A Nutrient Index Quantifying Productivity of Agaves and Cacti

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A NUTRIENT INDEX QUANTIFYING PRODUCTIVITY OF AGAVES AND CACTI

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SUMMARY

(1) Plant productivity is influenced by water status, temperature, and photosynthetically active radiation, the effects of which have been successfully incorporated into an environmental productivity index (EPI), and by element levels in the soil. Based on previously determined growth responses of four species of agaves and eleven species of cacti, individual multiplicative indices are proposed for soil levels of five elements (N, P, K, B, and Na) to give a first approximation of the influence of these elements on the productivity of agaves and cacti; the product of the N, P, K, B, and Na indices is termed the nutrient index (NI), which has a maximum value of unity when no element limits productivity.

(2) The rate of leaf unfolding from the central spike of folded leaves, which is highly correlated with EPI and productivity for agaves, was determined for *Agave deserti* at two sites in Arizona with similar values of EPI; leaf unfolding was 73% higher at the site whose NI was 74% higher, primarily because of a 47% higher nitrogen index.

(3) For *Agave tequilana* at ten sites in Jalisco, soil levels of N, P, K, B, and Na each varied about 3-fold, leading to a 2·4-fold variation in the NI; variations in the NI were positively correlated ($r^2 = 0{\cdot}96$, $P < 0{\cdot}001$) with the more than 2-fold variation in the annual rate of leaf unfolding.

(4) Although the proposed NI is only an estimate of edaphic influences on productivity of agaves and cacti, it satisfactorily explains the variation in productivity with soil element level at various sites for the two species tested.

INTRODUCTION

Plant productivity, often measured as dry weight increase, is influenced by physical factors of the environment (Beadle *et al.* 1985). Recently, a procedure has been developed to predict productivity based on the effect of soil water status, air temperature, and ambient photosynthetically active radiation (PAR) on net CO_2 uptake over 24-h periods (Nobel 1984, 1988). This approach introduces an Environmental Productivity Index (EPI) representing the fraction of maximal net CO_2 uptake expected, based on ambient environmental conditions. So far, EPI has apparently been applied only to agaves and cacti (Nobel 1988), although the underlying assumptions are quite general. Namely, it is assumed as a first approximation that water, temperature, and PAR can all simultaneously and independently limit net CO_2 uptake. The effects of these environmental factors thus become multiplicative, so when a particular parameter reduces net CO_2 uptake to zero, even optimal values of the other parameters cannot overcome such a limitation. Interactions occur between factors with respect to CO_2 uptake, but they have proved to be only secondary influences on productivity for agaves and cacti (Nobel 1988).

The EPI approach has been applied to situations where water status, air temperature, and PAR are the primary determinants of plant productivity. For instance, the effects of a nearly 4-fold increase in rainfall and a 10°C decrease in temperature with elevation on the productivity of *Agave deserti* are satisfactorily accounted for by EPI (Nobel & Hartsock 1986a). That study had been initiated to evaluate the influence on productivity of soil element levels over a 1 km elevational change, but variation in soil element levels proved to be minimal. Nevertheless, edaphic factors presumably influence productivity in other situations and thus could be incorporated as an additional multiplicative factor in EPI (Nobel 1988).

The present study first develops a Nutrient Index (NI) based on previously determined element effects on the productivity of agaves and cacti. It is recognized that species respond differently to nutrients, that availability of elements depends on the particle size distribution in the soil and the soil type, and that the physiological responses of a plant depend on the ratios of various elements in the soil. In the light of these complications, the present philosophy is to refine the predictions of EPI to accommodate different soil conditions, not to incorporate all the subtle interactions between elements and exchange surfaces within soils. In this way, a rough estimate of the primary edaphic effects on growth and productivity of agaves and cacti can hopefully be obtained for soils whose levels of various elements are known. Agaves were chosen for field studies of the nutrient index, because the unfolding of their leaves from the central spike of folded leaves has proved to be a simple, non-destructive morphological measure of productivity that is highly correlated with EPI, including for the two agave species selected here (Nobel 1984; Nobel & Valenzuela 1987; Nobel 1988).

