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SPUR LIGHT EXPOSURE AS A PRIMARY EXTERNAL CAUSE FOR DERIVATION OF DRIS NORMS IN WALNUT TREES

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ABSTRACT: Spur leaf macroelement profile of walnut (*Juglans regia*, cvs. 'Hartley' and 'Serr') was characterized by a modified diagnostic and recommendation integrated system (DRIS), using canopy photosynthetic photon flux (PPF) density exposure as a primary external determinant (5) of leaf mineral content. Spur N, P, Ca and Mg content was linearly correlated with PPF and SLW when expressed on the basis of leaf area (A) while that of K was linearly correlated with SLW on % DW basis (W). Mineral ratios, relevant for the DRIS analysis, were calculated using all four possible combinations of Area and Weight expressions (A/A, A/W, W/A, W/W) and correlated with spur leaf SLW. The particular expressions chosen for the DRIS analysis were based on their highest correlation to spur SLW and included N/K and P/K, based on A/W expression of the respective nutrients, and the reciprocal (W/A) expression for all other ratios. The dimensionless mineral ratios based on Weight per Weight (W/W) or Area per Area (A/A), which eliminated the DW contribution, were not related to light exposure and SLW.

Derivation of DRIS norms were based on the mineral profile of highly exposed spurs (10.8 ± 3.1 and 8.8 ± 3.9 mol m⁻²d⁻¹ PPF in 'Hartley' and 'Serr', respectively), characterized previously to be highly productive. Calculated DRIS indices of gradually less exposed and less productive spurs revealed a strong exponential imbalance of K or K and N (increasingly positive) in 'Hartley' and 'Serr', respectively, vs Ca and Mg (increasingly negative). DRIS indices of P became slightly negative in 'Hartley' and positive in 'Serr', as spur light exposure decreased. The calculated Nutritional Imbalance Index (NII) value of walnut spurs exposed to decreasing light intensities increased exponentially. The

modification of the existing procedures of DRIS analysis that reflects the light exposure of the leaf and takes into account its DW component, is proposed.

INTRODUCTION

The Diagnosis and Recommendation Integrated System (DRIS) developed by Beaufils (4, 5) was considered to be either superior (6, 15, 16, 37, 41) or supplementary (2, 21) to the critical level or sufficiency range method of interpreting plant nutritional status. The method, as envisioned by Beaufil (5), recognizes the following sequence:

Primary cause \rightarrow f (Resulting effects, Secondary causes) \rightarrow ϕ (Final effects)

The function f refers to soil or plant (internal character) response, while ϕ is the yield.

An advantage of the DRIS method is the assignment of relative nutrient limitations and excesses (5, 35, 36, 37, 41). Leaf analysis, using the critical or sufficiency range method, may, or may not identify deficiencies or excesses.

An additional advantage of the DRIS method is the use of nutrient ratios, rather than concentrations in DW, thereby focusing on nutrient content and disregarding DW changes within the plant. Accordingly, for the DRIS method, the plant can be sampled at any time, rather than at standard physiological stages (21, 37, 38, 41). This is particularly advantageous for annuals which could be diagnosed at an early stage of growth and their nutritional imbalances corrected immediately for better yield. In perennials, identification of a nutritional imbalance, characteristic of a particular soil-plant-management complex, is usually the basis of a long term remedy since correction is not always possible within the same growing season.

DRIS norms for tree crops have been derived only for a few species (2, 4, 6, 11, 29, 32). In some cases a DRIS analysis of the data was unsatisfactory and its use is considered only supplementary to the critical level or sufficiency range methods (2, 32).

We hypothesize that some of the difficulties with the DRIS method, at least as far as fruit trees are concerned, may arise because norms are derived from internal secondary functions, such as plant mineral content, disregarding the

primary causes. A major primary cause, strongly affecting leaf mineral content is light. Leaf dry weight, N (12, 13, 14, 22, 23, 26, 30) and other macroelement content on a leaf area basis, with the exception of K (42), have been found to be highly correlated with exposure to photosynthetic active radiation. Potassium, in contrast, has been related to light exposure when expressed as % DW. Leaf mineral content expressed per area is considered by Weinbaum et al. to have more physiological significance than % DW, since it more accurately reflects changes in mineral content irrespective of changes in leaf DW (42). Thus, in accord with the original DRIS procedure, the expression of mineral content per unit leaf area should be an ideal expression for DRIS.

In previous research we have shown that the SLW of walnut spur leaves is correlated positively with spur productivity (22). Increased light exposure, as reflected in SLW and N content, was associated with reduced catkin abortion, increased pistillate flower formation and fruit set, and reduced spur alternation (22). In the present work we have characterized the macroelement profile of walnut spur leaves in relation to light exposure and productivity of individual spurs. The DRIS procedure which uses mineral ratios in an integrated form was chosen for this analysis. The calibration of DRIS norms was derived from a population of spurs of high SLW, from highly exposed positions, where flowering and fruit set have been shown to be maximal with a minimal amount of biennial bearing. The calibration, therefore, was directly related to productivity and not dependent on broad correlations of yield and leaf mineral content.

