 660 parameter b_1) and the period of storage tissue accumulation (i.e., parameter b_2) (Duchenne et al.,
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22 661 1997; Plénet & Lemaire, 2000; Gastal et al., 2015). Our study, however, did not directly evaluate
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24 662 if the rate of N dilution during the pre-tuber initiation (i.e., vegetative growth) and post-tuber
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26 663 initiation (i.e., accumulation of storage tissue) periods varies due to $G \times E \times M$ interactions.
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28 664 Variation in parameters b_1 and b_2 across $G \times E \times M$ effects is a plausible physiological mechanism
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30 665 that could occur in addition to the non-ontogenetic allometric effects (i.e., timing of tuber
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32 666 initiation, relative rate of tube bulking) identified in the present study and used to explain variation
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34 667 in parameter b . This alternative hypothesis could be evaluated by modifying the Bayesian
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36 668 hierarchical method of the present study to include another hierarchical level representing the pre-
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38 669 and post-tuber initiation periods to determine if parameter b varies within these periods across to
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40 670 $G \times E \times M$ interactions.
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49 671 4.2. Implication of $G \times E$ Variation on N Use Efficiency
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52 672 Understanding and properly interpreting the impact of $G \times E \times M$ effects on NUE is a critical goal
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54 673 necessary to improve N fertilizer use; however, this must be done while controlling for the effect
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56 674 of crop N status (Lemaire & Ciampitti, 2020). The previous findings of Bohman et al. (2021)
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58 675 demonstrated that interpreting NUE and its constituent component of N utilization efficiency
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4 676 [NUtE] is directly related to the parameters of the CNDC through the critical N utilization
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6 677 efficiency curve [CNUtEC] which defines the critical value of NUtE [NUtE_c]:
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10 678 $NUtE_c = 1000 (10 a W^{-b})^{-1}$ [11]
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14 679 where parameters *a* and *b*, and W have the same meaning and units as previously defined in the
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16 680 present study and NUtE_c has units of g dry wt. g⁻¹ N. When NUtE is greater than NUtE_c, crop N
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18 681 status is deficient (i.e., NNI less than 1); conversely, when NUtE is less than NUtE_c, crop N status
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20 682 is excessive (i.e., NNI greater than 1).
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24 683 The finding in the present study that the CNDC can vary across G × E × M interactions and the
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26 684 finding from Bohman et al. (2021) of the intrinsic relationship between NUE and the CNDC
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28 685 together lead to the conclusion that the CNUtEC must also vary across the same G × E × M effects
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30 686 as the CNDC. Therefore, the effect of G × E × M on variation of NUtE_c is one of the multiple set
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32 687 of factors that ultimately control NUE. Understanding and accounting for the G × E × M effect on
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34 688 the CNUtEC is therefore critically important to understand the impacts of G × E × M interactions
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36 689 on NUE. In other words, controlling for this G × E × M effect represents an additional requirement
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38 690 when evaluating and interpreting NUE above and beyond the previously known requirements of
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40 691 controlling for both NNI and biomass (Barraclough et al., 2010; Caviglia et al., 2014; Sadras &
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42 692 Lemaire, 2014; Gastal et al., 2015; Lemaire & Ciampitti, 2020).
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50 693 Following from the above discussion of the CNUtEC and the findings of Giletto et al. (2020), G ×
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52 694 E × M effects that increase the relative proportion of biomass partitioned to tubers and reduce the
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54 695 time to tuber initiation will both decrease the %N_c and increase the NUtE_c values. Therefore, future
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56 696 efforts to systematically improve NUE in potato through either management practices (e.g.,
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58 697 Bohman et al. (2021)) or crop breeding (e.g., Tiwari et al. (2018); Jones et al. (2021); Stefaniak et
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4 698 al. (2021)) should focus on identifying $G \times E \times M$ interactions that result in an increased proportion
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6 699 of biomass partitioned to tubers or result in earlier timing of tuber initiation.
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10 700 *4.3. Uncertainty in Critical N Concentration*
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13 701 4.3.1. Communicating Uncertainty in Critical N Concentration
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17 702 This study as well as others that implemented Bayesian statistical methods to derive critical N
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19 703 dilution curves (Makowski et al., 2020; Ciampitti et al., 2021; Yao et al., 2021) clearly indicate
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21 704 that there is meaningful uncertainty in $\%N_c$ values. Therefore, the use of $\%N_c$ in subsequent
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23 705 calculations should include this inherent uncertainty. However, the direct use of the credible region
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25 defined from posterior distribution of the fitted Bayesian hierarchical model in subsequent
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27 706 calculations is impractical, and a method to concisely and accurately communicate the credible
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29 707 region remains necessary.
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35 709 Our finding that the credible region can be satisfactorily estimated using an equation of the same
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37 710 form as the CNDC (Figure 5) suggests that an additional pair of negative exponential curves
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39 711 representing the upper and lower boundary of the credible region for $\%N_c$ (i.e., $CNDC_{lo}$ and
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41 712 $CNDC_{up}$) should be reported in future studies. In this manner, the median value and credible region
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43 713 for $\%N_c$ is defined by a set of three, two-parameter curves (i.e., $CNDC - a, b$; $CNDC_{up} - a_{up}, b_{up}$;
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45 714 $CNDC_{lo} - a_{lo}, b_{lo}$) which can be easily communicated and used in subsequent computations (Table
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53 716 4.3.2. Computing Uncertainty of Derived Parameters
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57 717 Critical N concentration and the associated CNDC parameters are commonly used to derive and
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59 718 calculate other related parameters. For example, the calculation of NNI depends on both $\%N_{Plant}$
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4 719 and %N_c. (Eq. [1] and Eq. [2]). However, to properly account for the uncertainty in %N_c when
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6 720 computing NNI, the upper [%N_{c,up}] and lower [%N_{c,lo}] bounds of the credible interval for %N_c
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8 721 should also be used to determine the upper [NNI_{up}] and lower [NNI_{lo}] bounds of the credible
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10 722 interval for NNI, where %N_{c,up} and %N_{c,lo} are calculated using the CNDC_{up} and CNDC_{lo},
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12 723 respectively:
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17 724 $\text{NNI}_{\text{up}} = \% \text{N}_{\text{Plant}} / \% \text{N}_{c,\text{up}} = \% \text{N}_{\text{Plant}} / (a_{\text{up}} W^{-b_{\text{up}}})$ [12]
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21 725 $\text{NNI}_{\text{lo}} = \% \text{N}_{\text{Plant}} / \% \text{N}_{c,\text{lo}} = \% \text{N}_{\text{Plant}} / (a_{\text{lo}} W^{-b_{\text{lo}}})$ [13]
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24 726 This has important practical implications for interpreting NNI values. For example, in a case where
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26 727 NNI is less than 1 but NNI_{up} is greater than 1, it follows that crop N status would not be considered
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28 728 deficient (i.e., NNI is not significantly different from 1). In contrast, when both NNI and NNI_{lo} are
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30 729 greater than 1, it follows that crop N status would be considered surplus (i.e., NNI is significantly
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32 730 greater than 1). However, the threshold for considering significant differences in NNI will
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34 731 necessarily depend upon the threshold used for calculating %N_{c,lo} and %N_{c,up} (e.g., 90%
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36 732 confidence region). For example, the conclusions of a small-plot trial evaluating the effect of
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38 733 various N fertilizer treatments on yield and biomass (e.g., Bohman et al. (2021)) may draw
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40 734 different conclusions when uncertainty in calculated NNI values is explicitly considered (e.g., N
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42 735 treatments were or were not limiting).
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50 736 Additionally, the parameters of the CNDC (i.e., a , b) are also used to parameterize other related
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52 737 curves such as the critical N uptake curve [CNUC] or the critical N utilization efficiency curve
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54 738 [CNUtEC] (Bohman et al., 2021). When computing the critical N uptake [N_c] or critical N
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56 739 utilization efficiency [NUtE_c] values defined by these curves, respectively, the parameters from
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58 740 the CNDC_{lo} (i.e., a_{lo} , b_{lo}) and CNDC_{up} (i.e., a_{up} , b_{up}) should be used to calculate the upper and
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4 741 lower bounds of these derived values. In general, any calculation depending on either %N_c or any
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6 equation that uses the parameters of the CNDC, should also additionally use the CNDC_{lo} and
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8 CNDC_{up} to account for uncertainty in %N_c.
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13 744 *4.4. Evaluating Differences between Statistical Methods*
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16 745 While the occurrence of differences between CNDCs derived using the Bayesian hierarchical
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18 model compared to the conventional statistical methods (Figure 6) is itself notable, the magnitude
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20 of the differences found in the present study is especially remarkable for the following reasons.
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24 748 Because of its strong theoretical underpinning, %N_c and NNI are typically considered to be high
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26 fidelity measurements of crop N status, not affected by the subjectivity or relativity found in most
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28 other methods (Lemaire et al., 2019). However, the findings of the present study strongly suggest
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30 that this conception of the NNI framework must be qualified within a particular application by the
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32 statistical methods used to derive the CNDC for a given experimental dataset.
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38 753 Unfortunately, the direct evaluation of different statistical methods to calculate the CNDC from
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40 the same experimental dataset cannot directly answer the question of which statistical method or
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42 resulting CNDC is “correct” (i.e., most accurate, least biased). However, we can reasonably
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44 conclude from both deduction and from the findings of the present study that a Bayesian
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46 hierarchical model utilizing the linear-plateau method and leveraging partial pooling across effect
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48 levels will result in inference that is less subjected to potential bias in the experimental data set
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50 compared to the conventional statistical methods. Additionally, it extracts the greatest amount of
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52 information from a given dataset, as no data are excluded from the fitting of the total model.
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4 761 Therefore, it appears preferable for the future development of CNDCs to utilize the Bayesian
5 hierarchical method to both quantify uncertainty and reduce bias in %N_c. Without addressing these
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7 762 limitations (i.e., bias and uncertainty), both directly resulting from the statistical methods used, the
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9 763 NNI framework cannot fulfill its core objective of providing an absolute reference of crop N status.
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15 765 Additionally, with further development of standardized tools for this scientific computing task, the
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17 766 implementation of the partially-pooled Bayesian hierarchical framework for deriving the CNDC
18 can be made trivial and may enable the development of CNDCs from existing but unutilized
19 experimental datasets. Therefore, the development of a dedicated software library to implement
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21 767 the partially-pooled Bayesian hierarchical method developed in the present study is a priority for
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23 768 future research efforts because it will enable other researchers to implement this preferred method
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25 769 of deriving CNDCs. This is of timely importance given the increased availability of high-quality,
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27 770 consolidated datasets suitable for fitting CNDCs across G × E × M effects (Ciampitti, et al., 2022).
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34 773 Given the increased availability of data, future research should expand the partially-pooled
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36 774 Bayesian hierarchical method to fit models simultaneously using data from multiple crop species.
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40 775 Finally, having sufficient quantity and quality of experimental data remains an essential criterion
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43 776 to consider when deriving a CNDC independent of the statistical method used (Fernández et al.,
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45 777 2021; Fernández et al., 2022). Even with the advantages of the partially-pooled Bayesian
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47 778 hierarchical method, insufficient experimental data quality and quantity may still result in
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49 779 inferential bias of the CNDC for an individual G × E × M interaction level. Given the limitations
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51 780 of the quantity and quality of experimental data used in this study (i.e., bias towards N limiting
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53 781 conditions for Argentina, bias towards non-N limiting conditions for Belgium and Minnesota), it
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55 782 is plausible that estimates of CNDCs from this study are biased relative to estimates of CNDCs
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57 783 derived using an “ideal” experimental dataset and identical statistical methods. Therefore, future
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4 784 studies utilizing the partially-pooled Bayesian hierarchical method should ensure that the
5 experimental dataset for each $G \times E \times M$ interaction level meets the sufficiency criteria identified
6 by Fernández et al. (2022) (i.e., at least eight experimental trials containing at least three N
7 treatments and at least three sampling dates).
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16 788 **5. Conclusions**
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20 789 First, this study demonstrated that there are significant differences between CNDCs developed
21 across $G \times E \times M$ effects for potato. Therefore, any application of $\%N_c$ must use an appropriate
22 CNDC (i.e., not significantly different) for the $G \times E \times M$ interaction being considered. Second,
23 this study developed an approach to communicate uncertainty in $\%N_c$ through the concise set of
24 six parameters defined by the CNDC (i.e., a, b), $CNDC_{lo}$ (i.e., a_{lo}, b_{lo}), and $CNDC_{up}$ (i.e., a_{up}, b_{up}),
25 and the $\%N_c$ value computed from these three curves should be used in all subsequent
26 computations to propagate uncertainty. Third, this study demonstrated that the statistical method
27 used to derive CNDCs affects the inferred $\%N_c$ values, and that the partially-pooled hierarchical
28 Bayesian framework is less susceptible to bias due to insufficient quantity and quality of
29 experimental data than the conventional statistical methods. Therefore, future efforts to derive
30 CNDCs should utilize the partially-pooled hierarchical Bayesian framework whenever possible.
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32 794 Fourth, the findings of this study suggest that variation in $\%N_c$ across $G \times E \times M$ interactions
33 necessarily extends to NUE, via the relationship between the CNDC and the CNUtEC. Therefore,
34 795 NUE is dependent on the mechanisms that control N dilution (i.e., biomass partitioning), and future
35 efforts to improve NUE should explicitly consider how $G \times E \times M$ interactions affect N dilution.
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1 **Quantifying critical N dilution curves across G × E × M effects for potato using a partially-
2 pooled Bayesian hierarchical method**

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15 **Abstract:** Multiple critical N dilution curves [CNDCs] have been previously developed for potato;
16 however, attempts to directly compare differences in CNDCs across genotype [G], environment
17 [E], and management [M] interactions have been confounded by non-uniform statistical methods,
18 biased experimental data, and lack of proper quantification of uncertainty in the critical N
19 concentration [%N_c]. This study implements a partially-pooled Bayesian hierarchical method to
20 develop CNDCs for previously published and newly reported experimental data, systematically
21 evaluates the difference in %N_c [$\Delta\%N_c$] across G × E × M effects, and directly compare CNDCs
22 from the Bayesian framework to CNDCs from conventional statistical methods. The partially-
23 pooled Bayesian hierarchical method implemented in this study has the advantage of being less
24 susceptible to inferential bias at the level of individual G × E × M interactions compared to
25 alternative statistical methods that result from insufficient quantity and quality of experimental
26 datasets (e.g., unbalanced distribution of N limiting and non-N limiting observations). This method
27 also allows for a direct statistical comparison of differences in %N_c across levels of the G × E ×
28 M interactions. Where found to be significant, $\Delta\%N_c$ ~~was attributed to~~ was hypothesized to be
29 ~~related to~~ variation in the timing of tuber initiation (e.g., maturity class) and the relative rate of
30 tuber bulking (e.g., planting density) across G × E × M interactions. In addition to using the median
31 value for %N_c (i.e., CNDC), the lower and upper boundary values for the credible region (i.e.,
32 CNDC_{lo} and CNDC_{up}) derived using the Bayesian framework should be used in calculation of N
33 nutrition index (and other calculations) to account for uncertainty in %N_c. Overall, this study
34 provides additional evidence that %N_c is dependent upon G × E × M interactions; therefore,
35 evaluation of crop N status or N use efficiency must account for variation in %N_c across G × E ×
36 M interactions.