DEVELOPMENT OF ELEMENT INDICES

Nitrogen

Various studies have shown that net CO_2 uptake, shoot volume, and dry weight of agaves and cacti increase approximately logarithmically with the nitrogen level in soil or in hydroponic solution (Nobel 1983; Nobel & Berry 1985; Nobel & Hartsock 1986b). Therefore, by analogy with the three component indices in EPI, a nitrogen index has been proposed that quantifies the influence of N on net CO_2 uptake over 24-h periods (Nobel 1988):

$$\text{nitrogen index} = \frac{\text{net CO}_2\text{ uptake under new N condition}}{\text{net CO}_2\text{ uptake under original N condition}} = \frac{1 + n_{\mathrm{N}} \ln \mathrm{N}_{\mathrm{new}}}{1 + 1n_{\mathrm{N}} \ln \mathrm{N}_{\mathrm{orig}}} \qquad (1)$$

where n_{N} is the nitrogen coefficient and $\mathrm{N}_{\mathrm{new}}$ and $\mathrm{N}_{\mathrm{orig}}$ represent the soil nitrogen levels at the new and the original site.

The units proposed for N, which affect the value for n_{N}, are the relative level of nitrogen in solution for plants grown hydroponically and the % total N by dry weight in the root zone for plants in soil (full-strength Hoagland solution contains 236, 212, and 32 mg l^{-1} of K, N and P, respectively). For seedlings of *Agave deserti, Carnegiea gigantea, Ferocactus acanthodes*, and *Trichocereus chilensis* grown hydroponically, linear regressions of increases in shoot volume or in plant dry weight against the logarithm of the relative N level (the N level in full-strength Hoagland solution was taken as 1·00) show that n_{N} averages 0·20, as determined from the slope of the equations (eqn (1); Nobel 1983; Nobel & Hartsock 1986b). Slopes of similar regressions of plant dry weight against the logarithm of soil N in the field show that n_{N} averages 0·24 for *A. deserti* (Nobel & Hartsock 1986b) and 0·25 for *Opuntia phaeacantha* (Nobel *et al.* 1987). In conjunction with EPI, the nitrogen index has been used successfully to explain the different growth rates of *A. deserti* in the open compared with under the canopy of a nurse plant, where soil N levels tend to be higher, a situation in which edaphic factors modify the EPI predictions (Franco & Nobel 1988).

A surface application of 500 kg N ha^{-1}, which increases soil N in the root zone to 0·3%, leads to less growth of *A. deserti* in the first year but more in the second year than does 100 kg N ha^{-1} (Nobel, Quero & Linares 1988). Shoot dry weight of *Opuntia engelmannii* increases with soil N up to the highest observed level of 0·3% (Nobel *et al.* 1987) and application of 100 kg N ha^{-1} to *A. lechuguilla* in soils with 0·25% N can enhance growth by 37% (Nobel, Quero & Linares 1988). Soil N averages 0·52% for *Agave fourcroydes* at a site where fertilizer in the form of leaf residue is applied, resulting in much nitrogen in organic matter that is hence not readily available to the plants (Nobel & Berry 1985). Based on these observations, it is assumed as a first approximation that the nitrogen index increases linearly with soil N up to 0·3%.

Using the same nitrogen index as before (eqn (1)), with n_N determined from soil data (0·245) and setting the N index to unity at 0·3% N (which requires 0·705 in the denominator, because $1+0{\cdot}245 \ln (0{\cdot}3)=0{\cdot}705$), leads to the following relation:

$$\text{nitrogen index}=\frac{1+0{\cdot}245 \ln N}{0{\cdot}705}=1{\cdot}418+0{\cdot}348 \ln N \qquad (2)$$

for $N \leqslant 0{\cdot}3\%$ (note that $0{\cdot}348 \ln 0{\cdot}3=-0{\cdot}419$, so the nitrogen index is essentially unity for 0·3% N in the soil). Nitrogen is assumed not to limit growth of agaves and cacti above 0·3% N in the soil, in which case the nitrogen index is unity.

