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FORUM

Production as a function of resource availability: Slopes and efficiencies are different

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Abstract

A number of investigators have interpreted the slope of a linear production-resource relationship as a measure of efficiency of resource utilization. However, this is rarely true and may lead to incorrect conclusions. Here, by means of simple mathematical equations and conceptual definitions, we point out the theoretical differences between slope and efficiency. While a slope represents the change in the dependent variable per unit change in the independent variable, efficiency expresses the amount of output produced by a unit amount of input. Practical implications of using slopes as indicators of resource-use efficiency are less important as the resource amount increases. Slopes may be used as indicators of the sensitivity of production to changes in input, which is by itself an interesting property of biological systems. Finally, production function intercepts determine whether the efficiency will decrease, increase, or remain constant as resources increase.

Keywords: Fertilization; Marginal response; Precipitation; Primary production; Production function; Resource-use efficiency.

Introduction

Production functions essentially describe a transformation process where a given input yields a given quantity of output. For example, above-ground net primary productivity (the net increment of aerial plant mass, *ANPP*) may be analysed as a linear function of precipitation (*PPT*) (Sala et al. 1988), and photosynthesis may be represented as a non-rectangular hyperbolic function of irradiance (Farquhar & von Caemmerer 1982). In many cases, the slope of the linear part of a production function has been equalled to the resource use efficiency (Noy-Meir 1973; Lambers et al. 1998; Paruelo et al. 1999; Lauenroth et al. 2000; Chapin et al. 2002; Tilman et al. 2002; Huxman et al. 2004). However, is the slope of an input-output relationship the same as the efficiency of utilization of a resource?

Hafner (2003) showed that decreasing fertilization efficiency is not related to a decreasing slope between production and fertilization as suggested by Tilman et al. (2002). Given that efficiency is a basic concept in several disciplines, we provide novel elements to develop Hafner's argument and make it useful to a wider audience. We show why the slope of a production function is not necessarily a measure of resource use efficiency, and highlight the usefulness of slopes by themselves.

Slopes and efficiencies

In our context slope is the tangent of the angle between a straight line and the *x*-axis in a co-ordinate system and efficiency is the output (or production) per unit input (or resource). Thus, while a slope represents the change in the dependent variable per unit change in the independent variable, efficiency expresses the amount of output produced by a unit amount of input. Therefore, slope and efficiency are measures of different attributes.

In spite of the conceptual differences stated above, there are certain cases where both variables display similar values. This may have led some authors to interpret the slope of a linear production function as an efficiency. Let us consider a simple example based on three general production functions (Fig. 1) to illustrate this issue. The functions represent positive linear relationships of the form:

$$y = a + bx \qquad (1)$$

where x is the amount of a given input and y is the quantity of a given output, b is the slope, and a is the y-intercept. The three types of production functions have the same slope, b, but type 1 has a zero intercept, type 2 has a positive intercept and type 3 has a negative intercept. For a linear function, the utilization efficiency (*UE*) is equal to (Hafner 2003):

$$UE = \frac{y}{x} = \frac{a}{x} + b \qquad (2)$$

Eq. 2 reveals three features that are relevant to our problem. First, it indicates that the only case where *UE* would be equal to *b* is when *a* is zero, that is, in type 1 functions (Fig. 1a). Second, when *a* is different from zero (types 2 and 3), the efficiency changes with *x*, with a slope that decreases in magnitude, the value of which depends on *a* and *x* (Fig. 1b, c). If *a* is positive, the efficiency will decrease at increasing levels of the independent variable (Fig. 1b), whereas the opposite will occur when *a* is negative (Fig. 1c). The reason is simple: when the independent variable tends to zero the denominator of the ratio *a*/*x* gets smaller and, so, the efficiency tends either to positive infinity if the numerator is positive or to negative infinity if the numerator is negative. The third feature is that, as seen in Fig. 1b, c, the difference between the efficiency and the slope, when *a* is different from 0, depends on the range of values of the independent variable considered. Thus the difference between *UE* and *b* will decrease as *x* increases.

We focus on linear functions because relationships which are central topics in grassland ecology and agronomy, such as the cited *ANPP-PPT* and fertilizer rate-grain yield, are generally linear or nearly so for a considerable range of values (Sala et al. 1988). However, we believe our mathematical analysis is still relevant for other types of function mainly because, independently of whether a production function is linear or not, at any given level of *x* the slope will be different from the efficiency if the *y*-intercept is not zero.

