



Using simple environmental variables to estimate below-ground productivity in grasslands

R. A. GILL^{*1}, R. H. KELLY², W. J. PARTON², K. A. DAY³, R. B. JACKSON¹, J. A. MORGAN⁴, J. M. O. SCURLOCK⁵, L. L. TIESZEN⁶, J. V. CASTLE⁷, D. S. OJIMA² and X. S. ZHANG⁸

¹Department of Biology, Duke University, Durham, NC 27708, U.S.A. E-mail: rgill@wsu.edu ²Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, U.S.A., ³Department of Natural Resources, Climate Impacts and Grazing Systems, Indooroopilly, Queensland 4068, Australia, ⁴USDA/ARS Rangeland Resources (1701) Center Avenue, Fort Collins, CO 80526, U.S.A., ⁵Environmental Sciences Division, Oak Ridge National Laboratory, TN 37831–6407, U.S.A., ⁶EROS Data Center, US Geological Survey, Sioux Falls, SD 57198, U.S.A., ⁷Department of Biology, University of New Mexico, Long-term Ecological Research Network Office, 801 University Boulevard SE, Suite 104, Albuquerque, NM 87106, U.S.A., ⁸Institute of Botany, Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, PR China

ABSTRACT

In many temperate and annual grasslands, above-ground net primary productivity (NPP) can be estimated by measuring peak above-ground biomass. Estimates of below-ground net primary productivity and, consequently, total net primary productivity, are more difficult. We addressed one of the three main objectives of the Global Primary Productivity Data Initiative for grassland systems to develop simple models or algorithms to estimate missing components of total system NPP. Any estimate of below-ground NPP (BNPP) requires an accounting of total root biomass, the percentage of living biomass and annual turnover of live roots. We derived a relationship using above-ground peak biomass and mean annual temperature as predictors of below-ground biomass ($r^2 = 0.54$; $P = 0.01$). The percentage of live material was 0.6, based on published values. We used three different functions to describe root turnover: constant, a direct function of above-ground

biomass, or as a positive exponential relationship with mean annual temperature. We tested the various models against a large database of global grassland NPP and the constant turnover and direct function models were approximately equally descriptive ($r^2 = 0.31$ and 0.37), while the exponential function had a stronger correlation with the measured values ($r^2 = 0.40$) and had a better fit than the other two models at the productive end of the BNPP gradient. When applied to extensive data we assembled from two grassland sites with reliable estimates of total NPP, the direct function was most effective, especially at lower productivity sites. We provide some caveats for its use in systems that lie at the extremes of the grassland gradient and stress that there are large uncertainties associated with measured and modelled estimates of BNPP.

Key words Below-ground biomass, biomass to NPP conversion, functional equilibrium, grassland NPP, net primary production, NPP estimation, root turnover.

INTRODUCTION

Ecologists and land managers have invested considerable energy in recent decades to find reliable methods for estimating net primary productivity (NPP). This effort to quantify NPP is critical because of the central role of NPP in ecosystem functioning, determining plant biomass accumulation and herbivore production, as well as influencing nutrient cycling and ecosystem carbon exchange (McNaughton *et al.*, 1989; Jackson *et al.*, 2000; Sala & Austin, 2000). Measuring NPP is

also important if we are to understand annual changes in organic matter in natural and managed systems and to understand the controls over carbon fluxes. Furthermore, understanding controls over NPP will be crucial in developing models of these processes at large spatial scales. While advances have been made in accurately determining above-ground NPP (Paruelo *et al.*, 1997; Raich *et al.*, 1997; Sala & Austin, 2000), the amount of NPP allocated below-ground remains among the most poorly understood attributes of ecosystems (Lauenroth, 2000).

Two primary approaches have been used to estimate below-ground net primary production (BNPP): (1) sequential biomass sampling or (2) turnover coefficients coupled with biomass estimates. Most BNPP studies have sampled biomass

*Corresponding author: Dr R.A. Gill, Program in Environmental Science and Regional Planning, Washington State University, P.O. Box 644430, Pullman, WA 99164-4430, USA. E-mail: rgill@wsu.edu

through time, either by sequential coring or by root in-growth cores, and have assumed that positive increases in biomass summed through the growing season are reliable estimates of BNPP (Böhm, 1979; Milchunas & Lauenroth, 1992; Neill, 1992; Gill & Jackson, 2000). The strength of sequential biomass sampling lies in its direct assessment of below-ground plant biomass. However, biomass sampling has limitations, including both sampling bias and an inability to account for coincidental growth and death between sampling dates (Sala *et al.*, 1988a; Hendrick & Pregitzer, 1993; Lauenroth, 2000). Alternatively, several researchers have used radiocarbon or minirhizotrons to determine root turnover coefficients, which are then multiplied by a measured biomass to estimate BNPP (Aerts *et al.*, 1989; Milchunas & Lauenroth, 1992; Hendrick & Pregitzer, 1993). Turnover coefficients are the proportion of root biomass that is produced or that dies annually, and their use overcomes some of the problems found in sequential biomass sampling. However, these methods may be hampered by difficulties implicit in the use and disposal of radioactive materials or the soil disturbance occurring with the installation of minirhizotrons, and the processing requirements for minirhizotron images. Where these limitations can be overcome it appears that turnover coefficients may provide better assessments of BNPP than many other methods (Milchunas & Lauenroth, 1992; Lauenroth, 2000).