37 **Keywords:** critical N concentration; critical nitrogen dilution curve; nitrogen nutrition index;
38 nitrogen use efficiency; potato; Bayesian; genotype-by-environment-by-management interactions

39

40 **Abbreviations:** NUE, nitrogen use efficiency; NUpE, nitrogen uptake efficiency; NUtE, nitrogen
41 utilization efficiency; NNI, nitrogen nutrition index; CNDC, critical nitrogen dilution curve;
42 CNUC, critical nitrogen uptake curve; CNUtEC, critical nitrogen utilization efficiency curve; W,
43 total dry weight plant biomass; N_{Plant} , plant nitrogen content, $\%N_{Plant}$, plant nitrogen concentration;
44 $\%N_c$, critical plant nitrogen concentration; NUtE_c, critical nitrogen utilization efficiency; $\Delta\%N_c$,
45 difference in critical nitrogen concentration; $\%N_{c,up}$, upper bounds of credible interval for critical
46 nitrogen concentration; $\%N_{c,lo}$, lower bounds of credible interval for critical nitrogen
47 concentration; NNI_{up}, upper bound of credible interval for nitrogen nutrition index value; NNI_{lo},
48 lower bound of credible interval for nitrogen nutrition index value; CNDC_{lo}, lower boundary of
49 credible region for critical nitrogen dilution curve; CNDC_{up}, upper boundary of credible region for
50 critical nitrogen dilution curve; G, genotype; E, environment; M, management; EONR,
51 economically optimum nitrogen rate

52

53 1. Introduction

54 Identifying optimal crop nitrogen [N] status to maximize growth and yield production is an elusive
55 goal. Traditionally, either the yield-goal approach or rate-response curves have been used to
56 identify optimal N fertilizer application rate (Morris et al., 2018). The N nutrition index [NNI] is
57 an alternative approach to the current paradigm and comprises a well-developed framework to
58 determine optimal crop N status (Lemaire et al., 2019). Typically, NNI is used to determine crop
59 N status using whole plant analysis and to direct adaptive N management within a growing season
60 (Houlès et al., 2007; Morier et al., 2015). ~~Unlike the yield goal or rate response approach where~~
61 ~~the optimal N fertilizer rate is empirically based on the marginal economic returns to yield from N~~
62 ~~fertilizer (i.e., economic optimum N rate [EONR]) under a given set of genotype [G], environment~~
63 ~~[E], and management [M] factors (Morris et al., 2018; Nigon et al., 2019),~~ ~~t~~he NNI framework
64 has conventionally been considered generalizable across E × M effects (e.g., year-to-year,
65 geographic, or cultural practices variability) and can be defined for any particular G effect (e.g.,
66 crop species or cultivar). In this manner, NNI ~~reflects intrinsic physiological properties and is~~
67 ~~considered to represent intrinsic physiological properties (Sadras & Lemaire, 2014)~~ ~~reflects~~
68 ~~absolute crop N status across rather than a parameter otherwise subject to variation in~~ ~~under~~
69 environmental conditions (e.g., net soil N supply) or management practices (e.g., rate, source,
70 timing, and placement of N fertilizer) (Sadras & Lemaire, 2014).

71 The NNI approach is defined based on the allometric relationship of declining plant N
72 concentration [%N_{Plant}] with increasing plant biomass, referred to as the critical N dilution curve
73 [CNDC], which defines the critical N concentration [%N_c] below which relative growth rate is
74 reduced (Gastal et al., 2015):

75 $\%N_c = a W^{-b}$ [1]

76 where W represents dry weight plant biomass, and a and b are empirically fitted parameters.
77 Parameter a is numerically equivalent to $\%N_c$ expressed in units of $g N 100 g^{-1}$ when W is equal
78 to 1 Mg ha^{-1} , and parameter b effectively represents the ratio of the relative rate of decline in $\%N_c$
79 to the relative rate of increase in $\%N_c$ as W increases. Using the CNDC, NNI values are then calculated
80 as ratio of $\%N_{\text{Plant}}$ and $\%N_c$:

81 $\text{NNI} = \%N_{\text{Plant}} / \%N_c$ [2]

82 When NNI is greater than 1.0, crop N status is said to be in excess, and crop growth is not limited
83 by N, while when NNI is less than 1.0, crop N status is deficient, and crop growth is limited by N.
84 At NNI equal to 1.0, crop N status is optimal (Lemaire & Gastal, 1997).

85 A robust theoretical framework has been developed to explain decline in N concentration as
86 biomass increases, but the application of this theory is most commonly restricted to the vegetative
87 period where only metabolic and structural tissues are present (Greenwood et al., 1990; Justes et
88 al., 1994; Sadras & Lemaire, 2014). Dilution of N in vegetative tissue occurs in relationship to an
89 increasing proportion of structural biomass, with low N concentration, relative to metabolic (i.e.,
90 photosynthetic) biomass, with high N concentration (Lemaire & Gastal, 1997; Gastal et al., 2015).

91 Multiple previous studies have extended and empirically validated the CNDC relationships beyond
92 its typical applications to describe declining N concentration over the entire crop growth cycle,
93 including periods of reproductive growth, by including consideration of storage tissues in addition
94 to structural and metabolic tissues (Greenwood et al., 1986; Duchenne et al., 1997; Plénet &
95 Lemaire, 2000; Herrmann & Taube, 2004). Acceleration of N dilution of N beyond the vegetative

96 period primarily occurs as low N biomass (i.e., starch) accumulates in storage tissues such as grain
97 or tubers,and where the rate of decline is determined by the relative N concentration in storage
98 biomass compared to vegetative biomass (Duchenne et al., 1997; Plénet & Lemaire, 2000).

99 Duchenne et al. (1997) observed that as an increasing proportion of biomass accumulates in tubers,
100 the rate of decline in N concentration increases with increasing biomass. Certain crops, such as
101 potato, exclusively use a CNDC based on whole plant biomass due to the complex relationship
102 between vine growth and tuber production (Duchenne et al., 1997; Bélanger et al., 2001a; Giletto
103 & Echeverría, 2015; Ben Abdallah et al., 2016). Despite the validity of this approach, interpreting
104 variation in CNDC observed between cultivars and geographies has been challenging.

105 However, recent work by Giletto et al. (2020) identified a mechanistic relationship underpinning
106 the observed empirical relationships in N dilution for potato. The CNDC based on whole plant
107 biomass reflects dilution in both the tuber and vine biomass, individually, and the increasing
108 proportion of biomass allocated to low concentrations of N in biomass (i.e., tubers) as whole plant
109 biomass increases. Giletto et al. (2020) also observed that varieties and locations with a greater
110 proportion of biomass allocated to tubers have a greater value for parameter b of the CNDC, where
111 parameter b of the CNDC represents the relative rate of decline in $\%N_c$ as biomass increases.

112 Based on this framework developed by Giletto et al. (2020), it is reasonable to expect that variation
113 in CNDC for potato would occur due to variation in total biomass and harvest index (i.e., timing
114 of tuber initiation, relative rate of tuber bulking) across $G \times E \times M$ gradients. Understanding the
115 effects of $G \times E \times M$ interactions on crop N requirements and status is critical to improving
116 agronomic outcomes and N use efficiency [NUE] within cropping systems (Lemaire & Ciampitti,
117 2020).

118 Previous CNDCs for potato have been developed with different statistical methods and limited
119 quantification of their uncertainty Previous development of CNDCs for potato (Duchenne et al.,
120 1997; Bélanger et al., 2001a; Giletto & Echeverría, 2015; Ben Abdallah et al., 2016). ~~has been~~
121 ~~conducted using a non uniform set of statistical methods and with limited quantification of~~
122 ~~uncertainty in either the range of plausible %N_e values or the fitted parameter values themselves.~~
123 This makes it difficult to ascertain whether observed differences in CNDCs result from underlying
124 G × E × M effects, are confounded by the limitations of the statistical approach, or biased due to
125 insufficient quantity or quality of experimental data (e.g., unbalanced distribution of N limiting
126 and non-N limiting observations).

127 The conventional approach to fit a CNDC consists of a two-step process: first, the critical points
128 from the relationship of %N_{Plant} as a function of biomass are selected using statistical criteria;
129 second, a negative exponential curve is fit to the subset of critical points using non-linear
130 regression. There are two commonly used statistical approaches to identify critical points: (1)
131 linear-plateau curve fit and (2) ANOVA and protected multiple comparison.

132 Using a linear-plateau curve to derive critical points was originally suggested by Justes et al.
133 (1994). This approach is rigorous and requires sufficient empirical data such that a linear-plateau
134 curve can be identified (i.e., at least one N limiting and at least two non-N limiting data points) for
135 each observation date. Therefore, this approach can be difficult or impossible to implement due to
136 potential limitations of the experimental data used such as insufficient levels of N treatments (i.e.,
137 fewer than three treatment levels) or interactions between management practices and
138 environmental conditions (i.e., all observations are either N limiting or non-N limiting).

139 In contrast, many studies use methods similar to Ben Abdallah et al. (2016) where critical points
140 are determined using a simplified statistical method. In this approach, ANOVA is first used to
141 identify experimental dates where variation in biomass is statistically significant. Subsequently, a
142 protected multiple comparisons analysis is used to identify which experimental treatments had the
143 highest level of biomass – the treatment level with the significantly greatest level of biomass is
144 then defined as the critical point. While this statistical method is more flexible to implement, it
145 cannot resolve deficiencies in the underlying empirical data (e.g., insufficient level of N
146 treatments, interactions with environmental conditions) ~~that the linear plateau method was~~
147 ~~designed to discriminate against~~. Therefore, the critical points selected using the simplified method
148 may be biased due to inherent deficiencies of the underlying experimental data used.

149 Novel statistical methods developed first by Makowski et al. (2020) provide a framework which
150 allows for standardization in statistical approach and quantification of uncertainty for deriving in
151 CNDCs which enables comparison of %N_c across G × E × M interactions. In short, this framework
152 implements a hierarchical Bayesian model which simultaneously identifies critical points using
153 the linear-plateau method (e.g., Justes et al. (1994)) while fitting the negative exponential curve
154 which defines %N_c. The advantage of this method is that it fits the CNDC from the entire set of
155 experimental data for a given G × E × M interaction level and removes the arbitrary intermediate
156 step of separately identifying critical points. This approach has already been successfully used by
157 Ciampitti et al. (2021), Yao et al. (2021), and Fernández et al. (2021) to evaluate differences in
158 CNDCs across G × E × M interactions for maize, wheat, and tall fescue cropping systems,
159 respectively. Through this single-step process, the Bayesian hierarchical method both eliminates
160 the need to separately identify critical points and implements the theoretically preferred method
161 (e.g., linear-plateau curve fit) to select critical points.

162 The Bayesian hierarchical method, however, remains subject to inferential bias due to both limited
163 quantity and quality of experimental data (Fernández et al., 2021; Fernandez et al., 2022). With
164 respect to quantity, having an insufficient number of observations from a limited number of
165 experimental trials to derive an individual CNDC will result in increased bias in %N_c. With respect
166 to quality, using experimental data that does not reflect a full range of biomass values or does not
167 sufficiently represent both limiting and non-limiting N conditions will result in increased bias in
168 %N_c. Datasets used to derive the CNDC using the Bayesian hierarchical method should contain at
169 least eight experimental trials containing at least three N treatments and at least three sampling
170 dates (Fernández et al., 2022).

171 However, there are multiple approaches to pooling across G × E × M interactions within the
172 Bayesian hierarchical method to address this bias due to experimental data limitations: no pooling,
173 full pooling, and partial pooling.

174 The no pooling approach treats each experimental data level independently where experimental
175 data from one level is not used in inference for any other level (McElreath, 2020). The no pooling
176 approach was used by Makowski et al. (2020), Ciampitti et al. (2021), Yao et al. (2021), and
177 Fernández et al. (2021) to develop independent models for each G × E × M interaction. For the
178 Bayesian hierarchical method, the no pooling approach is directly limited by the quantity and
179 quality of experimental data for each G × E × M interaction level.

180 The full pooling approach, in contrast, treats each experimental data level in an equivalent manner
181 where the experimental data from all levels are used simultaneously for inference (McElreath,
182 2020). The full pooling approach was used by Fernández et al. (2021) to develop a single model
183 across G × E × M interaction levels. While this approach was found by Fernández et al. (2021) to

184 potentially reduced inferential bias from the Bayesian hierarchical method (i.e., by increasing the
185 combined quantity and quality of data used to fit a given CNDC), the fully pooled approach has
186 the explicit tradeoff that inference at individual levels of $G \times E \times M$ interactions is not possible.

187 The partial pooling approach balances the tradeoffs between fitting a single population-level model
188 (i.e., full pooling) and fitting multiple independent group-level models (i.e., no pooling) by using
189 the entire set of experimental data to fit a single model with where the data from all other levels of
190 an effect influence the inference for a particular level and reduce inferential bias (McElreath,
191 2020). In this manner, individual effect levels are said to be “borrowing strength” through the
192 process of “shrinkage”, where more extreme values are pulled toward the average (Lindstrom &
193 Bates, 1990; Bates, 2010). Therefore, using a partially-pooled Bayesian hierarchical method
194 should reduce ~~both reduce~~ the inferential bias for a given $G \times E \times M$ interaction level where the
195 quantity and quality of experimental data are not otherwise sufficient and enable inference for each
196 individual $G \times E \times M$ interaction level. However, the partial pooling approach has not yet been
197 implemented within in the Bayesian hierarchical method to derive CNDCs.

198 Building upon previous work, the objectives of this study are to 1) develop CNDCs using the
199 hierarchical Bayesian framework for potato varieties in Minnesota (from both previously
200 published and unpublished experimental data) and for potato varieties in Argentina (Giletto &
201 Echeverría, 2015), Canada (Bélanger et al., 2001a), and Belgium (Ben Abdallah et al., 2016) (from
202 previously published experimental data), 2) extend the implementation of the hierarchical
203 Bayesian framework using a partial pooling approach to compare CNDCs across $G \times E \times M$
204 interactions based on the uncertainty in $\%N_c$ and curve parameters a and b , 3) identify the optimal
205 methods to determine uncertainty in $\%N_c$ for use in calculating NNI and other derivative metrics,

206 and 4) compare CNDCs developed with the hierarchical Bayesian framework methods to
207 previously published CNDCs for the same data with different statistical methods.