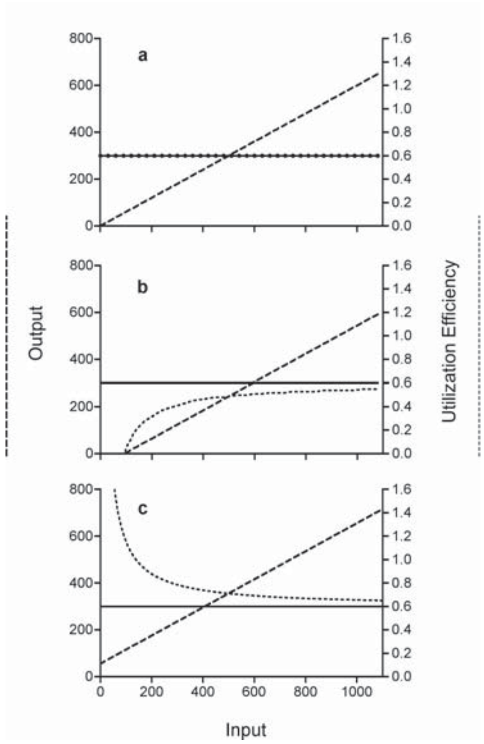

Fig. 1. Output and utilization efficiencies for three production function types, differing only in *y*-intercept: **a**. Intercept = 0 (type 1); **b**. Positive intercept (type 2); **c.** Negative intercept (type 3). In all cases the output is represented by the dashed line in each panel, the slope of the production function is the same (*b* = 0.6) and is represented by a solid, horizontal line, and the utilization efficiency is represented by the dotted line.

Examples

A first example of lack of distinction between a slope and an efficiency is provided by the relationship between *ANPP* and *PPT*. Some authors have interpreted the slope of this relationship as a measure of the amount of precipitation required to produce a unit of biomass (rain use efficiency, *RUE*) (Paruelo et al. 1999; Lauenroth et al. 2000; Huxman et al. 2004), whereas other authors (e.g. Varnamkhasti et al. 1995; Nicholson et al. 1998; Prince et al. 1998) have calculated *RUE* as the ratio between *ANPP* and *PPT*.

This confusion may be explained by the difference between water use by plants and precipitation. Noy-Meir (1973) suggested that the slope of the relationship between *ANPP* and precipitation could be interpreted as the Water Use Efficiency (*WUE*) of the community, as long as the ineffective precipitation (runoff and soil evaporation) was subtracted from precipitation (*PPT*). In this case, as the intercept of the relationship must be 0, the slope becomes a measure of *WUE* (i.e. the ratio of net photosynthesis to transpiration (de Wit 1958; Noy-Meir 1973). Le Houérou (1984) subsequently defined *RUE* as: "the quotient of annual primary production by annual rainfall i.e. the number of kg of aerial dry matter phytomass produced over 1 ha in 1 year per mm of total rain fallen". Le Houréou's *RUE* includes the unmeasured components of runoff, evaporation and drainage, which are not used by plants. In this case, as the intercept is different from 0, the slope is not an estimate of *RUE*.

A second example of the indistinct use of slopes and efficiencies is found in many plant physiology or ecology textbooks when discussing the light-response curve of photosynthesis (Lambers et al. 1998; Aber & Melillo 2001; Chapin et al. 2002). The light-response curve illustrates the response of net photosynthesis (measured as the rate of CO_2 assimilation, *A*, in µmol-CO_2.m^{-2}.s^{-1}) to irradiance *I* in µmol.m^{-2}.s^{-1} (Fig. 2). The initial slope of this curve – where *A* increases almost linearly with irradiance – has been used by some authors as a descriptor of the efficiency with which light is converted into fixed carbon(Lambers et al. 1998; Aber & Melillo 2001; Chapin et al. 2002). However, this is not true as the light response curve has a negative intercept. Thus, net photosynthetic light use efficiency (*LUE*) rather than remaining constant, first increases and then decreases asymptotically (Fig. 2). The same rationale was applied to functions relating net ecosystem exchange (*NEE*) with irradiance (Chapin et al. 2002, p. 118). In both cases, what remains constant at low to medium irradiances is the response of photosynthesis or NEE to increases in light availability (the slope), not the utilization efficiency.

A third example concerns the global agricultural production in relation to the amount of fertilizer globally used (Tilman et al. 2002). This was explained as a decreasing 40-year trend in global efficiency (cereal produced/nitrogen added), as a result of diminishing returns (a decreasing slope of production as a function of fertilization). Hafner (2003) showed, with a reasoning similar to ours, that a decline in efficiency was not necessarily due to diminishing returns: the slope of production as a function of nitrogen addition was not synonymous with the efficiency of utilization of nitrogen fertilizer.

How important is it to distinguish between slope and efficiency in practice? As shown in Fig. 1, it will depend on the range of values considered for the *x* (resource) variable. We will illustrate this point with our first example, the relationship between *ANPP* and *PPT* reported by Lauenroth & Sala (1992), and summarized by the function *ANPP* ($g.m^{-2}.a^{-1}$) = 55.8 + 0.13 *PPT* ($mm.a^{-1}$) (Fig. 3). We found that mean rain use efficiency for this 49-year data set was 0.32 $g.m^{-2}.mm^{-1}$, almost three times larger than the slope (Fig. 3). Maximum efficiencies, up to five times larger than the slope, are observed at low precipitation values. However, efficiency gradually converges towards the slope as precipitation increases. Thus, at low precipitation values, the implications of using the slope as a measure of efficiency are stronger. For example, Prince et al. (1998) found strikingly high *RUE* in dry years. In general, this will be the case as long as the relationship between *ANPP* and precipitation is linear with a positive y-intercept as it usually happens when annual series of *ANPP* and *PPT* are considered (i.e. temporal models) (Paruelo et al. 1999). Consequently, temporal models belong to the type 2 function and the decreasing pattern of *RUE* is an unavoidable outcome (Fig. 1b).