Understanding below-ground NPP (BNPP) is particularly important in grassland ecosystems. In most grasslands a large proportion of biomass is below-ground (Coupland, 1992), making estimates of total NPP in grasslands particularly sensitive to estimates of below-ground production. Early estimates of grassland NPP were based solely on above-ground peak standing matter, and even the co-ordinated efforts to characterize grassland NPP by the International Biological Programme were based mainly on changes in above-ground biomass, with relatively few estimates of below-ground production (Milner & Hughes, 1968; Singh & Joshi, 1979; Long *et al.*, 1989). Because few studies present quantitative measurements of total NPP, including above-ground and below-ground components, the Global Primary Productivity Data Initiative (GPPDI) was established as a Focus 1 Activity of the International Geosphere–Biosphere Programme Data and Information System (IGBP-DIS; Olson *et al.*, 1997). As part of this activity, several working group meetings on the ‘Development of a Consistent Worldwide Net Primary Productivity Database’ were held from December 1997 to October 1998 in Santa Barbara, California, USA at the National Center for Ecological Analysis and Synthesis. This activity has led to the development of a database available from the Oak Ridge National Laboratory (<http://daac.ornl.gov/NPP>).

This paper presents an algorithm for estimating below-ground NPP in grasslands to fulfil one of the three main objectives of the GPPDI: to develop simple models or algorithms to estimate missing components of total system NPP

(Scurlock *et al.*, 1999). This model is not strictly mechanistic. We are seeking relationships between environmental variables and NPP that allow us to predict below-ground NPP. The patterns identified in this analysis may then be useful in identifying candidate mechanisms that could be used to develop more detailed, process-orientated models. The patterns may also be useful in making preliminary predictions for the many sites around the world where no data exist. We use a method that requires estimating below-ground biomass when those data are unavailable, and then converting that biomass number to BNPP using a turnover coefficient. In this paper we used both climate and vegetation data to estimate maximum below-ground biomass and root turnover coefficients.

In addition to providing an algorithm to estimate BNPP in grasslands, we test three candidate root turnover functions that might be used to describe root dynamics in grasslands. It is possible that root turnover increases in productive environments, so one of the models that we considered had root turnover increasing with above-ground NPP. Several studies in forests have shown shorter root life spans in fertilized soils compared to control plots, indicating that site fertility has some bearing on root turnover (Aber *et al.*, 1985). Alternatively, root turnover may not be influenced by environmental factors, making root turnover constant in grasslands. A third possibility is that root turnover is controlled by a suite of factors, including root herbivores, water stress and growing season length, that are correlated with mean annual temperature (Gill & Jackson, 2000). By comparing the ability of these three models to predict patterns of BNPP, we hope to provide some insights into regional controls over root dynamics.

METHODS

Development data

There were three sources of biomass or productivity data available to us: (1) the core NPP database compiled at the US Oak Ridge National Laboratory (Scurlock *et al.*, 1999), (2) the Osnabrück dataset (Esser *et al.*, 1997) and (3) Australian pasture data provided by K.A. Day (unpublished data). Using three independent data sources allowed us to develop empirical relationships between climate and vegetation data with one set and then validate the model with independent datasets. We included in our consideration all available measurements made on predominately grassland, non-wetland sites with limited woody cover. We then filtered the selected biomass and NPP data for the availability of simultaneous above-ground and below-ground measurements. In addition, we required below-ground biomass measurements to be taken at the approximate time of peak above-ground biomass, since this is the most widespread analogue for above-ground NPP.

Of the sites and treatments (e.g. burning, grazing) reported in the Oak Ridge grassland NPP database, we were able to

Table 1 Characteristics of grassland sites included in the development data set. MAP = mean annual precipitation; MAT = mean annual temperature. Treatments = number of datasets available per site for different grazing and burning treatments (NB not irrigation or fertilization). Total number of treatments = 52. ORNL = Oak Ridge National Laboratory DAAC (URL), DNR = Queensland Department of Natural Resources