208 **2. Materials and Methods**

209 *2.1. Experimental Data*

210 This study combines experimental data from both newly reported and previously published sources
211 (Ben Abdallah et al., 2016; Giletto et al., 2020). The data used for analysis in this study are
212 summarized in Table 1 and the relevant methods related to the experimental trials are reported
213 below. All individual experimental observations used in this study are presented in the
214 Supplemental Materials (Table S1).

Table 1. Summary of experimental data used in this study.

Study	Location	Variety	Site-Years	Sampling Dates	Samples
Present Study	Minnesota	Clearwater	2	10	30
		Dakota Russet	2	14	70
		Easton	2	14	70
		Russet Burbank	9	52	328
		Umatilla Russet	2	10	30
Giletto et al. (2020)	Argentina	Bannock Russet	3	13	52
		Gem Russet	4	18	72
		Innovator	4	18	72
		Markies Russet	2	9	36
		Umatilla Russet	3	14	56
Canada		Russet Burbank	4	30	104
		Shepody	4	30	105
Ben Abdallah et al. (2016)	Belgium	Bintje	17	49	238
		Charlotte	7	24	114

215
216 2.1.1. Newly Reported Data – Minnesota
217 Six individual plot-scale field experiments were conducted over a total of eight years (MN-1:
218 1991–1992; MN-2: 2014–2015, MN-3: 2016, MN-4: 2018–2019, MN-5: 2019, MN-6: 2020) ~~on~~

219 irrigated plots at the Sand Plain Research Farm [SPRF] in Becker, MN ($45^{\circ} 23' N$, $93^{\circ} 53' W$).A
220 summary of the treatments and sampling design for each experiment is presented in Table 2, and
221 a summary of key experimental factors across G, E, and M effects are presented in Table 3. (Table
222 2). The soil is characterized as a Hubbard loamy sand (Sandy, mixed, frigid Entic Hapludolls) with
223 organic matter content ranging from 1.3 to 2.5% and is excessively well drained with low available
224 water holding capacity (Hansen & Gieneke, 1988; USDA NRCS, 2013). For a typical growing
225 season beginning on 1 May and ending on 15 September, mean temperature is $18.9^{\circ}C$, cumulative
226 precipitation is 383 mm, cumulative growing degree days are $1638^{\circ}C$ days, mean daily solar
227 radiation is 22.7 MJ m^{-2} , and mean diurnal temperature difference is $11.6^{\circ}C$ based on a historical
228 climate reconstruction for the period of 1980–2016 (Gelaro et al., 2017; Weather Spark, 2021).

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Table 2. Summary of newly reported experimental small-plot trials in Minnesota, USA.

Experiment	Year	Reference
MN-1	1991–1992	Rosen et al. (1992); Rosen et al. (1993); Errehbi et al. (1998)
MN-2	2014–2015	Sun (2017); Sun et al. (2019); Sun et al. (2020)
MN-3	2016	Crants et al. (2017)
MN-4	2018–2019	Gupta and Rosen (2019); Gupta et al. (2020); Li et al. (2021)
MN-5	2019	Bohman et al. (2020)
MN-6	2020	Rosen et al. (2021)

232 Apart from experimental N and variety treatments, all management and cultural practices were
233 managed by the staff at the SPRF in accordance with common practices for the region (Egel, 2017).
234 Nutrients were applied based on soil samples and University recommendations (Franzen et al.,
235 2018; Rosen, 2018), and supplemental irrigation was applied based on the University

236 recommended checkbook method (Wright, 2002; Steele et al., 2010). Additional details on
237 experimental procedures for these studies have been previously reported (Table 2).

238 A randomized complete block design with three or four replicates was used in each field
239 experiment. All experiments evaluated at least three nitrogen-N rates (0 – 400 kg N ha⁻¹)
240 for Russet Burbank potato [*Solanum tuberosum* (L.)], with some studies evaluating additional
241 potato varieties (Table 2). Nitrogen fertilizer was applied using various source and timing regimes
242 including polymer coated urea applied at planting and/or emergence, split-applied urea and urea-
243 ammonium nitrate at emergence and/or post-emergence, ammonium nitrate at planting,
244 emergence, and/or post-emergence. The maturity class of varieties evaluated in these experiments
245 included: medium late Clearwater and Dakota Russet; medium late to late Umatilla Russet;
246 late Easton; late to very late Russet Burbank (Thompson, 2013; Porter, 2014; Stark et al., 2020;
247 OSU, 2021). Planting density was 36,000 plants ha⁻¹ for all experiments except for MN 1 which
248 was planted at a density of 48,000 plants ha⁻¹.

249 EThe experiments that evaluated multiple varieties had either a factorial design, or split-plot design
250 with variety treatment as the whole-plot and nitrogen-N treatment as the split-plot. Plots in these
251 studies were between 5.4 – 6.4 m wide (6 or 7 x 0.9 m rows) and 6.1 – 9.1 m long. Experiments
252 were planted each year in late-April to early-May and were mechanically harvested in mid-
253 September with vines terminated one to two weeks prior to harvest. Apart from experimental N
254 and variety treatments, all management and cultural practices were managed by the staff at the
255 SPRF in accordance with common practices for the region (Egel, 2017). Nutrients were applied
256 based on soil samples and University recommendations (Franzen et al., 2018; Rosen, 2018), and
257 supplemental irrigation was applied based on the University recommended checkbook method

258 (Wright, 2002; Steele et al., 2010). Additional details on experimental procedures for these studies
 259 have been previously reported (Table 2).

260 A summary of N management practices and varieties evaluated for each of these studies is given
 261 below (Table 3).

Table 2. Summary of newly reported experimental small-plot trials in Minnesota, USA

<u>Experiment</u>	<u>Year</u>	<u>N trts.[†]</u>	<u>N rates [kg ha⁻¹]</u>	<u>Varieties</u>	<u>Sampling Dates</u>	<u>Reference</u>
<u>MN-1</u>	1991	10	0, 135,		12 June, 24 June, 2 July,	
			180, 225,	Russet Burbank	16 July, 30 July, 13 Aug.	Rosen et al. (1992);
			270		10 Sept.	Rosen et al. (1993);
	1992	10	0, 135, 180, 225, 270	Russet Burbank	10 June, 25 June, 17 July, 5 Aug., 26 Aug., 15 Sept.	Errebhi et al. (1998)
<u>MN-2</u>	2014	5	135, 200, 270, 335,	Russet Burbank, Dakota Russet,	30 June, 15 July, 24 July, 11 Aug., 26 Aug., 8 Sept.,	Sun (2017);
			400	Easton	15 Sept.	Sun et al. (2019);
			135, 200, 270, 335,	Russet Burbank, Dakota Russet,	23 June, 7 July, 21 July, 4 Aug., 17 Aug., 1 Sept.,	Sun et al. (2020)
	2015	5	400	Easton	16 Sept.	
<u>MN-3</u>	2016	4	45, 180, 245, 335	Russet Burbank	28 June, 13 July, 26 July, 3 Aug., 10 Aug., 13 Sept.	Crants et al. (2017)
<u>MN-4</u>	2018	3	135, 270, 400	Russet Burbank, Clearwater, Umatilla Russet	26 June, 10 July, 18 July, 1 Aug., 13 Sept.	Gupta and Rosen (2019); Gupta et al. (2020);
			135, 270, 400	Russet Burbank, Clearwater, Umatilla Russet	26 June, 11 July, 24 July, 7 Aug., 16 Sept.	Li et al. (2021)
			45, 155, 245, 290, 335	Russet Burbank	25 June, 9 July, 23 July, 6 Aug., 21 Aug., 16 Sept	Bohman et al. (2020)
<u>MN-6</u>	2020	8	55, 155, 245, 270, 290, 335	Russet Burbank	24 June, 7 July, 22 July, 4 Aug., 16 Sept.	Rosen et al. (2021)

[†] Including N source, timing, and placement combinations occurring at an equivalent N rate

Table 3. Summary of experimental treatments evaluated in small-plot trials in Minnesota, USA.

Experiment	N treatments*	N rates [kg ha ⁻¹]	Varieties
MN-1	10	0, 135, 180, 225, 270	Russet Burbank
MN-2	5	135, 200, 270, 335, 400	Russet Burbank, Dakota Russet, Easton
MN-3	4	45, 180, 245, 335	Russet Burbank
MN-4	3	135, 270, 400	Russet Burbank, Clearwater, Umatilla Russet
MN-5	8	45, 155, 245, 290, 335	Russet Burbank
MN-6	8	55, 155, 245, 270, 290, 335	Russet Burbank

* Including N source, timing, and placement combinations occurring at an equivalent N rate

264

265 Samples of vine biomass were harvested immediately prior to mechanical termination for
266 determination of fresh weight vine yield. Harvested tubers were mechanically sorted into weight
267 classes and graded (USDA, 1997), and fresh weight tuber yield was determined as the sum of all
268 weight classes and tuber grades. Harvested biomass was oven dried at 60°C to determine dry matter
269 content of vines and tubers. Dry weight tuber and vine biomass was calculated as the product of
270 fresh weight and dry matter content for each tissue respectively. Total N concentration of vines
271 and tubers was determined from subsamples of plant tissues with either combustion analysis
272 (Elementar Vario EL III, Elementar Americas Inc., Mt. Laurel, NJ) using standard methods
273 (Horneck & Miller, 1998), or with the salicylic Kjeldahl method (Horwitz et al., 1970). Total N
274 content of vines and tubers was calculated as the product of N concentration and dry weight
275 biomass for each tissue respectively. Total plant N content [N_{Plant}] (kg N ha⁻¹) was calculated from
276 the sum of tuber and vine N content. Total plant dry weight biomass [W] (Mg dry wt. ha⁻¹) was
277 calculated from the sum of vine and tuber dry weight biomass. Plant N concentration [%N_{Plant}] (g
278 N 100 g⁻¹ dry wt.) was calculated as the ratio of N_{Plant} to W.

279 Whole-plant samples were also regularly collected during the period of late-May to early-
280 September (Table 24). Two to three plants were harvested from each plot on four to six dates each
281 year with vines, roots, and tubers each measured separately. Dry weight biomass, N concentration,
282 and N content for vines and tubers were determined for these in-season plant tissue samples using
283 the methods described above. Calculations for W, N_{Plant}, and %N_{Plant} were the same as methods
284 previously described above.

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Table 4. In-season and harvest sampling dates for the experimental small-plot trials in Minnesota, USA.

Experiment	Year	1	2	3	4	5	6	Harvest
MN-1	1991	12 June	24 June	2 July	16 July	30 July	13 Aug	10 Sept.
MN-1	1992	10 June	25 June	17 July	5 Aug.	26 Aug.		15 Sept.
MN-2	2014	30 June	15 July	24 July	11 Aug.	26 Aug.	8 Sept.	15 Sept.
MN-2	2015	23 June	7 July	21 July	4 Aug.	17 Aug.	1 Sept.	16 Sept.
MN-3	2016	28 June	13 July	26 July	3 Aug.	10 Aug.		13 Sept.
MN-4	2018	26 June	10 July	18 July	1 Aug.			13 Sept.
MN-4	2019	26 June	11 July	24 July	7 Aug			16 Sept.
MN-5	2019	25 June	9 July	23 July	6 Aug	21 Aug		16 Sept.
MN-6	2020	24 June	7 July	22 July	4 Aug			16 Sept.

286

287 2.1.2. Previously Published Data – Belgium, Argentina, and Canada

288 Experimental data reported in two previous studies, Giletto et al. (2020) and Ben Abdallah et al.
289 (2016), were included in the analysis conducted for the present study. The data from Giletto et al.
290 (2020) comprises two separate experimental data sets from small-plot experiments conducted in
291 Balcarce in the province of Buenos Aires, Argentina (37° 45' S; 58° 18' W) Argentina (Giletto &
292 Echeverría, 2015) and in the upper St. John River Valley of New Brunswick, Canada (47° 03' N;
293 67° 45' W) Canada (Bélanger et al., 2000, 2001a, 2001b). All data from the Giletto et al. (2020)
294 study used in the present analysis was included in this previous publication.

295 In the Canadian study, two varieties (Russet Burbank and Shepody) and four N fertilization rates
296 (0, 50, 100, and 250 kg ha⁻¹) were evaluated under irrigated and non-water limiting conditions with
297 each variety having four site years of experimental data and either seven or eight sampling dates
298 per site year (Table 1). These small plot experiments were conducted in the upper St. John River
299 Valley of New Brunswick, Canada (47° 03' N; 67° 45' W). Nitrogen fertilizer for all treatments
300 was ammonium nitrate applied at planting. The maturity class of varieties evaluated in these
301 experiments included: early to medium—early—Shepody; late to very late—Russet Burbank (Stark
302 et al., 2020; OSU, 2021). Planting density was 29,000 and 44,000 plants ha⁻¹ for Russet Burbank
303 and Shepody, respectively. The soil texture for these experiments was classified as either loam or
304 clay loam with organic matter content ranging from 2.6 to 3.0%. For a typical growing season
305 beginning on 1 June and ending on 10 October, mean temperature is 15.7°C, cumulative
306 precipitation is 371 mm, cumulative growing degree days are 1150 °C days, mean daily solar
307 radiation is 19.1 MJ m⁻², and mean diurnal temperature difference is 10.0 °C based on a historical
308 climate reconstruction for the period of 1980–2016 (Gelaro et al., 2017; Weather Spark, 2021).

309 In the Argentina study, five varieties (Bannock Russet, Gem Russet, Innovator, Markies Russet,
310 and Umatilla Russet) and four N fertilization rates (0, 80, 150, and 250 kg N ha⁻¹) were each
311 evaluated under irrigated and non-water limiting conditions for between two and four site years
312 with between four and five sampling dates per site year (Table 1). These small plot experiments
313 were conducted in Balcarce in the province of Buenos Aires, Argentina (37° 45' S; 58° 18' W).
314 Nitrogen fertilizer for all treatments was urea applied at planting. The maturity class of varieties
315 evaluated in these experiments included: early to medium—Innovator; medium to late—Gem
316 Russet; medium late to late—Umatilla Russet; late to very late—Bannock Russet and Markies
317 Russet (Giletto & Echeverría, 2015; Stark et al., 2020; OSU, 2021). The planting density was

318 59,000 plants ha⁻¹ for all varieties. Soil texture for these experiments was classified as a loam with
319 organic matter content ranging from 4.2 to 5.2%. For a typical growing season beginning on 10
320 October and ending on 10 March, mean temperature is 18.4°C, cumulative precipitation is 428
321 mm, cumulative growing degree days are 1739 °C days, mean daily solar radiation is 25.5 MJ m⁻²,
322 and mean diurnal temperature difference is 13.6 °C based on a historical climate reconstruction
323 for the period of 1980–2016 (Gelaro et al., 2017; Weather Spark, 2021).

