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## **Percolation Model for Universal Scaling of Vegetation Net Primary Productivity with Climate Variables**

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**Abstract** We show that a quantitative, physically-based model of water balance, combined with a model for the dependence of net primary productivity (NPP) of vegetation on evapotranspiration  $E$  leads to the universal scaling of NPP with the climate variables, namely, precipitation  $P$  and potential evapotranspiration  $E_p$ . The model for NPP is based on percolation theory. The water balance is derived based on the hypothesis that ecosystem selection is driven by optimizing NPP with respect to the principal hydrologic fluxes i.e.,  $E$  and  $Q$  ( $=P - E$ ; known as run-off), with the flux dependence of  $E$  being applied self-consistently to the NPP’s model. The predictions are compared separately with Budyko’s compilation of the NPP data as a function of  $E_p$  and  $P$  using the aridity index,  $A_I = E_p/P$ , and  $E_p$  for each set of experimental data, and are shown to be in excellent agreement with the data.

**Plain Language Summary** Predicting the dependence of the net primary production on the climate variables, namely, precipitation  $P$  and potential evapotranspiration  $E_p$ , has been the subject of numerous studies. We develop a model by combining percolation theory, which describes the morphology of heterogeneous soil and plants’ root structure, with a model of water balance, which is based on the prevalent view in ecology that, to access and utilize resources for growth and reproduction, plant ecosystems exploit diversity optimally. We show that one obtains an equation describing universal scaling of NPP with  $P$  and  $E_p$ . The agreement between the predictions of the scaling equation and the relevant data at *global scale* is excellent.

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## 1. Introduction

Earth’s soil has been called “the crucible of life, a self-regulating, biophysical factory, acting like a composite living entity.” (Hillel, 2005). It represents a critical nexus (Brantley et al., 2007; Anderson et al., 2007) where plants grow, carbon is sequestered, and precipitation  $P$  is partitioned into run-off  $Q$  and evapotranspiration  $E$  (Falkenmark and Rockström, 2006; Gentine et al., 2012; Maxwell and Condon, 2016). Partitioning of the precipitated water into its primary fluxes has a profound effect on what happens in soil and the environment and, therefore, life and its diversity. Consider, for example, biodiversity. Precipitation promotes biodiversity (Krishnaswamy et al., 2009), which in turn promotes the assimilation of carbon

by plants, i.e, the net primary productivity (NPP),  $N_p$  (Oehri et al., 2017). Despite its high importance to the food-energy-water nexus (D’Odorico et al., 2018) to understanding climate stability and change (Tapley et al., 2019) and for managing water resources and optimizing agricultural production (Huang et al., 2012), there is currently no parsimonious model for accurately predicting the NPP of individual ecosystems, as well as trends across biomes. Ever since the work of Rosenzweig (1968) and Webb et al. (1986), research on NPP has tended to focus on far more complex process-based models (Cramer et al., 1999; Adam et al., 2004). For Example, Raich et al. (1991) stated that as a preferred alternative, “We can more successfully predict rates of NPP in terrestrial ecosystems, if we model the basic processes controlling productivity and how they are influenced by environmental factors.”

Nevertheless, it remains true that evapotranspiration  $E$  is the most important single input for predicting NPP (Rosenzweig, 1968), since it represents a measure of two highly variable inputs in photosynthesis, namely, light and water. The monotonic increase in NPP as a power of  $E$  (Rosenzweig, 1968) is bounded only by limits on solar energy (de Wit, 1965; Krause-Jensen and Sand-Jensen, 1998) at about  $3500 \text{ g cm}^{-2} \text{ yr}^{-1}$  (Hunt, 2017). Predicting  $E$  as a function of climatological variables  $P$  and potential evapotranspiration  $E_p$  - the central problem of hydrology (Horton, 1931) and known as the water balance - is thus the key missing ingredient for a model of NPP in terms of climatological variables.

As a report by the National Academy of Sciences (1991) suggested, the foundation for a solution of the water balance must be based on the link between hydrology and ecological optimality, since the fluxes of the key biological variables, such as biomass, are also linked with such operating chemical processes as carbon assimilation, which in turn are linked to hydrological processes, such as evapotranspiration. Such relationships make it clear that hydrology is a fundamental component of the biogeochemical cycles. A recent theoretical development (Hunt et al., 2021) that accurately predicts  $E$  as a function of solar energy and precipitation, *without* using adjustable parameters, is in the spirit of such a strategy, which was derived by optimizing NPP with respect to the principal hydrologic fluxes.

