1 **Simulated effects of elevated CO₂ on nitrogen cycling using the NuCM**
2 **model.** Tree Physiology (in press)

3

4 D.W. JOHNSON¹

5

6 ¹*Biological Sciences Center, Desert Research Institute, P.O. Box 60220, Reno, NV 89506*

7 *and Environmental and Resource Science, University of Nevada, Reno, NV 89512*

8

1 Summary

2

3 The interactions between elevated CO₂ and N cycling were explored using simulations
4 generated by the Nutrient Cycling Model (NuCM) for a *Pinus taeda* site at Duke, North
5 Carolina and a mixed deciduous site at Walker Branch, Tennessee. The simulations tested
6 whether N limitation would prevent growth increase in response to elevated CO₂ and
7 whether growth response to CO₂ in N-limited systems could be facilitated by increased
8 biomass/N (reduced concentration) and/or increased litter N mineralization. Nitrogen
9 limitation precluded additional growth when target growth rates and litterfall were increased
10 (simulating potential response to elevated CO₂) at the Duke site. At the Walker Branch site,
11 increasing target growth and litterfall caused a slight (7%) increases in growth. Reducing
12 foliar N concentrations caused reduced growth because of N limitation created by reduced
13 litter quality (C/N ratio), reduced decomposition and N accumulation in forest floor. These
14 effects were most pronounced at the Duke site, where the forest floor N turnover rate was
15 lower than at the Walker Branch site. Reducing wood N concentration allowed prolonged
16 increases in growth because of greater biomass/N; however, N uptake was reduced,
17 allowing greater N immobilization in the forest floor and soil. Increased N mineralization
18 caused increased growth at the Duke site but not at Walker Branch.

19 These simulation pose the counter-intuitive hypothesis that increased biogeochemical
20 cycling of N (via increased litterfall N) will cause reduced growth in an N-limited system
21 because of increased accumulation of N in the forest floor and soil. Translocation (removal
22 of N from senescing leaves prior to litterfall) mitigates this response by allowing the trees
23 to maintain a greater proportion of N taken up rather than recycle it back to the forest floor
24 and soil where it can be immobilized. Eliminating translocation at Walker Branch changed
25 the sign as well as the magnitude of the responses in three of the four scenarios simulated.
26 NuCM currently does not allow translocation in coniferous species, and thus the effects of
27 translocation on N cycling in the Duke simulations are not known.

DISCLAIMER

This report was prepared as an account of work sponsored by an agency of the United States Government. Neither the United States Government nor any agency thereof, nor any of their employees, make any warranty, express or implied, or assumes any legal liability or responsibility for the accuracy, completeness, or usefulness of any information, apparatus, product, or process disclosed, or represents that its use would not infringe privately owned rights. Reference herein to any specific commercial product, process, or service by trade name, trademark, manufacturer, or otherwise does not necessarily constitute or imply its endorsement, recommendation, or favoring by the United States Government or any agency thereof. The views and opinions of authors expressed herein do not necessarily state or reflect those of the United States Government or any agency thereof.

DISCLAIMER

Portions of this document may be illegible in electronic image products. Images are produced from the best available original document.

1

2 **Introduction**

3

4 The long-term effects of elevated CO₂ on growth and C sequestration are highly dependent
5 on the availability and cycling of other elements such as N. Elevated CO₂ can mitigate
6 nutrient deficiencies by facilitating increased uptake and/or biomass production per unit
7 uptake, especially in the case of N (Zak et al. 1993, McGuire et al. 1997, Johnson et al.
8 1997, 1998). On the other hand, elevated CO₂ can exacerbate nutrient deficiencies by
9 introducing high-C/nutrient ratio litter and/or labile organic compounds into the soil which
10 in turn cause immobilization of nutrients (especially N) (Diaz et al. 1993, Strain, 1985).
11 Many of these nutrient mobilization-immobilization processes have been studied in detail in
12 isolation from the ecosystem; however, the feedbacks among these processes are numerous
13 and complicated, and currently there is no consensus as to how they will affect the final
14 outcome in growth response and C sequestration.