Site	Data source	Treatments	MAP (mm)	MAT (°C)	Latitude	Longitude
Calabozo, Venezuela	ORNL	3	1306	28.3	8.93	-67.42
Charleville, Queensland, Australia	ORNL	2	483	20.7	-26.40	146.27
Klong Hoi Khong, Thailand	ORNL	2	1541	28.0	6.33	100.93
Lamto, Ivory Coast	ORNL	1	1165	28.6	6.22	-5.03
Matador, Saskatchewan, Canada	ORNL	1	350	2.4	50.70	-107.72
Matopos, Zimbabwe	ORNL	1	603	18.8	-20.26	28.37
Nairobi, Kenya	ORNL	2	677	20.1	-1.33	36.83
Kursk, Russia	ORNL	1	583	5.2	51.67	36.50
Otradnoe, Russia	ORNL	2	485	4.2	60.83	30.25
Shortandy, Kazakhstan	ORNL	1	350	1.6	51.67	71.00
Tumugi, Inner Mongolia, China	ORNL	1	411	2.1	46.10	123.00
Tuva, Russia	ORNL	1	285	-4.3	51.83	94.42
Montecillos, Mex., Mexico	ORNL	2	580	14.3	19.46	-98.91
Osage, Oklahoma, USA	ORNL	2	916	14.3	36.95	-96.55
Bridger, Montana, USA	ORNL	2	349	8.7	45.78	-110.78
Dickinson, Nebraska, USA	ORNL	2	422	4.8	46.90	-102.82
Hays, Kansas, USA	ORNL	1	586	12.0	38.87	-99.38
Jornada, New Mexico, USA	ORNL	2	262	14.4	32.60	-106.85
Roma (Euthella), Queensland, Australia	DNR	2	540	20.4	-26.48	148.68
Roma (DPI Research Station), Queensland, Australia	DNR	1	553	20.5	-26.58	148.77
Roma (Roselea), Queensland, Australia	DNR	2	541	20.4	-26.76	148.82
Crows Nest, Queensland, Australia	DNR	1	848	17.5	-27.03	152.02
Grandchester, Queensland, Australia	DNR	1	917	18.5	-27.75	152.45
Calliope (Galloway Plains), Queensland, Australia	DNR	3	797	21.2	-24.16	150.95
Biloela (Callide Range), Queensland, Australia	DNR	1	797	21.2	-24.19	150.69
Parkhurst, Queensland, Australia	DNR	1	812	22.4	-23.30	150.51
Bowen (Ida Creek), Queensland, Australia	DNR	1	816	23.4	-20.27	148.12
Normanton (Milgarra), Queensland, Australia	DNR	1	653	27.3	-18.12	140.88
Julia Creek (Toorak), Queensland, Australia	DNR	1	403	25.2	-20.98	141.80
Tambo (Lisnatee), Queensland, Australia	DNR	1	473	20.4	-25.08	146.50
Clermont (Epping Forest Nat. Pk.), Queensland, Australia	DNR	1	500	23.1	-22.37	146.69
Gayndah (Brian Pastures Res. Stn.), Queensland, Australia	DNR	6	666	20.6	-25.67	151.75

include 23 treatments at 16 sites that met our requirements. We used these data for algorithm development. The Osnabrück compilation of NPP measurements and estimates includes 720 total sites, 116 of which met our minimal requirements (non-forest, non-wetland), and 51 satisfied our requirement for above-ground and below-ground values reported (Esser *et al.*, 1997). The Osnabrück and K.A. Day data were not used in algorithm development so they could be used *post facto* to test the relationship.

Our complete set of development data (Table 1) span a range of peak above-ground biomass from 80 to 930 g/m², with concurrent below-ground measurements ranging from 120 to 3400 g/m². The data encompass mean annual precipitation ranging from 262 to 1541 mm, and mean annual temperature between -4.3 and 28.6 °C.

Algorithm development and data analysis

To determine the relationship between environmental factors and below-ground biomass and to use environmental and above-ground plant characteristics to determine below-ground NPP we conducted multiple pairwise regressions. Once we determined the variables most strongly related to below-ground biomass, we ran a multiple regression to describe most fully the relationship. Below-ground biomass was then converted to BNPP using estimates of the percentage of live material and root turnover rate. The resulting relationship was then tested against an independent database of NPP compiled from the literature by Esser *et al.* (1997). In addition, we conducted a site level test of the complete BNPP algorithm for two sites with extensive NPP measurements. All

relationships discussed in this paper are statistically significant at $P \leq 0.05$ unless otherwise noted. To give an estimate of the error associated with our model calculation, we assess the error of estimation:

$$\left(\left(\frac{\text{Modelled BNPP} - \text{reported BNPP}}{\text{Reported BNPP}} \right) \times 100 \right)$$

for the six most productive and the six least productive sites in the database. We also determine the error of estimation for site-level tests.

RESULTS AND DISCUSSION

Algorithm development

Our complete algorithm of below-ground NPP from simple and widely available measurements is:

$$\text{BNPP} = \text{BGB} \times \frac{\text{Live BGB}}{\text{BGB}} \times \text{turnover} \quad (1)$$

where: BGB is below-ground biomass in g m^{-2} and equals $0.79(\text{AGBIO}) - 33.3(\text{MAT} + 10) + 1289$; AGBIO = peak above-ground live biomass (g m^{-2}); MAT = mean annual temperature; ($^{\circ}\text{C}$) or, an observed value of below-ground biomass may be used.

$$\frac{\text{Live BGB}}{\text{BGB}} = 0.6$$

Turnover is the proportion of roots that are produced or die annually in year^{-1} . We consider three options:

- 1 Direct function: turnover is directly related to above-ground NPP, $\text{turnover} = 0.0009 \text{ g/m}^2 (\text{AGNPP}) + 0.25 \text{ year}^{-1}$.
- 2 Constant function: turnover is constant proportion of root biomass, $\text{turnover} = 0.65 \text{ year}^{-1}$ regardless of above-ground NPP.
- 3 Exponential function: turnover increases exponentially with mean annual temperature, $\text{turnover} = 0.2884e^{0.046 \text{ MAT}}$.