324

325 The data from Ben Abdallah et al. (2016) represents multiple experimental data set from small-
326 plot experiments were conducted in Gembloux, Belgium (50° 33' N; 4° 43' E)Belgium. Only a
327 portion of the data from the Ben Abdallah et al. (2016) study used in the present analysis was
328 included in this previous publication – while the dry weight biomass data were previously reported,
329 the N concentration data from the Ben Abdallah et al. (2016) experiment is reported for the first
330 time in this work.

331

332 In the Belgium studies, three to six N rates (ranging from 0 to 250 kg N ha⁻¹) were evaluated for
333 two varieties (Bintje and Charlotte) for 17 and 7 site-years, respectively, with between one and
334 eight sampling dates per site year (Table 1). These small plot experiments were conducted in
335 Gembloux, Belgium (50° 33' N; 4° 43' E). Nitrogen fertilizer for all treatments was ammonium
336 nitrate applied at planting. The maturity class of varieties evaluated in these experiments included:
337 medium—Charlotte; late—Bintje (CFIA, 2013; AHDB, 2015; OSU, 2021). The planting density
338 was 38,000 plants ha⁻¹ for all varieties. The soil texture for these experiments was classified as
339 loam, sandy loam, silt loam, or silty clay loam with organic matter content ranging from 1.3 to

340 2.6%. For a typical growing season beginning on 20 April and ending on 20 September, mean
341 temperature is 15.5°C, cumulative precipitation is 244 mm, cumulative growing degree days are
342 1313 °C days, mean daily solar radiation is 20.0 MJ m⁻², and mean diurnal temperature difference
343 is 8.3 °C based on a historical climate reconstruction for the period of 1980–2016 (Gelaro et al.,
344 2017; Weather Spark, 2021). A summary of experimental data from each trial used in the present
345 study is presented in Table 1, and a summary of key experimental factors across G, E, and M
346 effects is presented in Table 3.

347
348 A comparison of G (i.e., maturity class), E (i.e., soil texture, growing season weather conditions),
349 and M (i.e., planting density, source and timing of N fertilizer) factors across the G × E × M
350 interaction levels evaluated in this study is presented in Table 5.

351

Table 5. Comparison of key experimental factors including for Genotype [G]; variety maturity class [Maturity Class]; Environment [E]: soil texture classification [Soil Texture], soil organic matter content [OM], growing season mean daily temperature [T_{Mean}], growing season cumulative precipitation [Precip.], growing season mean diurnal temperature difference [$\Delta T_{Diurnal}$], growing season cumulative growing degree days [GDD], growing season mean daily incident solar radiation [Sol. Rad.]; and Management [M]: planting density [Density], and N fertilizer application source and timing.

		G	E									M										
Location	Variety	Maturity Class [†]	Soil Texture [‡]	OM [%]	Growing Season [§] ¶		T _{Mean} [°C]	Precip. [mm]	ΔT _{Diurnal} [°C]	GDD [°C d]	Sol. Rad. [MJ m ⁻²]	Density [plants ha ⁻¹]	N Source & Timing [¶]	Irr.								
Argentina	Bannock Russet	L to VL	L	4.2 – 5.2	1 June –		18.4	428	13.6	1739	25.5	59,000	Urea @ PL	Yes								
	Gem Russet	M to L			10 Oct. 4.2 –																	
	Innovator	E to M			Oct. 4.2 –																	
	Markies Russet	L to VL			to 5.2																	
	Umatilla Russet	ML to L																				
Belgium	Bintje	L	SiCL, SiL, L, SL	1.3 – 2.6	10 Oct. –		15.5	244	8.3	1313	20.0	38,000	AN @ PL	No								
	Charlotte	M			10 Mar. 1.3 –																	
Canada	Russet Burbank	L to VL	CL, L	2.6 – 3.0	20 Apr. –		15.7	371	10.0	1150	19.1	29,000	AN @ PL	Yes								
	Shepody	E to ME			20 Sept. 2.6 –																	
Minnesota	Clearwater	ML	LS	1.3 – 2.5	1 May –		18.9	383	11.6	1638	22.7	36,000*	AN, Urea, UAN, and/or PCU @ PL, EM, and/or P-EM	Yes								
	Dakota Russet	ML			15 Sept. 4.3 –																	
	Easton	L			to 2.5																	
	Russet Burbank	L to VL																				
	Umatilla Russet	ML to L																				

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† Early [E], medium-early [ME], medium [M], medium-late [ML], late [L], very late [VL] as classified by Stark et al. (2020), OSU (2021), Giletto & Echeverría (2015), CFIA (2013), AHDB (2015), Thompson (2013), and Porter (2014)

‡ Silty clay loam [SiCL], clay loam [CL], silt loam [SiL], loam [L], sandy loam [SL], loamy sand [LS]

§ Summary weather data based on typical growing season dates and historical climate reconstruction for the period of 1980-2016 (Gelaro et al., 2017; Weather Spark, 2021)

¶ Ammonium nitrate [AN], urea-ammonium nitrate [UAN], polymer-coated urea [PCU], planting [PL], emergence [EM], post-emergence [P-EM]

* Russet Burbank in MN-1 was planted at a density of 48,000 plants ha⁻¹

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354

355

356 2.2. Statistical Methods

357 Based on the general approach outlined by Makowski et al. (2020), this study implemented a
358 partially-pooled Bayesian hierarchical framework to infer CNDC parameters for each location and
359 variety within location, assess the uncertainty in model parameters and %N_c, and compare fitted
360 CNDCs across the effects of location and variety.

361 In summary, this statistical approach uses the entire set of experimental data (Figure 1a) and does
362 not require any preliminary or intermediary statistical analysis. At the level of each experimental
363 sampling date, a linear plateau curve is fit for biomass as a function of N concentration (Figure
364 1b) and the join point of the linear plateau curve is used to define the %N_c. Simultaneously, a
365 negative exponential curve (i.e., CNDC) is fit across all experimental sampling dates for a given
366 effect level of the hierarchical model (e.g., location, variety) where the critical point of each linear
367 plateau curve lies exactly upon the negative exponential curve (Figure 1b). In this manner, the
368 linear plateau curve fitted for any given date is influenced by the data from all other experimental
369 sampling dates through the fitting of the negative exponential curve. In comparison, the
370 conventional statistical approach fits a negative exponential curve to the subset of critical points
371 (Figure 1c) which are identified via an intermediate statistical analysis (i.e., ANOVA and protected
372 multiple comparisons).

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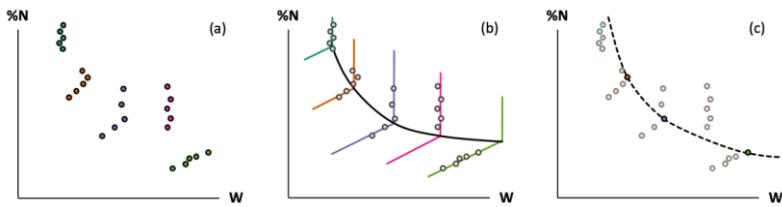


Figure 1. Hypothetical example comparing various statistical methods where plant N concentration [%N] as a function of biomass [W] on five experimental sampling dates for (a) raw experimental data, (b) linear-plateau curves (solid colored lines) fitted for each experimental sampling date (points for each date distinguished by color) and the critical N dilution curve (solid black line) fitted using the hierarchical Bayesian method based on Makowski et al. (2020), and (c) critical points (opaque) and non-critical points (transparent) selected using conventional statistical analysis (i.e., ANOVA and protected multiple comparison) with critical N dilution curve (dotted line) fitted using conventional methods (i.e., non-linear regression using only the critical points).

374

375 The Bayesian hierarchical framework outlined by Makowski et al. (2020) was extended to
 376 explicitly include the $G \times E \times M$ interaction levels within the fitted model using a partial pooling
 377 approach. Experimental data were nested according to location and variety within location, where
 378 the linear-plateau curve fitted for each experimental sampling date is nested within a given level
 379 of variety within location (Figure 2Figure 1). This model structure leverages the advantages of
 380 partial pooling to address the limitations identified by Fernández et al. (2021) that a sufficient
 381 quantity and quality of experimental data are required while still enabling direct inference on the
 382 individual $G \times E \times M$ interaction levels. Using *R* (R Core Team, 2021a), the *brms* package
 383 (Bürkner, 2017, 2018) was used to implement the statistical framework outlined by Makowski et
 384 al. (2020) with the modifications as previously described (Figure 2Figure 1). The *brms* package,
 385 an interface to *Stan* (Carpenter et al., 2017), was chosen due to the ability to include group-level
 386 effects (i.e., random effects) which allows for the fit of this particular partially-pooled Bayesian
 387 hierarchical model. The *brms* package includes a user-friendly modeling language, robust
 388 documentation, and a diverse set of tools to analyze and assess models.

389

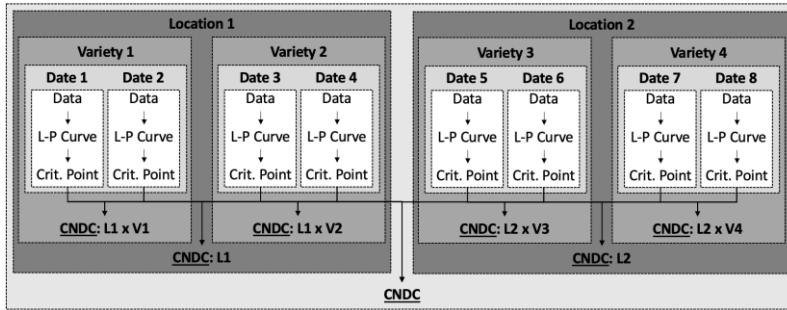


Figure 12. Flowchart showing nested structure used to fit critical N dilution curves [CNDC] using the hierarchical Bayesian method based on Makowski et al. (2020). Linear-plateau (L-P) curves and critical points (i.e., the fitted join point of each linear-plateau curve) are identified at the level of each experimental sampling date and pooled at various levels of location and variety within location to determine the CNDC for that level. This hierarchical model structure simultaneously fits all individual levels of location and variety within location, as well as for the global level of all experimental data, which allows for direct comparison across levels.

390

391 A non-linear *brms* model was defined by combining the two separate expressions used by
 392 Makowski et al. (2020) to parameterize the Bayesian hierarchical model as previously
 393 implemented with *rjags* (Plummer, 2019) and *JAGS* statistical software (Plummer, 2013).

394 The first expression from Makowski et al. (2020) represents the linear-plateau component:

$$395 \quad W = \min(W_{Max,i} + S_i \cdot (\%N_{Plant} - \%N_c), W_{Max,i}) \quad [3]$$

396 where S_i and $W_{Max,i}$ are the slope of the linear-plateau curve and the maximum value of biomass
 397 (i.e., plateau) for a given date [i], respectively, \min represents the minima function (i.e., the plateau
 398 component), and W , $\%N_{Plant}$, and $\%N_c$ have the same meaning as previously defined in this present
 399 study. This linear-plateau curve is defined with N concentration as the independent variable and
 400 biomass as the dependent variable and is written in point-slope form where the reference point
 401 used is the critical point.

402 The second expression from Makowski et al. (2020) represents the CNDC component:

403 $\%N_c = a W_{Max,i}^{-b}$ [4]

404 where a and b are the parameters that define the negative exponential curve and $\%N_c$ and $W_{Max,i}$
405 have the same meanings as defined above.

406 Using algebraic substitution (i.e., for $\%N_c$), these two expressions (Eq. [3] and Eq. [4]) were
407 combined to produce following non-linear *brms* model formula:

408 $W \sim min(W_{Max,i} + S_i (\%N_{Plant} - (a W_{Max,i}^{-b})), W_{Max,i})$ [5]

409 Two group-level (i.e., random) effects were specified for this *brms* model to parameterize the
410 nested structure ([Figure 2](#)[Figure 1](#)). First, the parameters S and W_{Max} included group-level effects
411 to fit a linear-plateau curve to each experimental sampling date:

412 $W_{Max} + S \sim 1 + (1 | index)$ [6]

413 where $index$ represents the unique level of each experimental sampling date, nested within a given
414 level of variety within location. Second, the parameters a and b included group-level effects to fit
415 the CNDC:

416 $a + b \sim 1 + (1 | location) + (1 | location:variety)$ [7]

417 where *location* and *location:variety* represents the unique effect level for location and variety
418 within location, respectively. Models were fit using treatment-level means (i.e., an effect of
419 replicate was not included in the model).

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420 The *brms* model was fitted using 4 chains and 10000 iterations with 3000 warmups per chain.
421 Model convergence was verified by determining that all parameters had satisfactory R-hat values
422 of less than 1.01 with bulk-ESS and tail-ESS values of at least 100 samples per chain (Vehtari et

423 al., 2021). The priors for this model were chosen based on expert knowledge (i.e., previously
 424 reported values), empirical observations (i.e., summary values from the data set), and inspection
 425 of, and the joint prior predictive distribution. Evaluating the joint prior predictive distribution is
 426 particularly important for hyperparameters dealing with the standard deviation between groups in
 427 a hierarchical model due to the propagation of variance throughout model levels. (i.e., If a set of
 428 relatively uninformative priors led to biologically or physically impossible predictions which
 429 prevented model convergence, the prior ranges were narrowed) (Schad et al., 2021). In particular,
 430 a positive value for S is required to represent the positive physiological relationship between W
 431 and $\%N_{Plant}$ (i.e., linear-plateau curve where W increases as $\%N_{Plant}$ up to W_{max} at $\%N_c$). Similarly,
 432 having non-positive value for W_{max} is physically impossible. This is particularly important for
 433 hyperparameters dealing with the standard deviation between groups in a hierarchical model. A
 434 summary of the prior values used in this model is given below (Table 46).

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Table 64. Priors used in fitting the hierarchical Bayesian model with *brms*.