In this Letter we propose to use the model by Hunt et al. (2021) for the evapotranspiration in order to develop a theoretical framework for predicting NPP as a function of solar energy and precipitation with *at most* one adjustable parameter. Given its central position in Earth’s water and biogeochemical cycles, an accurate model is critical to water resources (Klemeš, 1988;

Arora, 2002) and models of climate (Olesen, 2007; Friend, 2010) as well.

## 2. The Percolation Model

Soil is a highly heterogeneous medium in which the connectivity of its pores is described by the sample-spanning percolation cluster (SSPC) near the percolation threshold (Katz and Thompson, 1986; Sahimi, 2011, 2023). The SSPC is made of the backbone - the multiply-connected cluster of pores through which flow and transport occur - and the singly-connected or dead-end pores. The SSPC is a self-similar fractal object with a fractal dimension  $D_f \approx 1.9$  and  $2.5$  in two and three dimensions (2D and 3D), as is the backbone with a fractal dimension,  $D_b \approx 1.64$  and  $1.87$  in 2D and 3D, respectively (Sheppard et al., 1999). Likewise, plants' roots system also possesses a fractal structure (Dannowski, 2005; Yang et al., 2022). Although the fractal dimension  $D_r$  of plant root depends on the soil depth, its typical value is close to that of the SSPC (Levang-Brilz and Biondini, 2002). Thus, we assume that,  $D_r \approx D_f$ .

Hunt (2017) employed Rosezweig's ideas to a model of root mass based on percolation theory, in order to develop the scaling relation,  $N_p \propto E^{D_f}$ , for the NPP. Briefly, since the root radial extent equals transpiration after one growing season and the cumulative transpiration after multiple seasons, and given that the plant's root structure is fractal, its mass equals transpiration raised to the power of fractal dimension  $D_f$ . We replace  $E$  with its dependence on  $E_p$  and  $P$ . Since we assume that plants' root network represents a 2D percolation cluster with  $D_r \simeq D_f = 91/48 \approx 1.9$ , we obtain,  $N_p \propto E_p^{1.9}$ . Although the general dependence of  $N_p$  on  $E_p$  has been verified, the proportionality factor is unknown and, thus, open to speculation.

Chemical weathering - disintegration of soil by chemical reactions - is limited by the rate of transport of cations (solute) in soil, while soil formation is limited by chemical weathering since plants and vegetables cannot use bare rock to grow, but need the cations in the minerals that are transported by flowing water, so that, in the absence of denudation, the chemical weathering depth is equal to the distance that a solute is transported. Solute transport in soil is described by the concepts of percolation theory (Sahimi, 2012; Ghanbarian-Alavijeh et al., 2012), which has been confirmed by experiments (Sahimi et al., 1986; Gist et al., 1990; Ghanbarian-Alavijeh et al., 2012), due to the predominance of flow at or near the percolation threshold. In the percolation representation of solute transport in soil, the total distance  $x$  that

a solute is transported by the flowing water is given by

$$x = d_0 \left( \frac{t}{t_0} \right)^{1/D_b} . \quad (1)$$

In Eq. (1)  $d_0$  is a characteristic median particle size, and  $x_0/t_0$  is the annual mean flow rate in the unsaturated zone, which has been verified for time scales ranging from a decade to millions of years (Hunt and Ghanbarian, 2016), and over four orders of magnitude of climate variability, representing a rainfall gradient from the Atacama desert to the New Zealand rainforest. Steady-state soil depths is reached when the soil production, defined as  $dx/dt$ , is equal to the denudation rate,  $q_d$ . The result provides the scaling of  $x$  with  $(P - E)$  (Hunt et al., 2020, 2021),

$$x = d_0 \left( \frac{P - E}{D_b \phi q_d} \right)^{1/(D_b - 1)} , \quad (2)$$

where  $\phi$  is the soil porosity. The accuracy of Eq. (2) has also been verified over two orders of magnitude variations in precipitation and almost three orders of magnitude variations in the denudation rate  $q_d$ .