Phosphorus

For seedlings of *A. deserti* grown hydroponically, raising phosphate from 0·01 to 1 times the level in full-strength Hoagland solution increases growth logarithmically, although the increase is only 32% as much as is caused by a similar increase in nitrate (Nobel & Hartsock 1986b). On the other hand, very little effect of P on growth over this same multiple of the P level in Hoagland solution occurs for seedlings of *Carnegiea gigantea*, *Ferocactus acanthodes*, and *Trichocereus chilensis* (Nobel 1983), indicating that species respond differently to levels of P. At field sites where the soil P level is 23 $\mu g\ g^{-1}$, application of 100 kg P ha^{-1} increases growth measured by leaf unfolding of *A. lechuguilla* by 24% (Nobel, Quero & Linares 1988) and 80 kg P ha^{-1} increases the dry weight gain of *Opuntia engelmannii* by 48% (Nobel *et al.* 1987). Because 100 kg of applied P ha^{-1} increases growth by only 5% for *A. deserti* where soil P is 54 $\mu g\ g^{-1}$ (Nobel, Quero & Linares 1988), approximately 60 $\mu g\ g^{-1}$ P may lead to maximal growth. Although it is recognized that the availability of P to plants is more crucial than total soil P, the latter will be used here as a first approximation.

Incorporating the logarithmic response of growth to P level observed in hydroponics (Nobel & Hartsock 1986b) and the proposed level of 60 $\mu g\ g^{-1}$ in soil for maximal growth leads to the following equation: phosphorus index $=1+n_P \ln (P/60)$. Assuming that application of 80–100 kg P ha^{-1} removes phosphorus limitations on growth, the data for *A. lechuguilla* and *O. engelmannii* indicate that growth can be increased an average of 36% from the level for soils containing 23 $\mu g\ g^{-1}$ P. On the other hand, the average growth enhancement for seedlings of *A. deserti* and the three cacti in hydroponics as the P level is increased 3-fold is only 10%. Although more data would help provide a better estimate of n_P, the available P responses of agaves and cacti suggest that growth, and hence the phosphorus index, may increase an average of 23% as the soil P level is increased about three-fold from 23 to 60 $\mu g\ g^{-1}$. Based on this average and the proposed logarithmic relationship, (1·00/1·23) equals $1+n_P$ ln (23/60), which leads to:

$$\text{phosphorus index} = 1 + 0{\cdot}195\ \ln\ (P/60) \qquad (3)$$

for P up to 60 $\mu g\ g^{-1}$ in the soil and unity above that level (note that 0·195 ln (60/60) = 0·000, so the phosphorus index is unity for 60 $\mu g\ g^{-1}$ P in the soil).

Potassium

Potassium has about 70% of the effect on seedling growth of *A. deserti* in hydroponics as does P when these nutrients are increased from 0·01 to 1 times their level in full-strength Hoagland solution and the response is again logarithmic with element level (Nobel & Hartsock 1986b). Over the same range, growth is enhanced an average of only 10% for seedlings of *Carnegiea gigantea*, *Ferocactus acanthodes*, and *Trichocereus chilensis* (Nobel 1988). Application of 500 kg K ha^{-1} increases leaf unfolding by 25% for *Agave lechuguilla* in soils with 32 $\mu g\ g^{-1}$ K but has no detectable effect on *A. deserti* in soils with 128 $\mu g\ g^{-1}$ K (Nobel, Quero & Linares 1988). Soil levels of 257 $\mu g\ g^{-1}$ K can occur for *Opuntia chlorotica* without leading to substantial enhancements in rates of nocturnal acid accumulation compared with 95 $\mu g\ g^{-1}$ K (Nobel 1983; P. S. Nobel, unpublished). Applying 100 kg K ha^{-1} leads to no significant increase in productivity for *Opuntia cochenillifera* in north-eastern Brazil (soil K level not specified; Metral 1965), although the most common nutrient deficiency disease for *Agave sisalana* in Kenya and Tanzania is attributable to a lack of K, which is alleviated by annual applications of 40 kg K ha^{-1} (Lock 1962, 1985).