Parameter	Distribution	Bounds	
		Lower	Upper
a	Normal (5.3, 0.1)	0	∞
$\sigma(a_{location})$	Normal (0.10, 0.02)	$-\infty$	∞
$\sigma(a_{location:variety})$	Normal (0.05, 0.01)	$-\infty$	∞
b	Normal (0.40, 0.01)	0	1
$\sigma(b_{location})$	Normal (0.05, 0.02)	$-\infty$	∞
$\sigma(b_{location:variety})$	Normal (0.02, 0.01)	$-\infty$	∞
W_{max}	Normal (8.0, 0.1)	1	∞
$\sigma(W_{max_index})$	Normal (7.0, 1.0)	$-\infty$	∞
S	Normal (6.0, 0.1)	0	∞
$\sigma(S_{index})$	Normal (1.0, 0.1)	$-\infty$	∞
σ	Student's t (3, 1.0, 0.1)	$-\infty$	∞

436

437 The entire statistical and data workflow used to generate this analysis is reproducible and available
 438 via GitHub repository (<https://github.com/bohm0072/bayesian-cndc-potato>). The *renv* package

439 (Ushey, 2021) was used to document the computing environment utilized while conducting this
440 analysis to ensure code portability and reproducibility.

441 2.3. Evaluating Uncertainty

442 2.3.1. Critical N Dilution Curve Parameter Uncertainty

443 After the statistical model was successfully fit to the data (n=28,000 draws), values for parameters
444 a and b of the CNDC were reported at the 0.05, 0.50 (i.e., median) and 0.95 quantiles for the effect
445 levels of *location* and *location:variety* to determine the 90% credible interval for each parameter.
446 The correlation between values for parameters a and b was determined for each effect level of
447 *location:variety* using the fitted parameter values at the level of the individual draws.

448 2.3.2. Critical N Concentration Uncertainty

449 Uncertainty in %N_c was characterized using three methods: (1) directly modeled 0.05 and 0.95
450 quantile value of posterior distribution of %N_c; (2) parameterized approximation of 0.05 and 0.95
451 quantile value of posterior distribution of %N_c; (3) indirect calculation of %N_c using 0.05 and 0.95
452 quantile values for a and b .

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453 For the directly modeled method, The %N_c for a set of discrete values of W between 1 Mg dry wt.
454 ha⁻¹ and the maximum observed value of W in the experimental data set was calculated for each
455 individual posterior draw based on the fitted values of parameters a and b for that draw. From the
456 distribution of %N_c values, the 0.05, 0.50 (i.e., median) and 0.95 quantile values were identified
457 for each effect level of *location:variety* to determine the 90% credible region for %N_c. This
458 approach makes maximal use of the jointly estimated parameters contained in the posterior
459 distribution.

460 For the parameterized approximation method, To develop curves approximating the upper and
461 lower boundaries of the 90% credible region for $\%N_c$ (i.e., the 0.05 and 0.95 quantile values,
462 respectively), two negative exponential curve of the same form as the CNDC (i.e., $y = a x^{-b}$)
463 whereas fit using *nls* (R Core Team, 2021b) to the set of data previously identified as defining the
464 boundaries of the 90% credible region (i.e., 0.05 and 0.95 quantile values of the posterior
465 distribution of $\%N_c$ computed using the directly modeled method described above). This approach
466 to derive parameterized approximation of the 90% credible region attempts to simplify the
467 complexity of communicating and propagating uncertainty in $\%N_c$. These parameterized curves
468 curves approximating the upper and lower boundaries of the credible region for the CNDC are
469 respectively referred to as CNDC_{up} and CNDC_{lo}, where parameters a_{up} and b_{up} correspond to
470 CNDC_{up} and parameters a_{lo} and b_{lo} correspond to CNDC_{lo}.

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$$471 \%N_{c,lo} = a_{lo} W^{-b_{lo}} \quad [8]$$

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$$472 \%N_{c,up} = a_{up} W^{-b_{up}} \quad [9]$$

473 For the indirect calculation method,

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474 Additionally, an estimate of the 90% credible region for $\%N_c$ was calculated by using the boundary
475 values of the 90% credible interval of parameters a and b . The estimate for the upper boundary of
476 the credible region for $\%N_c$ was determined from the 0.95 quantile value for parameter a and 0.05
477 quantile value for parameter b ; the estimate for the lower boundary of the credible region of $\%N_c$
478 was determined from the 0.05 quantile value for parameter a and 0.95 quantile value for parameter
479 b . This approach does not account for the joint estimation of parameters offered by the Bayesian
480 approach; therefore, the paired combination for parameters a and b (i.e., 0.05 and 0.95 quantiles,
481 respectively) might not actually occur in the posterior distribution.

482 To compare the various methods described above, the difference in critical N concentration
483 [$\Delta\%N_c$] whereas calculated as the difference between a reference value [$\%N_{c,ref}$] and a comparison
484 value [$\%N_{c,i}$]:

$$485 \Delta\%N_c = \%N_{c,ref} - \%N_{c,i} \quad [10]$$

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486 To compare differences between the various methods used to quantify uncertainty in $\%N_c$, $\Delta\%N_c$
487 was calculated (Eq. [10]) where $\%N_{c,ref}$ was set as the median value (i.e., 0.50 quantile) of $\%N_c$
488 from the directly modeled method, while $\%N_{c,i}$ was varied and set as the upper and lower values
489 of $\%N_c$ from the directly modeled, parameterized approximation, and indirect calculation methods
490 as described above.

491 between the 0.50 quantile (i.e., median) value for $\%N_e$, designated as the reference values (i.e.,
492 $\Delta\%N_e$ with constant value of zero), and the various methods to quantify uncertainty (i.e., 90%
493 credible region for $\%N_e$, CNDC_{up} & CNDC_{lo}, and estimates of credible region for $\%N_e$ using 90%
494 credible interval for parameters a and b). In this manner, the $\Delta\%N_e$ for each method to quantify
495 uncertainty in $\%N_e$ can be directly compared.

496 2.3.3. Comparing Critical N Concentration across G × E × M Effects

497 Similar to Using the directly modeled above method described above, the $\%N_c$ for each posterior
498 draw was calculated across a set of discrete values of W over the range of 1 Mg dry wt. ha⁻¹ and
499 the maximum observed value of W in the experimental data set. At the effect level of
500 location:variety, $\Delta\%N_c$ was calculated (Eq. [10]) the difference between the $\%N_e$ for a given
501 comparison and reference CNDC (i.e., $\Delta\%N_e$) was calculated at each value of W where $\%N_{c,ref}$ is
502 the median $\%N_c$ from the posterior distribution for the reference level and $\%N_{c,i}$ was the median

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503 %N_c from the posterior distribution for each pairwise comparison of all other levels. From this
504 computed set of $\Delta\%N_c$, the 0.05, 0.50 (i.e., median) and 0.95 quantile values were identified for
505 each effect level of pairwise comparison of location:variety levels to determine the 90% credible
506 region for $\Delta\%N_c$. ~~For a given range of W values, T~~he comparison curve was considered to be not
507 significantly different from the reference curve ~~when if the $\Delta\%N_e$ values for the 0.05 and 0.95~~
508 ~~quantile values of %N_e were respectively less than and greater than zero (i.e., the 90% credible~~
509 ~~region for $\Delta\%N_c$ contained~~s zero). In the case where the 0.05 quantile value for $\Delta\%N_e$ was greater
510 ~~than zero, the comparison curve was considered to have a significantly greater %N_e than the~~
511 ~~reference curve. In the case where the 0.95 quantile value for $\Delta\%N_e$ was less than zero, the~~
512 ~~comparison curve was considered to have a significantly lower %N_e than the reference curve. To~~
513 ~~evaluate $\Delta\%N_e$ in the present study, the %N_e for a given effect level of location:variety was~~
514 ~~compared to all other levels, and T~~his approach allows for the direct evaluation of differences in
515 $\Delta\%N_c$ across G × E × M effects (i.e., location:variety levels).

516 2.3.4. Comparing Critical N Concentration across Statistical Methods

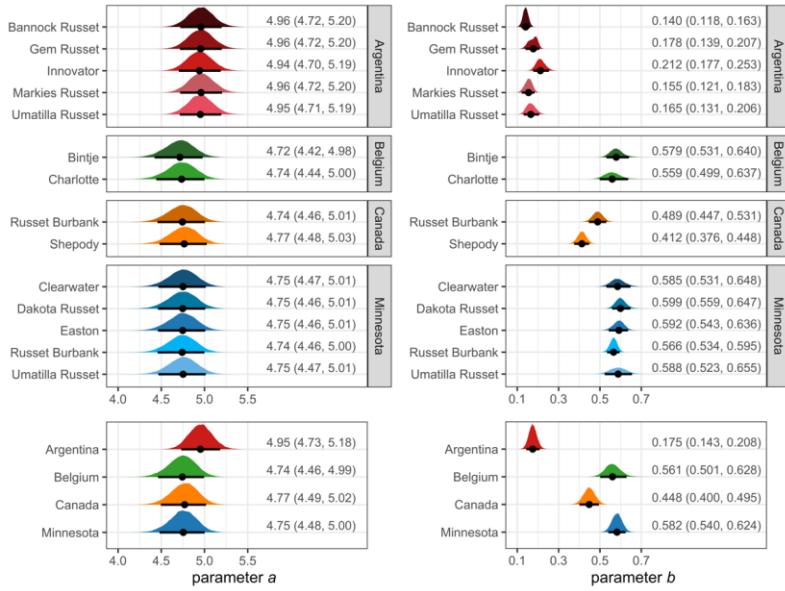
517 An analogous method was also used to compare the CNDCs fitted in the present study to the
518 CNDCs published in previous studies (i.e., Ben Abdallah et al. (2016); Giletto et al. (2020)).
519 Specifically, $\Delta\%N_c$ for each level of location:variety with previously published CNDC was
520 calculated (Eq. [10]) using where %N_{c,ref} was set as the median value (i.e., 0.50 quantile) of %N_c
521 from the directly modeled method, and %N_{c,i} was set as the previously published values of %N_c.
522 If $\Delta\%N_c$ falls outside of the the previously published curves were evaluated to see if they fell
523 within the 90% credible region for the corresponding curve fitted with the hierarchical Bayesian
524 method in the present study. Using the determined 90% credible region for the %N_c determined
525 from the directly modeled method, it is possible to identify the range for which two CNDCs are

526 significantly different. If the previously identified $\%N_e$ value falls outside of the credible region
527 for $\%N_e$ identified in this study, then the two curves are determined to be significantly different
528 over the range for which the previous value falls outside of the credible region. This approach
529 allows for direct evaluation of differences in $\%N_e$ for CNDCs developed from the same set of data
530 across various statistical methods.

531 **3. Results**

532 *3.1. Fitted Critical N Dilution Curve*

533 The posterior distribution of fitted values for CNDC parameters a and b are presented below in
534 ([Figure 3](#)[Figure 2](#)) showing the median value and 90% credible interval (i.e., 0.05 and 0.95 quantile
535 values). For parameter a , there was no significant difference for the effect of location at 90%
536 credible interval threshold ([Figure 3](#)[Figure 2a](#)). Although Argentina has a numerically greater
537 value of parameter a (4.95) than the other three locations (4.74 – 4.77), these differences are not
538 significant. Additionally, the variation in parameter a for the variety within location effect is
539 negligible and not statistically significant ([Figure 3](#)[Figure 2a](#)).
540



(a)

(b)

Figure 23. Posterior distribution of variety and variety within location effects for (a) parameter a ; and (b) parameter b . Points represent median value and line represents 0.05 and 0.95 quantile range. Values displayed with the figures are the median value with the 90% credible interval boundaries (i.e., 0.05 and 0.95 quantiles) displayed within the parentheses.

541

542 For parameter b , there were significant differences for both the effect of location and variety within
 543 location at a 90% credible interval threshold (Figure 3Figure 2b). For location, Argentina had the
 544 lowest value for parameter b (0.175), while Canada had a greater value for parameter b (0.448)
 545 than Argentina but lower than either Belgium (0.561) or Minnesota (0.582). The difference
 546 between parameter b for Belgium and Minnesota was not significant. For the variety within
 547 location effect, parameter b significantly varied for varieties in Argentina and Canada, while there
 548 were no significant differences in parameter b within either Belgium or Minnesota. For Argentina,
 549 Innovator had the greatest value for parameter b (0.212), followed by Gem Russet, Umatilla
 550 Russet, Markies Russet, and Bannock Russet (0.178, 0.165, 0.155, and 0.140, respectively). The

551 difference between Innovator and Umatilla Russet, Markies Russet, and Bannock Russet was
552 significant, while all other differences between varieties were not significant. For Canada, Russet
553 Burbank had a significantly higher value for parameter b (0.489) than Shepody (0.412).

554 There was a positive correlation found between parameters a and b ([Figure 4](#)[Figure 3](#)) which
555 indicates that quantifying differences in these parameter values independently ([Figure 3](#)[Figure 2](#))
556 is not appropriate to describe the uncertainty in $\%N_c$ determined by the correlated parameters.
557 Stated alternatively, significant differences for either parameter a or b do not necessarily imply
558 that differences in $\%N_c$ are also significant.

559

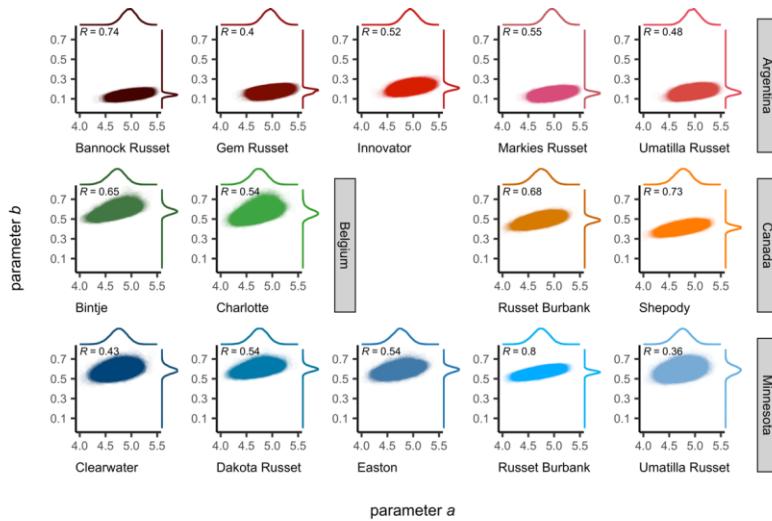
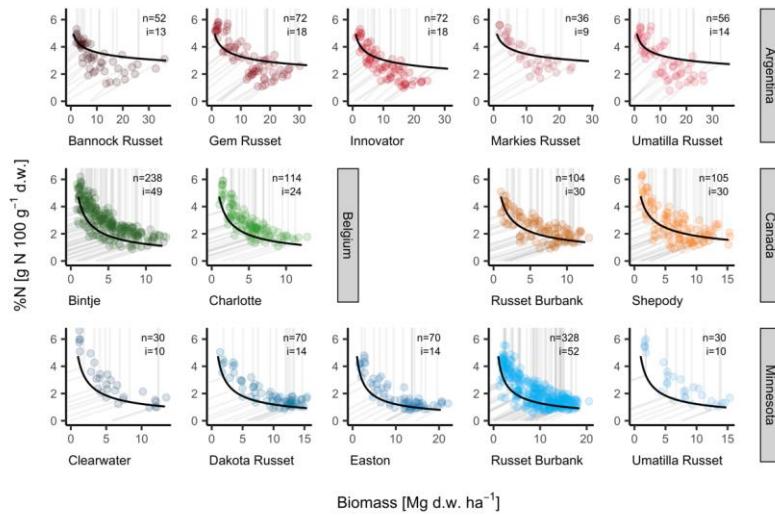


Figure 43. Distribution of posterior values for parameters a and b for each location within variety shown as a scatterplot with marginal density distribution given for each parameter. Pearson correlation coefficient [R] is displayed for the relationship between parameters a and b . Data are shown at the level of individual draws ($n=28,000$).