MATERIALS AND METHODS

Plant Material and Sampling Procedure. Five individual tree replicates of Persian walnut trees, (*Juglans regia* L) cvs. 'Serr' and 'Hartley', grafted on black walnut (*Juglans hindsii* L) rootstock, were selected in a commercial orchard near Winters CA. Trees were 16 years old and planted 8.5 x 8.5 m in a West - East orientation. Tree height reached 8-10 m with closed canopies at the top.

Effects of light exposure on spur SLW and productivity, including spur survival, return bloom, number of flowers per spur, fruit set and spur alternation have been published (22). Briefly, spur SLW and N content of 250 fruiting and non-fruiting paired spurs of 'Hartley' and 'Serr' walnuts, each, were measured close to harvest in 1988. Spurs were classified on the basis of their survival and

reproductive behavior in 1989. Spur classes were as follows: (a) dead spurs, (b) spurs that did not flower, (c) spurs flowered but did not fruit, (d) one of the tagged pair, either the vegetative or the reproductive spur, flowered and fruited and, (e) both, the vegetative and the reproductive pair flowered and fruited. The fifth class (e), where both the vegetative and the reproductive members of the pair flowered and set fruit, represented positions with better light exposure, as compared to positions where only one of the pair flowered and fruited (class d), and was therefore considered a distinct class.

The average SLW of the five distinct classes in 1988 were used as the basis for selection of SLW ranges (Table 1) for calculation of DRIS norms and indices in 1989. DRIS norms and indices were calculated from mineral analysis of 55 individual vegetative spurs of each cultivar, used in 1989 to establish the correlation between exposure to photosynthetically active radiation (PAR) and SLW (23). Measurements of PAR and sampling for SLW and mineral content of the individual spurs in 1989 were carried out after canopy closure (June 6-June 25 and June 26-July 8, in 'Serr' and 'Hartley', respectively).

Leaflet Sampling and Analysis. Several middle leaflets per spur were sampled, immediately after irradiance measurements were completed in 1989. Leaf areas were measured with a delta T area meter (Decagon, Seattle, WA) and then washed, dried at 55°C and ground to pass a 30-mesh screen. Leaf samples were digested for N, P, Ca, and Mg analysis. Potassium was extracted with 2% acetic acid. Nitrogen was determined by the conductimetric method of Carlson (9). Potassium, Ca, and Mg were measured by flame photometry and P by the molybdo-phosphate color reaction (8).

Calculations. Leaf mineral analyses were calculated and expressed on the basis of leaf area (A , $\mu\text{g} / \text{mm}^2$) and as % DW (W). All possible mineral ratios were calculated using both expressions (A/A , A/W , W/A , and W/W) and the best fit (linear or polynomial) was determined. Important expressions were selected on the basis of best fit to SLW. Predicted mineral ratios were recalculated from the curve fit for the average SLW of each spur class. DRIS norms for spur class e and indices of spur classes a-d were calculated from the following functions:

$$N \text{ index} = \frac{[f(N/P) + f(N/K) + f(N/Ca) + f(N/Mg)]}{4}$$

$$P \text{ index} = \frac{[- f(N/P) + f(P/K) + f(P/Ca) + f(P/Mg)]}{4}$$

$$K \text{ index} = \frac{[- f(N/K) - f(P/K) + f(K/Ca) + f(K/Mg)]}{4}$$

$$Ca \text{ index} = \frac{[- f(N/Ca) - f(P/Ca) - f(K/Ca) + f(Ca/Mg)]}{4}$$

$$Mg \text{ index} = \frac{[- f(N/Mg) - f(P/Mg) - f(K/Mg) - f(Ca/Mg)]}{4}$$

Where $f(N/P) = \left(\frac{N/P}{n/p} - 1 \right) \frac{1000}{CV}$, if $N/P > n/p$

Or $f(N/P) = \left(1 - \frac{n/p}{N/P} \right) \frac{1000}{CV}$, if $N/P \leq n/p$

where N/P is the ratio in spur classes a-d, and n/p and CV are used to calculate norms and coefficients of variation, respectively, in class e (the highest exposed position). The other functions were calculated similarly to provide an average index for N and the other nutrients. Standard deviations of DRIS indices were calculated similarly, from the SLW standard deviations of each spur class. A nutritional imbalance index (NII) was calculated, according to Meyer (28), as the sum of all indices irrespective of mathematical sign.