15 Shaver et al. (1992) described and summarized the results of a series of ecosystem-
16 level experiments in the Arctic tundra of Alaska. They noted that these ecosystems were not
17 responsive to either elevated CO₂ or increased light on a long-term basis because both
18 factors only affect photosynthesis directly and not the availability and cycling of limiting
19 nutrients (N and P). Shaver and his colleagues proposed that ecosystem productivity and
20 carbon cycling can only be affected significantly on a long-term basis through actions on
21 nutrient cycles. Using the Marine Biological Laboratory – Global Ecosystem Model (MBL-
22 GEM), McKane et al. (1997) simulated the field experiments described by Shaver et al.
23 (1992). According to the MBL-GEM model, increased biomass with elevated CO₂ in these
24 systems is due solely to the increase in C:N ratio in vegetation.

25 Rastetter et al. (1997) simulated the short- and long-term responses of a northern
26 hardwood forest to elevated CO₂ using the Multiple-Element Limitation (MEL) model.
27 Their simulations indicated that growth responses to elevated CO₂ were controlled by

1 different N cycling processes at four time scales: 1) an instantaneous response associated
2 with an increase in vegetation C:N ratio; 2) a response over a period of years facilitated by
3 greater N uptake (because of greater allocation of resources to uptake); 3) a net movement
4 of N from soils (low C:N ratio) to vegetation (high C:N ratio) over a period of decades; and
5 4) accumulation of N in the ecosystem over a period of centuries.

6 In this paper, some of the potential feedbacks that elevated CO₂ can cause in forest
7 nutrient cycles are explored with the Nutrient Cycling Model (NuCM). The NuCM model
8 addresses nutrient cycling processes on a smaller (stand-level) scale than the models
9 described above and includes very detailed and complex soil chemical components. Thus,
10 while NuCM may be too complex to be used on a regional or global scale, it can be used to
11 identify important processes that ought to be included in more general models.

12

13 **The Nutrient Cycling Model**

14

15 The Nutrient Cycling Model (NuCM) was developed primarily to explore the effects of
16 atmospheric deposition, fertilization, and harvesting in forest ecosystems (Johnson et al
17 1993, 1995). NuCM is a stand-level model that incorporates all major nutrient cycling
18 processes (uptake, translocation, leaching, weathering, organic matter decay, and
19 accumulation). NuCM simulates the cycling of N, P, K, Ca, Mg, and S based on expected
20 (target) growth rates (input by the user and reduced in the event of nutrient limitation),
21 user-defined litterfall rates, and weathering, N and S mineralization rates, soil minerals
22 composition, initial forest floor and soil organic pools, and C/N ratios. The model treats
23 decomposition as a three-stage process (litter moves into fine litter and two successive soil
24 organic fractions) during which nutrients are released from litter at rates depending upon
25 litterfall inputs and C/N ratios of litter and microbes.

26 The model has been previously calibrated for both the Duke (Johnson et al. 1995)
27 and Walker Branch (Johnson et al. in press, a) sites, and these sites were selected for the

1 following simulations because of their proximity to ongoing FACE studies. NuCM has no
2 physiological mechanisms built in that enable it to directly simulate the effects of elevated
3 CO₂; thus, the effects of elevated CO₂ on nutrient cycling were addressed by making
4 appropriate modifications to N cycling parameters: increased target growth, reduced foliar
5 N concentration, reduced wood N concentration, and increased litter N mineralization.

6 There are several features of NuCM that are important to note as background for
7 these simulations. First, vegetation biomass increment in the models will match the target
8 growth rate input by the user if no nutrient limitations develop and will fall short of the
9 target if nutrient limitations do develop. Both of the sites simulated are N-limited and
10 simulated growth rates therefore fall well below expected optimal values in the base case
11 (Johnson et al., 1995 and in press). Second, NuCM includes an algorithm which allows
12 increased or decreased vegetation nutrient concentrations according to nutrient supply. This
13 allows the vegetation to continue to produce greater biomass per unit nutrient uptake
14 (biomass/nutrient) when nutrients become limiting and also allows luxury consumption
15 (increased biomass/nutrient) when nutrients are in excess. Menus allow the user to specify
16 the percentage by which tissue stoichiometry is allowed to vary (by individual nutrient).
17 Thirdly, NuCM contains an algorithm for translocation (removal of nutrients from foliage
18 prior to senescence) for deciduous (but not coniferous) species. Menus allow the user to
19 specify the percentage the percentage of translocation that is allowed (by nutrient). The fact
20 that translocation is not allowed for coniferous species is not noted in the user's Manual
21 (Munson et al., 1992), an oversight noted previously by Kvindesland (1997).