560
561 Critical N dilution curves for each variety within location and the experimental data, median linear-
562 plateau curve for each experimental sampling date, and median value of $\%N_c$ are presented ([Figure](#)

563 [§Figure 4](#)). The individual linear-plateau curves fitted for each experimental sampling date nested
 564 within each level of the variety within location effect are presented in the Supplemental Materials
 565 (Figure S1).

566



567 **Figure 54.** Critical N dilution curves (i.e., median value of critical N concentration [%N_c]) fitted from the
 hierarchical Bayesian model are shown as a solid black lines for each variety within location. Biomass and N concentration [%N] data are displayed as points with the median linear-plateau curve for each
 sampling date shown as grey line. The number of samples [n] and the number of sampling dates [i] are
 displayed on each individual panel.

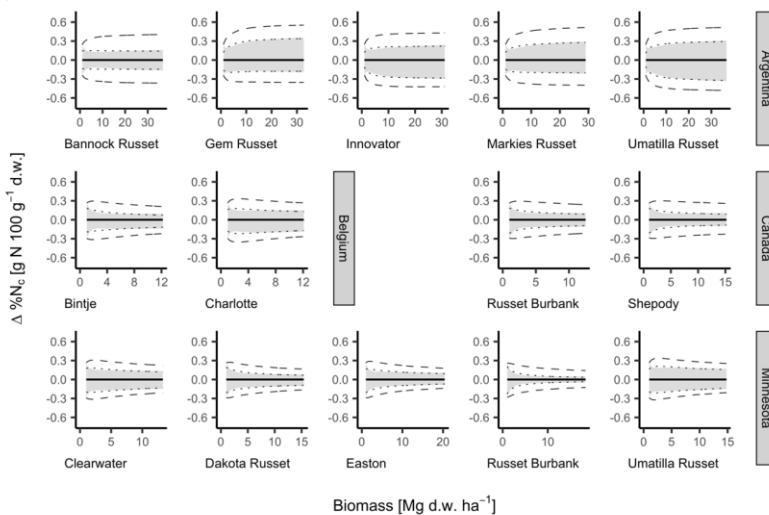
568 For the Argentina varieties, more than 60% of the observed data fall below the CNDC (i.e.,
 569 represent N limiting conditions) with over 40% of sampling dates having exclusively N limiting
 570 conditions observed. For both the Belgium and Minnesota varieties, more than 80% of the
 571 observed data fall above the CNDC (i.e., represent non-N limiting conditions) with almost 30% of
 572 sampling dates having exclusively non-N limiting conditions observed. For the Canada varieties,
 573 over 60% of observed data represented non-N limiting conditions but less than 10% of sampling
 574 dates had exclusively non-N limiting conditions observed (Figure S1).

575 3.2. *Critical N Concentration Uncertainty*

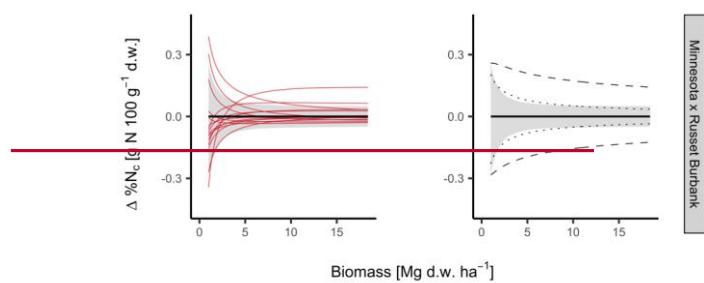
576 The credible region for %N_c varies across variety within location and across levels of biomass
577 ([Figure 6](#)[Figure 5](#)). The symmetry of the credible region distribution varies by variety within
578 location. Some levels of variety within location, such as Argentina × Gem Russet, have a skewed
579 distribution, while other levels, such as Canada × Shepody, have a symmetrical distribution ([Figure](#)
580 [6](#)[Figure 5a](#)). There are also differences in the range of the credible region, where some varieties
581 within location, such as Argentina × Umatilla Russet, have greater uncertainty in %N_c than others,
582 such as Minnesota × Russet Burbank. The uncertainty in %N_c also varies across the level of
583 biomass for a given CNDC. For example, as the level of biomass increases, Argentina × Umatilla
584 Russet has an increasing credible region range, Minnesota × Russet Burbank has a decreasing
585 credible region range, and Argentina × Bannock Russet has a nearly constant credible region range.

586

(a)



(b)



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Figure 65. Comparison of the difference in critical N concentration values [$\Delta\%N_c$] between the median reference critical N concentration [$\%N_{c,\text{ref}}$] represented as a solid black line at constant $\Delta\%N_c$ value of zero, and the various methods to quantify uncertainty in critical N concentration [$\%N_c$] where the magnitude of uncertainty in $\%N_c$ is equivalent the $\Delta\%N_c$ value. The grey shaded region represents the 90% credible region of $\%N_c$ (lower bound, 0.05 quantile; upper bound, 0.95 quantile) from the directly modeled approach (i.e., $\%N_c$ computed from parameter estimates of each posterior draw) fitted Bayesian hierarchical model. The dotted lines represent an estimation of the estimated upper and lower bounds of $\%N_c$ of the 90% credible region from the parameterized estimate approach using the non-linear regression method (i.e., CNDC_{lo} and CNDC_{up}). The dashed lines represent the approximated lower and upper bounds of $\%N_c$ from the indirect calculation approach (i.e., $\%N_c$ computed based on an approximation of uncertainty in $\%N_c$ based on the posterior distribution of critical N dilution curve (CNDC) parameters a and b). Data are presented for (a) all levels of variety within location, and (b) shown in greater detail for Minnesota \times Russet Burbank only for individual draws from the Bayesian hierarchical model, for the non-linear regression method, and for the approximation of the 90% credible region based on the posterior distribution of parameters a and b . For (b), the solid red line represents individual draws ($n=15$) from the posterior distribution of the fitted Bayesian hierarchical model.

588 Estimation of the upper and lower boundaries of the 90% credible region using the ~~non-linear~~
 589 ~~regression method parameterized estimate approach~~ (i.e., CNDC_{lo} and CNDC_{up}) (Table 57) appears
 590 to be reasonable based on graphical evaluation (Figure 6–Figure 5). However, these fitted CNDC_{lo}
 591 and CNDC_{up} curves do not themselves represent a draw directly from the posterior distribution
 592 and do not necessarily represent the most extreme possible curves (~~e.g., it is plausible to have an~~
 593 ~~individual draw that goes from the lower left to upper right corner of the interval, or vice versa~~)
 594 (Figure 6b). While credible regions with boundaries that are non-monotonic (e.g., Argentina ×
 595 Innovator) have portions of the curve fit approximation that are poorer performing, the credible
 596 regions with monotonic boundaries (e.g., Minnesota × Dakota Russet) seem to be satisfactory
 597 across the entire range of the curve.

598

Table 75. Paired ~~C~~ritical N dilution curve parameters for each variety within location, ~~with for~~
 the median value (~~CNDC~~) ~~from~~ the posterior distribution ~~for parameters a and b of the fitted~~
~~hierarchical Bayesian model (CNDC)~~, and the estimates for the credible region lower (CNDC_{lo})
 and upper (CNDC_{up}) boundaries using the ~~non-linear regression method parameterized estimate~~
~~approach~~.

Location	Variety	CNDC _{lo}		CNDC		CNDC _{up}	
		a _{lo}	b _{lo}	a	b	a _{up}	b _{up}
Argentina	Bannock Russet	4.82	0.146	4.96	0.140	5.10	0.135
	Gem Russet	4.80	0.190	4.96	0.178	5.07	0.152
	Innovator	4.83	0.241	4.94	0.212	5.06	0.193
	Markies Russet	4.82	0.167	4.96	0.155	5.08	0.135
Belgium	Umatilla Russet	4.85	0.195	4.95	0.165	5.06	0.143
	Bintje	4.52	0.606	4.72	0.579	4.90	0.567
	Charlotte	4.56	0.607	4.74	0.559	4.89	0.531
Canada	Russet Burbank	4.53	0.498	4.74	0.489	4.93	0.480
	Shepody	4.55	0.416	4.77	0.412	4.95	0.406
Minnesota	Clearwater	4.56	0.622	4.75	0.585	4.93	0.558
	Dakota Russet	4.54	0.619	4.75	0.599	4.94	0.588
	Easton	4.54	0.608	4.75	0.592	4.91	0.567
	Russet Burbank	4.51	0.562	4.74	0.566	4.95	0.567
	Umatilla Russet	4.56	0.631	4.75	0.588	4.92	0.546

599
 600 However, the approximation of uncertainty in %N_c based ~~directly on uncertainty in CNDC~~
 601 ~~parameters a and b on the indirect calculation method, using the previously determined credible~~
 602 ~~interval boundaries (Figure 3)~~, were found to contain the entire credible region for all varieties

603 within location evaluated (Figure 6Figure 5a). Therefore, ~~the this indirect calculation~~ approach
604 ~~directly using the based on~~ uncertainty in CNDC parameters is ~~quite less un~~informative ~~than either~~
605 ~~the directly modeled or parameterized estimate approaches and should be used as a last resort to~~
606 ~~estimate %N_c uncertainty when the credible region defined from either the original model fit or~~
607 ~~from the paired CNDC_{lo} or CNDC_{up} curves is unavailable~~. In the absence of the credible region
608 defined directly from the fitted hierarchical Bayesian model ~~(i.e., directly modeled approach)~~,
609 ~~using~~ the CNDC_{lo} and CNDC_{up} (Table 57) ~~(i.e., parameterized estimate approach)~~ is ~~are~~ a suitable
610 first-order representation of the credible region for %N_c.

611 3.3. *Evaluating Differences between Critical N Concentration*

612 3.3.1. Differences Related to G × E × M Effects

613 While an evaluation of the pairwise differences between all varieties within location was
614 conducted and is presented in the Supplemental Materials (Figure S2), a subset of the results
615 comparing Minnesota × Russet Burbank to all other varieties within location, Argentina ×
616 Innovator to all other varieties within Argentina, Canada × Russet Burbank to all other varieties
617 within Canada, and Belgium × Bintje to all other varieties within Belgium are presented in detail
618 here (Figure 7Figure 6).

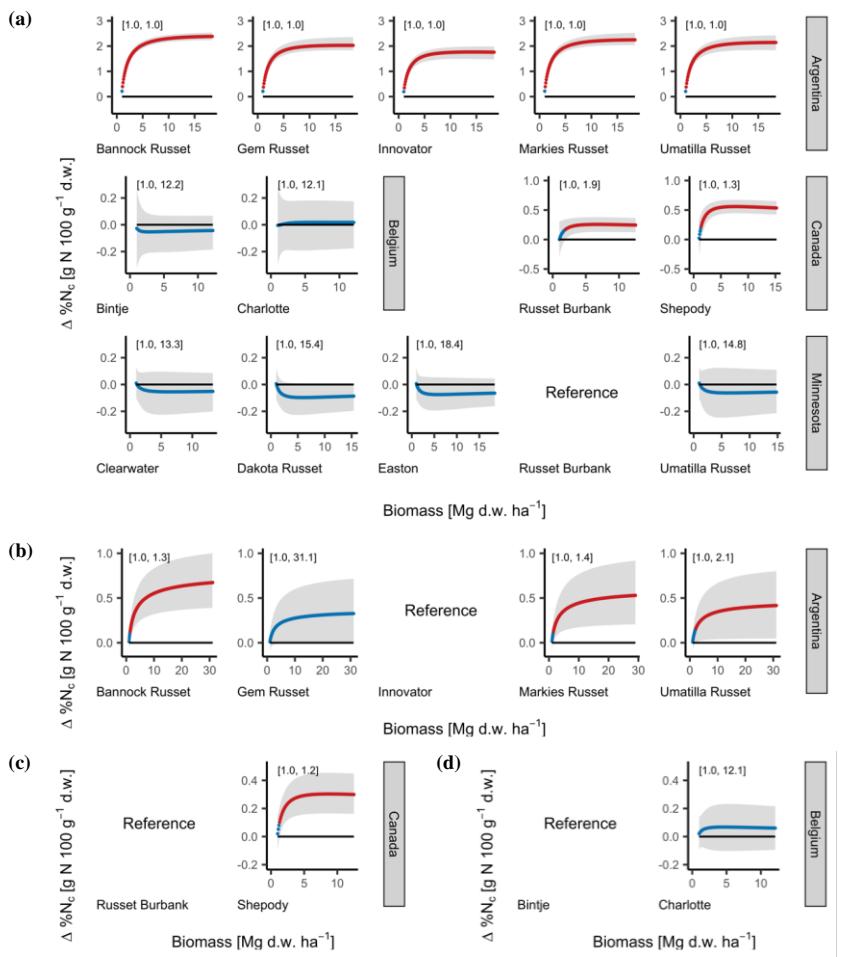


Figure 76. Comparison of the difference in critical N concentration values [$\Delta\%N_c$] between (a) Minnesota \times Russet Burbank and all other varieties within location, (b) Argentina \times Innovator and all other varieties within Argentina, (c) Canada \times Russet Burbank and all other varieties within Canada, and (d) Belgium \times Bintje and all other varieties within Belgium. ~~for critical N concentration [%N_c] determined by the hierarchical Bayesian method~~. The grey shaded region represents the 90% credible region (~~lower bound, 0.05 quantile; upper bound, 0.95 quantile~~) for $\Delta\%N_c$. The colored points represent the median value for $\Delta\%N_c$ at a given ~~b~~Biomass level where blue or red color respectively indicates ~~s~~ that the ~~90%~~ credible region for $\Delta\%N_c$ does or does not contain zero. The solid black line at constant $\Delta\%N_c$ value of zero represents %N_c for the reference curve [$\%N_{c,ref}$] (i.e., Minnesota \times Russet Burbank, Argentina \times Innovator, Canada \times Russet Burbank, and Belgium \times Bintje). The range of biomass values for which $\Delta\%N_c$ is not significantly different (i.e., ~~90%~~ credible region contains zero) is given in brackets.