Although, as described above, approximating transpiration by  $E$  results in the scaling relation,  $N_p \propto E^{D_f}$ , the soil depth is important as well, since carbon is sequestered throughout the soil, and plants' roots extend vertically into the critical zone with a depth roughly equal to the soil depth. Thus, the NPP is proportional to the product of  $E^{D_f}$  and  $x$ , i.e.,

$$N_p \propto E^{D_f} (P - E)^{1/(D_b - 1)} . \quad (3)$$

Optimizing  $N_p$  with respect to the hydrologic partitioning is accomplished by setting  $dN_p/dE = 0$ , which results in

$$E = \frac{D_f(D_b - 1)}{1 + D_f(D_b - 1)} P \equiv \alpha(d)P . \quad (4)$$

where  $d$  is the spatial dimension of the system. Since a solute carrying nutrients is transported by water through the backbone of the 3D SSPC, thus one may set  $D_b \approx 1.87$ . On the other hand, as discussed above, to access soil nutrients carried along by flowing water, trees' roots tend to grow horizontally, i.e., they constitute a 2D SSPC and, therefore,  $D_f = 91/48 \approx 1.9$ . Hence, we obtain,  $E = 0.623P$ , implying that the difference  $(P - E)$  is simply proportional to  $P$ . The denudation rate  $q_d$  is also generally proportional to  $P$ , implying that the net result for the soil depth is highly insensitive to climate details and explaining the consistency of soil depths of about 1 m around the world. It, however, adds no significant dependence of  $N_p$  on

climate variables, so that later substitution of the results for  $E$  into the equation for  $N_p$  is relevant only for the first factor.

Equation (4) was derived by neglecting both energy and water limitations on the vegetation productivity, when  $P$  and  $E_p$  are unequal. The energy limitation is taken into account by assuming that only  $P = E_p$  is optimized, and that the remaining  $(P - E_p)$  runs off, i.e.,

$$E = \alpha(d)E_p . \quad (5)$$

Thus, with  $D_f \approx 1.9$  and  $D_b \approx 1.87$ , we obtain,  $E = 0.623E_p$ . Water limitation is taken into account by assuming that only the surface covered by vegetation, shown to be proportional to  $P/E_p$  by Yang et al. (2009), and assumed here to equal  $P/E_p$ , is subject to the optimization, with  $E = P$  over the remaining area. The assumption, which neglects known routing of surface water towards vegetation, results in

$$E = P - (1 - \alpha) \left( \frac{P^2}{E_p} \right) = P - 0.377 \left( \frac{P^2}{E_p} \right) . \quad (6)$$

We emphasize that the numerical factor  $0.377 = 1 - 0.623 = 1 - \alpha(d)$ , is *not* a fitted number, but, as derived above, is derived based on percolation theory. Since both  $D_f$  and  $D_b$  represent universal fractal dimensions, the numerical factor  $0.377 = 1 - 0.623$  is also universal, which our theory predicts to be the fraction of  $P$  that represents  $E$  for a 2D plant root system with neither energy nor water limitations, a prediction that is within 1.5% of the measured global mean value of  $E/P$  (Hunt et al., 2021).

### 3. Universal Scaling of Net Primary Productivity

We now show that  $N_p$  follows a *universal* scaling law. To begin with, we note that according to Eq. (4),  $E$  is proportional to  $P$ . Moreover,  $q_d$ , the denudation rate, is also proportional to  $P$  (Reiners et al., 2003). Thus, in Eq. (2)  $(P - E)/q_d \sim \mathcal{O}(1)$  and, as a result,  $N_p \propto E^{D_f}$ . We define the aridity index as  $A_I = E_p/P$ . For  $A_I < 1$ ,  $E = E_p$  and thus,  $N_p \propto E_p^{D_f}$ . For  $A_I > 1$  we substitute Eq. (6) into  $N_p \propto E^{D_f}$  and derive

$$N_p \propto \begin{cases} \alpha(d)^{D_f} E_p^{D_f} & A_I < 1 , \\ E_p^{D_f} \left[ \frac{1}{A_I} - (1 - \alpha) \frac{1}{A_I^2} \right]^{D_f} & A_I > 1 \end{cases} \quad (7)$$

Thus, Eq. (7) implies that for  $A_I < 1$  the ratio  $N_p/E_p^{D_f}$  should saturate at a universal value,  $\alpha^{D_f} = 0.623^{1.9} \approx 0.4$ , whereas for  $A_I > 1$  it should be a universal function of the aridity index

$A_I$ . This means that separate curves of data taken at various solar irradiance, the flux of radiant energy  $Rn$ , should collapse onto a single universal function of  $A_I$ . Thus, one has a theory that satisfies simultaneously the criteria of Rosenzweig (1968), namely, that the principal input to NPP should be evapotranspiration, and of Budyko (1958) according to which the variables of relevance to NPP are  $A_I$  and  $E_p$ , while demonstrating that the critical variable missing from Rosenzweig’s analysis, i.e.,  $E_p$ , was already anticipated by Budyko (1958). The data that Budyko (1974) reported were a function of  $A_I$  for various values of the irradiance  $Rn$ , which we use as a proxy for potential evapotranspiration  $E_p$ .