Even though more data would be desirable before defining a potassium index, the available data suggest that growth of agaves and cacti may be logarithmic with soil K level up to about 250 $\mu g\ g^{-1}$. If 500 kg K ha^{-1} raises the soil K from 32 $\mu g\ g^{-1}$ to that leading to maximal leaf unfolding for *A. lechuguilla*, then solving the equation (1·00/1·25) equals $1+n_K$ ln (32/250) indicates that the coefficient n_K multiplying ln (K/250) is 0·097. On the other hand, the data for *A. deserti* in hydroponics indicate that the coefficient should be 70% of that for P (eqn (3)), or 0·137. Taking the average of these observations, the following preliminary index is proposed:

$$\text{potassium index} = 1 + 0{\cdot}117\ \ln\ (K/250) \qquad (4)$$

up to 250 $\mu g\ g^{-1}$ K and unity above that level.

Boron

For *Opuntia engelmannii* and *O. rastrera* at eleven sites in Coahuila, Mexico, growth measured as dry weight gain increases with soil B up to about 1·0 $\mu g\ g^{-1}$ B in the root zone (Nobel *et al.* 1987). Growth measured as leaf unfolding is not enhanced by applications of 10 or 100 kg B ha^{-1} for *A. deserti* in soils containing 1·36 $\mu g\ g^{-1}$ B (Nobel *et al.* 1987). Thus, 1·00 $\mu g\ g^{-1}$ B is assumed to yield a boron index of 1·00. For *A. lechuguilla* in soils containing 0·48 $\mu g\ g^{-1}$ B, leaf unfolding is enhanced 11% by application of 10 kg B ha^{-1} and 17% by 100 kg B ha^{-1} (Nobel, Quero & Linares 1988), the latter application level presumably removing any limitation of boron deficiency on growth. Assuming that growth is zero in the absence of soil B, a function consistent with these observations is:

$$\text{boron index} = B^{0{\cdot}213} \qquad (5)$$

for B up to 1·00 $\mu g\ g^{-1}$ and unity above that level (note that $0{\cdot}48^{0{\cdot}213} = 0{\cdot}855 = 1/1{\cdot}17$ and that $1{\cdot}00^{0{\cdot}213}$ is unity).

Sodium

Compared with no purposely added Na, 100 mM NaCl in a hydroponic solution decreases growth about 50% for *Carnegiea gigantea* and *Ferocactus acanthodes*, 20% for *Trichocereus chilensis* (Nobel 1983), and 50% for *Agave deserti* (Nobel & Berry 1985). In sand culture, growth is inhibited 10% by watering with 100 mM NaCl for *F. acanthodes* and 54% for *Opuntia ficus-indica* (Berry & Nobel 1985). Application of 100 mM NaCl reduces growth by 55% for *Opuntia humifusa* from the marine strand, but by 72% for an ecotype of the same species from an inland site (Silverman, Young & Nobel 1988). For a purportedly salt-tolerant cactus, *Cereus validus* (Yensen *et al.* 1981), 100 mM NaCl reduces nocturnal acid accumulation by about 40% (Nobel *et al.* 1984). The average of these various observations is a growth decrease of 44% at 100 mM NaCl. In all cases, the decrease in growth is approximately linear with NaCl concentration up to 100 mM.

Agaves and cacti under wet conditions take up water from the soil down to a soil water potential of about $-0{\cdot}5$ MPa, which for a representative sandy soil corresponds to about 10% water by volume (Nobel 1988). In this case and for a soil particle density of 1500 kg m^{-3} (Nobel 1988), 100 mM NaCl for the aqueous phase corresponds to 153 $\mu g\ g^{-1}$ Na by dry weight of the soil. Hence, the Na effect will be approximated as follows:

$$\text{sodium index} = 1 - 0{\cdot}00288\ \text{Na} \qquad (6)$$

which applies up to about 150 $\mu g\ g^{-1}$ Na (note that (0·00288) (153) = 0·44). At higher soil Na levels, the inhibition of growth is greater, but most agaves and cacti occur in soils with less than 100 $\mu g\ g^{-1}$ Na (Nobel 1983; Nobel & Berry 1985; Nobel *et al.* 1987; Nobel, Quero & Linares 1988; Silverman, Young & Nobel 1988).