RESULTS

SLW of spurs used to calibrate productivity in 1988 ranged from 4.09 to 7.36 mg/cm² and 4.01 to 5.66 mg/cm² in 'Hartley' and 'Serr', respectively (Table 1). Averages of spur classes b, c and d, used in DRIS calculation in 1989, were similar to the corresponding spur class averages in the previous year. The lowest and the highest classes in 1989 (a and e) had lower and higher values as compared to 1988 values. SLW of spurs in

TABLE 1. Average SLW of Various Spur Classes and Ranges of SLW Used in Calculation of DRIS Norms and Indices of 'Hartley' and 'Serr' Walnuts

Spur Class ^z	SLW (mg / cm ²)			
	Average 1988	Range for DRIS, 1989	DRIS Averages 1989	PPF, 1989 (mol m ⁻² d ⁻¹)
Hartley				
a	4.09±0.13	<4.35	3.77±0.45	1.60±1.4
b	4.60±0.09	4.35 - 5.04	4.77±0.19	2.68±1.3
c	5.47±0.17	5.04 - 5.73	5.36±0.19	3.84±1.9
d	5.98±0.40	5.73 - 6.67	6.09±0.26	5.76±2.1
e	7.36±0.25	>6.67	7.86±0.83	10.84±3.1
Serr				
a	4.01±0.10	<4.25	3.41±0.41	1.32±1.1
b	4.48±0.07	4.25 - 4.70	4.51±0.14	2.04±0.8
c	4.92±0.24	4.70 - 5.12	4.96±0.14	2.97±1.4
d	5.31±0.27	5.12 - 5.49	5.33±0.07	3.93±3.3
e	5.66±0.25	>5.49	6.71±1.12	8.80±3.9

^z Reproductive behavior of 1988 spurs in the following year were as follows:
a; spurs died,
b; spurs not flowering,
c; spurs flowering but not setting fruit,
d; Either vegetative or reproductive spur setting fruit ,
e; Both, vegetative and reproductive spurs setting fruit.

1989 were measured earlier in the growing season than in 1988 (June - July as compared to September and their value probably increased slightly at a later stage. Significant intra-canopy differences in SLW have been measured by the time the tree canopy was closed, with subsequent increases throughout the growing season (26, 30). The quality of class e spurs, which served as norms for DRIS calculation in 1989, was probably higher than the equivalent class in 1988 since SLW was higher already in June - July, and very likely increased thereafter.

Spur leaf N, P, Ca and Mg were linearly and positively correlated with PPF (Fig. 1) and SLW (Fig. 2 and Table 2) when mineral content was expressed on the basis of leaf area. In contrast, K was linearly and negatively correlated with PPF and SLW, but only when expressed as % DW (Figs. 1-2 and Table 2). Similar correlations were found in prunes, with the exception of P, which was negatively correlated with SLW (42). Correlations with SLW were, in all cases, higher than with PPF (compare Figs. 1 and 2).

The dimensionless values of mineral ratios, based on calculation of either area (A/A) or weight (W/W), were not related to SLW (Table 2) or PPF (data not shown), except for those ratios involving potassium (N/K, P/K, K/Ca and K/Mg). With the exceptions of N/K and P/K, the highest correlations of mineral ratios to PPF or SLW were found when the basis for calculation was W/A (weight/area). The highest correlations of N/K and P/K occurred when the basis for calculation was A/W (area/weight, Table 2). In some mineral ratios a linear regression (data not shown) fitted the data as well as a polynomial fit while in others a polynomial regression improved the fit.

The choice of the more important expressions for DRIS calculations was based on the highest correlations with SLW (Table 2). Plotting these expressions (Fig. 3) showed that N/P (W/A), N/K (A/W) and P/K (A/W) ratios were linearly related to SLW while all other mineral ratios (W/A) were polynomially related. The equations for the curves in Fig. 3 were used to calculate the predicted ratios for the average SLW of the various spur classes listed in Table 1. The calculated ratios, which differed slightly from the measured averages, were used in the calculation of the DRIS indices. Using the calculated ratios from the equations from Fig. 3 (rather than the measured values) and a balanced equation of DRIS (outlined in Material and Methods), set the DRIS norms of all nutrients, and the NII value, in spur class e (the highest spur quality) to zero.

DRIS indices (Table 3) of spur classes a-d, based on spur class e norms, were calculated for the PPF and SLW ranges listed in Table 1. When calculating DRIS indices, the values of mineral ratios for average SLW and ± 1 SD of SLW were derived from equations from the curves of Fig. 3.