Ideally, any algorithm used to predict below-ground NPP would use variables that are easily measured and are broadly available. Because above-ground biomass is one of the most easily obtained field measurements, this state variable is likely to be included in any NPP database. Also, remote sensing allows researchers to determine peak above-ground biomass remotely for large areas. If BNPP can be related to above-ground biomass and climate variables, estimates could be made for ecosystem carbon exchange for entire regions. In addition, the functional equilibrium theory (Thornley, 1977; Brouwer, 1983), and other frameworks of carbon partitioning (e.g. Farrar & Jones, 2000), suggest that there is a balance between shoot and root growth because plants need both

above-ground and below-ground resources in a somewhat stable ratio. Therefore, both shoot and root growth should increase with favourable plant growth conditions. After accounting for the influence of climate on root : shoot ratios, above-ground production should be an important covariate in estimating BNPP.

In support of the functional equilibrium concept, Farrar & Williams (1991) discuss how a reduction in temperature might lead to increased root : shoot ratios through differential effects of temperature on plant C sources and sinks. The model of Hunt *et al.* (1998) used the concept of balanced growth to model C partitioning responses of *Bouteloua gracilis* (H.B.K.) Lag. ex Steud. and *Pascopyrum smithii* P.A. Love. In line with balanced growth, Hunt *et al.*'s model represented increased biomass partitioning below-ground under low N and low soil water. In the development data set (Table 1) the ratio of root biomass to shoot biomass increased with declining precipitation ($r^2 = 0.15$) and decreasing temperature ($r^2 = 0.65$).

The data in the Osnabrück database (Esser *et al.*, 1997) support the concept that both above-ground and below-ground NPP are increased by favourable environmental conditions since below-ground NPP increased with above-ground NPP ($r^2 = 0.22$). Below-ground biomass was inversely related to mean annual temperature ($r^2 = 0.44$), while there was a poor relationship between below-ground biomass and mean annual precipitation ($r^2 = 0.02$). The poor correlation between below-ground biomass and precipitation was surprising. Sala *et al.* (1988b) found that above-ground NPP is increased both with mean annual precipitation and water holding capacity of soils. The effect of the precipitation relationship on above-ground NPP is clearly seen in the productivity estimates derived from the STATSGO (State Soil Geographic) database (USDA, 1991) as well as those from remotely sensed data (Tieszen *et al.*, 1997). Yang *et al.* (1998) quantified the increase in NDVI (normalized difference vegetation index, an index of biomass) with moisture in some grassland classes in the steppe grasslands of the northern Great Plains of the USA. Lauenroth & Sala (1992) found that above-ground forage productivity in the northern shortgrass steppe is positively related to annual precipitation on a year-to-year basis, and that the predictive power increases when precipitation event size is taken into account at the drier end of the grassland region. However, Gill & Jackson (2000) showed that the absence of a relationship between precipitation and below-ground processes at a regional scale does not necessarily mean that precipitation is not important in site-level root dynamics.

Based upon these concepts, we regressed observed below-ground biomass against above-ground biomass (as a surrogate for ANPP) and mean annual temperature. We arrived at an equation [$\text{BGB} (\text{g m}^{-2}) = 0.79 \text{ AGBIO} (\text{g m}^{-2}) - 33.3 (\text{g m}^{-2} \text{ } ^{\circ}\text{C}^{-1}) (\text{MAT} + 10)(^{\circ}\text{C}) + 1290 (\text{g m}^{-2})$] that predicted below-ground

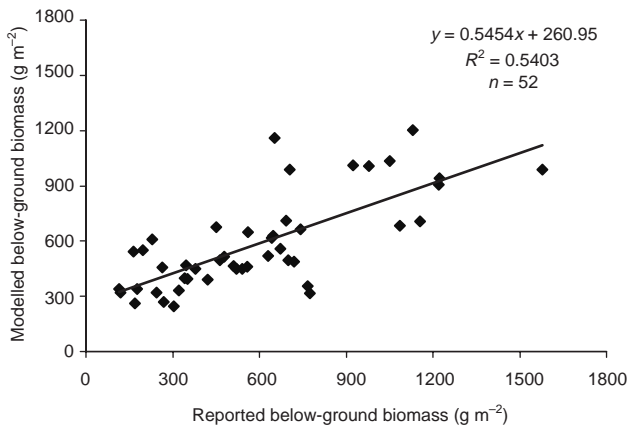


Fig. 1 Comparison of reported below-ground biomass values and those estimated with the equation derived herein based on mean annual temperature and above-ground biomass.

biomass with reasonable confidence ($r^2 = 0.54$) for a plot of observed below-ground biomass vs. simulated below-ground biomass (Fig. 1). There was a slight departure from a 1 : 1 relationship, indicating that the model has a tendency to predict that below-ground biomass is lower than reported at sites with the greatest below-ground biomass.