Nutrient index

Applications of Ca have little effect on the growth of *A. deserti* or *A. lechuguilla* in the field (Nobel, Quero & Linares 1988; P. S. Nobel and E. Quero, unpublished) or on *F. acanthodes* and *O. ficus-indica* in sand culture (Berry & Nobel 1985), so this macronutrient is not included in the NI. Although omission of the micronutrients Cu, Fe, Mn, Mo, and Zn inhibits leaf unfolding for *Agave sisalana* grown hydroponically (Pinkerton 1971), the only micronutrient whose level in the soil has been directly shown to influence growth of agaves and cacti is B (Nobel 1988), so only this micronutrient is included in the present form of the NI. Combining the above component indices therefore leads to the following preliminary definition of a nutrient index for agaves and cacti in soil:

$$\begin{aligned} \text{NI} &= \text{nitrogen index} \times \text{phosphorus index} \times \text{potassium index} \\ &\quad \times \text{boron index} \times \text{sodium index} \\ &= (1{\cdot}418 + 0{\cdot}348\ \ln \text{N}) \times [1 + 0{\cdot}195\ \ln(\text{P}/60)] \times \qquad (7) \\ &\quad [1 + 0{\cdot}117\ \ln(\text{K}/250) \times \text{B}^{0{\cdot}213} \times (1 - 0{\cdot}00288\ \text{Na}) \end{aligned}$$

where N is in % by dry weight, P, K, B, and Na are in $\mu g\ g^{-1}$ by dry weight, and the component indices become unity when $N \geqslant 0{\cdot}3\%$, $P \geqslant 60\ \mu g\ g^{-1}$, $K \geqslant 250\ \mu g\ g^{-1}$, and $B \geqslant 1{\cdot}0\ \mu g\ g^{-1}$ (the sodium index is appropriate up to about 150 $\mu g\ g^{-1}$ Na).

MATERIALS AND METHODS

Agave deserti

Small plants of *Agave deserti* Engelm. (Agavaceae) with an average dry weight of 32 g, raised from seed in a glasshouse in Los Angeles, were transplanted to field sites in Arizona in March 1986 (Nobel & McDaniel 1988). One site was the University of Arizona Marana Agricultural Center (32°27′N, 111°14′W, 580 m elevation) about 30 km north-west of Tucson and the other was the University of Arizona Oracle Agricultural Center (32°36′N, 110°50′W, 1120 m). A plant spacing of 2 m was used to avoid interplant shading. In addition to natural rainfall, which averaged 284 mm annually at the Marana Agricultural Center and about 440 mm at the Oracle Agricultural Center (National Oceanic and Atmospheric Administration, 1986–88), the plants at the Marana Agricultural Center were irrigated twice per year, leading to similar water availability at the two sites. The mean daily minimum temperatures averaged over the month at the Marana Agricultural Center increased from 4°C in December and January to 23°C in July and August (Nobel & McDaniel 1988). Based on observed variations of air temperature with elevation near the two sites (National Oceanic and Atmospheric Administration, 1986–88), mean daily minimum temperatures at the Oracle Agricultural Center average 4°C lower than at the Marana Agricultural Center. Dry weights were determined by drying excavated plants in a forced-draft oven at 80°C until no further weight changes occurred (about four days).

Agave tequilana

Agave tequilana Weber was studied on various plantations in the tequila-producing region within 5 km of Amatitán (20°50′N, 103°43′W, 1250 m elevation), which is 15 km south-east of Tequila, Jalisco (Mexico). Twenty, adjacent, 2-year-old plants were chosen at each of ten sites in November 1986; the average ground area occupied per plant was 3 m^2. The tips of the most recently unfolded leaves were clipped then so that leaves unfolding during the 1-year study period could be determined. The various sites were at the same elevation (±40 m) in a region relatively free of large topographical features, presumably leading to similar temperature and rainfall regimes.