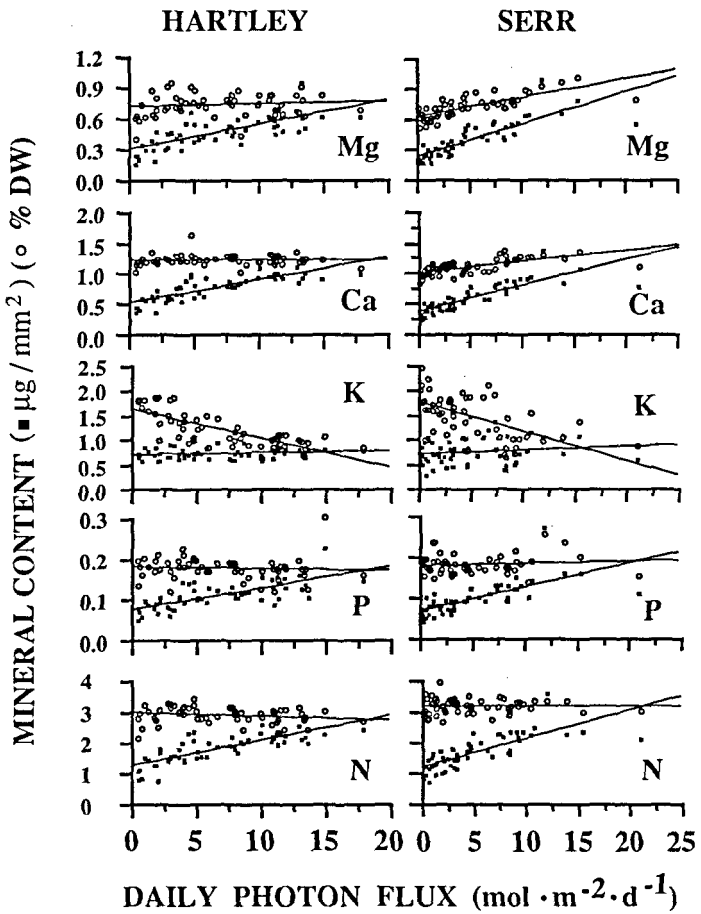


Figure 1. Walnut (cvs. Hartley and Serr) spur leaf mineral content as a function of daily photon flux irradiance.

TABLE 2. Correlations (r^2) Between Mineral Content and Ratios, and Spur SLW of 'Hartley' and 'Serr' Walnuts. (n=55 for Each Cultivar)

Parameter	A	W	A/A	A/W	W/A
	(mg/mm ²)	(% DW)	W/W		
	*		**	**	**
'Hartley'					
N	0.877	0.027			
P	0.654	0.020			
K	0.037	0.779			
Ca	0.916	0.001			
Mg	0.719	0.025			
N/10P			0.069	0.734	0.751
N/K			0.645	0.863	0.081
N/Ca			0.118	0.913	0.936
N/Mg			0.151	0.720	0.881
10P/K			0.530	0.815	0.076
10P/Ca			0.032	0.678	0.833
10P/Mg			0.231	0.590	0.844
K/Ca			0.740	0.034	0.937
K/Mg			0.665	0.068	0.888
Ca/Mg			0.252	0.779	0.897
'Serr'					
N	0.953	0.001			
P	0.824	0.033			
K	0.220	0.171			
Ca	0.942	0.389			
Mg	0.925	0.516			
N/10P			0.075	0.831	0.814
N/K			0.177	0.613	0.228
N/Ca			0.303	0.856	0.903
N/Mg			0.421	0.728	0.890
10P/K			0.207	0.642	0.198
10P/Ca			0.240	0.835	0.855
10P/Mg			0.340	0.739	0.846
K/Ca			0.253	0.075	0.646
K/Mg			0.318	0.049	0.658
Ca/Mg			0.139	0.851	0.890