The *y*-intercept of the relationship between annual *ANPP* and annual *PPT* (i.e. temporal models) thus becomes a key descriptor of interannual variation in *RUE*. Most *ANPP-PPT* temporal relationships found in the literature have a linear best fit, which is described by two parameters, intercept and slope. Intercepts may be positive or negative depending on the system considered (e.g. perennial or annual grasslands) but they are seldom zero (Paruelo et al. 1999). We highlight the relevance of intercepts as indicators of interannual variation of *RUE*, not as indicators of the *ANPP* that a system will have in a year with zero rainfall, which only occurs in extremely arid environments. Intercepts different from 0 can be explained by statistical or ecological reasons. For example, a lag in recovery of populations and thus of plant production after drought years (Lauenroth & Sala 1992; Paruelo et al. 1999), or factors other than water (e.g. light or nutrients) limiting production in years with high rainfall (Paruelo et al. 1999; Verón et al. 2002) will statistically reduce (i.e. flatten) the slope of the regression line and push the intercept to positive values. Thus, a positive intercept may simply result from fitting a linear regression to the relationship between *ANPP* and *PPT* for a system that has a low response to rainfall and may never experience near-zero rainfall. Among the ecological reasons, a developing body of evidence suggests that, in grasslands, there are important resource (e.g. water, N) or information (e.g.

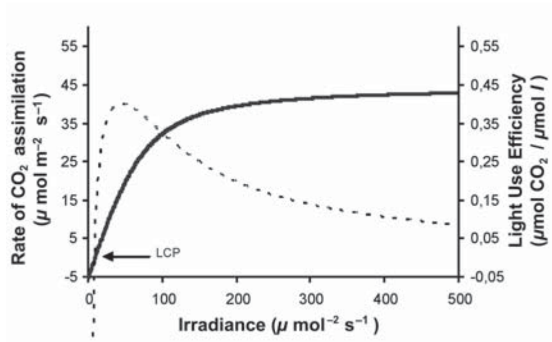

Fig. 2. Response of photosynthesis (solid line) and Light Use Efficiency (dotted line) to irradiance (I). The light response curve was calculated from the nonrectangular hyperbola presented in Lambers et al. 1998. The *y*-intercept is the rate of dark respiration. Arrow indicates the light-compensation point (the intercept with the *x*-axis). The initial slope of the light response curve is 0.53 $\mu mol\text{-}CO_2.\mu mol\text{-}I^{-1}$.

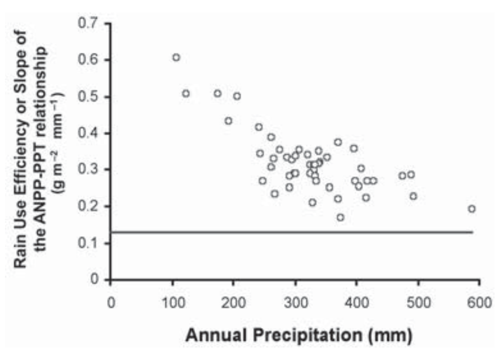

Fig. 3. *RUE* estimated as *ANPP*.PPT^{-1} (❍) vs. *RUE* derived from the slope of the *ANPP-PPT* relationship (line). Annual ANPP and PPT from data in Lauenroth & Sala (1992).

seeds, tillers) transference mechanisms from one year to the other (Paruelo et al. 1999; Oesterheld et al. 2001). These mechanisms would explain positive *ANPP* in years with zero rainfall. In other words, the artifact is to divide time into years assuming complete independence between them. Similarly, negative intercepts may occur in annual systems where a minimum rainfall threshold is required for key processes such as seed germination.

Slopes describe marginal responses

Although slopes of production functions are rarely indicators of efficiencies, they are very useful descriptors of ecological phenomena. They represent the response of production per unit increase in resource input (i.e. a marginal response). In the case of relationships between annual *ANPP* and precipitation, the slope provides key information about vegetation sensitivity to changes in precipitation (e.g. the response of the vegetation to changes in water availability). As this information is so useful, we propose that in the future it be referred to as the Precipitation Marginal Response (PMR).

Conclusions

A clear understanding of what constitutes an efficiency is crucial to prevent misinterpretations. By means of simple mathematical equations and conceptual definitions, we have made explicit the theoretical differences between a slope and an efficiency. Practical implications of using slopes as indicators of resource-use efficiency are less important as the resource amount increases. In addition, slopes may be used as indicators of the sensitivity of production to changes in input, which is by itself an interesting property of biological systems. Finally, intercepts determine whether efficiency will decrease, increase, or remain constant as resources increase.

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