621 For Minnesota × Russet Burbank, there were no significant differences in %N_c for any level of W
622 evaluated with any of the other varieties in Minnesota (i.e., Clearwater, Dakota Russet, Easton,
623 and Umatilla Russet) or with the Belgium varieties (i.e., Bintje, and Charlotte) ([Figure 7](#)[Figure](#)
624 [6a](#)). The %N_c values for both of the Canadian varieties (i.e., Russet Burbank, and Shepody) were
625 significantly greater than that for Minnesota × Russet Burbank when biomass values were greater
626 than 2 Mg ha⁻¹ dry wt. The %N_c for Canada × Russet Burbank and Canada × Shepody were up to
627 0.3 and 0.6 g N 100 g⁻¹ dry wt. greater than that for Minnesota × Russet Burbank, respectively.
628 The %N_c for the Argentina varieties (i.e., Bannock Russet, Gem Russet, Innovator, Markies
629 Russet, and Umatilla Russet) were significantly greater than for Minnesota × Russet Burbank,
630 except at a biomass value of 1.0 Mg dry wt. ha⁻¹, with a difference in value depending on variety
631 of up to 2.4 g N 100 g⁻¹ dry wt.

632 For Argentina × Innovator, %N_c was significantly lower than for Argentina × Bannock Russet,
633 Argentina × Markies Russet, and Argentina × Umatilla Russet but was not significantly different
634 from Argentina × Gem Russet ([Figure 7](#)[Figure](#) [6b](#)). The %N_c values for Argentina × Bannock
635 Russet, Argentina × Markies Russet, and Argentina × Umatilla Russet were up to 0.5 g N 100 g⁻¹
636 dry wt. greater than that for Argentina × Innovator. For Canada × Russet Burbank, %N_c was
637 significantly lower than for Canada × Shepody ([Figure 7](#)[Figure](#) [6c](#)), with a difference in %N_c of
638 up to 0.3 g N 100 g⁻¹ dry wt. For Belgium × Bintje, %N_c was not significantly different from
639 Belgium × Charlotte ([Figure 7](#)[Figure](#) [6d](#)).

640 There are two notable findings to point out. First, there were no significant differences between
641 Minnesota × Russet Burbank and any other varieties evaluated in Minnesota or between Belgium
642 × Bintje and Belgium × Charlotte. This finding did not hold true for all varieties within location
643 evaluated, however; Significant differences between varieties were found for both Argentina and

644 Canada. Second, the comparison between the Minnesota \times Russet Burbank and Canada \times Russet
 645 Burbank curves as well as the comparison between the Minnesota \times Umatilla Russet and Argentina
 646 \times Umatilla (Figure S2) were both significantly different.

647 3.3.2. Differences Related to Statistical Methods

648 When comparing the curves fit in the present study with the Bayesian hierarchical method to the
 649 curves fit in the previous studies using conventional statistical methods, there were significant
 650 differences between statistical curve fit methods for all varieties within location evaluated (Figure
 651 [8](#)[Figure 7](#)). None of the previous CNDCs fall entirely within the credible region for the respective
 652 CNDCs developed in the present study.

653

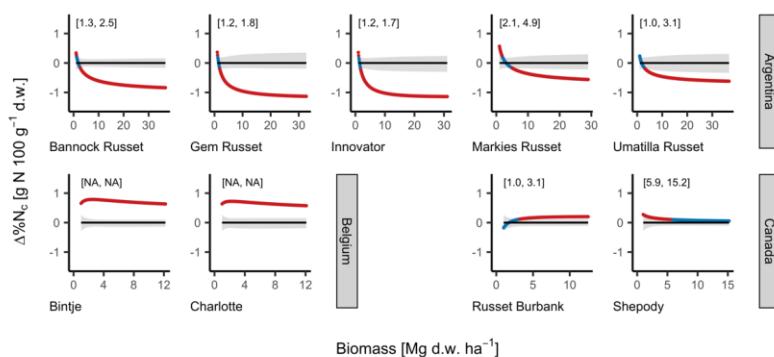


Figure 87. Comparison of the difference in critical N concentration values [$\Delta\%N_c$] between the conventional statistical methods used in previous studies (i.e., Argentina – Giletto and Echeverría (2015); Belgium – Ben Abdallah et al. (2016); Canada – Bélanger et al. (2001a)) and the hierarchical Bayesian method used in the present study [for each variety within location](#). The grey shaded region represents the 90% credible region ([lower bound, 0.05 quantile; upper bound, 0.95 quantile](#)) for critical N concentration [$\%N_c$] [using the directly modeled method](#) from the hierarchical Bayesian method. The solid black line at a constant $\Delta\%N_c$ value of zero represents the median value for $\%N_c$ [using from the hierarchical Bayesian method directly modeled method](#). Red or blue points respectively indicate that $\Delta\%N_c$ falls outside of (i.e., is significant) or falls within (i.e., is not significant) the 90% credible region for $\%N_c$ [determined by the directly modeled method](#). The range of biomass values for which $\Delta\%N_c$ is not significant is given in brackets.

654

655 The %N_c values from the previously developed CNDCs for the Argentina varieties (Giletto &
656 Echeverría, 2015) were significantly less than that from the present CNDCs across all varieties for
657 biomass levels of greater 5 Mg dry wt. ha⁻¹ ([Figure 8](#)[Figure 7](#)). The magnitude of this difference
658 was relatively large, with the Δ%N_c between the previous and present method ranging up to -0.6
659 to -1.1 g N 100 g⁻¹ dry wt., depending on variety. Therefore, relative to the statistical method used
660 in this study it appears that the statistical methods used by Giletto and Echeverría (2015) selected
661 biased critical points due to an overrepresentation of N limiting observations in the experimental
662 dataset ([Figure 5](#)[Figure 4](#), Figure S1) leading to a systematic underestimation of %N_c.

663 The %N_c from the previously developed CNDCs for Belgium (Ben Abdallah et al., 2016) were
664 significantly greater than that from the CNDCs developed in the present study ([Figure 8](#)[Figure 7](#)).
665 For all levels of biomass, Δ%N_c between the previous and present methods was significantly
666 different with a value of 0.7 g N 100 g⁻¹ dry wt. Therefore, relative to the statistical method used
667 in this study, it appears that the statistical methods used by Ben Abdallah et al. (2016) selected
668 biased critical points due to overrepresentation of non-N limiting observations in the experimental
669 dataset leading to a systematic overestimation of the %N_c.

670 The %N_c from the previously developed CNDCs for Canada (Bélanger et al., 2001a) was
671 significantly greater for both Canada × Russet Burbank and Canada × Shepody than the present
672 CNDCs for biomass levels of less than 3 Mg dry wt ha⁻¹ and greater than 6 Mg dry wt ha⁻¹,
673 respectively ([Figure 8](#)[Figure 7](#)). Relative to the other locations, however, the CNDCs for Canada
674 were the most similar between statistical methods, with a small value for Δ%N_c of only 0.2 g N
675 100 g⁻¹ dry wt. Therefore, relative to the statistical method used in this study, it appears that the
676 statistical method used by Bélanger et al. (2001a) did not select biased critical points likely due to
677 the minimal lesser bias observed in this experimental dataset.

678 Because a CNDC using the conventional statistical methods has not been previously published for
679 potato in Minnesota, no comparison across statistical methods is made for this experimental
680 dataset. However, the bias observed in the Minnesota experimental dataset is similar to the bias
681 found in the Belgium experimental dataset; therefore, using the conventional statistical methods
682 to derive a CNDC for Minnesota would likely overestimate %N_c relative to the hierarchical
683 Bayesian method.

684 **4. Discussion**

685 *4.1. Mechanisms of Dilution*

686 While the present study presents direct evidence of significant differences between CNDCs for
687 potato across G × E × M effects, previous studies help describe the potential physiological
688 mechanisms for this source of variation. Reviewing previous work on this topic, Lemaire et al.
689 (2019) described a framework with which to consider the variation in relative partitioning of dry
690 matter. First, relative partitioning varies as biomass varies over the growing season indicating that
691 there is an ontogenetic relationship between harvest index and biomass. Second, the allometric
692 trajectory of relative allocation (e.g., harvest index at a given level of biomass) is subject to
693 variation in non-ontogenetic factors (i.e., G × E × M interactions).

694 The findings of Giletto et al. (2020) suggest that the variation in CNDCs for potato are due to non-
695 ontogenetic factors. In general, G × E × M interactions that result in greater and more rapid relative
696 partitioning of biomass from vines (i.e., high N metabolic and structural tissue) to tubers (i.e., low
697 N storage tissues) will result in greater N dilution (i.e., lower %N_c) at the same level of total plant
698 biomass (Lemaire et al., 2019). The two factors described by Giletto et al. (2020) affecting N

699 dilution due to non-ontogenetic factors are total plant biomass at tuber initiation (i.e., timing of
700 tuber initiation) and relative rate of tuber growth to plant growth (i.e., relative rate of tube bulking).
701 These two factors are affected by various physiological mechanisms and G × E × M interactions;
702 however, relatively limited work has been conducted to comprehensively evaluate the combined
703 effect of G × E × M interaction on these two physiological mechanisms for potato.

704 4.1.1. Timing of Tuber Initiation

705 The timing of tuber initiation is affected primarily by variety maturity class (i.e., G). Potato
706 varieties are classified on a spectrum of growth patterns where early maturing varieties are
707 considered to be determinate and later maturing varieties are considered to be indeterminate
708 (Thornton, 2020). Compared to indeterminate varieties, determinate varieties progress more
709 quickly to the tuber initiation growth stage (i.e., at lower total plant biomass) and have a more
710 rapid tuber bulking (i.e., biomass increase) with limited additional canopy and vine biomass
711 growth (i.e., increased harvest index for a given level of biomass) (Kleinkopf et al., 1981).
712 Therefore, it is expected that increasing earliness of maturity for a potato variety would result in
713 an increase in N dilution.

714 In the present study, differences in maturity class between varieties resulted in differences in %N_c.
715 For example, Argentina × Innovator, which has an early to medium maturity class, had
716 significantly lower %N_c than Argentina × Bannock Russet, Argentina × Markies Russet, and
717 Argentina × Umatilla Russet, which have either a medium-late to late or late to very late maturity
718 class; however, Argentina × Gem Russet, which has a medium to late maturity class did not have
719 a significantly different %N_c from Argentina × Innovator ([Table Figure S27](#)). This finding supports

720 the hypothesis that varieties with an earlier maturity class (i.e., earlier tuber initiation) will have
721 lower %N_c (i.e., greater N dilution).

722 Timing of tuber initiation is also subject to G × E × M interactions. Ideal conditions for tuber
723 initiation are moderate to low soil N availability, shorter day length, high light intensity, and cool
724 nighttime temperatures (Ewing & Struik, 1992; Thornton, 2020); when N fertilizer management
725 results in excessively high soil N availability (Kleinkopf et al., 1981), under conditions of reduced
726 solar irradiance (Menzel, 1985), or when nighttime soil temperatures_S are elevated (Slater, 1968;
727 Kim & Lee, 2019), tuber initiation can be delayed. Therefore, both M effects that result in
728 excessive early-season soil N availability (e.g., all N applied at planting in a soluble form) and E
729 effects that result in increased solar irradiance or reduced nighttime temperatures (i.e., increased
730 diurnal temperature difference) could result in an increase in N dilution.

731 However, due the limitation of the experimental studies (i.e., the effect of M was not systematically
732 varied across a given G ~~×~~ E interaction), it is not possible to directly assess the impact of diurnal
733 temperature difference, solar ~~radiation~~irradiance, or N fertilizer source and timing (Table 35) on
734 the timing of tuber initiation and N dilution distinct from the combined effect of G ~~×~~ E ~~×~~ M
735 interactions.

736 4.1.2. Rate of Tuber Bulking

737 The rate of tuber bulking and allocation of biomass to tubers is subject to the effects of E.
738 Conventionally, potential biomass production has been considered as the product of total solar
739 radiation and radiation use efficiency (Monteith, 1977; Sinclair & Muchow, 1999) as has been
740 successfully applied to potato (Allen & Scott, 1980). Previous studies have suggested that
741 decreasing diurnal temperature difference results in a reduction in tuber bulking rate (i.e., radiation

742 use efficiency), most likely as a result of increasing utilization of photosynthesis assimilates for
743 maintenance (via increased respiration) as nighttime temperature increases (Benoit et al., 1986;
744 Bennett et al., 1991; Lizana et al., 2017); however, Kim & Lee (2019) did not observe any effect
745 of increasing diurnal temperature difference on tuber bulking rate.

746 Given the limitation of the experimental studies (i.e., the effect of E was not systematically varied
747 across a given G x M interaction), it is not possible to directly assess the impact of diurnal
748 temperature difference and solar radiation (Table 35) on the rate of tuber bulking across G x E x
749 M interactions.

750 Planting density is an important effect of M that may play a key role in determining the relative
751 partitioning of biomass for to tuber. Previous studies investigating this effect have found that as
752 planting density increases, leaf area index increases (Bremner & Taha, 1966; Ifenkwe & Allen,
753 1978; Allen & Scott, 1980), tuber dry weight biomass on a per area basis increases (Bremner &
754 Taha, 1966; Ifenkwe & Allen, 1978), while tuber dry weight biomass on a per plant basis decreases
755 (Bremner & Taha, 1966; Ifenkwe & Allen, 1978). The combination of the effect of increasing
756 planting density could plausibly result in the net effect of an increased relative proportion of
757 biomass allocated to vines (i.e., reduction in harvest index) (Vander Zaag et al., 1990), therefore
758 reducing N dilution and resulting in an increased %N_c.

759 In the present study, variations in %N_c due to variation in planting density were observed. For
760 example, Argentina has the highest planting density of any location (Table 35) which resulted in
761 greater %N_c than all other locations (Figure S2). The relative effect of planting density also appears
762 to be of greater magnitude than other sources of variation (e.g., maturity class). For example,
763 Canada × Russet Burbank, which has a late to very late maturity class and planting density of

764 29,000 plants ha⁻¹, had a lower %N_c than Canada × Shepody, which has an early to medium-early
765 maturity class and planting density of 44,000 plants ha⁻¹ (Table 35, Figure 7Figure 6c). Therefore,
766 this finding suggests that the effect of planting density (i.e., rate of tuber bulking) may be relatively
767 more important at controlling %N_c than the effect of maturity class (i.e., timing of tuber initiation).