* Linear **Polynomial, 3d degree

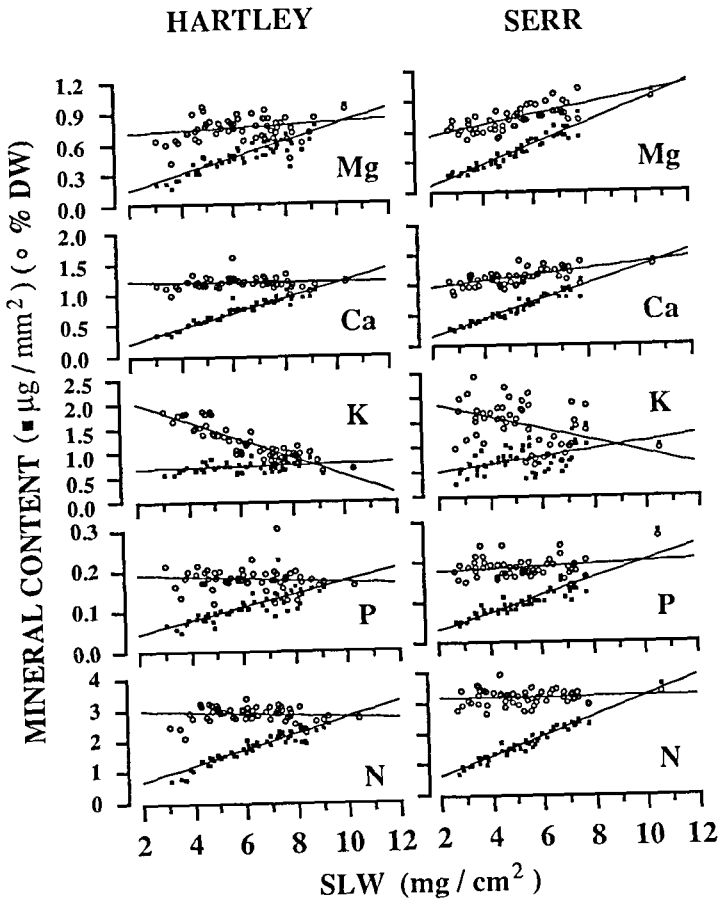


Figure 2. The relation between SLW and mineral content of walnut (cvs. Hartley and Serr) spur leaves.

TABLE 3. Dris Indices of Walnut Spurs (\pm SD)

Parameter	Spur Class				
	a	b	c	d	e
	Hartley				
PAR	1.60 \pm 1.4	2.68 \pm 1.3	3.84 \pm 1.9	5.76 \pm 2.1	10.84 \pm 3.1
SLW	3.77 \pm 0.45	4.77 \pm 0.19	5.36 \pm 0.19	6.09 \pm 0.26	7.86 \pm 0.83
N	11.3 \pm 4.6	16.5 \pm 0.6	13.8 \pm 1.9	9.5 \pm 2.6	0 \pm 4.3
P	-13.0 \pm 1.3	-6.1 \pm 0.1	-5.5 \pm 0.4	-4.6 \pm 0.7	0 \pm 2.3
K	142.8 \pm 13.2	65.4 \pm 5.3	41.3 \pm 12.8	21.9 \pm 5.0	0 \pm 6.2
Ca	-56.4 \pm 5.4	-35.1 \pm 2.1	-25.2 \pm 5.5	-15.2 \pm 3.3	0 \pm 4.8
Mg	-84.7 \pm 11.0	-40.7 \pm 3.8	-24.3 \pm 9.5	-11.5 \pm 3.6	0 \pm 3.4
NII	308 \pm 36	164 \pm 11	110 \pm 30	63 \pm 15	0 \pm 21
	Serr				
PAR	1.32 \pm 1.1	2.04 \pm 0.8	2.97 \pm 1.4	3.93 \pm 3.3	8.80 \pm 3.9
SLW	3.41 \pm 0.41	4.51 \pm 0.14	4.96 \pm 0.14	5.33 \pm 0.07	6.71 \pm 1.12
N	37.0 \pm 2.4	20.9 \pm 1.4	15.2 \pm 1.4	11.0 \pm 0.9	0 \pm 7.3
P	14.3 \pm 1.1	10.6 \pm 0.3	8.0 \pm 0.1	5.9 \pm 0.3	0 \pm 3.7
K	44.3 \pm 7.5	21.3 \pm 2.6	17.7 \pm 2.6	12.9 \pm 0.5	0 \pm 9.6
Ca	-23.3 \pm 2.3	-12.1 \pm 1.5	-10.8 \pm 1.1	-7.6 \pm 0.3	0 \pm 4.5
Mg	-72.3 \pm 6.4	-40.7 \pm 2.9	-30.2 \pm 2.9	-22.2 \pm 1.4	0 \pm 16.1
NII	191 \pm 20	106 \pm 9	82 \pm 8	60 \pm 3	0 \pm 41

Reduced spur quality, associated with decreasing light exposure and SLW, was characterized by a leaf mineral imbalance. Magnesium and Ca became limiting (negative values), balanced by excess K or K+N in 'Hartley' or 'Serr', respectively. It is difficult to ascertain in the DRIS analysis whether a relative deficiency is of greater importance than the accompanying excesses (11). In the case of walnut spurs, the relative deficiency of Ca and Mg and the accompanying excess of K, and N in the case of 'Serr', are a manifestation of essentially the same process of response to light and allocation of nutrients within the tree canopy.