In order to extrapolate BNPP from below-ground biomass, it is necessary to describe the proportion of below-ground biomass that is live (%live). A number of studies have made efforts to separate live and dead roots. Data indicate that %live ranges from approximately 35% (Garcia-Moya & Castro, 1992; Kinyamario & Imbamba, 1992; Ojima *et al.*, 1994) to 67% (Singh & Coleman, 1973, 1974; Kamnalrut & Evenson, 1992; Gilmanov *et al.*, 1997). The range of %live for temperate grasslands is approximately 30% to 65%, although seven of eight estimates cover a much narrower range (52% to 67%; Singh & Coleman, 1973, 1974; Hayes & Seastedt, 1987; Gilmanov *et al.*, 1997). The mean value for temperate grasslands is 60% (Jackson *et al.*, 1997). The value for tropical grasslands is more variable, with a mean of 50% and a range of 38% to 69% (Fiala & Herrera, 1988; Garcia-Moya & Castro, 1992; Kamnalrut & Evenson, 1992; Kinyamario & Imbamba, 1992; Scholes & Walker, 1993; Jackson *et al.*, 1997). The %live root biomass is lowest for tundra graminoids, 35–40% (Dennis *et al.*, 1978). Such mean estimates ignore seasonal variability of this system property, which is probably dynamic and may depend on plant ontogeny, environmental factors influencing decomposition and soil depth (Troughton, 1957; Casper & Jackson, 1997; Eissenstat & Yanai, 1997). Nevertheless, many of the above estimates are based on averages of monthly measurements over many years and should provide reasonable annual estimates for each site. Due to the uncertainty associated with estimates of %live, we used a constant value of 60%. It is important to

recognize that in systems where the proportion of live roots is consistently greater or lesser than the value used here, this algorithm would need to be adjusted to take into account this discrepancy. This difference is likely to be especially important in systems with slow rates of decomposition (e.g. tundra).

To arrive at a reliable estimate of below-ground NPP, we must have some knowledge of patterns of root turnover. Turnover is the death and subsequent detachment of roots, expressed as an annual proportion. A great deal of scientific effort has been made to quantify root turnover (reviewed in Cheng *et al.*, 1991; Gill & Jackson, 2000), and although the methods have improved over time it is still one of the most difficult ecosystem characteristics to describe. Our analysis is used to evaluate three alternative assumptions about the controls over root turnover. First, it might be assumed that as above-ground productivity increases the conditions favouring faster turnover also increase, such as greater rainfall, higher nitrogen availability and faster decomposition (Schimel *et al.*, 1997). Therefore, we used above-ground biomass as an environmental surrogate and independent variable in this equation. The resulting equation allows for annual root turnover rates of 0.3–1.0 year⁻¹, based on above-ground biomass values between 0 and 800 g/m², although Scurlock & Hall (1998) and Gill & Jackson (2000) suggest that root turnover rates occasionally exceed 1.0 year⁻¹. Alternatively, we modelled turnover as a constant, which implies that for all grasses the proportion of roots that die annually is invariant. The third possibility is that temperature, with its accompanying suite of covariates, controls root turnover. This assumes that higher maintenance respiration, nutrient availability, water stress and pathogen load are the dominant controls over patterns of turnover (Gill & Jackson, 2000).

Model validation

We tested the efficacy of the three turnover estimates in two ways: (1) through a comparison of modelled results with the Esser *et al.* (1997) dataset and (2) through direct comparison of model output and values reported for two sites in the USA with reliable below-ground NPP measurements. The Shortgrass Steppe (SGS), LTER (National Science Foundation Long-term Ecological Research Network) site (<http://sgs.cnr.colostate.edu/sgshome.html>), was the location of an in-depth study of below-ground NPP using carbon isotopes (Milchunas & Lauenroth, 1992). The Konza Prairie Research Natural Area (KNZ, <http://www.ksu.edu/konza/>), also an LTER Network site, was the site of another below-ground NPP study (Hayes & Seastedt, 1987) using minirhizotrons. The SGS's above-ground productivity (including crowns) was 165 g biomass m⁻², with below-ground productivity ranging from 151 to 175 g biomass m⁻² (Milchunas & Lauenroth, 1992). At KNZ, above-ground NPP was 450 g biomass m⁻²,