#### 4. Comparison with Experimental Data

Beyond the difficulties in prediction lie those in finding suitable data to test the predictions of the percolation model, as very few researchers have chosen to represent  $N_p$  as a function of  $A_I = E_p/P$ . As mentioned above, one of the few who made such a systematic study was Budyko (1974). We have used a digitized version of his original data and figures, reported by Gupta et al. (2002), for evaluating the accuracy of the predicted universal scaling of  $N_p$ . Given that, for example, Adams et al. (2004) needed 20 journal pages to describe ten representative models of NPP and 15 more to list the equations and their constants, we believe that there is an important place for a model with only two parameters,  $P$  and  $E_p$ , which are simultaneously independent variables in the related fundamental problem of hydrology, namely, the water balance.

Figure 1 presents the original data of Budyko for NPP versus  $P/E_p$ . Figure 1(b) exhibits the data, rescaled according to Eq. (7). Interestingly, the crossover in the data from energy- to water-limited regimes occurs at  $A_I < 1$  around 0.8. We, therefore, present simultaneously the predictions of Eq. (7), but scaled to a crossover from energy to water limitations at  $A_I/0.8 = 1$ . As a consequence of the tendency for solar energy to arrive continuously, but for water to arrive in lumps, ecosystems are water-limited even for  $A_I$  less than, but close to 1. One can see that the simple uncertainty in the position of the crossover point from water- to energy-limitations suffices to map out the range of the data in arid ecosystems, since the predicted curve maps out the lower boundary of the data in both regimes.

In Figure 2, we compare the individual sets of data with the predictions, but using the modification of Eq. (7) scaled to  $A_I/0.8$ . As Figure 2 demonstrates, the predicted  $N_p$  are around the

1 : 1 line, indicating accurate theoretical predictions by the percolation model.

## Discussion

In ecology, null models (Harvey et al., 1983) can be developed to determine whether data are “structured.” In physics, scaling plots of data reveal universality of certain functions. The scaling plot of Figure 2 reveals that, even in the presence of some discrepancies, the fundamental structure of the data is compatible with the predictions of Eq. (7). The inputs are climatic variables  $P$  and  $E_p$ . The origin of the structure in the ecological dataset of Budyko (1974) can be thought of as the hypothesis that ecosystems, or clades (Doolittle, 2017), are selected on the basis of productivity within limitations primarily of energy and water, in such a way that the ensemble of species fills the niches that are most productive. Thus, given a set of inputs, the plant ecosystem that we actually find is the one that is best adapted to growing and reproducing itself, subject to the climate limitations present.

Other limiting factors may exist: there are portions of Figure 1 where the curves fall short of the predicted productivity. Approximations made in order to develop theory lead to differences with the data. For example, we underestimate the productivity of ecosystems with  $A_I < 1$  and small values of the solar irradiance  $Rn$ . We, however, have based our predictions on the concept that total biomass scales consistently with below-ground biomass. Thus, it is possible that in such ecosystems where water and nutrients are not as important limiting factors as light, a larger share of plant biomass is found above-ground than on average across the remaining ecosystems, leading to the underprediction. In order to realize the full predictive potential of the theory, we also have to admit the potential relevance of water limitations to systems in which the input energy, as measured in potential evapotranspiration, is less than the total precipitation. The reason for such an asymmetry in the response of vegetation to the water balance - a crossover from energy- to water-limitations before the energy can evaporate all the water - presumably lies in the distinct characters of solar energy and precipitation inputs to the ecosystem: Water arrives less regularly and in lumps, some of it flowing off when not needed and unavailable when needed, whereas energy arrives nearly continuously.

In a related study, Huxman et al. (2004) found convergence to a common water-use strategy in the arid limit. Our results appear to suggest a similar convergence. We note also that our scaling analysis of NPP as a function of aridity index in Figure 2 illuminates a striking



tendency of ecosystems towards common behavior in the arid limit, in accord with the discussion of Huxman et al. (2004).