22

23 **Hypotheses "tested"**

24

25 The following hypotheses, based on the review and discussion in the Introduction, were
26 "tested" with NuCM:

27

- 1 (1) N limitations will preclude growth increases in response to elevated CO₂ in the
2 absence of any increases in N availability;
- 3 (2) Reductions in foliar N will cause increased biomass/N and temporarily increased
4 growth; this will be reversed as increased litter C/N slows decomposition and
5 reduces N availability
- 6 (3) Reduced wood N concentration will cause increased biomass production per unit N
7 uptake and, consequently, increased growth;
- 8 (4) Increases in N mineralization will temporarily increase N cycling and growth, but
9 this will diminish over time as the system re-equilibrates.

10

11 These hypotheses were "tested" by applying the following scenarios to both the
12 Walker Branch and Duke sites: 1) no change, 2) increasing target growth and litterfall by
13 40% (+40% NPP), 3) reducing foliar N concentration by 40% (-40% Fol N), 4) reducing
14 wood N concentration by 40% (-40% Wood N), and 5) increasing litter N mineralization
15 by 40% (+40% N Min). The simulations were run twice for the Walker Branch site, once
16 with the measured rate of N translocation (47%, WBW-T; Johnson and Van Hook, 1989)
17 and once with no translocation (WBW-NT).

18 These simulations address two basic ways in which N-limited systems could
19 respond to elevated CO₂: 1) increased biomass/N (reduced concentration), and 2) increased
20 N mineralization. With regard to 1), there is the added factor of negative feedbacks via the
21 litterfall-decomposition pathway when foliar N concentration is reduced whereas this is not
22 a factor when woody N concentration is reduced. Hypotheses 2 through 4 address these
23 issues; Hypothesis 1 addresses the premise that N limitation actually precludes growth
24 response in the absence of any change in nature of the N cycle.

25

26 Results

27

1 *Duke*

2 Hypothesis (1) was only partially supported by the Duke simulations: increasing target
3 growth and litterfall (+40% NPP) caused increases in growth, vegetation N content and
4 vegetation N increment between years 1 and 5 in the +40% NPP scenario compared to the
5 Base scenario. This was followed by a decline to levels well below the Base scenario in
6 later years (Figures 1 and 2; Table 1). This shift in response coincided with a steep decline
7 in N status between years 1 and 6, as reflected in the litterfall N, N increment, and N
8 uptake patterns in all scenarios (Figure 2). The +40% NPP caused the expected increase in
9 litterfall N compared to the Base scenario except for a brief crossover between years 4 and
10 6 (Figure 2). This increased litterfall N in turn caused an increase in forest floor N and soil
11 N (Figure 1 and Table 1), apparently at the expense of vegetation N increment (Figure 2
12 and Table 1)¹. N leaching was slightly lower in the +40% NPP than in the Base scenarios
13 because of greater N immobilization in forest floor and soil.

14 Hypothesis (2) was supported in the Duke simulations: biomass in the -40% Fol. N
15 scenario increased slightly compared to the Base scenario between years 4 and 9, and this
16 was followed by a decrease relative to the Base scenario in later years (Figure 1). Litterfall
17 N was considerably lower in the -40% Fol N scenario than in the Base scenario, as
18 expected, and this allowed some additional available N to be allocated to (woody)
19 increment (Figure 2). However, the reduction in litterfall was outweighed by the increase in
20 increment, and thus N uptake was reduced compared to the Base scenario. Despite the
21 greatly reduced litterfall N flux in the -40% Fol. N scenario, reduced decomposition
22 (caused by reduced litter C/N ratio) caused increased forest floor N increment compared to
23 the Base scenario (Figure 1 and 2; Table 1). Reduced decomposition in the -40% Fol. N

¹ NuCM calculates initial litter N pools from user input values for litterfall and decomposition rates. Thus, the initial conditions for litter N differ; and simulated litter N increments may be greater than indicated by final simulated litter N pools. Unfortunately, NuCM does not display or output initial litter or soil N pools, but starts with the pool size at the end of year 1, precluding an exact mass balance calculation.