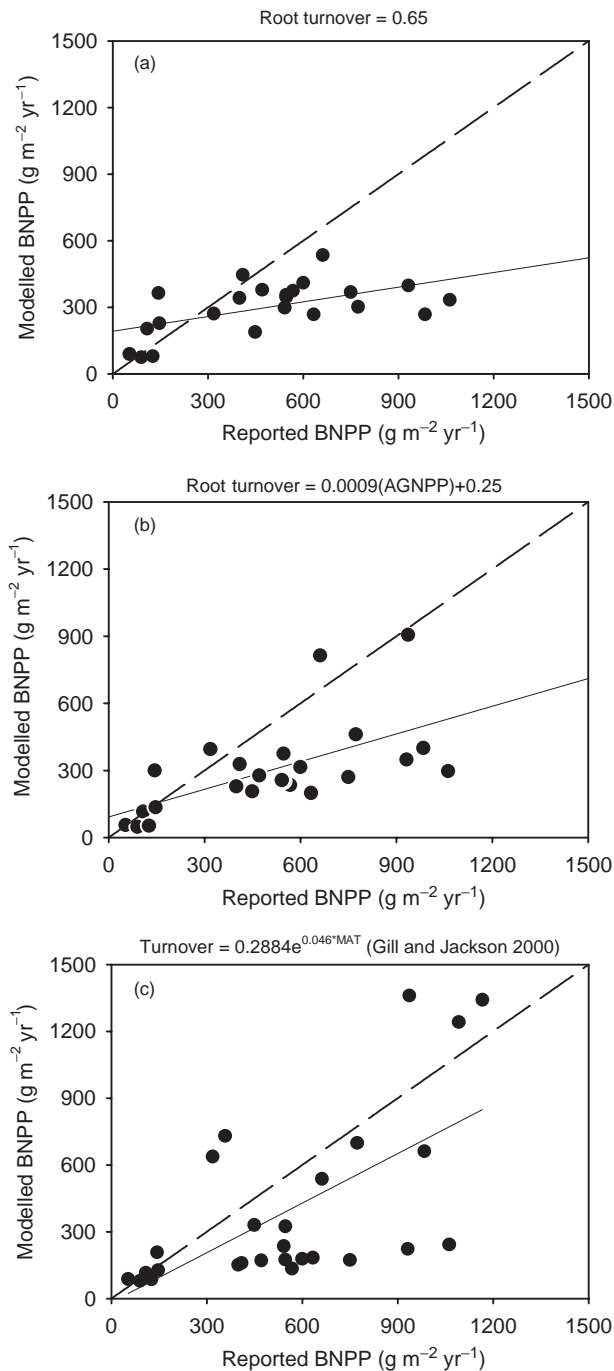


Fig. 2 Below-ground NPP calculated using simple environmental variables (mean annual temperature, above-ground biomass) with three different representations of root turnover rate. (a) Root turnover is represented as a direct function of above-ground biomass ($r^2 = 0.370$), (b) root turnover represented as a constant rate of 65% per year ($r^2 = 0.307$), and (c) root turnover represented as an exponential increase with mean annual temperature ($r^2 = 0.402$). Lines are the best fit linear models.

with a range of 335–486 g biomass m^{-2} below-ground (Hayes & Seastedt, 1987). These root observations were made in surface soils (to 40-cm depth, maximum), which include > 50% of total root biomass.

We tested our algorithm against the largest database of above-ground and below-ground grassland productivity known to us (Esser *et al.*, 1997). The constant ($r^2 = 0.307$, Fig. 2a) and direct ($r^2 = 0.370$, Fig. 2b) functions tended to predict lower values of BNPP than reported in the database, especially at the high productivity end and this is reflected in the error estimation. For the most productive six sites, the constant function diverged from reported values by an average of -68%, with a range from -48 to -80%. The error of estimation for these productive sites was slightly less using the direct function, with a mean divergence from reported values of -65% and a range from -55 to -79%. The exponential turnover model ($r^2 = 0.402$, Fig. 2c) represented BNPP more effectively at the productive end of the gradient, where there appears to be a strong disparity between the reported and modelled values in the first two models. Using the exponential turnover model, the mean error of estimation for the six most productive sites was -19%, with a range of +45% to -76%. Since neither the direct or constant functions did a reasonable job in predicting BNPP in the most productive end of the gradient, we suggest that the exponential function is the most useful of the three functions in predicting regional patterns of BNPP.

These three methods of estimating turnover result in annual BNPP estimates for the development dataset (Table 1) ranging from 68 to 646 g biomass m^{-2} for eqn 1, 95 to 469 g biomass m^{-2} for eqn 2, and 79–1341 g biomass m^{-2} for eqn 3. When applied to our test site in Colorado (SGS), the direct function was most effective, yielding BNPP of 188 g biomass m^{-2} per year. Constant turnover yielded a BNPP much higher than reported values (Table 2). The exponential function was higher than the reported values at the SGS site, while it was lower than the reported values at KNZ. The constant and direct representations of turnover resulted in somewhat low, but reasonable BNPP for KNZ (Table 2).

Based on a need for a simple way to estimate missing components of total system NPP, formalized as the Global Primary Productivity Data Initiative (GPPDI), we offer the algorithm that utilizes an exponential root turnover function. Our simple method of estimating below-ground NPP is not designed to replace more sophisticated techniques informed by direct observation or sampling. However, the use of these methods, including sequential biomass sampling, root in-growth cores and radiocarbon and minirhizotron estimates of root turnover rate is limited because they are time-consuming and expensive. The algorithm we present here allows the estimation of below-ground NPP when field observation is impractical, due to cost or when estimates are to be made over large areas. In addition, it will be possible to estimate below-ground NPP

Table 2 Comparison of the reported and modelled values of NPP for SGS and KNZ (in g biomass m⁻² per year). Error of estimation was calculated using the equation:

$$\left(\left(\frac{\text{Modelled BNPP} - \text{reported BNPP}}{\text{Reported BNPP}} \right) \times 100 \right)$$

Positive values indicate that the model overestimated BNPP, while negative values are the result of the model underestimating BNPP

Below-ground NPP	SGS	Error of estimation	KNZ	Error of estimation
Reported				
Minimum	151		335	
Maximum	175		486	
Modelled				
Constant root turnover	307	75%(max) 103% (min)	349	-28%(max) 4% (min)
Direct root turnover	188	7%(max) 25% (min)	352	-28%(max) 5% (min)
Exponential turnover	210	20%(max) 39% (min)	281	-42%(max) 16% (min)

based on above-ground NPP measurements made in years past, making it possible to estimate historic changes in total NPP.

ACKNOWLEDGMENTS

This work was conducted as part of the 'Development of a Consistent Worldwide Net Primary Productivity (NPP) Database' Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (grant no. DEB-94-21535), the University of California — Santa Barbara, and the State of California. Financial support for NREL authors was provided by NASA-EOS NAGW 2662. We thank Mike Coughenour and Jim Clark for their helpful comments on an earlier version of this manuscript.