TABLE 1. Growth of *Agave deserti* in Arizona, soil element levels, and calculated element indices

	Marana Agricultural Center	Oracle Agricultural Center
Growth parameter	Value per plant	
Leaves unfolding	20·2±0·9 (20)	11·7±0·4 (14)
Dry weight increase (g)	343±41 (8)	188±18 (6)
Element	Soil level	
N (%)	0·101±0·014 (5)	0·057±0·003 (5)
P (μg g^{-1})	90·8±1·7 (6)	48·9±2·9 (6)
K (μg g^{-1})	526±15 (6)	114±7 (6)
B (μg g^{-1})	0·692±0·037 (6)	0·403±0·042 (6)
Na (μg g^{-1})	55·8±6·0 (6)	29·1±3·5 (6)
Index	Calculated value	
Nitrogen index	0·620	0·421
Phosphorus index	1·000	0·960
Potassium index	1·000	0·908
Boron index	0·925	0·824
Sodium index	0·839	0·916
Nutrient index	0·481	0·277

Growth is for the 2-year-period from 3 March 1986 to 8 March 1988. Data are presented as mean±S.E., with the number of measurements in parentheses.

Elemental analysis

Soil samples were taken from the centre of the root zone at a depth of about 0·10 m. Elemental analyses other than nitrogen were performed using inductive-coupled plasma (Alexander & McAnulty 1981) on 1 M ammonium acetate extracts of the non-gravel soil fraction (particle size under 2 mm). Total soil N for the non-gravel fraction was determined using 1-g samples following Kjeldahl digestion and titration of the released ammonia after conversion to ammonium (Bremner 1965). All element levels are expressed per unit dry weight of soil.

RESULTS

Agave deserti

Growth of *Agave deserti* over a 2-year period in Arizona was much greater at the Marana Agricultural Center than at the Oracle Agricultural Center (Table 1). The rate of leaf unfolding was 73% higher and the dry weight increase was 83% greater at Marana, which had an elevation about half that of Oracle.

Water availability and photosynthetically active radiation are similar at the two sites, so the temperature index was calculated to see whether differences in it could lead to large

TABLE 2. Soil element levels and calculated indices for *Agave tequilana* at ten sites near Tequila, Jalisco

Soil element level				
N (%)	P (μg g^{-1})	K (μg g^{-1})	B (μg g^{-1})	Na (μg g^{-1})
0·097	20·6	274	0·397	3·23
0·108	46·4	246	0·350	12·37
0·121	31·9	437	0·608	13·72
0·151	34·9	306	0·547	11·05
0·111	29·9	235	0·477	9·53
0·168	43·8	243	0·652	1·85
0·226	49·9	270	0·687	6·42
0·152	34·4	229	0·675	2·35
0·285	56·1	331	0·805	2·85
0·091	44·6	140	0·585	4·78

Calculated component indices					
N	P	K	B	Na	Nutrient index
0·606	0·792	1·000	0·821	0·991	0·390
0·643	0·950	0·998	0·800	0·964	0·470
0·683	0·877	1·000	0·899	0·960	0·517
0·760	0·894	1·000	0·879	0·968	0·578
0·653	0·864	0·993	0·854	0·973	0·466
0·797	0·939	0·997	0·913	0·995	0·678
0·900	0·964	1·000	0·923	0·982	0·786
0·762	0·892	0·990	0·920	0·993	0·615
0·981	0·987	1·000	0·955	0·992	0·917
0·584	0·942	0·932	0·892	0·986	0·451

Element analysis was done in quadruplicate, the standard deviation for each site averaging 5% of the means for N, P, and K and 9% for B and Na.