1 scenario also caused less N input to the soil, however, and thus N increment in the soil was
 2 less than in the Base scenario (Table 1).

3 Hypothesis (3) was supported in the Duke simulations: reduced wood N concentration
 4 (-40% Wood N) caused greater biomass, reduced vegetation N content, and greater
 5 biomass/N than in the Base scenario (Figures 1 and 2). Total nitrogen uptake was reduced,
 6 however; thus, the increase in biomass did not offset the reduction in wood N concentration.
 7 Nitrogen not taken up by the vegetation in the -40% Wood N scenario did not leach
 8 (leaching was similar to that in the Base scenario) but was accumulated in the forest floor
 9 and soil (Table 1).

10 Hypothesis (4) was not supported in the Duke simulations: increased N mineralization
 11 (+40% N Min.) caused greater biomass and vegetation N content than in the Base scenario
 12 and these differences increased over time (Figure 1). As expected, increments in soil N
 13 were reduced in the +40% N Min. scenario, but forest floor N pools increased, apparently
 14 because of greater litterfall N input (Figure 2 and Table 1). Increased N mineralization had
 15 only a slight effect on N leaching (14.9 kg ha^{-1} , compared to 14.3 kg ha^{-1} in the Base
 16 scenario) (Figure 2 and Table 1).

17

18 *Walker Branch, Translocation (WBW-T)*

19 Hypothesis (1) was only partially supported in the Walker Branch, Translocation (47% N
 20 translocation) simulations: growth was slightly greater in the +40% NPP than in the Base
 21 scenario even though vegetation N content and uptake were nearly identical (Figures 3 and
 22 4; Table 1). Forest floor N accumulated at a greater rate in the +40% NPP than in the Base
 23 scenario, but soil N increment in this and all other scenarios was negative.

24 Hypothesis (2) was not supported in the Walker Branch simulations: reduced foliar N
 25 caused slightly reduced growth throughout the simulation despite the fact that biomass/N
 26 was greater (Figure 3). Forest floor N in the -40% Fol. N started at a lower value because
 27 of the lower litterfall N return (for the reasons previously described), but forest floor N

1 increment was slightly greater than in the Base scenario because of reduced decomposition
2 rate (Figure 4 and Table 1).

3 Hypothesis (3) was supported in the Walker Branch simulations: reduced wood N
4 concentration (-40% Wood N) caused slightly increased biomass, slightly reduced
5 vegetation N content, greatly reduced N increment, and greatly increased biomass/N
6 compared to the Base scenario (Figures 3 and 4). Only a small amount of the N not taken
7 up by the vegetation in this scenario leached (17.1 kg ha^{-1} , compared to 16.9 kg ha^{-1} in the
8 Base scenario) (Figure 4 and Table 1).

9 Hypothesis (4) was not supported in the Walker Branch simulation: biomass and
10 vegetation N were slightly decreased in the +40% N Min. scenario compared to the Base
11 scenario (Figure 3 and Table 1). Forest floor N was reduced and soil N became less
12 negative in the +40% N Min. scenario, but litterfall, increment, uptake and leaching were
13 only slightly affected (Figures 3 and 4; Table 1).