REFERENCES

- Aber, J.D., Melillo, J.M., Nadelhoffer, K.J., McClaugherty, C.A. & Pastor, J. (1985) Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: a comparison of two methods. *Oecologia*, **66**, 317–321.
- Aerts, R., Berendse, F., Klerk, N.M. & Bakker, C. (1989) Root production and root turnover in two dominant species of wet heathlands. *Oecologia*, **81**, 374–378.
- Böhm, W. (1979) *Methods of studying root systems*. Springer-Verlag, Inc, New York.
- Brouwer, H. (1983) Functional equilibrium: sense or nonsense? *Netherlands Journal of Agricultural Science*, **31**, 335–348.
- Casper, B.B. & Jackson, R.B. (1997) Plant competition underground. *Annual Review of Ecology and Systematics*, **28**, 545–570.
- Cheng, W., Coleman, D.C. & Box, J.E. Jr (1991) Measuring root turnover using the minirhizotron technique. *Agriculture, Ecosystems and Environment*, **34**, 261–267.
- Coupland, R.T. (1992) Mixed prairie. *Grasslands of the world* (ed. by R.T. Coupland), pp. 151–182. Cambridge University Press, Cambridge.
- Dennis, J.G., Tieszen, L.L. & Vetter, M.A. (1978) *Vegetation and production ecology of an Alaskan Arctic tundra*. Springer, Berlin.
- Eissenstat, D.M. & Yanai, R.D. (1997) The ecology of root lifespan. *Advances in Ecological Research*, **27**, 1–60.
- Esser, G., Lieth, H.F.H., Scurlock, J.M.O. & Olson, R.J. (1997) *Worldwide estimates and bibliography of net primary productivity derived from pre-1982 publications*. ORNL Technical Memorandum TM-13485. Oak Ridge National Laboratory, Oak Ridge, Tennessee.
- Farrar, J.F. & Jones, D.L. (2000) The control of carbon acquisition by roots. *New Phytologist*, **147**, 43–53.
- Farrar, J.F. & Williams, W.L. (1991) The effects of increased atmospheric carbon dioxide and temperature on carbon partitioning, source-sink relations, and respiration. *Plant, Cell, and the Environment*, **14**, 819–830.
- Fiala, K. & Herrera, R. (1988) Living and dead belowground biomass and its distribution in some savanna communities in Cuba. *Folia, Geobotanica and Phytotaxonomica*, **23**, 225–237.
- Garcia-Moya, E. & Castro, P.M. (1992) Saline grassland near Mexico City. *primary productivity of grass ecosystems of the tropics and sub-tropics* (ed. by S.P., Long, M.B. Jones & M.J. Roberts), pp. 70–99. Chapman & Hall, London.
- Gill, R.A. & Jackson, R.B. (2000) Global patterns of root turnover for terrestrial ecosystems. *New Phytologist*, **147**, 13–31.
- Gilmanov, T.G., Parton, W.J. & Ojima, D.S. (1997) Testing the 'CENTURY' ecosystem level model on data sets from eight grassland sites in the former USSR representing a wide climatic/soil gradient. *Ecological Modelling*, **96**, 191–210.
- Hayes, D.C. & Seastedt, T.R. (1987) Root dynamics of tallgrass prairie in wet and dry years. *Canadian Journal of Botany*, **65**, 787–791.
- Hendrick, R.L. & Pregitzer, K.S. (1993) Patterns of fine root mortality in two sugar maple forests. *Nature*, **361**, 59–61.
- Hendrick, R.L. & Pregitzer, K.S. (1993) The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. *Canadian Journal of Forest Research*, **23**, 2507–2520.
- Hunt, H.W., Morgan, J.A. & Read, J.J. (1998) Simulating growth and root-shoot partitioning in prairie grasses under elevated atmospheric CO₂ and water stress. *Annals of Botany*, **81**, 489–501.
- Jackson, R.B., Mooney, H.A. & Schulze, E.-D. (1997) A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Science USA*, **94**, 7362–7366.
- Jackson, R.B., Schenk, H.J., Jobbágy, E.G., Cnadell, J., Colello, G.D., Dickinson, R.E., Field, C.B., Friedlingstein, P., Heimann, M., Hibbard, K., Kicklighter, D.W., Kleidon, A., Neilson, R.P., Parton, W.J., Sala, O.E. & Sykes, M.T. (2000) Belowground consequences of vegetation change and their treatment in models. *Ecological Applications*, **10**, 470–483.
- Kamnalrut, A. & Evenson, J.P. (1992) Monsoon grassland in Thailand. *Primary productivity of grass ecosystems of the tropics*