## 5. Summary

In a recent theory for the water balance, the fraction of precipitation  $P$  returned to the atmosphere through evapotranspiration  $E$  was determined by optimizing the net primary productivity, NPP, of ecosystems with respect to the principal hydrologic fluxes,  $E$  and  $Q$ , the run-off. Here we substituted this result for  $E$  as a function of precipitation and potential evapotranspiration into an existing result for the NPP of ecosystems as a function of  $E$ . The result gives NPP as a universal function  $NPP(P, Ep)$  with a single unknown constant, which plays the role is of a universal carbon assimilation efficiency. Comparison with a compilation of the known global data (at the time) by Budyko in his book, *Climate and Life* (1974) demonstrates a strong predictive capability of the derived relationship with an  $R^2$  of 0.97 across biomes and climate variables. The predicted dependence on aridity index is strong in arid regimes, but saturates at low aridity. In contrast to the data, the predicted form of this saturation involves a discontinuous change in slope near aridity index 1. Although this introduces a slight discrepancy in the comparison with observation for NPP, the relevance of the slope discontinuity is proven in (separate) comparisons of streamflow elasticity with observation.

## Open Research

Data used in this study (A.G. Hunt et al., 2023) are available at:

<http://www.hydroshare.org/resource/eee62676c9874dc4b3bc44712c36315a> as well as in the Supplemental Material section.

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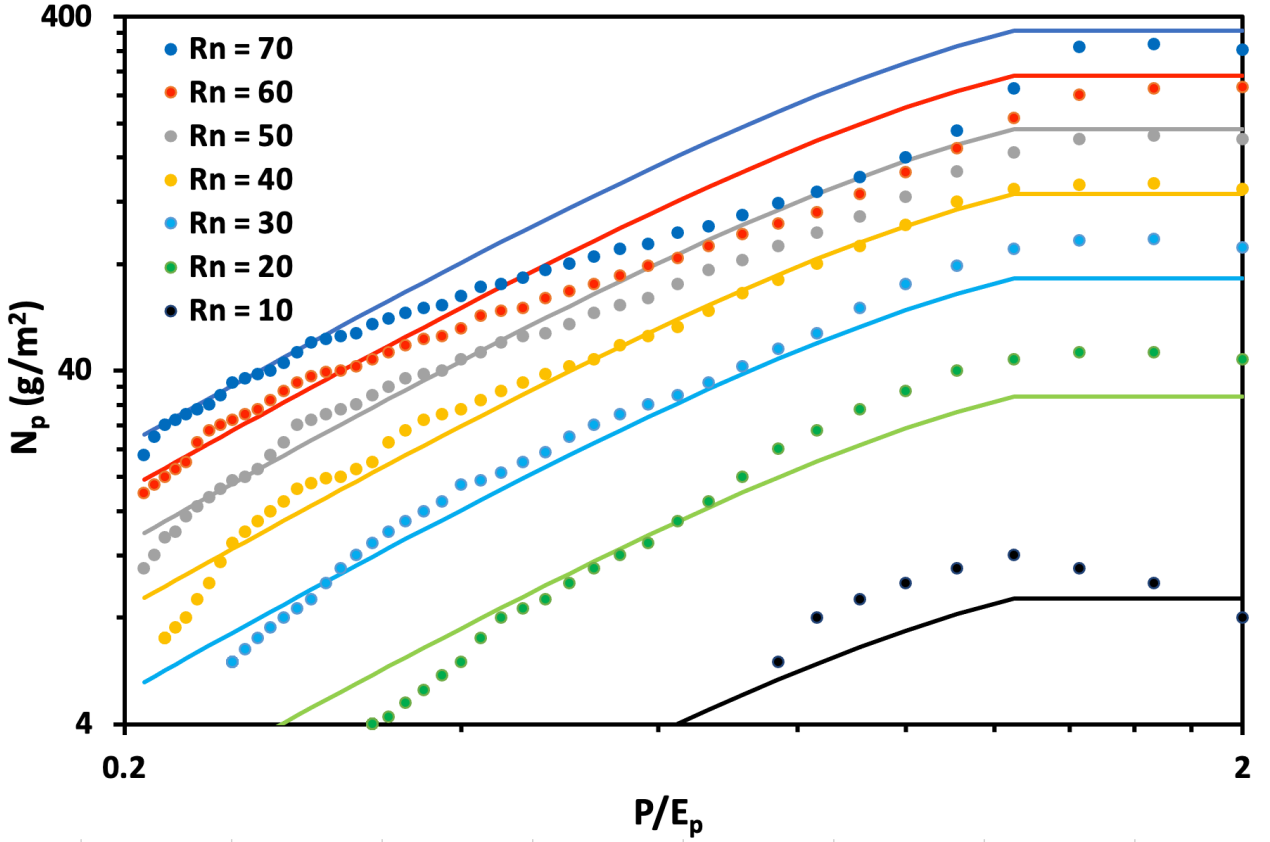