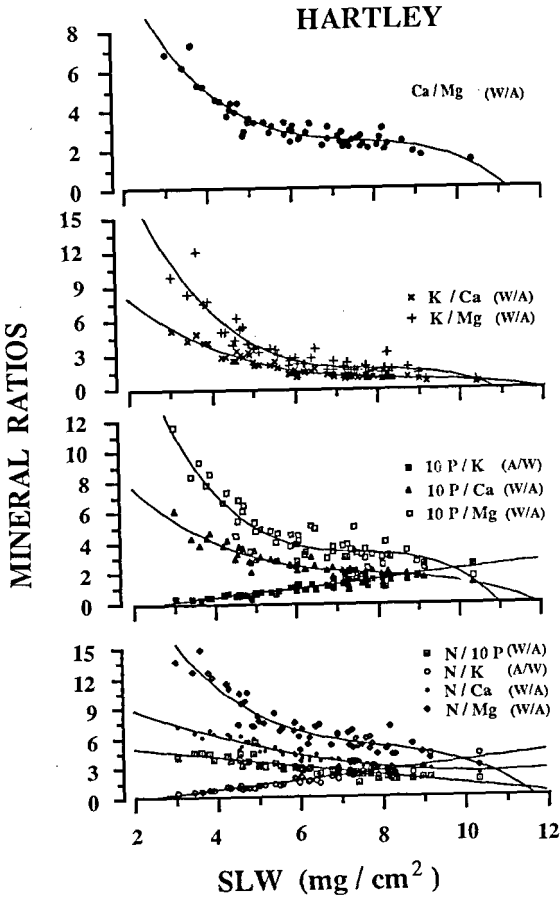


Figure 3a. The relation of SLW and mineral ratios of walnut (cv. Hartley) spur leaf. Ratios were calculated from nutrients expressed on leaf area (A) and % DW (W) basis.

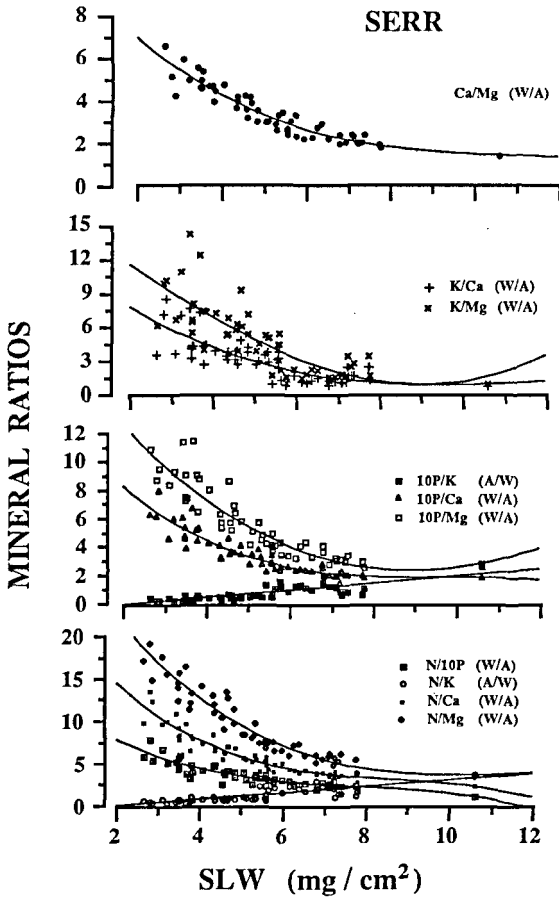


Figure 3b. The relation of SLW and mineral ratios of walnut (cv. Serr) spur leaf. Ratios were calculated from nutrients expressed on leaf area (A) and % DW (W) basis.

The negative indices of the less mobile, divalent cations, at low SLW, is presumably a consequence of reduced transpiration (31) and influx of Ca and Mg into shade leaves. Similar results were found in prunes (42). The imbalance of K (increase in shade) in these leaves is probably a consequence of reduced DW accumulation rather than actual K influx, since K was related to SLW only when its content was expressed on a DW basis. Nitrogen indices, particularly in 'Serr', increased and those of P decreased or increased, but the changes of P were relatively minor, even at the lowest spur quality. The present analysis indicated that in vegetative shaded 'off' spurs, N probably was not limiting since leaf N became positive rather than negative in the DRIS analysis, although N allocation to the spur was reduced. The DRIS analysis also indicated that P was probably not deficient.

The relationship between SLW and DRIS indices of walnut spur leaves was plotted and a continuous two term polynomial equation fitted to the data (Fig. 4). DRIS indices and NII values decreased or increased continuously as spur leaf exposure and SLW increased up to a value of approximately 8 mg/cm^2 in 'Hartley' and 6.5 mg/cm^2 in 'Serr'. Calculated SD values (Table 3) indicate that differences in DRIS values, between spur class e and d, were significant.