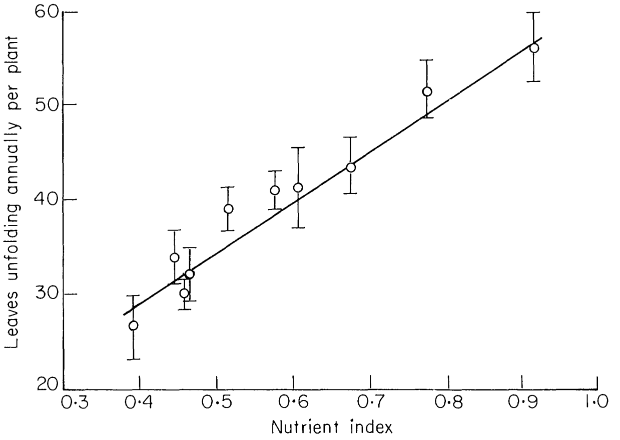

FIG. 1. Relation between the nutrient index and the number of leaves unfolding annually per plant for *Agave tequilana* at ten sites near Tequila, Jalisco. Leaf unfolding is the mean for twenty, initially 2-year-old plants at each site over the 1-year period 6 November 1986 to 6 November 1987. Vertical bars indicate standard deviations. See Table 2 for soil element levels and calculation of the nutrient index. The indicated regression line is: leaf unfolding = 54·9 × nutrient index + 7·19 ($r^2 = 0·96$, $P < 0·001$).

enough differences in EPI to account for the observed growth differences. For *A. deserti*, minimum night-time air temperatures closely (±1°C) approximate the average night-time leaf temperatures of this species, which in turn determine its net CO_2 uptake over 24-h periods (Nobel 1984). The average monthly temperature index at Marana was 0·90 and that at Oracle was 0·89. Hence, attention was turned to the soil to explain the large differences in growth observed.

Soil N levels were nearly 2-fold higher at the Marana Agricultural Center, leading to a 47% higher nitrogen index (eqn (2)) than at the Oracle Agricultural Center (Table 1). The product of the other four element indices was 0·776 at Marana, the main factor reducing this product from unity being the sodium index. At Oracle, the P, K, B, and Na indices were all less than unity (Table 1) and their product was 0·658. Primarily because of the effect of nitrogen, the NI for *A. deserti* was 74% higher at Marana than at Oracle (Table 1).

Agave tequilana

The major test of the relation between productivity and the Nutrient Index (eqn (7)) was with *Agave tequilana*, from which no data had been used to generate the index. A series of ten sites in the same general region but with widely differing soil element levels was selected. For soil from these sites, the N, P, and K levels varied 3-fold, the B level varied over 2-fold, and the Na level varied nearly 6-fold (Table 2). The soil K level tended to be high and the Na level low, so these two elements lowered the NI by at most only 7% and 4%, respectively. Suboptimal soil N levels produced the greatest lowering of the NI, leading to an average nitrogen index of 0·737 (Table 2). The phosphorus index averaged 0·910 and the boron index averaged 0·886 for the ten sites.

Because of the variation in soil element levels, especially of N, the NI varied considerably, from 0·390 to 0·917 (Table 2). Leaf unfolding for *A. tequilana* over the course of the year also varied considerably among the sites, from 26·5 leaves per plant to

56·2 leaves per plant. This rate of leaf unfolding was highly correlated with the NI (Fig. 1; $r^2 = 0{\cdot}96$). The correlation was nearly as high between the rate of leaf unfolding and the nitrogen index (leaf unfolding = 69·2 × nitrogen index − 11·58; $r^2 = 0{\cdot}91$, $P < 0{\cdot}001$), again showing the importance of soil nitrogen in accounting for differences in productivity among sites.

DISCUSSION

The proposed Nutrient Index accounted for over 95% of the variation in growth of *Agave deserti* between two sites and the variation in leaf unfolding rate for *A. tequilana* among ten sites. In particular, for two sites in Arizona where the environmental productivity index was approximately the same, growth measured by dry weight increases and the rate of leaf unfolding was nearly 2-fold higher for *A. deserti* where the NI was nearly 2-fold higher, primarily reflecting the higher soil N level at the site with the greater growth. The sites considered for *A. tequilana* in Jalisco had widely differing levels of the five elements considered for the NI (N, P, K, B, and Na; eqn (7)). The positive correlation of leaf unfolding with the NI for this species provided the more convincing test of this preliminary, approximate method for quantitatively predicting the influence of edaphic factors on the growth of agaves and cacti.