Figure 1: Comparison of the individual predictions for the data of Budyko (1974). In this case, the curve representing the prediction for  $Rn = 70$  is adjusted in order to produce the best match with the data at both large and small  $A_I > 1$ , and all the other predictions are scaled by the ratio of  $Rn/70$ , raised to the 1.9 power (the fractal dimension of two-dimensional percolation cluster). Owing to its superior performance, however, the scaling variable was chosen as  $A_I/0.80$ .

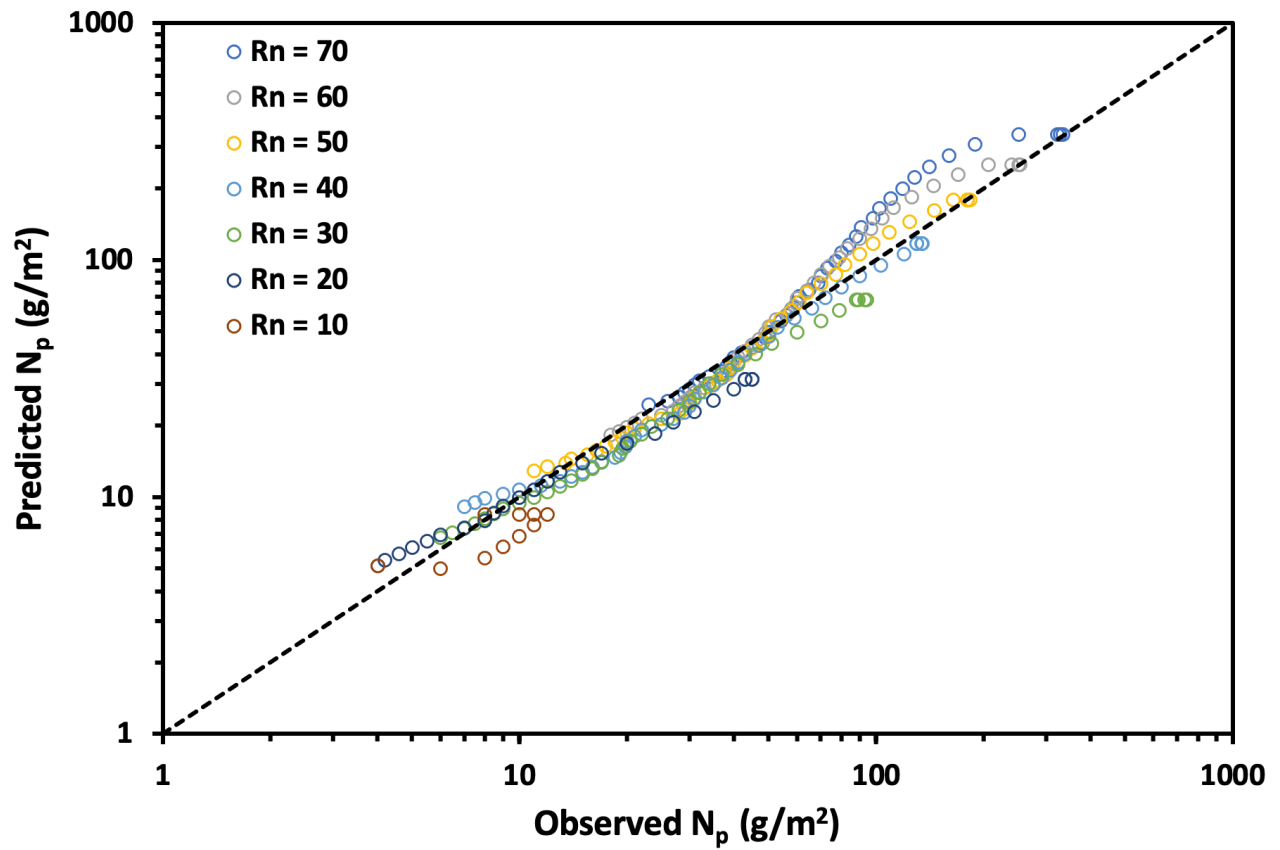


Figure 2: Comparison of the scaled plot of the data of Budyko (1974) with one of the predicted curves using Eq. (7), as well as its modification by substituting  $A_I/0.80$  for  $A_I$ .