14

15 *Walker Branch, No Translocation (WBW-NT)*

16

17 Setting translocation to 0% at Walker Branch caused major changes simulated growth and
18 N cycling. Litterfall N in the WBW-NT scenarios was greater than in the WBW-T
19 scenarios, as expected (e.g., $32\text{--}34 \text{ kg ha}^{-1} \text{ yr}^{-1}$ as opposed to $19\text{--}20 \text{ kg ha}^{-1} \text{ yr}^{-1}$,
20 respectively, in the Base scenarios) (Figures 4 and 6). The increase in litterfall N in turn
21 caused greater forest floor N mass in the WBW-NT simulations ($170\text{--}256 \text{ kg ha}^{-1}$ as
22 opposed to $162\text{--}248 \text{ kg ha}^{-1}$, respectively, in the Base scenarios) (Figures 4 and 6), but
23 no difference in the net increment in forest floor in the Base scenario (86 kg ha^{-1} in the Base
24 scenarios in each case; Table 1). Soil N increment became positive in the WBW-NT
25 simulations, apparently because of greater litterfall N input. Growth, vegetation N uptake,
26 N increment, and leaching were greatly reduced WBW-NT scenarios compared to the

1 WBW-T scenarios because of greater soil N increment and greater allocation of N away
2 from wood increment to litterfall (Figures 5 and 6; Table 1).

3 The responses of Walker Branch to the various scenarios also changed significantly
4 when translocation was set to 0. In contrast to the results from the WBW-T simulations,
5 Hypothesis (1) was supported in the WBW-NT simulations: the +40% NPP scenario had a
6 negative effect on biomass, vegetation N content, and vegetation N increment (Figures 5
7 and 6). The increments of N in the forest floor (98 kg ha^{-1}) was nearly identical to that in
8 the WBW-T simulation (97 kg ha^{-1}), but the increment in soil N was considerably greater
9 ($+59$ vs. -47 kg ha^{-1}) (Table 1).

10 In contrast to the WBW-T simulations, the -40% Fol. N scenario caused slightly
11 increased growth, reduced vegetation N, and increased biomass/N compared to the Base
12 scenario (Figures 5 and 6). Litterfall N was considerably lower in the -40% Fol N scenario
13 than in the Base scenario, as expected, allowing greater proportion of available N to be
14 incorporated into woody tissue (greater increment) (Figure 6). The increase in N increment
15 did not offset the reduced litterfall N to any major degree, however, because N uptake was
16 greatly reduced in the -40% Fol. N scenario compared to the Base scenario (Figure 6).
17 Forest floor N increment in the -40% Fol. N scenario (127 kg ha^{-1}) was greater than in the
18 Base scenario (86 kg ha^{-1}) and greater than in the WBW-T, -40% Fol. N scenario (91 kg
19 ha^{-1}). Soil N increment in the -40% Fol. N scenario was less than in the Base scenario
20 because of reduced N input from more slowly decomposing litter.

21 Hypothesis (3) was supported in the WBW-NT as in the WBW-T simulations: reduced
22 wood N concentration (-40% Wood N) caused increased biomass, reduced vegetation N
23 content and N increment and greatly increased biomass/N compared to the Base scenario
24 (Figures 5 and 6). Only a small amount of the N not taken up by the vegetation in this
25 scenario leached (0.35 kg ha^{-1} , compared to 0.25 kg ha^{-1} in the Base scenario) (Figure 6
26 and Table 1).

1 In contrast to the WBW-T simulation but similar to the Duke simulation, the +40% N
 2 Min. scenario in the WBW-NT simulation caused slightly increased biomass and vegetation
 3 N compared to the Base scenario (Figure 5 and Table 1). As in the Duke simulation, this
 4 pattern did not decrease over time but continued throughout the 24-year simulation. Also as
 5 in the Duke simulation, soil N increment was reduced in the +40% N Min. scenario, but
 6 forest floor N increment increased (Figure 6 and Table 1). Leaching was only slightly
 7 increased with increased N mineralization (0.32 kg ha^{-1} , compared to 0.25 kg ha^{-1} in the
 8 Base scenario) (Figure 6 and Table 1).