Agave tequilana is cultivated in rather sandy soils that are representative of those in which agaves and cacti occur naturally (Nobel 1988). In particular, the non-gravel fraction of the soil from its root zone averages 63% sand by mass (particles 0·05–2 mm in diameter), 27% silt (0·002–0·05 mm), and 10% clay (< 0·002 mm; Nobel & Valenzuela 1987), suggesting an ion exchange capacity similar to that for soils where other agaves and cacti grow (Nobel 1988). Although the soil texture for *A. tequilana* is typical for desert succulents, this species has an uncharacteristically high rate of leaf unfolding under adverse conditions. Specifically, even with a low monthly EPI (0·02–0·05), monthly leaf unfolding for 1-year-old and 3-year-old plants is about one leaf per plant (Nobel & Valenzuela 1987). The regression equation between the rate of leaf unfolding and the NI for *A. tequilana* (Fig. 1) has an intercept of about seven leaves unfolding annually per plant when the NI is zero. On the other hand, regression of leaf unfolding against the nitrogen index leads to an intercept of minus twelve leaves unfolding annually, which is inconsistent with field observations, underscoring the desirability of a NI based on five elements rather than on nitrogen alone.

The proposed NI is only a first approximation for estimating the influence of soil element levels on the productivity of agaves and cacti. Each of its component indices can be refined by further research, such as by using field soil whose element composition is experimentally varied; such data are crucially needed for all the component indices, especially the sodium index. Refinements can range from simply changing the coefficients in the proposed component indices, to introducing entirely new forms of the equations. For instance, no growth response may occur below a 'threshold' nutrient level in the soil, responses may be linear with higher levels, then reach saturation, and finally inhibition of growth may occur at even higher element levels in the soil (Epstein 1972). Growth of *A. deserti* can be reduced above 0·2% N present in the soil as nitrate (Nobel & Hartsock 1986b), which raises the further complication of the particular forms of each element (eqn (7) considers only total N). Nutrients can interact with each other, and other elements may need to be included in the NI in addition to the five whose effects on agaves and cacti have already been identified.

Agaves and cacti vary in their responses to soil element levels. For instance, *Pediocactus sileri* appears to be restricted to soils high in Ca (Benson 1982), *Echinocactus platyacanthus* also tends to occur in soils high in Ca (Trujillo Argueta 1982), whereas *Ferocactus histrix* apparently prefers soils low in Ca (del Castillo Sanchez 1982). Application of Ca in the form of limestone ($CaCO_3$) can increase the fibre yield of *Agave sisalana* in Tanzania, although the massive doses applied (for instance, 4600 kg Ca ha^{-1}; Lock 1962) may have influenced soil pH, a factor that is not included in the NI but which can influence ion uptake. In particular, soils in Tanzania, where *A. sisalana* is cultivated, tend to be acidic with a pH near 5; upon addition of limestone, the pH is raised, which can influence the uptake of nutrients other than Ca. The data used to derive the NI were obtained by many different methods. So far, the influence of N, P, K, and B on CO_2 exchange over 24-h periods, which is the basis for the variation in the component indices of EPI, has been related to dry weight increases in the field only for *Agave lechuguilla* (Nobel, Quero & Linares 1988). Thus, many improvements as well as restrictions for the application of the NI can reasonably be expected.

The NI can be used to evaluate the productivity in soils where agaves and cacti are native and to predict productivity where their cultivation is contemplated. For instance, at a site in the north-western Sonoran Desert (at 33°38′N, 116°24′W, 850 m) where the dominant vegetation is *Agave deserti* and various species of cacti, all the component indices are 0·9 or above, except for the nitrogen index, which is only about 0·5 (Nobel 1988), suggesting that nearly all the edaphic limitation on growth is by nitrogen. The NI can also be used in an agronomic context, permitting the consequences of application of various fertilizers to be evaluated in a quantitative manner. For instance, if a component index for N, P, K, or B were 0·5, then productivity could be doubled by suitable application of the deficient nutrient. In conjunction with EPI, productivity in new regions can be predicted for the many species of agaves and cacti that are already commercially exploited (Nobel 1988). In summary, the approximate guideline provided by the NI for predicting effects of soil on productivity of agaves and cacti can have financial ramifications for agronomically important species and also should help interpret growth in an ecological context.

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