DISCUSSION

Beaufil (5) and others (41, 37, 36, 21) recognized the need to define zones of normal vs slight and severe imbalances in the DRIS procedure, based on the natural variation within the high yielding population. Nevertheless they maintained that any deviation of a nutrient index from zero, zero, represents an imbalance and the greater the deviation, the greater is the imbalance. A concept of Nutritional Imbalance Index (NII), equal to the sum of all nutrient indices irrespective of sign, was introduced as an over all measure of the total nutritional balance (28, 41). Standard deviation has been used by several investigators to test the significance of deviation from zero of DRIS indices and NII values. Kelling and Schulte (21) pointed out that serious over-interpretation is nevertheless common, particularly when norms are based on locally calibrated data and used to diagnose samples from a

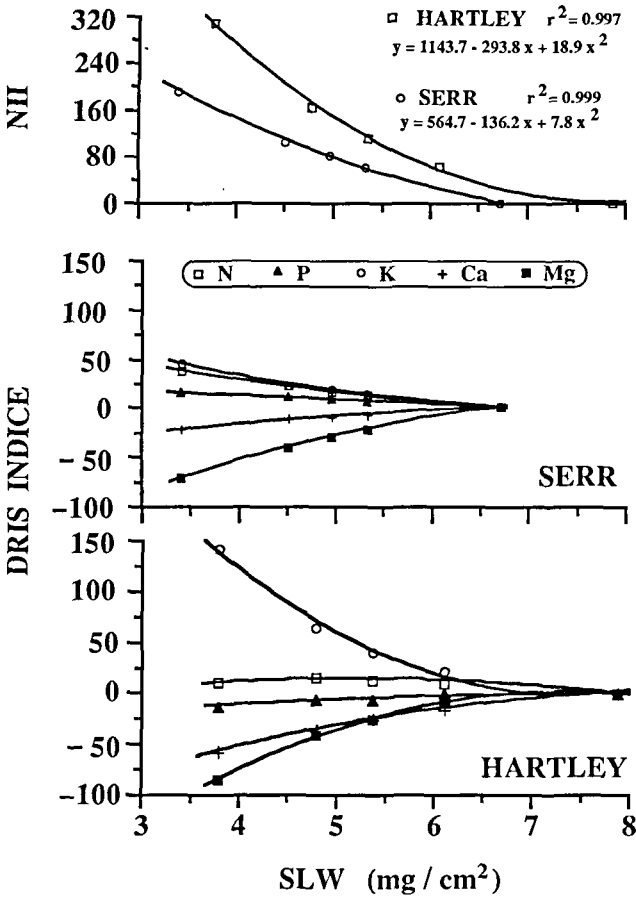


Figure 4. NII and DRIS N, P, K, Ca and Mg indices of walnut cvs. Hartley and Serr spur leaf as a function of SLW.

wide geographical area, because the statistical significance of the differences are frequently ignored and any negative number is diagnosed as a deficiency.

Hallmark et al. (18) recognized that the DRIS method always predicts one or more nutrients to be limiting, and re-introduced the dry matter factor into the DRIS procedure by using concentration values as well as ratios to separate limiting from non-limiting nutrients. Thus, one of the main advantages in the original DRIS method (eliminating DW contribution) was recognized also as a drawback. Sometimes the DRIS analysis does not properly point out the nutritional status of several elements simultaneously. Incompatibilities have been found mainly between DRIS indices of N, P, and K (18, 25). We maintain that some of the above difficulties may stem from the use of a secondary function (leaf mineral content), without taking into account the contribution of primary causes (i.e. light, manifested in leaf SLW, soil, etc.). Knowledge of relations to primary causes and inclusion of these fundamental relations into the DRIS procedure may improve the accuracy of diagnosis of any particular limiting (primary) cause. For example, errors of diagnosing soil limitations on plant nutrition may be avoided if radiation effects on leaf mineral profile are accounted for in the DRIS procedure. SLW integrates leaf exposure to radiation and may account, when integrated into the DRIS procedure, for variability of certain farm practices (planting densities, pruning, etc.), environmental variations (cloudiness in areas where summer rains prevail) and leaf sampling inconsistencies (errors due to sampling various tree sides, sampling within canopy and biennial growth effect on tree shade).

Non-identical expressions were chosen for the two categories of nutrients (A/W for some of the K ratios vs W/A for N, P, Ca, and Mg ratios), which differ in their relation to the primary cause of light and SLW. Ratios of N or P with K had the highest correlation to SLW when expressed as A/W. This expression is the relation of N or P per unit area (i.e. $\mu\text{g N mm}^{-2}$) to tissue K content in the DW ($100 \text{ (mg K) / } 100 \text{ mg DW} = \text{K/DW}$). All other ratios were most highly correlated with SLW when expressed as W/A (i.e. N in tissue DW in relation to $\mu\text{g P mm}^{-2}$). Both expressions are reciprocals as far as the unit of expressions are concerned but different with respect to the inverse of nutrient pairs. i.e.,

$$A/W \text{ for N/P is } \text{mg N mm}^{-2} / \text{P DW}^{-1}$$

$$W/A \text{ for N/P is } \text{N DW}^{-1} / \text{mg P mm}^{-2}$$

Both expressions, which are used for different ratios in the proposed DRIS procedure, include one term related to SLW and the other to tissue DW. The procedure presented here is, therefore, somewhat similar to the M-DRIS modification (18), which introduced the DW component into the analysis. The inclusion of the leaf area expression and particularly the choice of ratios correlated to light and SLW seems to integrate the fundamental relations between minerals found in the leaf and may, in future studies, improve the simultaneous diagnosis of all elements by the DRIS procedure.