9

10 Discussion

11 The simulation results suggest that reducing foliar N concentrations will not allow
 12 prolonged responses to elevated CO_2 because of negative feedbacks in the biogeochemical
 13 N cycle (i.e., (reduced litter C/N ratio, reduced decomposition and N immobilization in
 14 forest floor). These effects were most pronounced at the Duke site, where the forest floor
 15 N content was higher and N turnover rate was lower than at the Walker Branch site.
 16 Reducing wood N concentration, on the other hand, allowed prolonged increases in growth
 17 because of greater biomass/N without any significant slowing of the biogeochemical N
 18 cycle. As an aside, the -40% Wood N simulations illustrate the problem with using the
 19 term, "nutrient use efficiency" to describe the phenomenon of reduced concentration (or
 20 increased biomass/N). In this case, the vegetation was actually less "efficient" in taking up
 21 N and allowed more N to accumulate in the forest floor than in the Base scenario. Thus, a
 22 more precise term like reduced concentration or increased biomass/N to describe this effect
 23 is desirable.

24 In a more general sense, these simulation results suggest that the allocation of a limiting
 25 nutrient (like N) between litterfall and wood increment strongly affects overall N cycling
 26 and growth. The simulation results pose the counterintuitive hypothesis that increased
 27 biogeochemical cycling of N (via increased litterfall N) will cause reduced growth in an N-

1 limited system. The reduction in growth in the Duke +40% NPP scenario was due to
2 increased allocation of N to litterfall, resulting in increased accumulation of N in the forest
3 floor and soil. Given that the system is N-limited, N uptake and growth is constrained by
4 the supply of available N via atmospheric deposition and soil N mineralization. Thus,
5 forcing more N allocation to litterfall (as was done in these simulations) automatically
6 reduces the amount of N that can be incorporated into woody tissue, and this in turn
7 reduced growth. Translocation allows the trees to maintain a greater proportion of N taken
8 up rather than recycle it back to the forest floor and soil where it can be immobilized.
9 Translocation in the Walker Branch scenarios allowed the allocation of N between litterfall
10 and increment to remain stable, even when litterfall mass was increased in the +40% NPP
11 scenario, and this in turn allowed greater N availability and vegetation growth. When
12 translocation was eliminated in the Walker Branch simulations, growth was reduced
13 because of increased allocation to litterfall, as in the Duke simulations.

14 The Walker Branch simulations suggest that translocation is of major importance in N
15 cycling in the Walker Branch system and the effects of various perturbations upon it. In
16 three of the four scenarios simulated, setting translocation to 0 changed the sign as well as
17 the magnitude of the responses. It seems likely that varying translocation rates between 0
18 and the observed 47% or higher will also have major effects on simulated N cycling in this
19 system, and such simulations are now being planned.

20 The effects of translocation on N cycling in the Duke simulations cannot be known at
21 this stage because translocation is set to 0 for conifers in the current version of NuCM.
22 Cole and Rapp (1981) found that translocation in coniferous forests is approximately 0 on
23 average (i.e., N requirement for new growth is approximately equal to N uptake).
24 However, translocation for the Duke forest has been estimated at 66% (Johnson and
25 Lindberg, 1991), and thus the effects of translocation on N cycling in the Duke forest need
26 to be investigated.

27

1 **Acknowledgments**

2

3 This research was supported by funds provided by the USDA Forest Service Southern
 4 Research Station's Southern Global Change Program for the Integrated Modeling Project
 5 and the U.S. Department of Energy through subcontracts from Oak Ridge National
 6 Laboratory and the Smithsonian Institute. This paper has not been subject to Forest Service
 7 policy review and should not be construed to represent the policies of the Agency.

8

9 **References**

10

- 11 Cole, D.W. and M. Rapp. 1981. Elemental cycling in forest ecosystems. *In* Dynamic
 12 Properties of Forest Ecosystems. Ed. D.E. Reichle. Cambridge University Press,
 13 London. 341-409.
- 14 Diaz, S. J.P. Grime, J. Harris, and E. McPherson. 1993. Evidence of feedback
 15 mechanism limiting plant response to elevated carbon dioxide. *Nature* 364:616-617.
- 16 Johnson, D.W., J.T. Ball, and R.F. Walker. 1997. Effects of CO₂ and nitrogen fertilization
 17 on vegetation and soil nutrient content in juvenile ponderosa pine. *Plant and Soil*
 18 190:20-40.
- 19 Johnson, D.W., D. Binkley, and P. Conklin. 1995. Simulated effects of atmospheric
 20 deposition, harvesting, and species change on nutrient cycling in a loblolly pine forest.
 21 *For. Ecol. Manag.* 76:29-45.
- 22 Johnson, D.W., P.J. Hanson, D.E. Todd, R.B. Susfalk, and C.F. Trettin. Precipitation
 23 change and soil leaching: Field results and simulations from Walker Branch Watershed,
 24 Tennessee. *Water, Air, and Soil Pollut.* (in press)
- 25 Johnson, D.W., and S.E. Lindberg (eds). 1991. Atmospheric Deposition and Forest
 26 Nutrient Cycling: A Synthesis of the Integrated Forest Study. Ecological Series 91,
 27 Springer-Verlag, New York. 707 pages