- and sub-tropics (ed. by S.P., Long, M.B. Jones & M.J. Roberts), pp. 100–126. Chapman & Hall, London.
- Kinyamario, J.I. & Imbamba, S.K. (1992) Savanna at Nairobi National Park, Nairobi. *Primary productivity of grass ecosystems of the tropics and sub-tropics* (ed. by S.P., Long, M.B. Jones & M.J. Roberts), pp. 25–69. Chapman & Hall, London.
- Lauenroth, W.K. (2000) Methods of estimating belowground net primary production. *Methods in ecosystem ecology* (ed. by O.E., Sala, R.B., Jackson, H.A. Mooney & R.W. Howarth), pp. 58–71. Springer, New York.
- Lauenroth, W.K. & Sala, O.E. (1992) Long-term forage production of North American shortgrass steppe. *Ecological Applications*, **2**, 397–403.
- Long, S.P., Moya, E.G., Imbamba, S.K., Kamnalrut, A., Piedade, M.T.F., Scurlock, J.M.O., Shen, Y.K. & Hall, D.O. (1989) Primary productivity of natural grass ecosystems of the tropics: a reappraisal. *Plant and Soil*, **115**, 155–166.
- McNaughton, S.J., Osterheld, M., Frank, D.A. & Williams, K.J. (1989) Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, **341**, 142–144.
- Milchunas, D.G. & Lauenroth, W.K. (1992) Carbon dynamics and estimates of primary production by harvest, ^{14}C dilution, and ^{14}C turnover. *Ecology*, **73**, 593–607.
- Milner, C. & Hughes, R.E. (1968) *Methods for the measurement of the primary production of grassland*. Blackwell Scientific, Oxford.
- Neill, C. (1992) Comparison of soil coring and ingrowth methods for measuring belowground production. *Ecology*, **73**, 1918–1921.
- Ojima, D.S., Schimel, D.S., Parton, W.J. & Owensby, C.E. (1994) Long-term and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry*, **24**, 67–84.
- Olson, R.J., Scurlock, J.M.O., Cramer, W., Parton, W.J. & Prince, S.D. (1997) *From sparse field observations to a consistent global dataset on net primary production*. International Geosphere-Biosphere programme data and information system, Toulouse, France.
- Paruelo, J.M., Epstein, H.E., Lauenroth, W.K. & Burke, I.C. (1997) ANPP estimates from NDVI for the Central Grassland Region of the United States. *Ecology*, **78**, 953–958.
- Raich, J.W., Russell, A.E. & Vitousek, P.M. (1997) Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawai'i. *Ecology*, **78**, 707–721.
- Sala, O.E. & Austin, A.T. (2000) Methods of estimating aboveground net primary productivity. *Methods in ecosystem science* (ed. by O.E., Sala, R.B., Jackson, H.A. Mooney & R.W. Howarth), pp. 31–43. Springer, New York.
- Sala, O.E., Biondini, M.E. & Lauenroth, W.K. (1988a) Bias in estimates of primary production: an analytical solution. *Ecological Modelling*, **44**, 43–55.
- Sala, O.E., Parton, W.J., Joyce, L.A. & Lauenroth, W.K. (1988b) Primary production of the central grassland region of the United States. *Ecology*, **69**, 40–45.
- Schimel, D.S., VEMAP Participants & Braswell, B.H. (1997) Continental scale variability in ecosystem processes: models, data, and the role of disturbance. *Ecological Monographs*, **67**, 251–271.
- Scholes, R.J. & Walker, B.H. (1993) *An African savanna: synthesis of the Nylsvley study*. Cambridge University Press, Cambridge.
- Scurlock, J.M.O., Cramer, W., Olson, R.J., Parton, W.J. & Prince, S.D. (1999) Terrestrial NPP: towards a consistent data set for global model evaluation. *Ecological Applications*, **9**, 913–919.
- Scurlock, J.M.O. & Hall, D.O. (1998) The global carbon sink: a grassland perspective. *Global Change Biology*, **4**, 229–233.
- Singh, J.S. & Coleman, D.C. (1973) A technique for evaluating functional root biomass in grassland ecosystems. *Canadian Journal of Botany*, **51**, 1867–1870.
- Singh, J.S. & Coleman, D.C. (1974) Distribution of photo-assimilated ^{14}C in the root system of a shortgrass prairie. *Journal of Ecology*, **62**, 359–365.
- Singh, J.S. & Joshi, M.C. (1979) Tropical grasslands: primary production. *Grassland Ecosystems of the World* (ed. by R.T. Coupland), pp. 197–218. Cambridge University Press, Cambridge.
- Thornley, J.H.M. (1977) Root:shoot interactions. *Integration of activity in the higher plant* (ed. by D.H. Jennings), pp. 367–389. Cambridge University Press, Cambridge.
- Tieszen, L.L., Reed, B.C., Bliss, N.B., Wylie, B.K. & DeJong, D.D. (1997) NDVI, C_3 and C_4 production, and distributions in great plains grassland land cover classes. *Ecological Applications*, **7**, 59–78.
- Troughton, A. (1957) *The underground organs of herbage grasses*. Commonwealth Bureau of Pasture and Field Crops, Bucks, England.
- USDA (1991) *State soil geographic database (STATSGO): data users guide*. Soil Conservation Service miscellaneous publication number 1492.
- Yang, L., Wylie, B.K., Tieszen, L.L. & Reed, B.C. (1998) An analysis of relationships among climate forcing and time-integrated NDVI of grasslands over the U.S. northern and central Great Plains. *Remote Sensing of Environment*, **65**, 25–37.

BIOSKETCH

Richard Gill studies ecosystem dynamics and the physiological processes that underlie emergent ecosystem properties. His research focuses on the interaction between root dynamics and soil organic matter storage, particularly within a global change context. He is currently an Assistant Professor in the Program in Environmental Science and Regional Planning at Washington State University.