The dimensionless ratios (W/W or A/A) had no relation to light and SLW in walnut spurs, except where certain K ratios were involved. In the case of N, P, Ca, and Mg ratios, which increased proportionally to SLW on leaf area basis (Fig. 1), the highest correlations to SLW were found in the W/A expression (Table 2). Increases of SLW are attributed mainly to increases of leaf thickness, which is a function of the number of palisade layers in the leaf. The linear correlation of N/K and P/K with SLW, implies that P, N, and K vary linearly with the number and content of the palisade layers of the leaf. A major component of leaf N is RUBP-carboxylase (20), which is expected to increase as the number of cell layers in the leaf increases. Phosphorous, which in the case of walnut was positively correlated with SLW and in other studies negatively correlated with SLW (42), is a component of nucleic acids and may accumulate as a soluble fraction in leaf blades when its supply is abundant (34). Ratios in which divalent cations (Ca and Mg) are involved decrease polynomially as SLW increases (Figs. 3 and 4). Calcium and Mg contents, which are expressed in these ratios on area basis, are expected to change with the number of palisade layers as well. A polynomial correlation indicates influx of the divalent cations via the transpiration stream, in addition to the increase caused by changes in the number of palisade layers.

The use of mineral ratios, based either on dry weight or leaf area expressions, eliminates the apparent changes in mineral concentrations resulting from changes in DW. Eliminating the DW contribution was considered to be an important advantage in the DRIS method since the use of

mineral ratios or products, which had been shown in some cases to be constant for extended periods (35, 36,38,41) eliminated the need for standardization of sampling time. A constancy of mineral ratios or products in mature leaves implies, however, that either there are no influx and efflux of minerals from the leaf or that all minerals are changing simultaneously, at the same relative rate. Nutrients, however, are mobile and the potential for remobilization of the various nutrients is not identical (27). Leaf mineral constancy, therefore, is an unlikely premise, particularly when sink activity is present (10) or under deficient conditions. Indeed, several reports indicate that DRIS indices are dependent on sampling time (3, 6, 10, 19, 24, 29) or yearly variation caused by fruit load and tree age (29).

Nutrient uptake (40) and leaf mineral content (42) (Fig. 1) are influenced by irradiance and related to SLW. The data are not sufficient, however, to indicate how changes in leaf mineral content are related to changes in SLW throughout the growing season under variable nutrient supply. SLW of exposed leaves have been shown to increase during the growing season (26, 30, 33), but the increase, under variable nutrient supply (i.e. deficiency), may not be coupled to changes in leaf mineral content similar to those in Figs. 1 and 2. DRIS indices based on ratios related to SLW, therefore, can be expected to change throughout the growing season. Likewise, as mineral utilization is dependent on partitioning between vegetative and reproductive sinks, a computation of DRIS norms specific for distinct developmental stages (10) and spur type would probably be required. In walnuts, as an example, the presence of fruit reduced spur leaf N but had no significant effect on SLW (22), or K content (Klein, unpublished data). DRIS norms developed from adjacent vegetative and reproductive spurs on the same tree and year can be expected to differ. Standardization of leaf type, physiological age, and probably light exposure as well, remain essential for DRIS norm derivation and a meaningful interpretation of spur nutritional status. For characterization of tree productivity (not just spur productivity) as a function of light and nutrition, a leaf sampling procedure that adequately represents the average light exposure and mineral content of the tree as a whole, would be required.

In contrast to the other macroelements, leaf K content correlated with light and SLW on a DW, rather than a leaf area basis. The decrease of K as SLW increased implies that leaf DW may have increased in exposed positions, i.e. by cell wall deposition which may not require K influx. Alternately, K, which plays an important role in stomatal physiology (17, 31), may be concentrated at the epidermis and diluted by increasing palisade layers, which are known to increase as SLW increases (7). High K levels maintain high rates of transpiration and net photosynthesis by keeping stomates open (39) when water is readily available to the plant. From a regulatory standpoint and true to the mineral balance (ratio) concept, it can be argued that N utilization under K deficiency may be restricted. The regulation is probably indirect, through the control of stomatal closure, and involves imbalances of Ca and Mg at low SLW (Fig. 4). Regulation of stomatal closure at low K may be identical in sun and shade leaves, since K on an area basis is not related to light exposure. The overall result, however, could be manifested unevenly within the tree, with a restriction and nullification of light effects in the exposed leaves where a greater proportion of N is allocated.

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