- 1
2 Johnson, D.W., W.T. Swank, and J.M. Vose. 1993. Simulated effects of atmospheric
3 sulfur deposition on nutrient cycling in a mixed deciduous forest. *Biogeochemistry*
4 23:169-196.
- 5 Johnson, D.W., R.B. Thomas, K.L. Griffin, D.T. Tissue, J.T. Ball, B.R. Strain and
6 R.F. Walker. 1998. Effects of CO₂ and N on growth and N uptake in ponderosa and
7 loblolly pine. *J. Environ. Qual.* 27: 414-425.
- 8 Johnson, D. W. and R. I. Van Hook (eds.) 1989. Analysis of biogeochemical cycling
9 processes in Walker Branch Watershed. Springer-Verlag, New York. 401p.
- 10 Kvindesland, H.S.B. 1997. Modeling nutrient cycling in forest ecosystems. Doctor
11 Scientarium Theses 1997: 35. Department of Soil and Water Science, Agricultural
12 University of Norway, Ås, Norway.
- 13 McGuire, A.D., J.M. Melillo, D.W. Kicklighter, Y. Pan, X. Xiao, J Helfrich, B. Moore,
14 C.J. Vorosmarty, and A. Schloss. 1997. Equilibrium responses of global net primary
15 production and carbon storage to doubled atmospheric carbon dioxide: Sensitivity to
16 changes in vegetation nitrogen concentration. *Global Biogeochemical Cycles*, 11: 173-
17 189.
- 18 McKane, R.B., E.B. Rastetter, G.R. Shaver, K.J. Nadelhoffer, A.E. Giblin, J.A.
19 Laundre, and F.S. Chapin III. 1997. Climatic effects on tundra carbon storage inferred
20 from experimental data and a model. *Ecology* 78: 1170-1187.
- 21 Munsen, R.K., S. Liu, S.A. Gherini, D.W. Johnson, K.J. Wilkinson, R.J.M. Hudson,
22 K.S. White, and K.V. Summers. 1992. NuCM Code Version 2.0: An IBM PC code
23 for simulating nutrient cycling in forest ecosystems. Tetra-Tech, Inc. Hadley, MA.
- 24 Rastetter, E.B. 1996. Validating models of ecosystem response to global change.
25 *Bioscience* 46:190-198.
- 26 Rastetter, E.B., G. Ågren, and G.R. Shaver. 1997. Responses of N-limited ecosystems to
27 increased CO₂: A balanced-nutrition, coupled-element-cycles model. *Ecol. Appl.* 7:
28 444-460.

- 1 Shaver, G.R., W.D. Billings, F.S. Chapin III, A.E. Giblin, K.J. Nadelhoffer, W.C.
- 2 Oechel, and E.B. Rastetter. 1992. Global change and the carbon balance of arctic
- 3 ecosystems. *Bioscience* 42:433-441.
- 4 Strain, B.R. 1985. Physiological and ecological controls on carbon sequestering in
- 5 terrestrial ecosystems. *Biogeochemistry* 1:219-232.
- 6 Zak, D.R., K.S. Pregitzer, P.S. Curtis, J.A. Teeri, R. Fogel, and D.L. Randlett. 1993.
- 7 Elevated atmospheric CO₂ and feedback between carbon and nitrogen cycles. *Plant Soil*
- 8 151:105-117.

Table 1. Simulated biomass and N increments between years 1 and 24 and leaching fluxes over 24 years.