768 Because there was only a single level of M (e.g., planting density) within each level of G × E for
769 the experimental trials considered here, additional experimentation is required to fully consider the
770 independent effects of G, E, and M on critical N dilution. Therefore, future experimental studies
771 explicitly investigating the effect of M (e.g., planting density) on %N_c should be conducted to
772 properly consider the combined effects the G × E × M interaction.

773 4.1.3. Comparison to Other Crops

774 These findings contrast somewhat with the previous studies evaluating G × E × M effects on %N_c.
775 Yao et al. (2021) found a similar magnitude of effect on %N_c for both G and E effects for wheat
776 in China; however, Yao et al. (2021) also reported an E effect where %N_c for wheat in China was
777 significantly different from that reported by Makowski et al. (2020) for wheat in France. Ciampitti
778 et al. (2021) identified variation in %N_c for maize as a result of G × M interactions due to variation
779 in hybrid and planting density. Fernández et al. (2021) found that variation in %N_c for tall fescue
780 across G × E × M effects was negligible. In any case, the magnitude of the difference in %N_c
781 across G × E × M interactions reported by the previous studies for wheat, maize, and tall fescue
782 (Makowski et al., 2020; Ciampitti et al., 2021; Fernández et al., 2021; Yao et al., 2021) is less than
783 that was observed in the present study for potato.

784 Therefore, the impact of G × E × M on %N_c is not only significant for potato, but is also of
785 potentially of much greater relative importance compared to other crops (e.g., wheat, maize, tall

786 fescue). This is because the magnitude of variability in %N_c due to G × E × M interactions found
787 in the present study is relatively greater for potato than other crops; however, further additional
788 experimental data are needed to confirm that this finding is not an artifact of the statistical methods
789 or limitations of experimental data used in the present study.

790 **4.1.4. Limitations of Interpretation**

791 Previous studies, including that of Giletto et al. (2020) on potatoes, have identified that N dilution
792 follows a two-step process where the rate of N dilution varies between the vegetative period (i.e.,
793 parameter b_1) and the period of storage tissue accumulation (i.e., parameter b_2) (Duchenne et al.,
794 1997; Plénet & Lemaire, 2000; Gastal et al., 2015). Our study, however, did not directly evaluate
795 if the rate of N dilution during the pre-tuber initiation (i.e., vegetative growth) and post-tuber
796 initiation (i.e., accumulation of storage tissue) periods varies due to G × E × M interactions.
797 Variation in parameters b_1 and b_2 across G × E × M effects is a plausible physiological mechanism
798 that could occur in addition to the non-ontogenetic allometric effects (i.e., timing of tuber
799 initiation, relative rate of tube bulking) identified in the present study and used to explain variation
800 in parameter b . This alternative hypothesis could be evaluated by modifying the Bayesian
801 hierarchical method of the present study to include another hierarchical level representing the pre-
802 and post-tuber initiation periods to determine if parameter b varies within these periods across to
803 G × E × M interactions.

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804 ***4.2. Implication of G × E Variation on N Use Efficiency***

805 Understanding and properly interpreting the impact of G × E × M effects on NUE is a critical goal
806 necessary to improve N fertilizer use; however, this must be done while controlling for the effect
807 of crop N status (Lemaire & Ciampitti, 2020). The previous findings of Bohman et al. (2021)

808 demonstrated that interpreting NUE and its constituent component of N utilization efficiency
809 [NUtE] is directly related to the parameters of the CNDC through the critical N utilization
810 efficiency curve [CNUtEC] which defines the critical value of NUtE [NUtE_c]:

811
$$\text{NUtE}_c = 1000 (10 a W^{-b})^{-1}$$
 [118]

812 where parameters *a* and *b*, and W have the same meaning and units as previously defined in the
813 present study and NUtE_c has units of g dry wt. g⁻¹ N. When NUtE is greater than NUtE_c, crop N
814 status is deficient (i.e., NNI less than 1); conversely, when NUtE is less than NUtE_c, crop N status
815 is excessive (i.e., NNI greater than 1).

816 The finding in the present study that the CNDC can vary across G × E × M interactions and the
817 finding from Bohman et al. (2021) of the intrinsic relationship between NUE and the CNDC
818 together lead to the conclusion that the CNUtEC must also vary across the same G × E × M effects
819 as the CNDC. Therefore, the effect of G × E ~~×~~ M on variation of NUtE_c is one of the multiple set
820 of factors that ultimately control NUE. Understanding and accounting for the G × E × M effect on
821 the CNUtEC is therefore critically important to understand the impacts of G × E × M interactions
822 on NUE. In other words, controlling for this G × E × M effect represents an additional requirement
823 when evaluating and interpreting NUE above and beyond the previously known requirements of
824 controlling for both NNI and biomass (Barraclough et al., 2010; Caviglia et al., 2014; Sadras &
825 Lemaire, 2014; Gastal et al., 2015; Lemaire & Ciampitti, 2020).

826 Following from the above discussion of the CNUtEC and the findings of Giletto et al. (2020), G ×
827 E × M effects that increase the relative proportion of biomass partitioned to tubers and reduce the
828 time to tuber initiation will both decrease the %N_c and increase the NUtE_c values. Therefore, future
829 efforts to systematically improve NUE in potato through either management practices (e.g.,

830 Bohman et al. (2021)) or crop breeding (e.g., Tiwari et al. (2018); Jones et al. (2021); Stefaniak et
831 al. (2021)) should focus on identifying $G \times E \times M$ interactions that result in an increased proportion
832 of biomass partitioned to tubers or result in earlier timing of tuber initiation.

833 *4.3. Uncertainty in Critical N Concentration*

834 4.3.1. Communicating Uncertainty in Critical N Concentration

835 This study as well as others that implemented Bayesian statistical methods to derive critical N
836 dilution curves (Makowski et al., 2020; Ciampitti et al., 2021; Yao et al., 2021) clearly indicate
837 that there is meaningful uncertainty in $\%N_c$ values. Therefore, the use of $\%N_c$ in subsequent
838 calculations should include this inherent uncertainty. However, the direct use of the credible region
839 defined from posterior distribution of the fitted Bayesian hierarchical model in subsequent
840 calculations is impractical, and a method to concisely and accurately communicate the credible
841 region remains necessary.

842 Our finding that the credible region can be satisfactorily estimated using an equation of the same
843 form as the CNDC ([Figure 6](#)[Figure 5](#)) suggests that an additional pair of negative exponential
844 curves representing the upper and lower boundary of the credible region for $\%N_c$ (i.e., $CNDC_{lo}$
845 and $CNDC_{up}$) should be reported in future studies. In this manner, the median value and credible
846 region for $\%N_c$ is defined by a set of three, two-parameter curves (i.e., $CNDC - a, b$; $CNDC_{up} -$
847 a_{up}, b_{up} ; $CNDC_{lo} - a_{lo}, b_{lo}$) which can be easily communicated and used in subsequent computations
848 (Table [57](#)).

849 4.3.2. Computing Uncertainty of Derived Parameters

850 Critical N concentration and the associated CNDC parameters are commonly used to derive and
851 calculate other related parameters. For example, the calculation of NNI depends on both %N_{Plant}
852 and %N_c. (Eq. [1] and Eq. [2]). However, to properly account for the uncertainty in %N_c when
853 computing NNI, the upper [%N_{c,up}] and lower [%N_{c,lo}] bounds of the credible interval for %N_c
854 should also be used to determine the upper [NNI_{up}] and lower [NNI_{lo}] bounds of the credible
855 interval for NNI, where %N_{c,up} and %N_{c,lo} are calculated using the CNDC_{up} and CNDC_{lo},
856 respectively:

$$857 \quad \text{NNI}_{\text{up}} = \% \text{N}_{\text{Plant}} / \% \text{N}_{\text{c,up}} = \% \text{N}_{\text{Plant}} / (a_{\text{up}} W^{-b}_{\text{up}}) \quad [\underline{129}]$$

$$858 \quad \text{NNI}_{\text{lo}} = \% \text{N}_{\text{Plant}} / \% \text{N}_{\text{c,lo}} = \% \text{N}_{\text{Plant}} / (a_{\text{lo}} W^{-b}_{\text{lo}}) \quad [\underline{130}]$$

859 This has important practical implications for interpreting NNI values. For example, in a case where
860 NNI is less than 1 but NNI_{up} is greater than 1, it follows that crop N status would not be considered
861 deficient (i.e., NNI is not significantly different from 1). In contrast, when both NNI and NNI_{lo} are
862 greater than 1, it follows that crop N status would be considered surplus (i.e., NNI is significantly
863 greater than 1). However, the threshold for considering significant differences in NNI will
864 necessarily depend upon the threshold used for calculating %N_{c,lo} and %N_{c,up} (e.g., 90%
865 confidence region). For example, the conclusions of a small-plot trial evaluating the effect of
866 various N fertilizer treatments on yield and biomass (e.g., Bohman et al. (2021)) may draw
867 different conclusions when uncertainty in calculated NNI values is explicitly considered (e.g., N
868 treatments were or were not limiting).

869 Additionally, the parameters of the CNDC (i.e., a , b) are also used to parameterize other related
870 curves such as the critical N uptake curve [CNUC] or the critical N utilization efficiency curve
871 [CNUtEC] (Bohman et al., 2021). When computing the critical N uptake [N_c] or critical N

872 utilization efficiency [NUtE_c] values defined by these curves, respectively, the parameters from
873 the CNDC_{lo} (i.e., a_{lo} , b_{lo}) and CNDC_{up} (i.e., a_{up} , b_{up}) should be used to calculate the upper and
874 lower bounds of these derived values. In general, any calculation depending on either $\%N_c$ or any
875 equation that uses the parameters of the CNDC, should also additionally use the CNDC_{lo} and
876 CNDC_{up} to account for uncertainty in $\%N_c$.

877 *4.4. Evaluating Differences between Statistical Methods*

878 While the occurrence of differences between CNDCs derived using the Bayesian hierarchical
879 model compared to the conventional statistical methods ([Figure 7](#)[Figure 6](#)) is itself notable, the
880 magnitude of the differences found in the present study is especially remarkable for the following
881 reasons.

882 Because of its strong theoretical underpinning, $\%N_c$ and NNI are typically considered to be high
883 fidelity measurements of crop N status, not affected by the subjectivity or relativity found in most
884 other methods (Lemaire et al., 2019). However, the findings of the present study strongly suggest
885 that this conception of the NNI framework must be qualified within a particular application by the
886 statistical methods used to derive the CNDC for a given experimental dataset.

887 Unfortunately, the direct evaluation of different statistical methods to calculate the CNDC from
888 the same experimental dataset cannot directly answer the question of which statistical method or
889 resulting CNDC is “correct” (i.e., most accurate, least biased). However, we can reasonably
890 conclude from both deduction and from the findings of the present study that a Bayesian
891 hierarchical model utilizing the linear-plateau method and leveraging partial pooling across effect
892 levels will result in inference that is less subjected to potential bias in the experimental data set

893 compared to the conventional statistical methods. Additionally, it extracts the greatest amount of
894 information from a given dataset, as no data are excluded from the fitting of the total model.

895 Therefore, it appears preferable for the future development of CNDCs to utilize the Bayesian
896 hierarchical method to both quantify uncertainty and reduce bias in %N_c. Without addressing these
897 limitations (i.e., bias and uncertainty), both directly resulting from the statistical methods used, the
898 NNI framework cannot fulfill its core objective of providing an absolute reference of crop N status.

899 Additionally, with further development of standardized tools for this scientific computing task, the
900 implementation of the partially-pooled Bayesian hierarchical framework for deriving the CNDC
901 can be made trivial and may enable the development of CNDCs from existing but unutilized
902 experimental datasets. Therefore, the development of a dedicated software library to implement
903 the partially-pooled Bayesian hierarchical method developed in the present study is a priority for
904 future research efforts because it will enable other researchers to implement this preferred method
905 of deriving CNDCs. This is of timely importance given the increased availability of high-quality,
906 consolidated datasets suitable for fitting CNDCs across G × E × M effects (Ciampitti, et al., 2022).
907 Given the increased availability of data, future research should expand the partially-pooled
908 Bayesian hierarchical method to fit models simultaneously using data from multiple crop species.

909 Finally, having sufficient quantity and quality of experimental data remains an essential criterione
910 to consider when deriving a CNDC independent of the statistical method used (Fernández et al.,
911 2021; Fernández et al., 2022). Even with the advantages of the partially-pooled Bayesian
912 hierarchical method, insufficient experimental data quality and quantity may still result in
913 inferential bias of the CNDC for an individual G × E × M interaction level. Given the limitations
914 of the quantity and quality of experimental data used in this study (i.e., bias towards N limiting

915 conditions for Argentina, bias towards non-N limiting conditions for Belgium and Minnesota), it
916 is plausible that estimates of CNDCs from this study are biased relative to estimates of CNDCs
917 derived using an “ideal” experimental dataset and identical statistical methods. Therefore, future
918 studies utilizing the partially-pooled Bayesian hierarchical method should ensure that the
919 experimental dataset for each $G \times E \times M$ interaction level meets the sufficiency criteria identified
920 by Fernández et al. (2022) (i.e., at least eight experimental trials containing at least three N
921 treatments and at least three sampling dates).

922 **5. Conclusions**

923 First, this study demonstrated that there are significant differences between CNDCs developed
924 across $G \times E \times M$ effects for potato. Therefore, any application of $\%N_c$ must use an appropriate
925 CNDC (i.e., not significantly different) for the $G \times E \times M$ interaction being considered. Second,
926 this study developed an approach to communicate uncertainty in $\%N_c$ through the concise set of
927 six parameters defined by the CNDC (i.e., a, b), $CNDC_{lo}$ (i.e., a_{lo}, b_{lo}), and $CNDC_{up}$ (i.e., a_{up}, b_{up}),
928 and the $\%N_c$ value computed from these three curves should be used in all subsequent
929 computations to propagate uncertainty. Third, this study demonstrated that the statistical method
930 used to derive CNDCs affects the inferred $\%N_c$ values, and that the partially-pooled hierarchical
931 Bayesian framework is less susceptible to bias due to insufficient quantity and quality of
932 experimental data than the conventional statistical methods. Therefore, future efforts to derive
933 CNDCs should utilize the partially-pooled hierarchical Bayesian framework whenever possible.
934 Fourth, the findings of this study suggest that variation in $\%N_c$ across $G \times E \times M$ interactions
935 necessarily extends to NUE, via the relationship between the CNDC and the CNUtEC. Therefore,

936 NUE is dependent on the mechanisms that control N dilution (i.e., biomass partitioning), and future
937 efforts to improve NUE should explicitly consider how G × E × M interactions affect N dilution.
938

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943

944 7. References

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