	<u>Base</u>	<u>+40% N Min</u>	<u>-40% Fol. N</u>	<u>-40% Wood N</u>	<u>+40% NPP</u>
	----- kg ha ⁻¹ -----				
Duke					
Biomass	63	72	56	71	41
Vegetation N	176	200	201	126	112
Biomass/N	358	360	278	563	366
Forest Floor N	45	83	133	74	85
Soil N	225	137	98	232	240
Leaching	14.3	14.9	19.3	14.9	12.7
Walker Branch – 47% Translocation					
Biomass	42	41	39	46	45
Vegetation N	110	106	101	83	116
Biomass/N	381	387	386	495	387
Forest Floor N	86	77	91	97	97
Soil N	-42	-26	-36	-39	-47
Leaching	16.9	16.7	15.1	17.1	13.6
Walker Branch – 0% Translocation					
Biomass	8	9	8	9	4
Vegetation N	21	24	23	17	9
Biomass/N	381	375	348	529	444
Forest Floor N	86	94	127	88	98
Soil N	47	30	12	48	59
Leaching	0.25	0.32	0.25	0.35	0.07

Table 1. Simulated biomass and N increments between years 1 and 24 and leaching fluxes over 24 years.

	<u>Base</u>	<u>+40% N Min</u>	<u>-40% Fol. N</u>	<u>-40% Wood N</u>	<u>+40% NPP</u>
	----- kg ha ⁻¹ -----				
Duke					
Biomass	63	72	56	71	41
Vegetation N	176	200	201	126	112
Biomass/N	358	360	278	563	366
Forest Floor N	45	83	133	74	85
Soil N	225	137	98	232	240
Leaching	14.3	14.9	19.3	14.9	12.7
Walker Branch – 47% Translocation					
Biomass	42	41	39	46	45
Vegetation N	110	106	101	83	116
Biomass/N	381	387	386	495	387
Forest Floor N	86	77	91	97	97
Soil N	-42	-26	-36	-39	-47
Leaching	16.9	16.7	15.1	17.1	13.6
Walker Branch – 0% Translocation					
Biomass	8	9	8	9	4
Vegetation N	21	24	23	17	9
Biomass/N	381	375	348	529	444
Forest Floor N	86	94	127	88	98
Soil N	47	30	12	48	59
Leaching	0.25	0.32	0.25	0.35	0.07

1 Figure Legends

2

3 Figure 1. Simulated biomass, vegetation N content, biomass per unit N content

4 (biomass/N), and forest floor N content at Duke, NC using NuCM. Scenarios include

5 no change (Base), increasing N mineralization by 40% (+40% N Min.), reduceing

6 foliar N concentration by 40% (-40% Fol. N), reducing wood N concentration by 40%

7 (-40% Wood N), and increasing litterfall mass and target growth by 40% (+40%NPP).

8 Figure 2. Simulated nitrogen fluxes via litterfall, vegetation increment, uptake, and leaching

9 Duke, NC using NuCM. See Fig. 1 for code.

10 Figure 3. Simulated biomass, vegetation N content, biomass per unit N content

11 (biomass/N), and forest floor N content at Walker Branch, TN using NuCM.

12 Translocation is set at 47%. See Fig. 1 for code.

13 Figure 4. Simulated nitrogen fluxes via litterfall, vegetation increment, uptake, and leaching

14 Walker Branch, TN using NuCM. Translocation is set at 47%. See Fig. 1 for code.

15 Figure 5. Simulated biomass, vegetation N content, biomass per unit N content

16 (biomass/N), and forest floor N content at Walker Branch, TN using NuCM.

17 Translocation is set at 0%. See Fig. 1 for code.

18 Figure 6. Simulated nitrogen fluxes via litterfall, vegetation increment, uptake, and leaching

19 Walker Branch, TN using NuCM. Translocation is set at 0%. See Fig. 1 for code.

20

21

Duke

Duke

Walker Branch - T

3

Walker Branch - T

4

— Base - · - +40% N Min - - - -40% Fol N -40% Wood N ——— +40% NPP

Walker Branch - NT

5

Walker Branch - NT